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Understanding human-carnivore conflict over livestock depredation and its implications for conservation in the Tarangire-Simanjiro ecosystem, Northern Tanzania

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UNDERSTANDING HUMAN-CARNIVORE CONFLICT OVER LIVESTOCK DEPREDATION AND ITS IMPLICATIONS FOR CONSERVATION IN THE TARANGIRE-SIMANJIRO ECOSYSTEM, NORTHERN TANZANIA

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A Dissertation Submitted in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy in Life Science of the Nelson Mandela African Institution of Science and Technology

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ABSTRACT

Human-carnivore conflict is one of the threats facing large carnivores across the globe and can have a significant negative financial impact on local people's livelihoods. Semi-structured interviews were conducted with 300 respondents to examine the level of reported conflict with large carnivores over depredation on livestock, and to assess the key drivers of any such conflict, the financial livestock losses to local communities, the perceived effectiveness of current conflict mitigation strategies and local perceptions and attitudes towards the main carnivore conflict species in the Tarangire-Simanjiro ecosystem in northern Tanzania. Additionally, a spoor-based occupancy modelling approach that incorporates detection probability was used to assess the occurrence of four focal carnivore taxa, and to identify the key environmental and anthropogenic drivers of their occurrence. Of the 300 respondents, 75% reported losses of their livestock to wild predators over the past 1.5 years, which represents an annual loss rate of 1.4% of their livestock holdings. The overall financial loss due to livestock depredation was estimated to be US$ 141,847 (US$ 633/household/year). Reported depredation frequency by all large carnivore species increased significantly with increasing number of livestock owned, respondent's residency time, distance from the park boundary and declined significantly with increasing education, number of herders and improved fortified boma for cattle. Three-quarters of respondents (79%) held negative attitudes towards large carnivores due to risks of wildlife damage, particularly livestock depredation, while 20% were generally positive linked to potential ecotourism benefits. Education, years at residency and knowledge were the most influential determinants (though dependent on species) of attitudes towards large carnivores than landscape, demographic or economic factors. Fortified bomas (97.7%) and adult herders (71%) were perceived to be the most effective intervention methods to reduce night and daytime depredations respectively. Overall occurrence was estimated at 0.85 (SE = 0.06) for hyena, 0.82 (SE = 0.15) for cheetah, 0.55 (SE = 0.10) for lion and 0.61 (SE = 0.21) for leopard. Lion occurrence was negatively associated with distance to park boundary. Hyena occurrence was positively associated with human population density and negatively associated with bushland, while cheetah and leopard occurrences were positively associated with grassland. These results suggest that lions may be more vulnerable to human impacts than other species, while hyenas may benefit from vicinity to humans. This study provides targeted areas to prioritize for future carnivore conservation efforts and mitigation efforts regarding human-carnivore conflict.

DECLARATION

I, **Felix Joseph Mkonyi**, do hereby declare to the Senate of Nelson Mandela African Institution of Science and Technology that this dissertation is my own original work and that it has neither been submitted nor being concurrently submitted for degree award in any other institution.

________________________ ________________

Signature of candidate Date

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CERTIFICATION

The undersigned certify that they have read and hereby recommend for acceptance by the Nelson Mandela African Institution of Science and Technology a dissertation entitled: **Understanding Human-carnivore Conflict over Livestock Depredation and its Implications for Conservation in the Tarangire-Simanjiro Ecosystem, Northern Tanzania,** in Partial fulfillment of the requirements for the degree of Doctor of Philosophy in Life Science.

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DEDICATION

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This dissertation is also dedicated to the memory of my father, Joseph Mkonyi, who sowed the seeds of education into my life and interest of constant learning, for which I am eternally grateful. Though you are dead your legacy lives on in us.

TABLE OF CONTENTS **Page**

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

LIST OF ABBREVIATIONS AND ACRONYMS

AICc	Akaike Information Criterion corrected for small sample size
COSTECH	The Tanzania Commission for Science and Technology
GIS	Geographic Information System
GPS	Global Positioning System
GLMMs	Generalized Linear Mixed Models
GLMs	Generalized Linear Models
IUCN	International Union for the Conservation of Nature
LULC	Land use/Land cover
NM-AIST	Nelson Mandela African Institution of Science and Technology
NGO	Non-governmental organization
PI	Principal Investigator
PAs	Protected areas
SSC	Species Survival Commission
SPSS	Statistical Package for Social Sciences
SSI	Semi-Structured Interview
TSE	Tarangire-Simanjiro Ecosystem
TAWIRI	Tanzania Wildlife Research Institute
TNRF	Tanzania Natural Resource Forum
TNP	Tarangire National Park
TANAPA	Tanzania National Parks Authority
TPW	Tanzania People and Wildlife Fund

CHAPTER ONE

General introduction and background

1.1 Introduction

1.1.1 Importance of large carnivore conservation

Large carnivores are an integral part of the ecosystem and play an important role in maintaining the healthy ecosystems through predation and inter-specific competition (Terborgh *et al.*, 1999). Furthermore, large carnivores fulfill many important ecological functions such as regulating or limiting the population of their prey by altering the structure and the function of the entire ecosystem, hence preventing trophic cascades (Terborgh *et al.*, 1999). Prey-predator relationships can influence population dynamics, behavior and evolutionary processes in ecosystems, which means that removal of top predators may result in cascading trophic effects, such as changes in biodiversity and herbivore community structure (Terborgh *et al.*, 2002). Conservation of large carnivores is also of vital importance because they are essential "indicators" of ecosystem health, such that their disappearance from an ecosystem indicates that the habitat has become very severely degraded. They also act as "umbrella species" as they are connected to several other species and protecting them will automatically protect many habitat types and other sympatric species (including rare and threatened species) that depend on those habitats (Caro and O'Doherty, 1999). Furthermore, large carnivores are often used as "flagship species" to coordinate landscape conservation efforts and protect smaller and less charismatic species (Caro, 2003). In addition to their inherent aesthetic, cultural, symbolic and spiritual values, large carnivores are often "charismatic species" that have economic importance because of tourism and trophy hunting (Lindsey *et al.*, 2007). Under this circumstance, large carnivores particularly spotted hyena *Crocuta crocuta*, cheetah *Acinonyx jubatus*, leopard *Panthera pardus,* lion *Panthera leo* and African wild dog *Lycaon pictus* can be employed as surrogates for biodiversity conservation (Dalerum *et al.*, 2008). Nevertheless, conservation of large carnivores poses a seemingly insurmountable challenge as they range widely and occur at relatively low densities such that human encroachment and changes in habitat quality may have serious impacts on their populations (Inskip and Zimmermann, 2009; Woodroffe, 2000).

1.1.2 Human-carnivore conflict in context

The increasing pressure of human population growth and the rapid expansion of agriculture have resulted in habitat loss and fragmentation of key habitats for wildlife, forcing wild animals to live in proximity to humans (Inskip and Zimmermann, 2009; Woodroffe, 2000). Large carnivores, particularly lions *Panthera leo*, leopards *Panthera pardus*, spotted hyena *Crocuta crocuta*, cheetah *Acinonyx jubatus* and wild dogs *Lycaon pictus* often come into conflict with local people, especially where people and large carnivores live in close proximity (Treves and Karanth, 2003). The conflict between humans and large carnivores has been acknowledged as a key cause of large carnivore declines throughout the world (Dickman, 2008; Holmern *et al.*, 2007; Treves and Karanth, 2003). Human-wildlife conflicts can be defined as interactions between humans and wildlife where negative consequences, whether perceived or real, exist for one or both parties (Decker *et al.*, 2002). This type of conflict has two important dimensions – the reality of damage caused by wildlife to humans, and the perceptions and behavior of humans who suffer wildlife-caused damage. Human-wildlife conflict can be categorized into five classes: depredation upon livestock, predation upon game species, attacks on humans, crop raiding and disease transmission (Sillero-Zubiri and Laurenson, 2001; Smith, 2007). Livestock depredation is the most common direct cause of human-wildlife conflict that occurs where livestock and large carnivores are known to co-exist, particularly near protected areas (hereafter PAs) (Kissui, 2008; Holmern *et al.*, 2007; Treves and Karanth, 2003). Consequently, when large carnivores come into direct contact with humans and livestock, competition for resources, particularly predation upon domestic animals and game species (Kolowski and Holekamp, 2006; Treves and Karanth, 2003; Woodroffe, 2000) or occasional attacks on humans (Packer *et al.*, 2005) is likely to occur. This often results in persecution and elimination of the carnivore species involved (Woodroffe *et al.*, 2005a). The degradation of habitat, the reduction of natural prey, and the proximity of livestock favor a shift in large carnivore diet towards livestock. Inskip and Zimmermann (2009) reported that at least 75% of the world's felid species come into conflict with humans. However, carnivore populations, conflict dynamics, and methods for alleviating conflict vary from region to region (Woodroffe *et al.*, 2005a).

Human-carnivore conflict due to livestock depredation is common worldwide and is experienced by many diverse species including wolves *Canis lupus* which kills sheep in North America

(Treves *et al*., 2004), jaguars *Panthera onca* (Conforti and De Azevedo, 2003) and pumas *Puma concolor* (Polisar *et al.*, 2003) attack cattle in South America, tigers *Panthera tigris* (Gurung *et al*., 2008), leopards (Kolowski and Holekamp, 2006) and snow leopards *Uncia uncia* kill livestock in India and Pakistan (Bagchi and Mishra, 2006) while spotted hyenas, lions (Patterson *et al*., 2004), African wild dogs (Woodroffe *et al.*, 2005a) and cheetahs (Dickman, 2008; Marker *et al*., 2003) prey upon cattle and small stock in Africa. Along with livestock disease, depredation by large carnivores can result in potentially severe impacts to local communities (Frank *et al*., 2005), although this varies both temporally and geographically. For instance, depredation by large carnivores accounted for 63% of all stock deaths in Nepal (Jackson *et al*., 1996). In western Serengeti National Park in Tanzania, village households lost 69.8% of their local income annually to large carnivores, equivalent to an average loss of US $97.7 per household (Holmern *et al.*, 2007). Livestock depredation can therefore have very significant economic impacts on livestock owners, and the perceived economic losses in particular often lead to retaliatory or preventative carnivore killing (Kolowski and Holekamp, 2006; Patterson *et al*., 2004).

Apart from the direct economic costs which are relatively easy to quantify, local communities living with large carnivores also incur indirect economic costs through investment in damage control strategies, such as husbandry, herding and guarding livestock (Ogada *et al*., 2003). It is very clear that investing in livestock protection costs time and money, while the costs of human fatalities are obviously incalculable for the families concerned (Thirgood *et al*., 2005). For instance, time invested in herding and guarding the stocks could have been used for other activities such as education or harvesting (Norton-Griffiths and Southey, 1995). Consequently, maintaining carnivores in a human-dominated landscape can incur significant direct and indirect economic and opportunity costs to individuals and local communities living in such areas.

1.1.3 Factors affecting human-carnivore conflict and attitudes toward large carnivores

Understanding the determinants of conflict with carnivores is fundamental to developing the most effective conflict mitigation strategies (Dickman, 2010; Inskip and Zimmermann 2009). However, determinants of conflict with carnivores are often complex and deep-seated (Dickman, 2010), and can change significantly over time perhaps due to cultural, ecological and economic factors (Dickman, 2005; Fritts *et al*., 2003). Conflict between humans and carnivores may be influenced by various ecological and socio-economic factors such as gender, age, wealth (i.e. numbers of stock owned), level of education and levels of stock loss (Lindsey *et al*., 2005; Oli *et al*., 1994), habitat characteristics (Treves *et al.*, 2004), abundance and distribution of natural prey (Patterson *et al*., 2004), human density (Newmark *et al*., 1994), carnivore density (Lugton, 1993), proximity to a protected area (Holmern *et al.*, 2007; Patterson *et al.,* 2004) husbandry practices (Ogada *et al*., 2003) and some climatic and environmental factors (Inskip and Zimmermann, 2009; Patterson *et al.*, 2004). On the other hand, people's attitudes and perceptions towards large carnivores are influenced by several factors including age, gender, education level, income, proximity to a protected area, experience with carnivores, benefits from conservation, religious and cultural factors (Lindsey *et al*., 2005; Naughton-Treves *et al*., 2003; Schumann *et al*., 2008).

1.1.4 Current strategies for human-carnivore conflict mitigation

Current mitigation methods to reduce conflict between humans and predators can be divided into two management groups: lethal and non-lethal control. Both lethal (Woodroffe and Frank, 2005) and non-lethal control methods (Ogada *et al*., 2003; Woodroffe *et al.*, 2007) have been empirically tested for their effectiveness. Lethal control methods such as shooting, poisoning, spearing, trapping or snaring are considered to be ineffective, inhumane, and often conducted indiscriminately, resulting in the deaths of non-target species (Treves and Naughton-Treves, 2005). Lethal control to prevent conflict can be a major driver of large mammal population declines throughout the world (Treves and Naughton-Treves, 2005). For instance, a combination of trapping for fur and poisoning to protect sheep led to the extinction of the Falklands wolf or Malvinas zorro (*Dusicyon australis*) in 1876 (Sillero-Zubiri *et al.*, 2004). In North America and Europe, non-lethal controls such as hi-tech livestock management practices have been employed such as toxic collars, radio-activated guards and the use of electric fencing (Breitenmoser *et al*., 2005), but these are costly and may be inappropriate for use in less developed countries with poor infrastructure. However, several studies conducted in Tanzania, Kenya, America and Europe demonstrate the effectiveness of low-tech mitigation measures such as use of boma enclosures, herders, guard dogs and compensation schemes in reducing livestock losses to predators (Ogada *et al.,* 2003; Breitenmoser *et al.,* 2005; Woodroffe *et al.,* 2007; Kissui, 2008).

In their review of conflict mitigation measures worldwide, Inskip and Zimmermann (2009) categorized the conflict mitigation measures into: financial schemes (e.g., compensation, economic incentives, ecotourism, trophy hunting); improved protection of livestock (e.g., husbandry, guarding and deterrents); community development and education initiatives; problem animal control (e.g., aversive conditioning, translocation, lethal control); and land management such as zoning; all of which have had varying levels of success and failure (Mishra *et al.*, 2003).

The financial mechanisms such as compensation for livestock losses are widely used across the globe in mitigating human-carnivore conflicts (Agarwala *et al.*, 2010). However, financial compensation schemes may be difficult to implement in the Tanzanian context where there is lack of capacity and little chance of verification of depredation. Community-based incentive programmes such as income generation from ecotourism or the sale of handicrafts have been used with much success in snow leopard conservation in Pakistan and India (Mishra *et al.*, 2003). Tourism revenue-sharing with communities living adjacent to PAs can be used as a human-wildlife conflict mitigation strategy (Dickman *et al.*, 2011). However, Dickman *et al.* (2011) affirm that revenue-sharing programmes alone may not always outweigh the cost of living with wildlife and their implementation should consider both financial and cultural incentives for local people. A number of studies have shown that husbandry practices can be effective for reducing conflict with carnivores (Ogada *et al.*, 2003; Ukio, 2010; Woodroffe *et al.*, 2007). However, despite their potentialities, our knowledge regarding livestock husbandry practices and their perceived effectiveness in reducing livestock depredation by large carnivores in the Tarangire-Simanjiro Ecosystem (TSE) is still limited. Clearly, there is a need to identify measures to prevent carnivore attacks on livestock, which will then reduce retaliatory or preventative carnivore killing. Identifying which husbandry techniques are most effective can help livestock owners to implement the most efficient ways of protecting their livestock, and this will not only reduce conflict with carnivores but will reduce the household's economic and non-economic costs.

In Tanzania, human-carnivore conflict is a major challenge to the long-term conservation of large carnivore populations both inside and outside PAs, which often end up in retaliatory or preventative carnivore killing (Kissui, 2008). Moreover, it is increasingly understood that existing PAs are not large enough to sustain long-term viable carnivore populations, especially of large-bodied species, which range over large distances and therefore come into contact with humans (Durant, 2007). In this case, landscapes outside PAs may therefore be essential for the persistence of viable populations of large carnivores (Breitenmoser *et al*., 2005). However, the question of whether large carnivores can persist outside PAs depends on the tolerance of local people (Breitenmoser *et al.*, 2005). Human antagonism against large carnivores is often compounded by an innate fear of large predators and deep-seated cultural hostility resulting from past experiences, even if carnivores are not causing present problems (Sillero-Zubiri and Laurenson, 2001; Quammen, 2003).

In the TSE in northern Tanzania, human expansion coupled with habitat loss and fragmentation is the main reasons for the escalated human-carnivore conflict. The TSE is part of the Maasai Steppe in northern Tanzania and one of the richest wildlife areas in Tanzania. The TSE incorporates a number of protected and unprotected areas subject to different forms of natural resource use. It covers the Tarangire National Park, forming the dry season range for the migratory herds, especially wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchellii*), hartebeest (*Alcelaphus buselaphus*) and fringe eared oryx (*Oryx beisa callotis*), and the Simanjiro Plains forming the wet season dispersal area and calving grounds (Kahurananga and Silkiluwasha, 1997). Most importantly, this ecosystem is essential to the subsistence of pastoralists and farmers in the communal lands. However, large carnivore populations are potentially threatened due to the conversion of these rangelands into agricultural land (TAWIRI, 2007). Many of the driving forces of habitat loss and fragmentation in the TSE are associated with increasing human populations, the conversion of land for agriculture and livestock grazing (Msoffe *et al*., 2011). This poses a critical threat to wildlife migration corridors, grazing and dispersal areas (TNRF, 2005).

1.2 Statement of the Problem

Most of the world's large carnivore populations are in rapid decline (Ripple *et al.*, 2014), with human-carnivore conflict primarily due to livestock depredation identified as one of the key reasons for this decline (Dickman, 2008; Holmern *et al.*, 2007; Treves and Karanth, 2003). Therefore, managing this conflict is one of the top priorities for conservation biologists for the continued coexistence of human and large carnivores (Marker and Dickman, 2004; Woodroffe *et* *al*., 2005a). Livestock depredation by large carnivores imposes substantial economic and cultural costs to local households, thereby impacting people's livelihoods, which may contribute to poverty and food insecurity (Treves and Karanth, 2003; Treves and Naughton-Treves, 2005), and generating greater negative attitudes towards large carnivores as negative attitudes are a major driver of large carnivore persecution (Ogada *et al.,* 2003; Dickman, 2005; Holmern *et al*., 2007; Kissui, 2008).

While studies have documented conflicts between humans and large carnivores in Tanzania (Dickman, 2008; Kissui, 2008; Maddox, 2003; Nyahongo, 2007), little is known about the extent, reported patterns and determinants of conflicts triggered by livestock depredation in the TSE. Previous studies in this ecosystem have focused either on actual livestock depredation events on a small set of carnivore species (Kissui, 2008; Mponzi *et al.,* 2014), or single species conflict i.e., human-lion conflict (Lichtenfeld, 2005). So far there is a gap in a more holistic understanding of perceived conflict focused across the whole range of large carnivores, drivers of conflict, attitudes and perceptions towards the main carnivore species and drivers behind human attitudes which may lead to conflict in this ecosystem. In addition, no empirical data are available on perceived financial livestock losses due to depredation by large carnivores and other causes such as disease and theft on people's livelihoods in this ecosystem. This dissertation builds upon these previous studies by looking more broadly at the reported patterns of livestock depredation focusing on a large set of carnivore species (i.e., lions, cheetahs, spotted hyenas, leopards and African wild dogs) and key factors influencing these patterns. Of the greatest concern is that more than 90% of wildlife habitat in the Maasai Steppe (in which TSE is part of) is outside PAs in communal grazing lands (Borner, 1985; Maasai Steppe Cheetah Conservation Programme, 2013) where wildlife, people, and livestock all interact and compete for the same natural resources, thereby escalating the intensity of conflict. The need to fill these information gaps is crucial especially as large carnivore populations are currently in global decline and livestock depredation may seriously undermine conservation goals and impact people's livelihoods. Although a wide range of mitigation measures have been tried to reduce livestock depredation, the effectiveness of these intervention methods in reducing livestock depredation has not always been adequately assessed (Rigg *et al*., 2011). Previously, Lichtenfeld *et al.* (2014) tested the actual effectiveness of fortified bomas versus traditional bomas but no previous studies have assessed the perceived effectiveness of this method in relation to other methods in this ecosystem. Likewise, Ukio (2010) evaluated husbandry techniques used in different villages in the Maasai Steppe and their effectiveness at reducing conflicts, but not the perceived effectiveness of these methods.

Moreover, in order to maintain co-existence between humans and large carnivores, it is important to understand how humans perceive, tolerate and accept risks associated with large carnivores. Human-carnivore conflict often engenders negative perceptions towards carnivores (Oli *et al*., 1994; Patterson *et al*., 2004) and many factors influence people's attitudes towards large carnivores (Lindsey *et al*., 2005). However, very few studies have attempted to understand people's attitudes and factors influencing these attitudes towards large carnivores in Tanzania e.g., Dickman (2005, 2008) around Ruaha landscape and Lichtenfeld (2005) in the Tarangire ecosystem.

Large carnivores are particularly vulnerable to anthropogenic disturbance (e.g., habitat loss and fragmentation, agricultural expansion, persecution by humans) and loss of prey base because they have large home ranges, occur at relatively low densities and require extensive, intact habitats to survive (Sillero-Zubiri and Laurenson, 2001). The detrimental impacts of land use change and decreased prey availability are well-documented in many areas where human carnivore conflict rates are high (Carbone and Gittleman, 2002; Patterson *et al.*, 2004). Despite the increasing levels of anthropogenic pressure on large carnivore community in human-dominated landscapes, relatively little is known about the status, distribution and habitat use outside protected areas (Durant *et al.*, 2017; Msuha, 2009). Information on large carnivores in the Tarangire landscape is limited to data from non-invasive camera trapping across relatively small areas, and where surveys on unprotected lands were hampered by camera theft (Msuha, 2009). More importantly this is one of the first studies to use spoor surveys data within a patch occupancy model framework to assess occurrence of four focal carnivore taxa (lions, leopards, hyenas and cheetahs) and to identify the key environmental and anthropogenic drivers of their occurrence across a multiple-use landscape of northern Tanzania.

1.3 Research Objectives

1.3.1 General Objective

The general objective of this study is to investigate and provide a better understanding of human-carnivore conflict over livestock depredation in the Tarangire-Simanjiro Ecosystem, Northern Tanzania, in order to inform conflict mitigation strategies in this region.

1.3.2 Specific Objectives

The specific objectives of this study are:

1. To investigate the reported patterns and extent of conflict with large carnivores, and to assess the key drivers of any such conflict, as well as the financial livestock losses to local communities in the study area;
2. To evaluate the perceived effectiveness of livestock husbandry techniques in limiting livestock depredation by large carnivores in the study area;
3. To assess people's perceptions of conflict and their attitudes towards the main carnivore conflict species, as well as to identify the key factors affecting these attitudes;
4. To assess the occurrence and detection probabilities of focal carnivore species and to identify the key drivers of their occurrence in the study area.

1.4 Research Questions

In order to achieve the specific objectives, this study attempts to address the following specific questions:

1. What are the reported patterns and levels of conflict related to livestock depredation in the studied region?
2. What are the underlying factors influencing livestock depredation by large carnivores in the study area?
3. What are the livestock husbandry techniques currently employed by local people in the study area and how effective are they perceived to be in limiting livestock depredation by large carnivores?
4. What perceptions and attitudes do the local people have towards large carnivores? What are the key factors influencing these attitudes in the study area?
5. What is the current occurrence of focal carnivore species and drivers of their occurrence in the study area?

1.5 Significance of the Study

This study seeks to fill the gaps in the existing knowledge of human-carnivore conflict by integrating biological and social sciences to determine the potential for conservation of large carnivores and mechanisms to effectively reduce livestock depredation in the study area. This study investigates some interesting aspects of carnivore ecology and local people's perceptions of the conflict situation. A better understanding of human-carnivore conflict, particularly over depredation on livestock as well as quantifying the associated impacts is critical to implement appropriate conflict mitigation techniques so as to minimize livestock loss, to safeguard conservation of large carnivores and to improve local livelihoods. This study is critical for identifying areas most prone to conflict in order to focus conflict mitigation strategies in such areas. This study contributes a broad suite of variables which influence conflict in the area – and so providing the model framework that can be used to understand the complexities of conflict in other regions. Furthermore, a sound understanding of local people's attitudes and perceptions of risk associated with large carnivores, as well as the factors influencing these attitudes is essential for developing the most appropriate human-carnivore conflict mitigation strategies within communities.

More importantly, the findings of this study will be of interest to a broad readership including policy-makers, wildlife managers, researchers, conservation agencies, and other stakeholders involved in human-carnivore conflicts mitigation and can help make informed decisions in mitigating human-carnivore conflicts elsewhere. This study should also benefit those interested in understanding the complexity of the human dimensions affecting human-carnivore coexistence in unprotected landscapes. In addition, this study will benefit those interested in understanding the determinants of attitudes towards large carnivores which may be useful indicators across different regions. Moreover, this study establishes a baseline of information that can eventually be used to monitor changes in spatial distribution and status of large carnivore populations over time-related to changes in habitat and/or management efforts. This study will critically improve our state of knowledge to prioritize habitat conservation, identify threats that limit large carnivore presence and inform management actions in the region. This study will also likely improve local knowledge of large carnivores and conservation and help pastoralist communities to adopt acceptable human–carnivore conflict mitigation strategies.

1.6 Justification

Large carnivores are involved in livestock depredation and can impose significant economic and cultural costs to local households and undoubtedly impact carnivore communities in various ways (Holmern *et al*., 2007; Kissui, 2008). Hence, in this context, it becomes important to understand what effect livestock losses have on the livelihood and wellbeing of the local people living in the TSE. This landscape is critically important for large carnivores – it supports the globally important populations of lions, cheetahs, leopards, hyenas and African wild dogs. However, inadequate understanding of the extent of livestock depredation, spatial and temporal patterns of reported depredation, the context of reported attacks, factors influencing livestock depredation and the perceived effectiveness of livestock husbandry practices often hinders the implementation of appropriate conflict mitigation techniques and conservation of large carnivores in this critical landscape. Furthermore, our knowledge about large carnivore status, distribution, occurrence and also the potential factors influencing their occurrence in this landscape is limited. Information on large carnivores in this landscape is limited to data from non-invasive camera trapping across relatively small areas, and where surveys on unprotected lands were hampered by camera theft (Msuha, 2009). Therefore, this study aims to investigate the extent, reported patterns and factors influencing livestock depredation, as well as to use spoor surveys data to assess the occurrence of large carnivores across landscapes characterized by different environmental and anthropogenic factors, and it builds upon previous studies, especially by Lichtenfeld (2005) and Msuha (2009).

In addition, little knowledge about large carnivores, few tangible benefits associated with living with large carnivores and poor livestock husbandry practices have been found to intensify human-carnivore conflict (Dickman, 2008). Hence, in this context, there is an urgent need for inter-disciplinary research to understand what perceptions people have towards large carnivores, what the factors are that shape these attitudes, and which livestock husbandry techniques are most effective in mitigating human-carnivore conflict in this critical landscape.

1.7 Study area

1.7.1 Geography and climate

This study was conducted in the Tarangire-Simanjiro Ecosystem (3°52′ and 4°24′ S and 36°05′ and 36°39′ E) located in northern Tanzania (Figure 1). The study covered much of Tarangire National Park (TNP) and adjacent villages outside the National Park. The study focused on five villages adjacent to TNP i.e., Loibor Siret, Sukuro, Terat, Emboret and Loiborsoit. The TSE is characterized by semi-arid climatic conditions with erratic rainfall of 400-600 mm per annum (Kahurananga, 1979). Rainfall in this region is bi-modal in pattern with short rains occurring between November to December and long rains from March to May. Generally the climate is warm and dry, coolest from July to December and warmest from January to June, with an average daily temperature ranging from 16 ˚C to 27˚C.

1.7.2 Wildlife and habitat

The Simanjiro plains in Simanjiro district are the main dispersal areas for wildlife during the wet season and grazing for pastoralists during the dry season. The plains are primarily used by migrating herbivores especially wildebeest, zebra, hartebeest and fringe eared oryx for grazing and calving, and resident herbivores such as Thomson's gazelle (*Gazella thomsoni*), impala (*Aepyceros melampus*) and greater kudu (*Tragelaphus strepsiceros)* (Kahurananga and Silkiluwasha, 1997). During the rainy season, the majority of the migratory large ungulates leave TNP, dispersing eastwards to the Simanjiro plains, or northwards towards Lakes Manyara and Natron. They eventually return to TNP during the dry season. The TSE also hosts globally threatened carnivore species such as lions, cheetahs, leopards, African wild dogs and spotted hyenas.

The study area is a mosaic of habitat consisting of four major vegetation types: (i) grassland (*Digitaria macroblephara* and *Panicum coloratum)*, (ii) woodland (*Acacia tortillis* and *Commiphora schimperi)*, (iii) bushland (*Acacia stuhlmannii* and *A. drepanolobium)* and (iv) seasonally water-logged bushed grassland (*Pennisetum mezianum* and *Acacia stuhlmannii)* (Kahurananga, 1979). To assess occurrence of large carnivores, the study area was stratified into three major blocks based on an assessment of land use and vegetation type (PAs, communal grazing land and village land). The communal grazing land is generally an open semiarid savanna with short grass plains and wooded grassland, encompassing the Simanjiro Game Controlled Areas which are administered by the Wildlife Division for licensed wildlife hunting and free grazing (Kahurananga and Silkiluwasha, 1997). The village land was selected within the Loibor Siret village on the southeastern border of TNP. It is characterized by semi-arid mixed grassland savannah composed of agriculture, dense thickets, woody savannah, open savannah, and swamps.

1.7.3 Geology and topography

The underlying volcanic soils on the plains possess phosphorus-rich grasses important for lactating female animals and their young (Kahurananga and Silkiluwasha, 1997). The flood plains contain black cotton soils while the well-drained areas contain the dark red, sandy clay loam (Kahurananga and Silkiluwasha, 1997). The primary topographic features in this region are related to large-scale volcanic rifting. The escarpment of the Rift Valley rises from broad expansive flatlands through scattered hills to elevations between 900 and 1200 meters above sea level west of TNP and between 1356 and 1605 meters a.s.l. in Simanjiro (Kahurananga and Silkiluwasha, 1997).

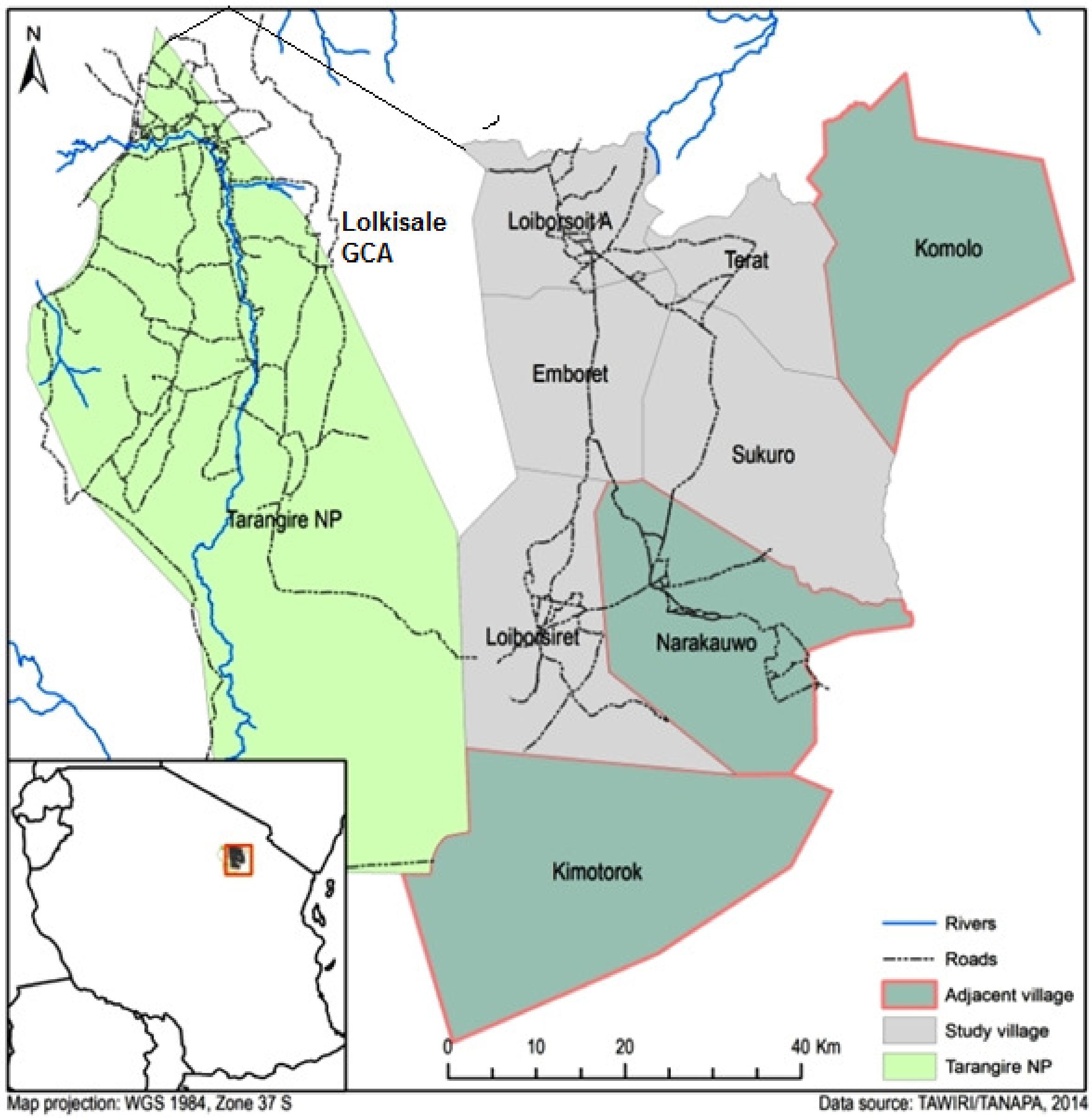

Figure 1. The Tarangire-Simanjiro ecosystem and its location in Tanzania

1.7.4 Major cultural groups in the study area

The major ethnic groups in this area are the Maasai and the Waarusha. Both groups historically depended on livestock. The Waarusha descended from the Maasai but have a higher frequency of practicing subsistence agriculture. Traditionally, the Maasai are semi-nomadic pastoralists, although many are now agro-pastoralists, as they are increasingly practicing subsistence agriculture. Pastoral and agro-pastoral communities keep a variety of livestock including cattle, goats, sheep, and donkeys. Farming is mostly based on food crops like maize (*Zeya mays*), beans (*Phaseolus* spp), sorghum (*Sorghum bicolor*), rice (*Oryza sativa*), cassava (*Manihot esculenta*), sweet potatoes (*Ipomoea batatas*), pigeon peas (*Cajanus cajan*) and green mung beans (*Phaseolus aureus*) and cash crops like wheat (*Triticum aestivum*), onions (*Allium cepa*), water melon (*Citrullus lanatus*) and sunflower (*Helianthus annuus)*.

1.8 General methods

The majority of the data were collected using interviews of pastoralists and agro-pastoralists living in Simanjiro district. The detailed and specific methods are provided in each relevant chapter, but the general methods are discussed below.

1.8.1 Semi-structured interviews

Semi-structured household interviews were used to collect information on characteristics and levels of human-carnivore conflict, livestock husbandry practices, attitudes, perceptions and knowledge of local people towards large carnivores. In designing the questionnaire, the similar format used by Maddox (2003) in northern Tanzania and by Dickman (2008) in southern Tanzania was followed. The questionnaires were pre-tested on a sample of 15 respondents in the region and revisions and modifications to the questions were made for clarification before further use. The questionnaire contained both closed-ended as well as open-ended questions in order to gain more information on participants' attitudes and reasoning. Semi-structured interviews (SSIs) were chosen instead of structured ones because SSIs allow for a wider range of responses and narratives, and are flexible enough to allow respondents to express their ideas and views in their own terms (Hunter and Brehm, 2003). Semi-structured interviews (SSIs) (Appendix I) were used to address objectives 1, 2 and 3 which provided specific data on characteristics and levels of human-carnivore conflict (Chapter 2), livestock husbandry practices (Chapter 3), people's attitudes and perceptions towards the five carnivore species (cheetah, lion, leopard, African wild dog and spotted hyena) (Chapter 4). During the interviews, the respondents' knowledge of carnivores was tested using the picture cards of 10 species (Appendix II). If the identification was incorrect, the respondent was told the correct animal before proceeding further, with discussions and explanations provided so that the respondent was clear exactly which species were being discussed and to ensure clarity for later questions. The cards included one picture of a tiger in order to judge respondents' reliability in recognizing local species. Details of the interview method are presented in Chapters 2, 3 and 4.

The questionnaire contained six thematic sections. The first section focused on information relating to respondents' sociodemographics such as name, gender, age, ethnicity, religious beliefs, household size, level of education, occupation, livestock holding (type and number of livestock kept), income sources, livestock type lost to predators and diseases in the month preceding the survey. The average market values of livestock species by age category (preferably adults) were obtained from traders and the prices were translated to US$ at the exchange rate of the time of the survey (1US$ = 1659TZS, June 2014).

The second section focused on attitudes, knowledge and perception regarding wildlife, particularly large carnivores. Respondents were also asked to independently list ('free-list') all wildlife species that they could think of that occurred around their household (defined as within a day's walk). The third section focused on the frequency of sightings of carnivore species. The fourth section focused on livestock depredation and human loss/injury experience with large carnivores. In this section, respondents were further asked to estimate the number and type of livestock they had lost to predators from 2013 to July 2014, place of attack, predators involved in the attack, time and season of attack. At least 1.5 years period was chosen because people could remember livestock depredation events within this time period with reasonable certainty. The fifth section focused on actions/anti-predation measures taken to control carnivores including lethal (use of poison, shooting, hunting, trapping) and non-lethal measures (guarding livestock or protective enclosures). The sixth section focused on livestock husbandry techniques and conflict mitigation measures.

1.8.2 Spoor surveys

Standard spoor survey methods were used to investigate occurrence and detection probabilities of four focal carnivore taxa in 3 land use types (i.e. Tarangire National Park (hereafter TNP), communal grazing land and village land). Spoor transects were established along the existing road network and heavily-used cattle trails. Roads and trails were assessed for their suitability in terms of substrate type, accessibility and traffic (Stander, 1998). Transects were systematically driven in a four-wheel-drive vehicle traveling at a constant speed of 10 to 15 km/hour (Funston *et al*., 2010; Houser *et al*., 2009; Stander, 1998). The experienced trackers (two Hadza Bushmen) sat on the bonnet/bumper and scanned for tracks directly ahead of the vehicle (Plate 1.1). Details of this method are presented in Chapter 5.

Plate 1. A researcher interviewing a local Maasai at Loibor Siret village (left), spoor tracking surveys (center), trackers counting the animal spoor (right)© Felix Mkonyi 2014

1.9 Structure of the dissertation

This dissertation is composed of six stand-alone chapters. In Chapter 1, an overview of the key issues concerning human-carnivore conflict around the world and, in particular, Tanzania, is provided; also the overall project aims, objectives and research questions to be addressed are presented. The study area where the study took place is also described in Chapter 1. General methods are also described in this chapter. However, details of study methodology are provided in each of the individual chapters. Besides the introduction and synthesis, each chapter has been written in publication format and represents a manuscript that is either published (Chapters 2-4) or in preparation for publication (Chapter 5). Chapter 6 finalizes the dissertation by giving a synthesis of the main findings and their implications for the management of human-carnivore conflict in the TSE. A brief overview of chapter's titles, aims and relevance of the research chapters is given below.

Chapter 2 titled **"Socio-economic Correlates and Management Implications of Livestock Depredation by Large Carnivores in the Tarangire Ecosystem, Northern Tanzania"** examines the reported patterns and extent of conflict with large carnivores, and also assesses the key drivers of any such conflict by integrating ecological, socio-economic and livestock husbandry variables. This chapter also seeks to evaluate the financial loss to local communities due to the perceived large carnivore depredation on livestock in relationship to other causes. All these were assessed using data collected from household interviews in five villages. The reported depredation levels were related to ecological, socio-economic and livestock husbandry variables. Species-specific and context-specific Generalized Linear Mixed Models (GLMMs) fitted with Poisson error distribution and log-link function were used to analyse the data. Information gained from this study has long-term implications on informing carnivore conflict issues essential for long-term conservation planning.

Chapter 3 titled "**Fortified Bomas and Vigilant Herding are Perceived to Reduce Livestock Depredation by Large Carnivores in the Tarangire-Simanjiro Ecosystem, Tanzania"** evaluates the perceived effectiveness of livestock husbandry techniques in reducing livestock depredation by large carnivores in the studied region. This chapter contributes valuable information that could help pastoralist communities to adopt acceptable human–carnivore conflict mitigation strategies and promote conservation of large carnivores. This chapter also seeks to identify interventions for further quantitative study in terms of measuring actual effectiveness of different livestock husbandry practices in reducing livestock depredation in the study area. The findings of this study are useful for evaluating the livestock husbandry practices perceived by people to be more effective in different contexts and hence facilitates informed management decisions towards human-carnivore conflict mitigation and large carnivore conservation.

Chapter 4 titled **"Local Attitudes and Perceptions Towards Large Carnivores in a Human-dominated Landscape of Northern Tanzania"** examines the human-carnivore relationships as determined by attitudes and perceptions towards large carnivores and potential factors influencing these attitudes. Using data collected from household interviews, attitudes of local people and risk perceptions associated with large carnivores (cheetahs, lions, leopards, spotted hyenas and wild dogs) in five villages adjacent to Tarangire National Park in northern Tanzania, were examined. Socio-economic factors (e.g., respondent's age, gender, sources of income, education level, occupation, livestock owned, livestock lost to predators), landscape factors (e.g., distance from protected area), years at residence (i.e. exposure to large carnivore-related risks) and knowledge of carnivores were used to find how best they predicted people's attitudes towards the main carnivore conflict species. This study provides valuable insights for the conservation of large carnivores within human-dominated landscapes and informs interventions that may mitigate the current and future status of the conflict and promote human-carnivore coexistence in the region.

Chapter 5 titled **"Large Carnivore Distribution in Relationship to Environmental and Anthropogenic Factors in a Multiple-use Landscape of Northern Tanzania"** investigates the occurrence and detection probabilities of four focal carnivore taxa and the factors that influence their occurrence and detection in a multiple-use landscape of northern Tanzania. Currently, very little information exists on the status, distribution and habitat use of large carnivores, especially outside the core PAs. In this chapter, spoor surveys data within a patch occupancy model framework were used to assess occurrence of large carnivores across three landscapes (the Tarangire National Park, communal grazing land and village land) characterized by different environmental and anthropogenic factors. This study provides a baseline of information which can be used to monitor changes in spatial distribution and status of large carnivore populations over time-related to changes in habitat and/or management efforts. This study also provides wildlife managers with a useful tool to identify priority sites for focused conservation of large carnivore populations and their habitats across the entire landscape.

The final section (Chapter 6) **"general synthesis and discussion"** provides a synthesis of the findings of the research, key implications for mitigating human-carnivore conflict, conservation of large carnivores and suggestions for further research.

CHAPTER TWO

Socio-economic Correlates and Management Implications of Livestock Depredation by Large Carnivores in the Tarangire Ecosystem, Northern Tanzania[1]

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Abstract

Livestock depredation by large carnivores is the key source of human-carnivore conflict worldwide and entails financial losses to livestock keepers. We examined the extent and patterns of livestock depredation, financial impacts of livestock losses and determinants of livestock depredation by large carnivores in the Tarangire ecosystem of northern Tanzania. Of 300 households surveyed, 74.7% reported losses of 1906 livestock to wild predators over 1.5 years, which represents an annual loss rate of 1.4% of their total herd. Spotted hyena (*Crocuta crocuta*) accounted for 70% of the total livestock loss, followed by leopard (*Panthera pardus*) (12%), African wild dog (*Lycaon pictus*) (8%), lion (*Panthera leo*) (7%) and cheetah (*Acinonyx jubatus*) (3%). This loss equated to a total financial loss of US$141,847 amounting to approximately US$ 633/household/year. Reported depredation frequency by all carnivore species increased significantly with increasing number of livestock owned, respondent's residency time, distance from the park boundary and declined significantly with increasing education, number of herders and improved fortified boma for cattle. Livestock depredation peaked during the wet season linked to seasonal migration of wild prey. Our study suggests that improving formal and conservation awareness education, boma fortification as well as improving herding practices could help mitigate the human-carnivore conflict.

Keywords: Financial losses, human-carnivore conflict, livestock depredation, livestock keepers, Tarangire ecosystem, wild predators

2.1 Introduction

Livestock depredation by large carnivores is one of the most important sources of human-carnivore conflicts as well as a major challenge threatening the conservation of large carnivores around the world (Treves and Karanth, 2003; Woodroffe, 2000). Large carnivores range widely, in such a way that existing protected areas (hereafter PAs) are not large enough to sustain their long-term viable populations (Woodroffe and Ginsberg, 1998). Hence, due to their large home ranges and high dietary protein requirements, large carnivores tend to move outside PAs and overlap with human-dominated landscapes (Patterson *et al*., 2004; Treves and Karanth, 2003; Woodroffe *et al.*, 2005). This close proximity to humans often results in conflict due to the damage they cause to livestock (Patterson *et al.*, 2004; Woodroffe and Ginsberg, 1998). Outside PAs, large carnivores are killed either deliberatively or accidentally, thus making the borders a "sink" in which human-caused mortality might limit survival of predators dispersing from the PAs (Kolowski and Holekamp, 2005; Kiffner *et al.*, 2009; Woodroffe and Ginsberg, 1998). The economic losses associated with livestock depredation on local communities often provoke retaliatory and preventative killing of the large predators (Ogada *et al.,* 2003; Patterson *et al*., 2004), which have a substantial impact on carnivore populations and thus jeopardize conservation efforts (Dickman, 2008; Woodroffe *et al*., 2005). Consequently, reducing antagonism towards large carnivores following depredation will contribute towards their conservation and promoting co-existence between humans and large carnivores.

Rates of livestock depredation by large carnivores may be influenced by environmental conditions, e.g., abundance and distribution of natural prey (Mizutani, 1999), seasonal patterns (Patterson *et al.,* 2004), socio-ecological factors, livestock husbandry practices and characteristics of livestock enclosures (Ogada *et al.,* 2003). In Tanzania, five large predators (lions, *Panthera leo*; leopards, *Panthera pardus*; cheetahs, *Acinonyx jubatus*; spotted hyenas, *Crocuta crocuta* and African wild dogs, *Lycaon pictus*) are chiefly responsible for livestock depredation (Dickman, 2008; Holmern *et al*., 2007; Kissui, 2008). Other carnivores (striped hyenas *Hyaena hyaena* and caracal *Caracal caracal*) occasionally prey on livestock as well. The Tarangire ecosystem is one of the richest wildlife areas in northern Tanzania. However, habitat loss and fragmentation associated with increasing human population, and the conversion of land for agriculture and livestock grazing (Msoffe *et al.,* 2011) have resulted in frequent encounters of large carnivores with humans and their livestock in this landscape. Livestock depredation by large carnivores entails economic damage to livestock keepers in Tanzania. However, diseases have been reported to contribute to far more livestock losses than depredation in other Tanzanian areas (Holmern *et al.*, 2007; Kissui, 2008; Nyahongo and Røskaft, 2012; Nyahongo, 2007).

Previous studies in the Tarangire ecosystem have focused either on actual livestock depredation events on a small set of carnivore species (Kissui, 2008; Mponzi *et al.*, 2014) or single species conflict i.e., human-lion conflict (Lichtenfeld, 2005). In addition, patterns of livestock depredation by large carnivores have been well-documented in Ruaha landscape (Dickman,

2008) and western Serengeti National Park (Holmern *et al.,* 2007). In this study, we build upon these previous studies by looking more broadly at the patterns of livestock depredation as well as ecological (distance to park boundary) and socio-economic factors (household size, education levels, number of livestock owned) influencing reported conflicts with a wide range of large carnivore species in the eastern part of the Tarangire ecosystem. There is currently limited information on these factors in our study area and across landscapes (Dickman *et al.,* 2014; Hampson *et al*., 2015). Correspondingly, no empirical data are available on perceived costs of livestock depredation by large carnivores and other causes of livestock losses such as disease and theft on people's livelihoods in this ecosystem. The cost of livestock depredation may play a critical role in shaping people's attitudes and behaviour towards carnivores (Bencin *et al.*, 2016; Hazzah, 2006; Kideghesho *et al.*, 2007; Lyamuya *et al*., 2016; Lyamuya *et al.,* 2014a; Lyamuya *et al.,* 2014b; Røskaft *et al.*, 2007). Furthermore, despite the existing studies on the extent of livestock depredation in Tanzania, relatively few studies have investigated the key determinants (ecological and socioeconomic factors) of perceived human-carnivore conflict (Dickman, 2008; 2010; Holmern *et al.,* 2007; Koziarski *et al.*, 2016). A better understanding of the extent and patterns of livestock depredation and its drivers is important to developing the most effective conflict mitigation and conservation management strategies (Dickman, 2008; Dickman *et al.,* 2014).

Our specific objectives were to (1) determine the reported extent of conflict and patterns of livestock depredation by large carnivores in relationship to other causes of livestock losses (2) estimate the financial livestock losses caused by large carnivores and other factors and (3) identify factors influencing livestock depredation by large carnivores. Based on our results, we suggest appropriate measures that might be taken to reduce human-carnivore conflict and contribute to improved conservation of large carnivores in the region. We hypothesized that (1) livestock depredation by large carnivores should be higher in households located closest to the protected area than further away (2) livestock depredation is influenced by socio-ecological (distance to park boundary, household size, education levels) and economic factors (number of livestock owned), and that (3) livestock husbandry practices will affect depredation rates. In this paper, we predicted that: (1) livestock depredation would decline significantly with increasing distance from the park boundary (Patterson *et al*., 2004; Holmern *et al*., 2007), (2) livestock depredation would be negatively associated with social factors (household size, education levels), positively associated with economic factors (number of livestock owned) (Holmern *et al.*, 2007; Woodroffe *et al.*, 2005) and respondent's residency time (Arjunan *et al*., 2006; Newmark *et al*., 1993), and (3) livestock depredation would increase significantly during the wet season for non-resident lions, spotted hyenas, cheetahs and wild dogs in response to seasonal migration of wild prey (Kahurananga and Silkiluwasha, 1997; Koziarski *et al*., 2016; Mponzi *et al*., 2014) – and vary independently with season by resident species such as leopard (Kissui, 2008) and (4) improved livestock husbandry practices would be negatively associated with depredation because fortified bomas and increased number of herders should result in decreased depredation (Lichtenfeld *et al.*, 2014; Ogada *et al*., 2003; Woodroffe *et al*., 2007).

2.2 Materials and methods

2.2.1 Study Area

The study was conducted in five villages (Loiborsoit, Terat, Emboret, Sukuro and Loibor Siret) of the Simanjiro Plains in Simanjiro district, northern Tanzania (Figure 2). Simanjiro district is located between 3°52′ and 4°24′ S and 36°05′ and 36°39′ E and lies within the Tarangire ecosystem located in the Maasai Steppe of northern Tanzania. The Tarangire ecosystem (20,000 km^2) is defined by the movements of its migratory animals, and consists of Tarangire National Park (TNP) (2,850 km^2) forming the dry season range for the migratory herds, and its wet season dispersal area and calving grounds in Monduli (including Lake Manyara National Park, Lolkisale Game Controlled Area, Manyara Ranch, Burunge and Randilen Wildlife Management Area) and Simanjiro districts (including Simanjiro plains, Mkungunero Game Reserve) (Borner, 1985). The area is characterized by bimodal rainfall averaging 650 mm per annum, with short rains from November to December and the long rains from March to May. The climate is highly seasonal with the dry season (June – October) and wet season (November - May).

The Simanjiro plains are one of the most important wet season dispersal and calving ranges for wildebeests (*Connochaetes taurinus*) and other ungulates such as zebra (*Equus burchellii*), hartebeest *(Alcelaphus buselaphus)* and fringe eared oryx (*Oryx beisacallotis)*. During the wet season (November – May), about 50% of the wildebeest move from the TNP to the northern plains and the other 50% to the Simanjiro plains (Morrison and Bolger, 2014). The plains are also important for non-migrant herbivores such as Thomson's gazelle (*Gazella thomsoni*), impala (*Aepyceros melampus*) and greater kudu (*Tragelaphus strepsiceros*) and an important area for livestock grazing by pastoralists during the dry season (June – October) (Kahurananga and Silkiluwasha, 1997). Large mammalian fauna of the area includes lions *P. leo,* cheetahs *A. jubatus*, leopards *P. pardus*, African wild dogs *L. pictus*, striped hyenas *Hyena hyena* and spotted hyenas *C. crocuta.* African wild dogs are listed as Endangered, lions, cheetahs and leopard are listed as Vulnerable, whereas striped hyenas are classified as Near Threatened and spotted hyenas as of Least Concern (IUCN, 2016). The major ethnic groups are the Maasai, Waarusha, and Ndorobo. The Maasai are semi-nomadic pastoralists, with a very high dependency on livestock although they have also been practicing subsistence agriculture. Pastoral communities keep a variety of livestock including cattle, goats, sheep, and donkeys. Waarusha, Ndorobo and some Maasai are agro-pastoralists who collectively practice subsistence agriculture and pastoralism.

2.2.2 Interview methods and questionnaire design

We used semi-structured questionnaire design to obtain data on perceived human-carnivore conflict. We consulted the village leaders and generated a numbered list of all eligible bomas included in the survey. Then, we selected 60 bomas from each village at random. The questionnaire survey was conducted between June and July in 2014. In designing the questionnaire, we followed the similar format used by Maddox (2003) in northern Tanzania and by Dickman (2008) in southern Tanzania (see Appendix I, Supplementary material). Pre-testing of the questionnaire was conducted on a sample of 15 respondents and revisions were made on the questionnaire to ensure clarity of the questions before the actual data collection started. The questionnaire contained both closed-ended as well as open-ended questions in order to gain more information on participant's attitudes and reasoning. We preserved the confidentiality of the respondent during the interviews. A questionnaire was administered in person by the principal investigator (PI) with the help of a local assistant and translator to 300 respondents. Within each boma, we counted the total number of households and utilized a random number generator to select a single household.

Where possible, respondents were selected from any of the three subjects (i.e. the head of the family (usually a man), the head's wife, or elder son according to seniority). Women deferred to men in seniority, so respondents were predominantly male, but interviews were conducted with women where they were comfortable to do so. During the interviews, we tested the respondents' knowledge of focal carnivores using the cards of coloured photographs.

The final questionnaire contained six main sections, however, only two are applicable in this part of the study (Appendix I). The first section focused on information relating to respondents' sociodemographics such as respondent's gender, age, ethnicity, religious beliefs, household size, education level, occupation, residency time, livestock holding, income sources and details on livestock number and type lost to wild predators compared with other causes in the month preceding the survey. The average market values of livestock species by age category (preferably adults) were obtained from livestock traders and the prices were translated to US$ at the exchange rate of the time of the survey (1US$ = 1659TZS, June 2014). We estimated the direct economic or financial losses to wild predators and other causes of livestock loss per household based on the prevailing market price of livestock at the time of conducting this survey. The average market value for cattle, calf, small stock and donkey was US$372, US$120, US$48 and US$90 respectively (Table 2). The second section focused on questions about the characteristics of livestock depredation. Respondents were asked to estimate the number and type of livestock they had lost in the previous one and a half years (2013 to July 2014) to wild predators, including place of attack, time and season of attack.

The focus of this study was the reported livestock loss to the wild predators; therefore we assume that the losses attributed to wild predators were often exaggerated, either deliberately, or due to the unintentional attribution of livestock deaths to wild predators. We assumed a 1.5 year period conservative enough for respondents to recall the depredation incidents, and the financial costs are estimates based on these incidents. All respondents were adults (≥18 years of age) who could freely express themselves. The household was chosen as the sampling unit, adapting Maddox (2003) and Dickman (2008), and interviews were restricted to one respondent per household. The questionnaire was conducted in a local language (i.e. Swahili language - with the aid of a translator speaking Maasai where needed) and took approximately 1 h to complete. The research was cleared by the Tanzanian authorities. The Tanzania Commission for Science and Technology reviewed and approved the research protocol (Ref. no. 2014-370-NA-97-20). Verbal

Informed Consent was obtained from all the subjects prior to participation and data were kept anonymously.

2.2.3 Statistical Analyses

Continuous variables were analysed using standard descriptive statistics (means, standard deviations (SD), ranges, percentages, and frequencies of counts, tables and charts). Categorical variables including gender, occupation and education level were converted into a set of dichotomous, dummy-coded variables. The intensity of livestock depredation expressed as the total number of livestock reportedly killed by all predators and by each predator species separately at bomas and in the grazing area was used as a response or dependent variable within generalized linear mixed models (GLMMs) with a Poisson error distribution and a log-link function. We included the number of owned livestock expressed in Tropical Livestock Units (TLU), respondent gender (male vs. female), respondent age (years), education level (none vs. primary, secondary and tertiary pooled), residency time (number of years since the respondent had arrived in the area), household size expressed in Adult Equivalent Units (AEU), number of herders, distance (km) from the park boundary (measured as the nearest distance between household and the park boundary using *ArcGIS v.10.1* (ESRI, Redlands, USA) and boma type (fortified or unfortified) as predictor variables. Since households from one village were not statistically independent of each other, we included the village ID as a random effect. Therefore, we used GLMMs to determine the nature of the potential relationship between response variables and all the potential predictor variables. Further descriptive statistics of explanatory variables used in the models are presented in Table 7, Supporting information.

To control for variation in household size, the household size was measured in terms of AEU. The adult-equivalent conversion factors for the number of people in the household by Latham, 1965, cited by Collier *et al.* (1990), were used to determine the AEU as presented in Table 8, Supporting information. First, in order to calculate AEU, the sex and age of surveyed household members were compiled (Cavendish, 2002). Second, the AEU by age and sex were summed up for all people in the household to compute the total AEU for the particular household. For better comparison of herd sizes across households and to account for differences in size and value of different livestock species, we converted number of reported livestock to standard units (i.e. Tropical Livestock Units (TLUs) (see also Table 1). The following conversion factors were used for each species of livestock: one head of cattle = 0.7, one goat or sheep = 0.1 and one donkey = 0.5 (Jahnke, 1982; LEAD/FAO, 1999). Total TLU = Livestock Nr x TLU factor. The overall TLU per respondent was then adjusted to 1 TLU being equivalent to an animal with a body weight of 250 kg (Jahnke, 1982; LEAD/FAO, 1999). Because the factors influencing depredation in the grazing area were distinct from those that influence depredation at bomas, we performed analyses separately for the two distinct contexts. Therefore, we analysed explanatory variables separately for each predator species and for all predators combined and eventually running six separate model sets with all possible variable combinations within GLMMs (Tables 10-12, Supporting information).

We checked for multicollinearity of the predictor variables using Spearman's correlation coefficients (r_s) for all possible variable pairs. We chose a cut-off of $r_s \geq 0.6$ to indicate high collinearity between predictor variables (Zuur *et al*., 2010). Using this approach resulted in the exclusion of one of the highly correlated variables from the analysis (see Table 7, Supporting information).

Age was correlated with education, respondent's residency time and number of herders. Moreover, gender was correlated with education, respondent's residency time, household size (adult equivalents) and number of owned livestock (livestock units). In addition, the number of owned livestock (livestock units) was correlated with household size (adult equivalents) and respondent's residency time (Table 9, Supporting information). However, there was no strong collinearity detected among these predictor variables (all $r_s < 0.6$), suggesting that any collinearity among variables was unlikely to affect statistical inference (Zuur *et al*., 2010). In contrast, boma type-small stock was highly correlated ($r_s = 0.76$) with boma type-cattle (Table 9, Supporting information) and we therefore excluded boma type-small stock from the analysis. Eventually, a total of nine variables were included in the models [age, gender, education level, respondent's residency time, household size (adult equivalents), livestock units, number of herders, distance to the park boundary and boma type-cattle] (Table 7, Supporting information). We ranked candidate models in order of parsimony based on the Akaike Information Criterion (AIC) corrected for small sample sizes (AICc) and model weights (ωi) (Burnham and Anderson, 2002). We computed model-averaged coefficients of predictor variables based on the top ranked models. We considered all models with ΔAICc < 2 to be equally plausible (Burnham and

Anderson, 2002). We chose GLMMs with a Poisson error, the most appropriate distribution for count data because they take into account both fixed and random effects in a single model and deal with non-normal response variables (Zuur *et al.,* 2010). We had six Poisson distributed target/response variables (i.e. number of livestock killed by all predators and number killed by lion, leopard, cheetah, spotted hyena and wild dog). We used the Pearson's chi-squared analyses to test the observed frequency of predation on various types of livestock, contexts of livestock attack events by the five carnivores and the nature of the relationships among independent variables. All statistical analyses were performed using *SPSS v. 22.0* (SPSS Inc., Chicago, IL, USA) and the significance level was measured at $p < 0.05$.

2.3 Results

2.3.1 Respondents' demographic, livestock holdings and socio-economic characteristics

Overall, the majority of respondents were the Maasai (96%, n = 288) and the rest were the Waarusha (4%, n = 12). The age group of the respondents ranged from 18 to 92 years old, with an overall mean age of 35.86± 14.19 (SD) years. Overall, more males (88.3%, n = 265) than females (11.7%, n = 35) participated in this survey, probably because the Maasai women do not speak in the presence of men or because women deferred to men in seniority. The mean household size, (in AEU) was 6.88± (SD 2.11) persons per household ranging from 2 to 12 persons.

Almost all respondents (99%) reported owning cattle, 99% reported owning goats and sheep (hereafter referred to as 'small stock') and 89.3% reported owning donkeys. Total stock holdings were estimated at 93,382 head of livestock (i.e., total TLUs = 7938) in all surveyed households. Mean TLU values ranged between 14.16 and 26.46 per household. The overall mean TLU per household was 25.61± (SD 5.53) (Table 1). Livestock number varied across households but consistently cattle were the dominant livestock species (Table 1, Figure 3). There was a slightly higher mean TLU per household in Loibor Siret and Sukuro due to a relatively high number of cattle and small stock in these villages (Figure 3). On average, respondents from Terat had less livestock (14.16 TLU) compared to other villages.

The majority of respondents were agro-pastoralists 95% (*n* = 285), while 5% (*n* = 15) were pastoralists. Of the 300 respondents, 51.3% (*n* = 154) had no formal education, while the rest had formal education: i.e. 36% (*n* = 108) primary education, 11.3% (*n* = 34) secondary education and 1.3% (*n* = 4) tertiary education. The main source of cash income for respondents was the sale of livestock (91%, *n* = 272), selling crops (27.3%, *n* = 82), off-farm activities (35%, *n* = 105, i.e. business, salaried or casual employment) and fewer people relied on other income generating activities (1.3%, *n* = 4, i.e. operating a restaurant business and sewing beads, construction works and bee keeping).

2.3.2 Livestock losses due to depredation in relationship to other causes

Seventy-five percent (*n* = 224) of respondents reported the loss of 1906 livestock to predators over a 19-month study period (Table 2). Spotted hyenas were reported to be responsible for most of the attacks on livestock (70.3%), followed by leopards (12.2%), African wild dogs (7.9%), lions (6.8%) and cheetahs (2.9%). In addition, cattle 23.5% (*n* = 56), small stock 75.6% (*n* = 180) and donkeys 0.8% (*n* = 2) were occasionally injured in these attacks. Cheetahs, spotted hyenas, leopards and African wild dogs were the main predators of small stock (98.5%) while lions depredated mostly on cattle (59.2%) (Figure 4). Depredation on donkeys was reported to be caused mainly by spotted hyenas (83.3%). Wild dogs (2.4%) were occasionally reported to prey on calves. Reported depredation frequency varied between livestock species (χ^2 = 846.49, *df* = 8, p <0.001; Figure 4). Non-predator livestock losses were reported to be associated with diseases particularly Heart water (77.3%), Contagious Bovine Pleuropneumonia (18.2%), East Coast Fever (2.5%), Contagious Caprine Pleuropneumonia (1.4%), diarrhoea (0.5%) and anthrax (0.2%).

Reported causes of livestock losses during a 1-month preceding the survey showed that disease was the main cause of livestock loss, followed by depredation, theft and other causes (snake bites, accidents and buffalo assaults). Overall, disease accounted for 90.8% of all stock losses initially reported, depredation 7.1%, theft 1.3% and all other losses 0.8%. On average, a significantly higher proportion of livestock were reportedly lost to diseases compared to other causes of livestock loss (χ^2 = 4205.70, *df* = 3, $p < 0.001$). The percentage of stock reportedly lost to depredation over a 1-month period showed that Sukuro (11.8%) had the highest rates of reported depredation, followed by Loibor Siret (6.5%) and Loiborsoit (5.8%), while the remaining villages constituted 4.4% in total. The average annual loss of the total herd to predators was 1.4% when considering the stocking rate in 2014 (ca. 93,382 total stock) and a total of 1906 depredated livestock.

2.3.3 Contexts of livestock depredation

The contexts of attacks on livestock varied among predators. Spotted hyenas were reported to attack livestock at bomas more often than when grazing at pasture ($\chi^2 = 1016.34$, $df = 1$, $p < 0.001$), whereas the attacks by cheetahs ($n = 55$) and wild dogs ($n = 150$) were reported to occur during the day (in the grazing areas). In contrast, lions and leopards were reported to attack livestock held in boma enclosures during the night as well as the grazing livestock during the day. However, attacks by lions ($\chi^2 = 0.12$, $df = 1$, $p = 0.724$) and leopards ($\chi^2 = 0.52$, $df = 1$, $p = 0.469$) did not vary significantly between the two contexts. Overall, 75.7% of predator attacks on livestock were reported to occur during the night at bomas, while 24.3% occurred during the day at pasture.

2.3.4 Spatial patterns of livestock depredation

We found that the spatial patterns of livestock depredation were unevenly distributed across the studied villages. The frequency of livestock reportedly lost to different predators differed significantly between villages ($\chi^2 = 657.51$, $df = 16$, $p < 0.001$). During the 19-month study period, the highest depredation levels were reported in Sukuro (23.2%), Emboret (22.9%) and Loiborsoit (21.9%), with slightly lower levels reported in Terat (17.0%) and Loibor Siret (14.9%). The mean annual livestock loss as reported for all predators was 8.51 head of stock per household (of those that reported loss) (Table 2). Wild dogs and leopards were reported to cause more attacks in Loibor Siret (67.3%, $n = 101$ and 39.2%, $n = 91$ respectively). Spotted hyenas were more often reported to have killed livestock than any other predator in all villages, but less frequent in Loibor Siret (3.5%, $n = 47$). In contrast, lions were reported to have killed more cattle in Loiborsoit (35.7%, $n = 46$).

2.3.5 Seasonal patterns of livestock depredation

More than three-quarters (76%) of reported attacks by all carnivore species occurred during the rainy season, while 24% were reported to have occurred in the dry season. Spotted hyenas, lions, cheetahs, leopards and wild dogs were reported to attack livestock significantly more often in the wet season than dry season (spotted hyenas: $\chi^2 = 448.23$, $df = 1$, $p < 0.001$; lions: $\chi^2 = 12.40$, $df = 1$, $p = 0.0004$; cheetahs: $\chi^2 = 21.02$, $df = 1$, $p < 0.001$; leopards: $\chi^2 = 40.56$, $df = 1$, $p < 0.001$; African wild dogs: $\chi^2 = 6.41$, $df = 1$, $p = 0.01$; Figure 5(a)). Overall livestock depredation peaks were greatest in April and May during the wet season (Figure 5(b)).

2.3.6 Financial valuation of livestock losses

The total estimated financial loss for those people interviewed corresponding to 1906 depredated livestock was US$141,847 (equivalent to 235,324,173 Tanzanian shillings) (Table 2). Spotted hyenas accounted for 70.3% (US$81,905) of the total herd and 57.7% economic loss, while lions accounted for 6.8% (US$38,705) of the total herd and 27.3% of financial loss (Table 2). The financial loss due to other predators was comparatively low (Table 2). On average, the annual financial loss per household was estimated to be US$633 (of those that reported loss), and US $473 (considering all the respondents). On average, the financial loss per household (of those that reported stock losses) was estimated to be US$464 during the wet season and US$168 during the dry season. The greatest proportion of stock and financial losses were reported on small stock in proportion to their relative abundance (US$82,189, $n = 1718$) (Tables 1 and 2). There was a significant difference in terms of financial valuation of losses of livestock species ($\chi^2 = 951$, $df = 12$, $p < 0.001$, $n = 1906$) and in terms of financial impact among the predators ($\chi^2 = 78020$, $df = 12$, $p < 0.001$). On average, the financial loss due to disease for the month preceding the survey ranked highest US$147,235 (US$ 491 per household), followed by depredation US$7968 (US$27 per household) and theft US$1695(US$6 per household) (Table 3). The total financial loss of livestock to large carnivores was relatively higher in Sukuro (US$339,559.30) and lowest in Loiborsoit (US$103,522.60) (Table 3).

2.3.7 Ecological and socio-economic factors associated with livestock depredation

For all predators combined, model selection using AICc identified two models (ΔAICc < 2; Table 10). In the top model, the reported frequency of livestock depredation (all predators combined) was positively associated with distance to park boundary, respondent's residency time and livestock units, but negatively associated with education level, boma type-cattle and number of herders in the grazing area (Table 4). Nevertheless, the reported frequency of livestock depredation by lions at bomas was best explained by the global model containing age, gender, education level, respondent's residency time, household size (AEU), distance to park boundary, boma type-cattle and livestock units as significant factors (Table 11, Supporting information). The reported frequency of livestock depredation by lions declined significantly with increasing level of education, distance from the park boundary and household size (AEU) (Table 5). Moreover, reported depredation frequency was lower among female interviewees compared to males. In addition, reported depredation frequency declined significantly with age and improved boma for cattle, but declined (non-significantly) with number of herders in the grazing area (Table 5). Conversely, reported depredation frequency increased significantly with increasing livestock units and respondent's residency time at their households. On the other hand, the top model for spotted hyenas contained education level, respondent's residency time, livestock units, distance to park boundary and boma type-cattle at bomas, while in the grazing area, contained livestock units and number of herders as significant factors (Table 11, Supporting information). The reported frequency of livestock depredation by spotted hyenas increased significantly with increasing distance from the park boundary, respondent's residency time, livestock units and declined significantly with improved boma for cattle. However, reported depredation frequency decreased (non-significantly) with increasing level of education and declined significantly with increasing livestock units and number of herders in the grazing area (Table 5).

At bomas, the reported frequency of livestock depredation by leopard was best explained by household size (AEU) (statistically significant) trend: reported depredation frequency declined with increasing household size), respondent's residency time [trend: reported depredation frequency increased (non-significantly) with residency time] and distance to park boundary [trend: reported depredation frequency declined (non-significantly) with increasing distance from the park boundary] (Table 4). The best fitting model for wild dog contained two variables; livestock units and number of herders, all showing a negative trend (Table 6, Table 12 Supporting information). However, only livestock unit reached a statistical significance. In the case of cheetahs, the reported frequency of livestock depredation decreased (non-significantly) with increasing livestock units and increased (non-significantly) with number of herders (Table 6).

2.4 Discussion

2.4.1 Livestock losses due to depredation in relationship to other causes

Our results showed that 75% of people reported carnivore attacks in their households, which is equivalent to an average of 1.4% of the total herd loss per annum. This figure is within the range of 0.02-2.6% worldwide losses to large carnivores reported by Graham *et al.* (2004), and is far more than 0.26% of the total herd reported in Ruaha National Park (Dickman, 2008); and much less compared to 12% of the total herd reported in Loliondo and Ngorongoro buffer zones (Maddox, 2003).

Interestingly, we found that carnivore species preyed selectively upon different livestock species corresponding to the size of the predator and in accordance with the size of their prey, prey preference and abundance. Cheetah, spotted hyena, leopard and African wild dog were the predominant predators of smaller prey species (small stock), while lions preyed mostly on larger prey species (cattle and donkey) and rarely on small-sized prey (small stock). This result confirms the preference of lions for larger prey species as reported in various studies (Hayward and Kerley, 2005) and the preference of cheetah, spotted hyena, leopard and African wild dog for smaller prey species (Hayward, 2006; Hayward *et al.*, 2006a; Hayward *et al.*, 2006b). Our results are consistent with previous findings that livestock species selection corresponds to the size of the predator (Patterson *et al.*, 2004) and in accordance with the size of their prey (Hayward, 2006). However, small stock were the most preferred prey by cheetah, spotted hyena, leopard and wild dog, probably related to their relative abundance in comparison to other livestock. In addition, spotted hyenas also preyed upon larger livestock such as cattle and donkey that are larger than their own body mass probably due to the fact that spotted hyenas do not have distinct prey species preference (Hayward, 2006). On the other hand, wild dogs occasionally preyed upon calves, i.e. prey sizes which are significantly larger than their own body mass due to their group hunting strategy (Hayward *et al.*, 2006b).

Overall, spotted hyenas and leopards accounted for more small stock attacks compared to other carnivore species. The high plasticity of spotted hyenas (Boydston *et al.*, 2003; Kruuk, 1972) and leopards (Nowell and Jackson, 1996) in habitat use and diets may explain their predominance as small stock predators compared to other carnivore species. Similar studies have also reported spotted hyenas and leopards being responsible for most of the small stock depredation, e.g., around the Serengeti National Park in Tanzania (Holmern *et al.*, 2007) and in the Maasai Steppe of northern Tanzania (Kissui, 2008; Mponzi *et al*., 2014). However, unlike Tarangire ecosystem, wild dogs and spotted hyenas were considered the most problematic species in the eastern part of the Serengeti ecosystem (Hampson *et al*., 2015; Lyamuya *et al*., 2014a) and lions in the Ruaha landscape (Dickman *et al.*, 2014).

The total financial loss of livestock depredation by spotted hyenas, lions and leopards reported in this study was much higher compared with other studies (Holmern *et al*., 2007). In this case, the financial costs of reported losses might be perceived as significant by households experiencing such losses. In Maasai culture, livestock act as a social capital, a sign of status and wealth (Hampson *et al.,* 2015), such that a single depredation event may be devastating for households owning very few animals, hence posing a significant economic impact on rural communities (Hazzah, 2006). Perception of costs may also be higher than actual costs because, for example, predators are blamed for livestock loss when the cause of livestock death may be due to other factors, such as disease, and a scavenger is blamed for killing livestock when in reality it is scavenging an animal already dead (Rasmussen, 1999). We observed that the total reported livestock loss due to leopard and wild dogs was slightly higher than that by lion, but lion killed cattle contributing to higher financial loss than leopard and wild dogs. Cattle have economic and cultural values placed on them by the Maasai; therefore loss of cattle is likely to have serious economic and social consequences (Spear and Waller, 1993). Our results suggest that diseases were responsible for higher livestock losses than any other cause within and among villages. Our findings concur with other studies conducted in Tanzania, in which disease was found to be the leading cause of livestock loss (Dickman, 2008; Holmern *et al*., 2007; Kissui, 2008; Nyahongo and Røskaft, 2012). Diseases are particularly known to be responsible for high loss in livestock production (3-6 times higher other than livestock depredation) in sub-Saharan Africa (Frank *et al.*, 2005; Gifford-Gonzalez, 2000). Generally, the impact of theft was very low compared to the impacts of livestock depredation and disease contrary to Nyahongo and Røskaft (2012) and Ogada *et al.,* (2003).

2.4.2 Spatio-temporal patterns of livestock depredation

We observed variation in the timing and contexts of depredation by different carnivore species similar to other reported findings. Cheetahs and wild dogs are diurnal, and typically attack grazing herds by day (Ogada *et al.*, 2003). Leopards, spotted hyenas and lions attack livestock at any time of the day, either in the grazing area or at bomas (Patterson *et al.*, 2004), although other studies found that spotted hyena and leopard attacks prevail at night at bomas (Kissui, 2008; Woodroffe *et al.*, 2007). Surprisingly, we found that the mean annual livestock loss due to depredation was relatively lower for households in Loibor Siret (1.29 per household) and Terat (1.45 per household) than expected compared to other villages. We expected that the reported frequency of livestock depredation would be relatively higher for households in Loibor Siret due to the proximity of this village to the Tarangire National Park. A possible explanation for the lower depredation rates in Loibor Siret could be due to the presence of fortified bomas which reduced incidences of carnivore attacks on livestock. Between 37% and 40% of respondents reported using fortified bomas in Loibor Siret to keep cattle and small stock respectively, which might have influenced our results in various ways (Mkonyi *et al.*, 2017c). In addition, boma type was a good predictor of livestock depredation levels (e.g., boma type for cattle associated negatively with livestock depredation by all predators, lions and spotted hyenas in our boma depredation model). The impact of fortified bomas on large carnivores has also been tested in Loibor Siret where overall depredation rates by lions, leopards and spotted hyenas declined by 90% (Lichtenfeld *et al.*, 2014). Similarly, there were fewer reported incidences of depredation in Terat households. The reason for the lower depredation in this village is uncertain, however, it could possibly reflect the low density of carnivore species around this village. Nevertheless, the highest depredation rates reported in Sukuro, Emboret and Loiborsoit may be related to many factors, including low density of wild prey species, continued human encroachment onto carnivore habitat and poorly constructed night-time enclosures (bomas). Studies show that livestock depredation is more common in areas with low prey abundance (Bagchi and Mishra, 2006), high human population, increased encroachment and poor livestock husbandry practices (Treves and Karanth, 2003).

2.4.3 Seasonal patterns of livestock depredation

Our study revealed that there was a seasonal variation in livestock depredation by lions, cheetahs, leopards, spotted hyenas and wild dogs, with clear peaks of depredation during the wet season. The depredation peak during the wet season has also been reported by Mponzi *et al.* (2014) and Koziarski *et al.* (2016) for the western part of this ecosystem. But in other areas of Africa, depredation mainly occurs during the dry season (e.g., Hemson *et al.,* 2009). Our findings somewhat contradict the "reduced natural prey hypothesis" which emphasizes that depletion in natural prey abundance promotes attacks on livestock (Khorozyan *et al*., 2015a). Our results could reflect the seasonal shifts in wild prey distributions from TNP into the communal village lands (Kahurananga and Silkiluwasha, 1997), with more predators (lions, cheetahs, wild dogs and spotted hyenas) following natural prey and hence coming into conflict with humans and livestock. This seasonal variability in depredation patterns has also been reported for hyenas and lions in the Maasai Steppe of northern Tanzania (Kissui, 2008; Mponzi *et al*., 2014) and for lions in Tsavo National Park in Kenya (Patterson *et al*., 2004). Patterson *et al*., (2004) found that livestock depredation by lions peaks during the wet season when natural prey are in better condition and more widely dispersed, hence difficult for predators to acquire. Interestingly, we found no support for the prediction that livestock depredation by leopards is independent of season. Hence, it is possible that even leopards could be moving in the same manner with ungulate migrations following the increase in livestock predation by leopards in the wet season. However, additional research with verified data would be appropriate in explaining this seasonal variation.

2.4.4 Ecological and socio-economic factors associated with livestock depredation

Our hypothesis that socio-ecological (distance to park boundary, education level) and economic factors (number of livestock owned) would influence the reported frequency of livestock depredation by all predator species was supported. Surprisingly, distance to park boundary was positively associated with reported frequency of livestock depredation, which was contrary to our prediction. This is a clear indication that the reported frequency of livestock depredation by all predator species was relatively lower in households located closer to PA than further away. Clearly, there is a high variation in this variable because the households ranged from 7 to 52km from the park boundary. Our findings contradict with findings reported elsewhere that livestock depredation declines significantly with increasing distance from the park boundary (Holmern *et al.*, 2007; Patterson *et al.*, 2004). This unexpected pattern may be explained by improved fortified bomas in households closest to the park (i.e. around 42% of the traditional bomas were fortified), while distant households had few or no fortified bomas. However, this trend varied significantly by species. For instance, reported lion attacks declined with increasing distance from the park boundary, although the reverse was true for spotted hyenas. This discrepancy can be partly explained by the fact that spotted hyenas killed the largest number of small stock in households located further away from the park where fortified bomas were mostly absent. Moreover, our findings suggest that lions were more likely to attack livestock in households that were closer to the PAs due to the fact that lions usually stay close to their natural habitat (Holmern *et al.*, 2007). However, spotted hyenas often move far from PAs and are able to survive well in human-dominated landscapes due to their opportunistic feeding patterns and adaptive ranging behaviour (Hofer and East, 1993; Kolowski and Holekamp, 2011). Our findings showed that respondents with formal education experienced lower depredation rates than those without any formal education, consistent with our prediction and previous studies (Holmern *et al.,* 2007; Woodroffe *et al.*, 2005). Consistent with other studies (Hemson *et al.,* 2009; Zimmermann *et al.,* 2005), our results indicate that people who owned large numbers of livestock experienced more livestock losses to large carnivores. This finding contradicts Koziarski *et al*. (2016) who found that education, psychological and demographic attributes were more influential in wildlife conflict perceptions than economic considerations (livestock ownership). However, consistent with our prediction, the incidences of attacks on livestock by predators declined with increasing number of herders and fortified bomas as it has been demonstrated in other studies (Lichtenfeld *et al.*, 2014; Ogada *et al.,* 2003; Woodroffe *et al.*, 2007). Our prediction that increased exposure to wildlife-related risks (i.e. long-term residency) would be positively associated with livestock depredation was supported, and this may be because long-term residency has been found to be associated with negative attitudes towards large carnivores (see Arjunan *et al.,* 2006; Newmark *et al.,* 1993).

Furthermore, we found that men reported more depredation frequency with lions than women in the study area. This may be because men claim ownership of livestock and they come more frequently into contact with lions during livestock herding (Hampson *et al.*, 2015; Koziarski *et* *al.*, 2016). We also found that reported depredation frequency with lions at bomas was negatively associated with interviewee age, suggesting that as interviewees get older, they perceive lower levels of depredation. It could be that older interviewees are more likely to have reinforced bomas and this corroborates our previous findings (Mkonyi *et al.,* 2017a), showing that the longer people are in a place; the more tolerant they are likely to become. In addition, we assume that retaliatory killing and also the culturally motivated killing of lions by humans in response to damages caused by lions is negatively affecting lion populations in this ecosystem (Kissui, 2008; Lichtenfeld L. Pers. Comm. 2014). Based on this evidence, we can assume that it is also likely for other species.

2.5 Conclusion and management implications

Human-carnivore conflict is a complex issue for management, especially where humans live adjacent to or within PAs (Dickman, 2010). Our study suggests that conflict due to livestock depredation could be significantly reduced by improving formal and conservation awareness education at all levels (i.e. during primary, secondary and tertiary school education), fortifying boma enclosures, improving herding practices such as increasing the number of herders (particularly adults) per herd. We also suggest the need for finding out high and low-risk areas where livestock is more or less susceptible while grazing and eventually educating herders to avoid grazing their livestock in high-risk areas (predator hotspots) or always be vigilant while grazing in such areas. Conservation efforts for mitigating conflicts should concentrate more on households that are situated further away from national park by improving boma enclosures for livestock. In addition, local people should receive tangible benefits (through benefit-sharing programmes) from large carnivore presence on village land that could offset costs of livestock losses and increase local people’s tolerance for these predators. While increased carnivore attacks on livestock in the study area can engender significant socio-economic costs to local households, conservation efforts would benefit from combined carnivore conservation initiatives and livestock depredation reduction.

Conservation education and awareness programmes focusing on large carnivore behavioral ecology may also reduce the human-carnivore conflict and increase local people’s tolerance for large carnivores (Sillero-Zubiri *et al.*, 2007). In order to control and prevent livestock depredation by large carnivores, there is a need to understand predator-specific protection measures which can then be integrated into conflict mitigation programmes. As disease was perceived to be a greater cause of livestock losses than depredation in the surveyed villages, interventions would be to control and manage livestock diseases through preventive vaccinations and increase access to veterinary services (Khorozyan *et al.*, 2015b).

Our study has provided new insights into the complexities of human-carnivore conflicts among the five large African carnivores and determinants of reported conflict with these species in the Tarangire ecosystem of northern Tanzania. We recommend further research along these lines to evaluate the actual frequency of conflict in the study area (using field verification methods) and continued monitoring of conflict situations over time or other causes of mortality. This might help in understanding the 'conflict hotspots' or sites predisposed to livestock depredation across the village land, allowing herders and wildlife managers to concentrate livestock protection and conservation education programs in such areas.

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Table 1. Livestock holdings expressed in Tropical Livestock Units (TLU) per adult equivalent unit (AEU) in the study villages in Simanjiro district, Tanzania (2014).

			Livestock type		
Village	N	Cattle	Small stock	Donkey	[a]Mean
Loibor Siret	60	20.90	5.05	0.52	26.46
Sukuro	60	20.76	4.58	0.46	25.80
Terat	60	10.55	2.98	0.63	14.16
Emboret	60	16.68	3.83	0.58	21.09
Loiborsoit	60	12.07	2.56	0.61	15.24
Mean ±SD		**16.19±4.29**	**5.87±1.26**	**3.55±1.22**	**25.61 ± 5.53**
% of the total herd		**37.15**	**61.05**	**1.80**	**100**
Livestock per AEU		**16.19**	**5.87**	**3.55**	**25.61**

N: number of households sampled in the study villages.

[a]Mean TLU per AEU

TLU conversion factor: 1 head of cattle = 0.7 TLU, 1 sheep or goat (small stock) = 0.1 TLU, 1 donkey = 0.5 (Source: Jahnke 1982, LEAD/FAO 1999)

The Tropical Livestock Unit (TLU) is commonly taken to be an animal of 250 kg live weight.

Table 2. Financial valuation (in US $) of reported livestock kills (*n*) by large carnivores in the study villages in Simanjiro district, Tanzania, over a period of 2013 - July 2014

	Unit value (US$)	Lion	Cheetah	Leopard	Spotted hyena	African wild dog	Overall
Cattle	$371.91	$37,191 (100)	$0	$0	$18,595.5 (50)	$0	$55,786.5(150)
Calf	$120.00	$0	$0	$0	$1,320 (11)	$480 (4)	$1,800(15)
Small stock	$47.84	$1,243.84 (26)	$2,583.36 (54)	$11,098.88 (232)	$60,278.4(1260)	$6,984.64 (146)	$82,189.12(1718)
Donkey	$90.04	$270.12 (3)	$ 90.04 (1)	$0	$1,710.76 (19)	$0	$2,070.92(23)
Total loss		$38,704.96 (129)	$2,673.4 (55)	$11,098.88 (232)	$81,904.66(1340)	$7,464.64 (150)	$141,846.5(1906)
Mean loss - per AEU[a]		129.02 (0.43)	8.91 (0.18)	37.00 (0.77)	273.02(4.47)	24.88 (0.50)	472.8(6.35)
Mean loss - per AEU[b]		172.79(0.58)	11.93 (0.25)	49.55 (1.04)	365.65(5.98)	33.32(0.67)	633.2(8.51)
Loss as % of total herd		6.77	2.89	12.17	70.30	7.87	100
Annual cost		$25,803	$1,782	$7,399	$54,603	$4,976	$94,563

Numbers in parentheses represent the numbers of individuals killed (*n*)

AEU: Adult equivalent unit

The conversion rate in accordance with prevailing market rates at the time of the survey 1US $ = 1659 Tanzanian shillings

[a]Considering all the respondents (*n* = 300)

[b]Considering only the respondents who reported loss (*n* = 224)

Table 3. Livestock reportedly lost to depredation, diseases, theft and other causes in the study villages in Simanjiro district, Tanzania.

	Loibor Siret		Sukuro		Terat		Emboret		Loiborsoit		Overall mean values (US $)	
	Cattle	Small stock	Cattle	Small stock	Cattle	Small stock	Cattle	Small stock	Cattle	Small stock	Cattle	Small stock
Mean value of livestock	348.6	36.9	431.9	57.1	369.2	57.1	331.5	42.6	378.2	45.5	371.9	47.8
Livestock loss (US $)												
*Overall depredation	6274.8 (18)	9557 (259)	9069.9 (21)	24096.2 (422)	7753.2 (21)	17244.2 (302)	11934 (36)	17082.6 (401)	20422.8 (54)	16243.5 (357)	11090.94	16844.72
**Depredation	6274.8 (18)	885.6 (24)	4319 (10)	14446.3 (253)	2953.6 (8)	5767.1 (101)	331.5 (1)	894.6 (21)	2647.4 (7)	1319.5 (29)	3305.26	4662.62
**Disease	101791 (292)	30516.3 (827)	218973 (507)	87077.5 (1525)	58703 (159)	70575.6 (1236)	70941 (214)	33313 (782)	44627 (118)	19656 (432)	99006.96	48227.68
**Theft	3834.6 (11)	1512.9 (41)	0	342.6 (6)	0	0	0	213 (5)	1891 (5)	682.5 (15)	1145.12	550.2
**Others	0	1217.7 (33)	0	0	0	57.06 (1)	331.52 (1)	0	0	0	66.30	254.95
Total financial loss (US $)	**111900 (321)**	**42804 (1160)**	**228043 (528)**	**111516.3 (1953)**	**66456 (180)**	**87876.8 (1539)**	**83206.5 (251)**	**50608 (1188)**	**66940.6 (177)**	**36582 (804)**	**111309.34**	**65877.55**

Only financial losses for adult cattle and small stock are calculated here.

**Based on numbers of livestock reported lost to depredation, diseases, theft and other causes for the 1-month preceding the survey (number of livestock lost are shown in Parentheses).

*Based on overall livestock reported lost to depredation over a period of 2013 – July 2014.

Mean value of livestock: Calculated using the exchange rate at the time of conducting this survey 1US $ = 1659 Tanzanian shillings.

Bold values signify the overall or total financial loss and number (in parentheses) of each livestock type due to depredation, disease, theft and other causes for the month preceding the survey across the villages

Table 4. Summary statistics of model-averaged estimates of coefficients (β) derived from the top model, standard error (SE), *t*-statistic and its 95% confidence interval (CI) from generalized linear mixed models (GLMMs) explaining the reported frequency of livestock depredation by all predators and by leopard in the Tarangire ecosystem, Tanzania 2014.

					95% Confidence interval	
Parameter	Estimate (β)	SE	*t*-statistic	*p*-value	Lower	Upper
a) *At bomas*						
All predators						
Intercept	1.380	0.208	6.646	<0.001	0.971	1.788
Education	-0.450	0.233	-1.933	0.044	-0.908	0.008
PA distance	0.008	0.006	2.202	0.030	0.005	0.020
Residence time	0.055	0.016	3.363	0.001	0.023	0.087
TLU	0.001	0.001	2.405	0.017	0.000	0.002
Boma type-cattle	-1.675	0.217	-7.712	<0.001	-2.102	-1.247
Leopard						
Intercept	-0.404	1.305	-0.310	0.757	-2.972	2.163
Residence time	0.026	0.025	1.048	0.296	-0.023	-0.075
Household size (AEU)	-0.344	0.038	-9.060	<0.001	-0.419	-0.269
PA distance	-0.016	0.041	-0.391	0.696	-0.096	0.064
b) *In the grazing area*						
All predators						
Intercept	1.758	0.456	3.854	<0.001	0.855	2.661
Number of herders	-0.999	0.244	-4.090	<0.001	-1.482	-0.515
Leopard						
Intercept	-0.075	0.482	-0.155	0.877	-1.029	.880
TLU	0.001	0.001	2.223	0.028	0.000	0.002
Number of herders	-0.982	0.290	-3.382	0.001	-1.556	-0.407

PA distance: distance from the park boundary; TLU: total number of livestock owned expressed in Tropical Livestock Unit; AEU: adult equivalent unit. Species-specific models were computed separately for (a) depredation at bomas and (b) depredation in the grazing area. All models consisted of village ID as a random effect. Significance level was set at $p < 0.05$.

Table 5. Summary statistics of model-averaged estimates of coefficients (β) derived from the top model, standard error (SE), *t*-statistic and its 95% confidence interval (CI) from generalized linear mixed models (GLMMs) explaining the reported frequency of livestock depredation by lions and spotted hyenas in the Tarangire ecosystem, Tanzania 2014.

Parameter	Estimate (β)	SE	*t*-statistic	*p*-value	95% Confidence interval	
					Lower	Upper
a) *At bomas*						
Lion						
Intercept	0.255	0.192	1.327	0.186	-0.123	0.633
Age	-0.045	0.002	-17.720	<0.001	-0.050	-0.040
Gender	-1.593	0.056	-28.318	<0.001	-1.704	-1.482
Education	-0.496	0.056	-8.800	<0.001	-0.607	-0.385
PA distance	-0.014	0.002	-6.964	<0.001	-0.018	-0.010
Residence time	0.012	0.002	4.919	<0.001	0.007	0.017
TLU	0.002	7.5074E-05	20.735	<0.001	0.001	0.002
Household size (AEU)	-0.156	0.016	-9.858	<0.001	-0.187	-0.125
Boma type-cattle	-1.607	0.045	-35.945	<0.001	-1.695	-1.519
Spotted hyena						
Intercept	1.149	0.589	1.948	0.052	-0.012	2.310
Education	-0.426	0.267	-1.598	0.111	-0.951	0.099
PA distance	0.016	0.001	11.333	<0.001	0.013	0.019
Residence time	0.059	0.020	2.919	0.004	0.019	0.098
TLU	0.001	0.001	2.259	0.025	0.000	0.002
Boma type-cattle	-1.981	0.233	-8.490	<0.001	-2.440	-1.522
b) *In the grazing area*						
Lion						
Intercept	-1.428	0.498	-2.865	0.005	-2.415	-0.441
Number of herders	-0.083	0.281	-0.296	0.768	-0.640	0.474
Spotted hyena						
Intercept	1.863	1.246	1.495	0.138	-0.605	4.331
TLU	-0.004	0.001	-5.144	<0.001	-0.006	-0.003
Number of herders	-2.207	0.692	-3.189	0.002	-3.577	-0.836

PA distance: distance from the park boundary; TLU: total number of livestock owned expressed in Tropical Livestock Unit; AEU: adult equivalent unit. Species-specific models were computed separately for (a) depredation at bomas and (b) depredation in the grazing area. All models consisted of village ID as a random effect. Significance level was set at $p < 0.05$.

Table 6. Summary statistics of model-averaged estimates of coefficients (β) derived from the top model, standard error (SE), *t*-statistic and its 95% confidence interval (CI) from generalized linear mixed models (GLMMs) explaining the reported frequency of livestock depredation by wild dogs and cheetah in the grazing area in the Tarangire ecosystem, Tanzania 2014.

Parameter	Estimate (β)	SE	*t*-statistic	*p*-value	95% Confidence interval	
					Lower	Upper
Wild dog						
Intercept	0.272	0.974	0.279	0.781	-1.658	2.201
TLU	-0.003	0.001	-3.038	0.003	-0.005	-0.001
Herders	-1.151	0.594	-1.937	0.055	-2.327	0.026
Cheetah						
Intercept	-1.916	0.598	-3.205	0.002	-3.100	-0.732
TLU	-0.003	0.001	-2.015	0.046	-0.006	-4.888E-05
Herders	0.312	0.458	0.682	0.497	-0.594	1.218

TLU: total number of livestock owned expressed in Tropical Livestock Unit; Herders: number of herders. All models consisted of village ID as a random effect. Significance level was set at $p < 0.05$.

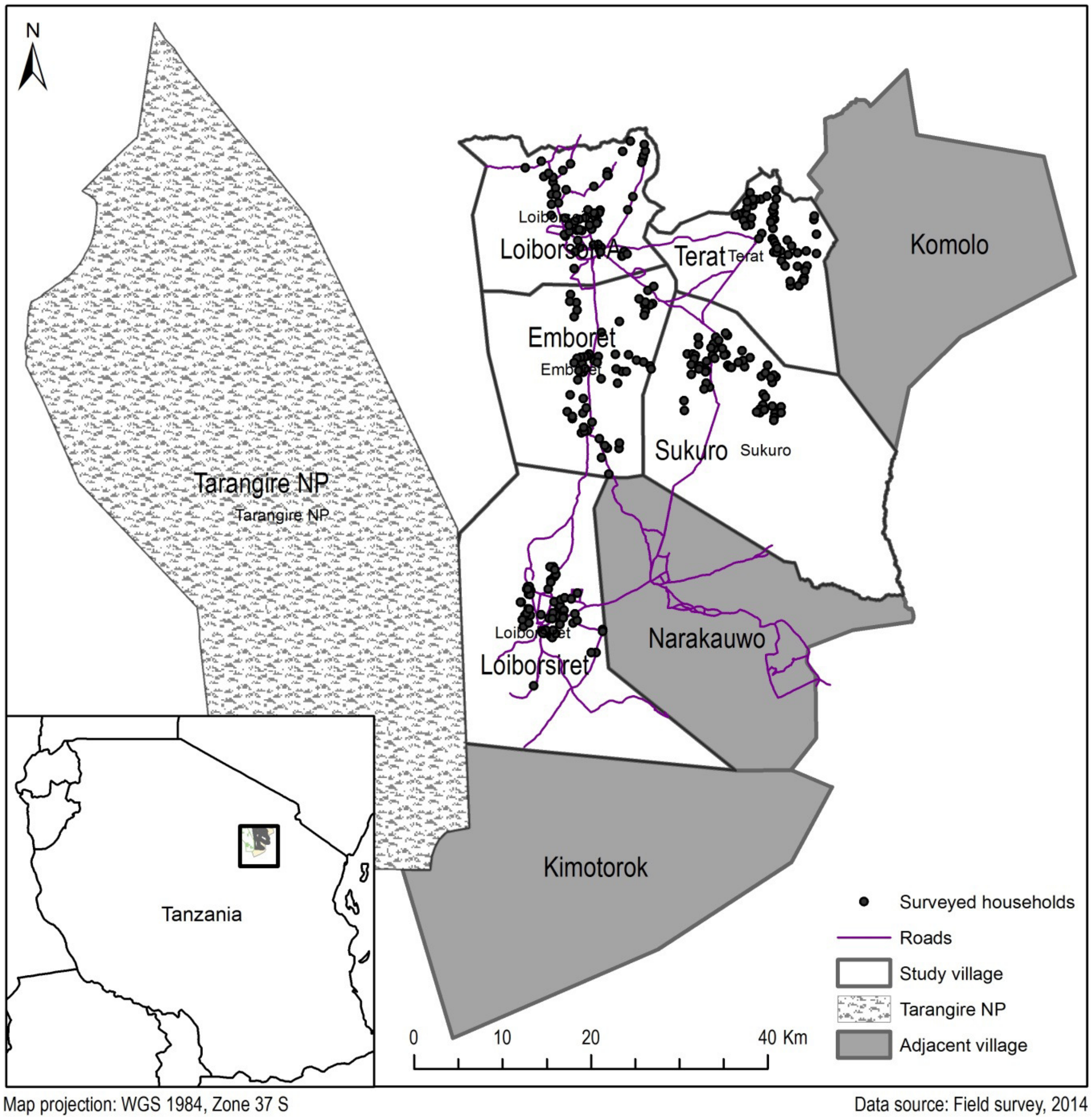


Figure 2. Map showing the location of the studied villages and the households interviewed in the survey.

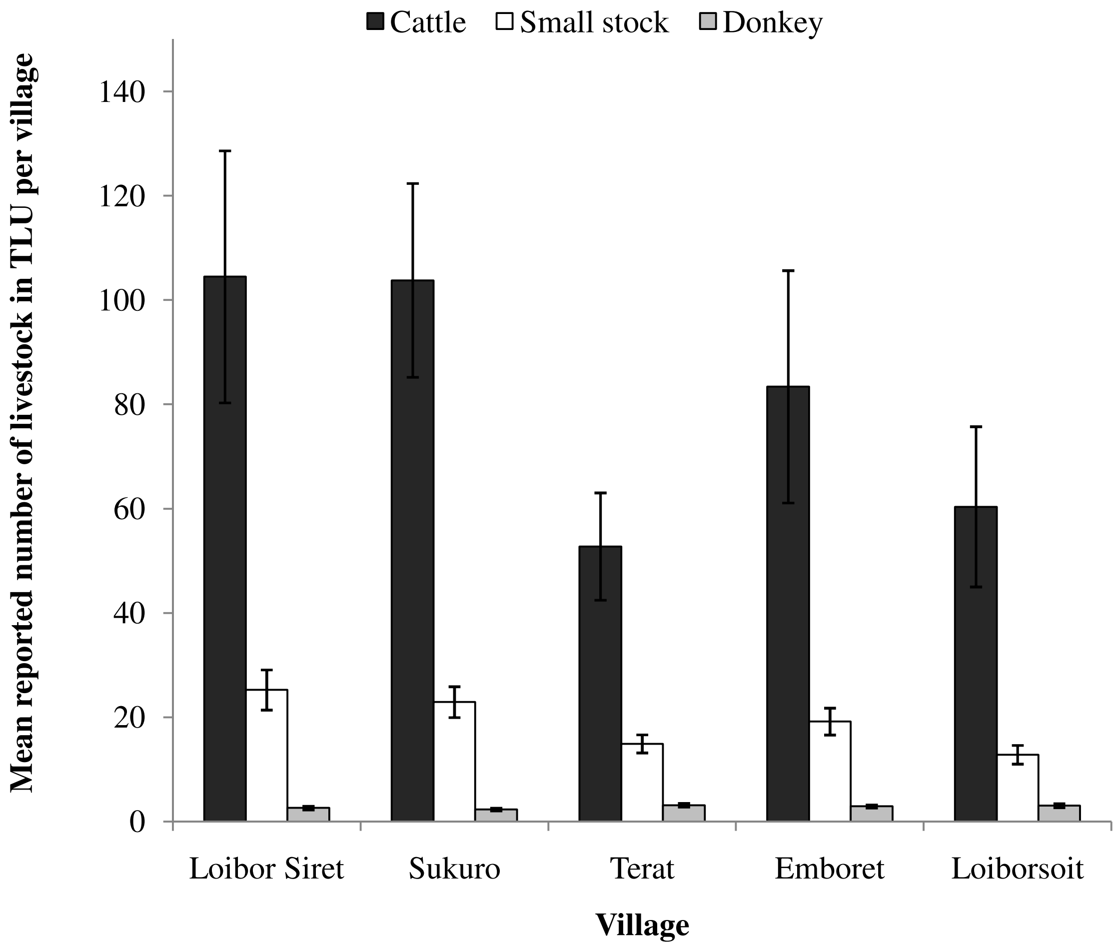


Figure 3. Mean livestock holdings recorded according to location surveyed in Simanjiro district, Tanzania, in 2014, expressed in tropical livestock units (Mean TLU ±SE).

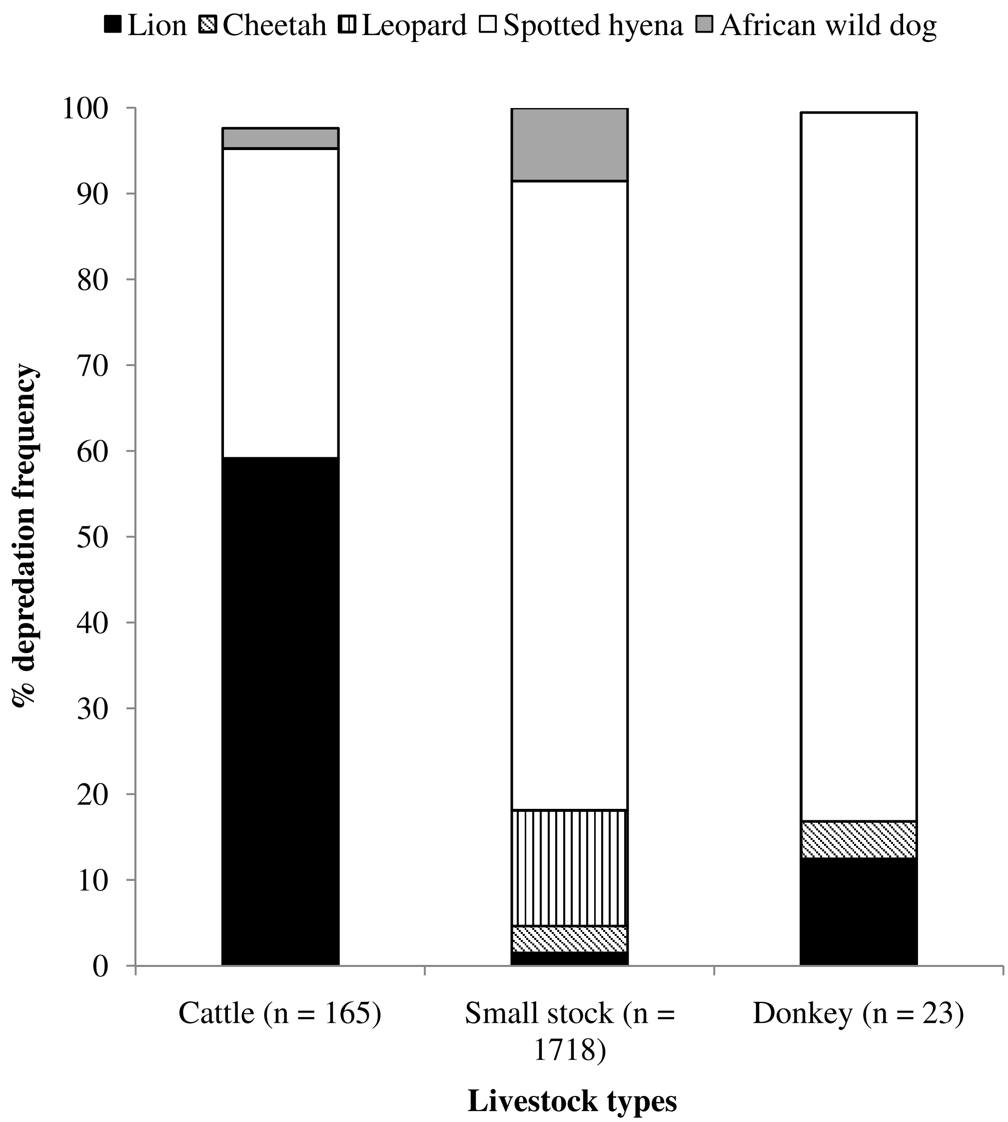
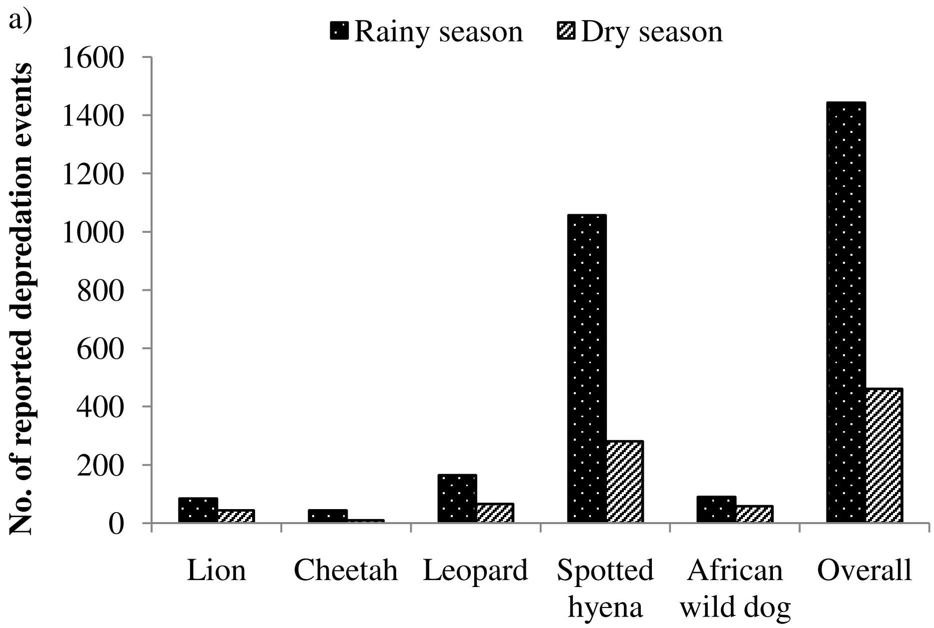


Figure 4. Percentage frequencies of reported attacks of predators on different livestock types in Simanjiro district, Tanzania, over a period of 2013-July 2014. Total numbers of attacks of each type are shown in parentheses.



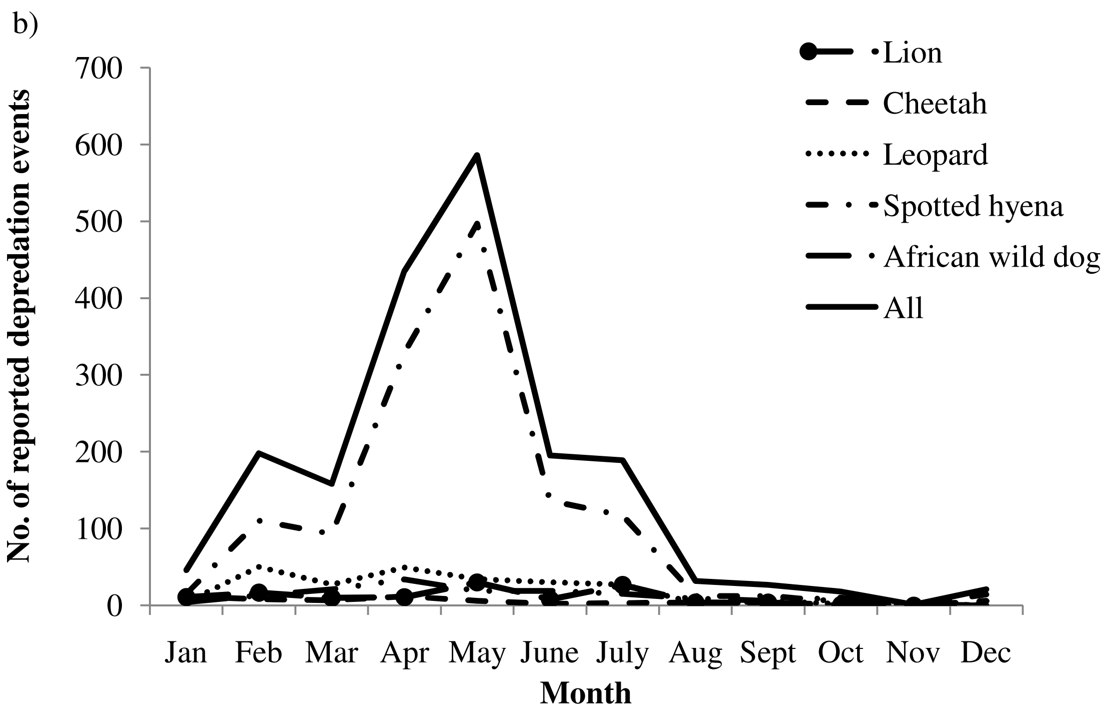


Figure 5. Reported frequencies of livestock depredation by predator species according to (a) season and (b) month in the Tarangire ecosystem during 2013-July 2014.

Supporting information:

Table 7. Descriptive statistics of explanatory variables (fixed effects) used to predict the likelihood of reported livestock depredation by large carnivores using Generalized Linear Mixed Models (GLMMs).

Variable	Description	Type	Mean	Std Dev.	Min.	Max.
HHsize_AEU	Household size (Adult Equivalents)	Continuous	6.88	2.11	2	12
Age	Age of respondent (years)	Continuous	35.86	14.19	19	92
Gender	Gender of respondent, dummy coded (1 = male, 2 =. female)	Categorical	-	-	-	-
Educ	Education level of respondent, dummy coded (1 = no education; 2 = primary, secondary and tertiary pooled)	Categorical	-	-	-	-
TLU	Total livestock units (TLUs)	Continuous	102.95	163.88	3	1385
PA_Dis	Distance to the nearest park boundary (km)	Continuous	28.81	12.64	7	52
Res_time	Respondent's residency time (years)	Continuous	9.90	7.30	1	42
Herders	Number of herders	Continuous	0.52	0.70	1	2
Bom_type_c	Boma type for cattle, dummy coded (1 = unfortified, 2 = fortified)	Categorical	-	-	-	-

Table 8. Adult-equivalent conversion factors for the number of people in the household to adult-equivalent units (AEU) according to age group and gender.

	Adult equivalents by sex	
Age group (years)	Male	Female
0-2	0.40	0.40
3-4	0.48	0.48
5-6	0.56	0.56
7-8	0.64	0.64
9-10	0.76	0.76
11-12	0.8	0.88
13-14	1.00	1.00
15-18	1.20	1.00
19-59	1.00	0.88
60+	0.88	0.72

Source: Latham 1965, cited by Collier *et al.* (1990)

Table 9. Spearman's correlation coefficients matrix of variables (r-values) used to predict the likelihood of reported livestock depredation by large carnivores

		1	2	3	4	5	6	7	8	9
1	Gender									
2	Age	0.03								
3	Education	-0.20***	-0.29***							
4	Livestock units	-0.20***	-0.04	0.06						
5	Household size, AEU	-0.13*	-0.02	0.02	0.17*					
6	Respondent's residency time	-0.16**	0.16*	0.09	0.26***	0.09				
7	Number of herders	0.05	-0.18**	0.08	-0.05	-0.03	-0.17			
8	Distance to park boundary	-0.09	-0.09	0.02	0.07	0.11	-0.05	0.11		
9	Boma type-cattle	-0.05	0.06	0.11	0.09	0.05	0.08	-0.05	0.07	
10	Boma type-small stock	-0.06	0.01	0.13*	0.18*	0.03	0.11	-0.05	0.00	0.76***

Note to Table S3: *p < 0.05, **p < 0.01, ***p < 0.001 (2-tailed)

Table 10. A *priori* candidate models of variables associated with the reported number of livestock killed by all predators and individual leopard at bomas and in the grazing area as ranked by AICc and AICc weights in the Tarangire ecosystem, Tanzania 2014. Models were analysed using generalized linear mixed models (GLMMs) fitted with Poisson error distribution and log-link function.

	~ All predators attack ~						**~Leopard~**					
Model rank	**Candidate models (At Bomas) †**	**-2LL**	**K**	**AICc**	**ΔAICc**	**ω_i**	**Candidate models (At Bomas) †**	**-2LL**	**K**	**AICc**	**ΔAICc**	**ω_i**
1	Education + PA distance + Residence time + TLU + Boma type-cattle	-3930.66	6	3932.68	0.00	0.665	Residence time + HHsize_AEU + PA distance	-2938.36	4	2940.37	0.00	1.000
2	Education + PA distance + Residence time + TLU + HHsize_AEU + Boma type-cattle	-3932.04	7	3934.05	1.37	0.335	Gender+Educ ation + PA distance+Residence time+TLU+HHsize_AEU+Boma type-cattle	-2999.94	8	3001.95	61.58	0.000
3	Gender + Education + PA distance + Residence time + TLU +HHsize_AEU + Boma type-cattle	-3991.00	8	3993.02	60.34	0.000	Age+ Gender+ Educ ation + PA distance + Residence time +TLU+HHsize_AEU + Boma type-cattle	-3000.07	9	3002.09	61.72	0.000
4	Age + Gender+ Education + PA distance + Residence time + TLU + HHsize_AEU + Boma type-cattle	-4007.23	9	4009.24	76.56	0.000	Education + PA distance+Residence time + TLU + HHsize_AEU + Boma type-cattle	-3012.33	7	3014.34	73.97	0.000
5	Education + Residence time + TLU	-4129.17	4	4131.18	198.50	0.000	Education + PA distance + Residence time+ TLU	-3030.60	5	3032.62	92.25	0.000
6	PA distance + Residence time + TLU + Boma type-cattle	-4155.20	5	4157.22	224.54	0.000	Education + PA distance + Residence time + TLU+ Boma type-cattle	-3055.95	6	3057.97	117.60	0.000
7	Education + PA distance + Residence time + HHsize_AEU	-4303.01	5	4305.02	372.34	0.000	Education + Residence time	-3128.46	3	3130.47	190.10	0.000
8	Education + Residence time	-4319.61	3	4321.62	388.94	0.000	Education + PA distance	-3165.79	3	3167.80	227.43	0.000
9	Residence time + TLU	-4395.29	3	4397.31	464.63	0.000	PA distance + Residence time + TLU + Boma type-cattle	-3521.69	5	3523.70	583.33	0.000
10	PA distance + Residence time + TLU	-4398.19	4	4400.20	467.52	0.000	PA distance + Residence time + TLU	-3594.45	4	3596.46	656.09	0.000
11	PA distance + Residence time	-4506.80	3	4508.81	576.13	0.000	Residence time	-3667.57	2	3669.59	729.22	0.000
12	Residence time	-4516.42	2	4518.43	585.75	0.000	PA distance + Residence time	-3696.01	3	3698.03	757.66	0.000
13	Education + TLU + HHsize_AEU	-4745.91	4	4747.93	815.25	0.000						
14	Education + PA distance	-5078.33	3	5080.34	1147.66	0.000						
15	TLU	-5079.67	2	5081.68	1149.00	0.000						
16	Education	-5136.10	2	5138.12	1205.44	0.000						
17	PA distance	-5313.96	2	5315.97	1383.29	0.000						
	Candidate models (in the grazing area) †						**Candidate models (in the grazing area) †**					
1	No. of herders	-775.12	2	777.16	0.00	0.997	TLU + no. of herders	-928.09	3	930.13	0.00	1.000
2	TLU + no. of herders	-787.09	3	789.12	11.96	0.003	No. of herders	-962.38	2	964.42	34.29	0.000

Notes: K: number of estimated parameters in the model plus 1 for intercept and error term; -2LL: value of the Restricted log-likelihood of the model; AICc: Akaike's Information Criterion corrected for small sample size; ΔAICc: difference in AICc values between the best-performing model and the model of interest; ωi: Akaike model weight. † All models consisted of village ID as a random effect. PA distance: distance from the park boundary; TLU: total number of livestock owned expressed in Tropical Livestock Unit; HHsize_AEU: household size in Adult Equivalent Unit.

Table 11. A *priori* candidate models of variables associated with the reported number of livestock killed by lions and spotted hyena at bomas and in the grazing area as ranked by AICc and AICc weights in the Tarangire ecosystem, Tanzania 2014. Models were analysed using generalized linear mixed models (GLMMs) fitted with Poisson error distribution and log-link function.

	~ Lion ~						~Spotted hyena~					
Model rank	**Candidate models (At Bomas) †**	**-2LL**	**K**	**AICc**	**ΔAICc**	**ω_i**	**Candidate models (At Bomas) †**	**-2LL**	**K**	**AICc**	**ΔAICc**	**ω_i**
1	Age+Gender+Education + PA distance + Residence time + TLU + HHsize_AEU + Boma type-cattle	-797.52	9	799.54	0.00	1.000	Education + PA distance + Residence time + TLU+Boma type-cattle	-3768.87	6	3770.89	0.00	0.997
2	Education + PA distance+TLU+Boma type-cattle	-1885.40	5	1887.42	1087.88	0.000	Education+PA distance+Residence time+TLU+HHsize_AEU+Boma type-cattle	-3780.41	7	3782.42	11.53	0.003
3	PA distance + TLU + Boma type-cattle	-1897.50	4	1899.52	1099.98	0.000	Gender+Education + PA distance + Residence time+TLU + HHsize_AEU + Boma type-cattle	-3836.91	8	3838.93	68.04	0.000
4	Education + PA distance + Residence time + TLU+Boma type-cattle	-1899.60	6	1901.62	1102.08	0.000	Age+Gender+Education + PA distance + Residence time + TLU + HHsize_AEU + Boma type-cattle	-3842.24	9	3844.25	73.36	0.000
5	Gender+Educ ation+ PA distance + Residence time + TLU + HHsize_AEU+Boma type-cattle	-1908.05	8	1910.06	1110.52	0.000	PA distance + Residence time + TLU	-4149.84	4	4151.85	380.96	0.000
6	Education + PA distance +Residence time+TLU + HHsize_AEU + Boma type-cattle	-1913.14	7	1915.15	1115.61	0.000	Education+ PA distance + Residence time + HHsize_AEU	-417134	5	4173.36	402.47	0.000
7	Education + PA distance + Residence time + Boma type-cattle	-1916.03	5	1918.04	1118.50		PA distance + Residence time	-4266.97	3	4268.98	498.09	0.000
8	PA distance + HHsize_AEU + TLU + Boma type-cattle	-1919.36	5	1921.37	1121.83	0.000	Residence time + TLU	-4302.62	3	4304.63	533.74	0.000
9	TLU + PA distance	-1959.02	3	1961.03	1161.49	0.000	Residence time + HHsize_AEU + TLU	-4312.85	4	4314.86	543.97	0.000
10	Education + PA distance+ Residence time+ TLU	-1962.81	5	1964.83	1165.29	0.000	Education+ Residence time	-4369.49	3	4371.50	600.61	0.000
11	PA distance + Residence time + TLU	-1967.93	4	1969.94	1170.40	0.000	Residence time	-4447.17	2	4449.18	678.29	0.000
12	TLU + HHsize_AEU+ PA distance	-1979.61	4	1981.62	1182.08	0.000	Education+ PA distance	-4949.47	3	4951.49	1180.60	0.000
13	Education + PA distance	-1984.17	3	1986.18	1186.64	0.000						
14	PA distance	-1995.94	2	1997.96	1198.42	0.000						
15	PA distance + Residence time	-2009.06	3	2011.08	1211.54	0.000						
16	Residence time	-2015.26	2	2017.27	1217.73	0.000						
17	Education+ Residence time	-2033.46	3	2035.48	1235.94	0.000						
18	Education	-2051.93	2	2053.94	1254.40	0.000						
	Candidate models (in the grazing area) †						**Candidate models (in the grazing area) †**					
1	No. of herders	-653.38	2	655.41	0.00	0.996	TLU + no. of herders	- 1064.39	3	1066.43	0.00	1.000
2	TLU+ no. of herders	-664.51	3	666.54	11.13	0.004	No. of herders	-1103.70	2	1105.74	39.31	0.000

Notes: K: number of estimated parameters in the model plus 1 for intercept and error term; -2LL: value of the Restricted log-likelihood of the model; AICc: Akaike's Information Criterion corrected for small sample size; ΔAICc: difference in AICc values between the best-performing model and the model of interest; ωi: Akaike model weight. † All models consisted of village ID as a random effect. PA distance: distance from the park boundary; TLU: total number of livestock owned expressed in Tropical Livestock Unit; HHsize_AEU: household size in Adult Equivalent Unit.

Table 12. A *priori* candidate models of variables associated with the reported number of livestock killed by wild dogs and cheetahs in the grazing area as ranked by AICc and AICc weights in the Tarangire ecosystem, Tanzania 2014. Models were analysed using generalized linear mixed models (GLMMs) fitted with Poisson error distribution and log-link function

	~ Wild dog ~						**~Cheetah~**					
Model rank	**Candidate models (in the grazing area) †**	**-2LL**	**K**	**AICc**	**ΔAICc**	**ω_i**	**Candidate models (in the grazing area) †**	**-2LL**	**K**	**AICc**	**ΔAICc**	**ω_i**
1	TLU + no. of herders	-838.91	3	840.95	0.00	1.000	TLU+ no. of herders	-742.18	3	744.21	0.00	0.987
2	No. of herders	-871.04	2	873.08	32.13	0.000	No. of herders	-750.82	2	752.85	8.64	0.013

Notes: K: number of estimated parameters in the model plus 1 for intercept and error term; -2LL: value of the Restricted log-likelihood of the model; AICc: Akaike's Information Criterion corrected for small sample size; ΔAICc: difference in AICc values between the best-performing model and the model of interest; ωi: Akaike model weight. † All models consisted of village ID as a random effect. TLU: number of livestock owned expressed in Tropical Livestock Unit.

CHAPTER THREE

Fortified Bomas and Vigilant Herding are Perceived to Reduce Livestock Depredation by Large Carnivores in the Tarangire-Simanjiro Ecosystem, Tanzania[2]

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Abstract

Human-carnivore conflict (HCC) is an increasingly important issue in Tanzania, especially where humans live adjacent to protected areas (PAs). We conducted semi-structured interviews (*n* = 300) to compile information on livestock husbandry practices and evaluate perceptions about the effectiveness of these methods in the Tarangire-Simanjiro ecosystem of northern Tanzania. Fortified bomas were perceived to be very effective (97.7%) in reducing nighttime depredations, while adult herders were perceived to be effective (71%) in reducing daytime depredations. Domestic dogs were perceived to be more effective at night, but an equal number of respondents found them to be effective during herding as those who found them to be not effective. Our results also show that boma type had a significant effect on livestock depredation. We recommend the use of fortified bomas as a long-term solution to prevent nocturnal livestock loss and adult herders for livestock during the day.

Keywords: Fortified bomas; human-carnivore conflict (HCC); livestock husbandry practices; livestock depredation; Tarangire-Simanjiro ecosystem.

3.1 Introduction

Most of the world's large carnivore populations are in rapid decline (Ripple *et al.,* 2014). Conflict with local populations, particularly over livestock depredation, is arguably one of the most important challenges in large carnivore conservation, and one of the major threats to large carnivore populations around the world (Woodroffe and Ginsberg, 1998; Holmern *et al.,* 2007; Dickman, 2008). In order to address human-carnivore conflict (HCC), there is need for effective, cost-effective, and sustainable solutions that allow people living adjacent to protected areas and large carnivores to coexist. Mitigation methods to reduce conflict between humans and predators can be divided into lethal and non-lethal management control. Both lethal and non-lethal control (Ogada *et al.,* 2003; Woodroffe and Frank 2005; Woodroffe *et al.,* 2007) have been experimentally tested for their effectiveness, and cost-benefit analyses demonstrate that non-lethal methods of human–wildlife conflict mitigation are cheaper and more effective and economically feasible (McManus *et al.,* 2014). Lethal control methods such as shooting, poisoning, spearing, trapping, or snaring are considered to be ineffective, inhumane, and are often conducted indiscriminately, resulting in the deaths of non-target species (Treves and Naughton-Treves, 2005).

Empirical evidence from Kenya, North America, and Europe shows that various forms of livestock husbandry can effectively reduce livestock depredation by wild carnivores (Ogada *et al.,* 2003; Breitenmoser *et al.,* 2005; Woodroffe *et al.,* 2007). Livestock husbandry practices such as boma enclosures, herders, and guard dogs play a crucial role in reducing livestock depredation (Ogada *et al.,* 2003; Kolowski and Holekamp 2006; Woodroffe *et al.,* 2007; Kissui, 2008; Loveridge *et al.,* 2010a). Recent studies show that fortified bomas (livestock enclosures, also called Living Wall bomas or bomas reinforced with chain-link fences) are effective at reducing nighttime depredations of livestock by over 90% (Lichtenfeld *et al.,* 2014). With effective husbandry strategies, it is presumed that large carnivores and livestock might coexist successfully on communal land bordering Tarangire National Park (TNP). In this study, *livestock husbandry* refers to the movement and management of livestock to reduce the number killed by predators. Despite studies that have suggested that livestock husbandry practices can be more effective at reducing conflict with large carnivores (Ogada *et al.,* 2003; Woodroffe *et al*., 2007; Ukio, 2010; Lichtenfeld *et al.,* 2014), our knowledge regarding the perceived effectiveness of different livestock husbandry practices in mitigating conflict with large carnivores in the Tarangire-Simanjiro ecosystem (TSE) is still limited. Lichtenfeld *et al.* (2014) tested the effectiveness of fortified bomas versus traditional bomas, but no previous studies have assessed the perceived effectiveness of this method in relation to other methods in this ecosystem. Likewise, Ukio (2010) evaluated husbandry techniques used in different villages in the Maasai Steppe and their effectiveness in reducing conflicts, but not the perceived effectiveness of these methods. The perceptions of the success of different measures within local communities will directly influence the likelihood of their use. We evaluated the perceived effectiveness of livestock husbandry techniques in the TSE to contribute theoretical insights and data that can be directly integrated into management decisions for effective human-carnivore conflict mitigation and carnivore conservation. Specifically, our objectives were (1) to assess the relative effectiveness of livestock husbandry practices employed by pastoral communities in mitigating livestock depredation in the TSE, and (2) to evaluate people's perceptions about the effectiveness of these techniques in preventing livestock depredation.

3.2 Materials and Methods

3.2.1 Study Area

This study was conducted in Simanjiro district in Manyara region, northern Tanzania (3°52′ and 4°24′ S and 36°05′ and 36°39′ E). It lies within the Maasai Steppe with a land area of 20,591 km^2. On the western part lies the TNP, which includes only 15% (2,850 km^2) of the TSE (approximately 20,000 km^2) (Figure 6). The area is characterized by semi-arid climatic conditions with erratic rainfall of 400-600 mm per annum (Kahurananga, 1979). The climate is highly seasonal with dry season (June – October) and wet season (November - May). Rainfall is bi-modal in pattern with short rains occurring between November to December and long rains from March to May. Generally, the climate is warm and dry, coolest from July to December and warmest from January to June, with an average daily temperatures ranging from 16˚C to 27˚C.
The vegetation can be classified into four broad types as (i) grassland (*Digitaria macroblephara* and *Panicum coloratum)*, (ii) woodland (*Acacia tortillis* and *Commiphora schimperi)*, (iii) bushland (*Acacia stuhlmannii* and *A. drepanolobium),* and (iv) seasonally water-logged bushed grassland (*Pennisetum mezianum* and *Acacia stuhlmannii)* (Kahurananga, 1979).

The area has four land use types: PAs (TNP), commercial farmland, communal grazing lands, and settlement. The Simanjiro plains are the main dispersal areas for wildlife during the wet season and grazing for pastoralists during the dry season. The plains are primarily used by migrating herbivores especially wildebeest (*Connochaetes taurinus*), zebra (*Equus burchellii*), hartebeest (*Alcelaphus buselaphus*), and fringe eared oryx (*Oryx beisacallotis)* for grazing and calving and non-migrant herbivores such as Thomson's gazelle (*Gazella thomsoni*), impala (*Aepyceros melampus*), and greater kudu (*Tragelaphus strepsiceros*) (Kahurananga and Silkiluwasha, 1997). During the rainy season, the majority of the migratory large ungulates leave the TNP, dispersing eastwards to the Simanjiro plains, or northwards towards Lakes Manyara and Natron. They return to TNP during the dry season.

The TSE is also inhabited by large carnivore species, including lions (*Panthera leo*), cheetahs (*Acinonyx jubatus*), leopards (*Panthera pardus*), African wild dogs (*Lycaon pictus*), striped hyenas (*Hyena hyena*), and spotted hyenas (*Crocuta crocuta*), that may prey upon game and livestock. In this ecosystem, large carnivores may be vulnerable to natural prey base depletion because they have large home ranges, occur at relatively low densities and require extensive, intact habitats to survive (Sillero-Zubiri and Laurenson, 2001). Nevertheless, the rapidly growing human population, expanding cultivation, and settlements in the plains are increasingly leading to the exclusion of wildlife (Msoffe *et al.,* 2011), suggesting that large carnivores will be increasingly shifting their diets to livestock over time. African wild dogs are listed as Endangered, lions, cheetahs, and leopards are listed as Vulnerable, whereas striped hyenas are Near Threatened and spotted hyenas are Least Concern (IUCN, 2016). The underlying volcanic soils on the plains possess phosphorus-rich grasses important for lactating female animals and their young (Kahurananga and Silkiluwasha, 1997). The flood plains contain black cotton soils while the well-drained areas contain dark red, sandy clay loam (Kahurananga and Silkiluwasha, 1997).

In the study area communities are of diverse ethnic groups. The major ethnic groups are Maasai, Waarusha and Ndorobo, with smaller numbers of Barbaig, Datoga, Pare, Hadzabe, Sandawe, Sonjo, Chagga, Fipa, Nyaturu, and Iraqw.

Traditional livestock husbandry is still practiced across Simanjiro district. Livestock herds are taken from the village to graze during the day, from early morning (between 06:30 – 08:00 am), and returned before sunset, often herded by 1–2 adults, but sometimes also by young boys, girls, and women. At night the herds are penned into traditional kraals known as '*bomas,*' a Swahili term for the circular livestock enclosures where Maasai pastoralists keep their animals at night, and/or an enclosing structure for a household compound (Lichtenfeld *et al.,* 2014). Bomas were traditionally fenced with acacia thorn branches, planted native trees only (i.e., *Commiphora africana*), a combination of acacia thorn bush branches and planted native trees) or more recently, fortified chain-link fencing (Plate 2a-d). Bomas are nested within bomas. Cattle and donkeys are usually kept together in an internal boma of an approximately 125 m circumference, while small stock are kept in bomas of a 25-50 m circumference. However, boma sizes can vary depending on the number of livestock owned. Each village has multiple bomas and one or more villagers may share the same boma. The boma fortification project is implemented by a local non-government organization (NGO), the Tanzania People and Wildlife Foundation (TPW). Since the construction of fortified bomas can be expensive for pastoralist communities, this NGO conducts a cost-sharing programme to upgrade traditional bomas with chain-link fencing and the addition of planted native trees (*Commiphora africana*) that act as thorny fence posts. Community members contribute 25% of the total costs (approximately $500 per boma) over an individually-tailored repayment period (Lichtenfeld *et al.,* 2014). Community members are also responsible for various stages of the fortified boma installation.

3.2.2 Interview methods

We conducted semi-structured interviews (SSIs) in five villages in the vicinity of TNP, northern Tanzania, to compile information on livestock husbandry practices and evaluate respondents' perceptions about the effectiveness of these methods. Interviews were conducted between June and July in 2014, and were designed using a similar format to Maddox (2003) and Dickman (2008) as a guide. The questionnaire contained both closed-ended as well as open-ended questions in order to gain more information on participant's attitudes and reasoning. Questionnaires are a useful tool to examine human attitudes and behaviors towards wildlife species (White *et al.,* 2005). Semi-structured interviews (SSIs) were chosen to allow for a wider range of responses and narratives, and are flexible enough to allow respondents to express their ideas and views in their own terms (Hunter and Brehm, 2003). In all cases the anonymity and confidentiality of the interviewee was preserved. We focused on five villages: Emboret, Terat, Sukuro, Loiborsoit and Loibor Siret (Figure 6). The villages are similarly laid out in a clustered settlement pattern. A questionnaire was administered by the principal investigator (PI) with the help of a local assistant and translator (Maa to Swahili) to 300 respondents via face-to-face personal interviews from 300 households.

We obtained a list of households from village offices and randomly selected an equal proportion from each sub-village. Sixty respondents were selected from each village at random. Within each boma (here referring to entire bush-fenced settlements), we counted the total number of households and utilized a random number generator to select a single household. The sample included the head of the family (usually a man), or the head's spouse or elder son according to seniority. The most senior members of the household were asked to participate in the survey in the expectation that they would be more informative and could more freely express themselves than junior members. Women often deferred to men, so respondents were predominantly male, but interviews were conducted with women where they were comfortable in doing so. All interviewees were ≥18 years of age. The household was chosen as the sampling unit (Maddox, 2003; Dickman, 2008), and interviews were restricted to one respondent per household.

During the interviews, we tested respondents' knowledge of carnivores using coloured photographs. If the identification was incorrect, the respondent was told the correct animal before proceeding further, with discussions and explanations provided so that the respondent was clear exactly which species was being discussed (particularly in the case of distinguishing between leopard, serval, and cheetah), before moving on to questions on livestock depredation. The main topics covered by the final questionnaire were (1) livestock husbandry practices, i.e., how respondents look after their livestock at night and during the day, and (2) perceptions of conflict mitigation methods, specifically what measures respondents take to avoid livestock depredation. In order to assess the perceived effectiveness of the mitigation methods respondents were further asked to rate how effective they thought potential mitigation methods were in preventing livestock depredation during both day and night. These were subjectively graded on a four-point Likert scale of (0) - not effective, (1) - slightly effective, (2) - effective, (3) - very effective. For those with fortified bomas who also reported cases of livestock depredation, we established whether depredation had occurred before or after boma fortification.

Interviews were conducted in the local language (i.e., Swahili - with the aid of a Maasai translator where needed) and took approximately one hour to complete.

3.2.3 Statistical analyses

Questionnaires completed in Swahili were translated into English for statistical analysis. Questionnaire data were numerically coded and entered into *SPSS v.* 22.0 software package (SPSS Inc., Chicago, Illinois, USA) to perform all analyses. All categorical and continuous variables were analysed using standard descriptive statistics (mean, standard deviation (SD), range, percentages and frequencies of counts, tables, and charts). A one-sample Kolmogorov-Smirnov test was used to determine if continuous variables were normally distributed and non-parametric tests were chosen especially where we felt that our data did not meet the assumptions of normality. Chi-squared tests using Yate's correction factor for tests with one degree of freedom were used to compare proportions. All statistical tests were two-tailed and significance was measured at $P < 0.05$.

3.3 Results

3.3.1 Livestock husbandry practices

Protective enclosures (bomas) to keep livestock at night were used by all respondents (100%, n = 300), guard dogs by 88% (n = 265), and herders by 100% (n = 300). Solar-powered lights around bomas were used by 2% (n = 5) of the respondents.

3.3.2 Boma type

The majority of the respondents use traditional bomas made of acacia thorn bush branches or a combination of acacia thorn bush branches and planted native trees (Figure 7). Overall, fewer respondents used fortified bomas and planted trees enclosures. Fortified bomas are the most commonly used enclosures in Loibor Siret. In Loiborsoit, fortified bomas are used by 2% and 22% of respondents to keep cattle/donkeys and small stock respectively; but are used by a relatively small proportion in Emboret and Terat, and by no households in Sukuro (Figure 7).

3.3.3 Guard dogs

Dogs are used to protect livestock against predators. Despite the fact that 88% (n = 265) of respondents reported having dogs in their households, only 54% (n = 162) reported having livestock accompanied by dogs, with an average of 1.46 ± 0.50 (range: 1 - 2) dogs per herd. Presence or absence of dogs did not have any significant influence on livestock depredation in the grazing areas ($\chi^2 = 451.97$, $df = 480$, $P = 0.816$).

3.3.4 Herders

According to Maasai tradition, while females and males of all age groups are responsible for herding livestock, males have greater responsibility. In this study, the majority of the respondents employed adults (33%), young boys (32.5%), and a combination of adults and young boys (31%) to herd livestock. However, in some cases, women (2%), girls (1.3%) or a combination of young boys and women (0.3%), or young boys and girls (0.3%) are used. Herders' age groups are associated with herding different livestock types. Young boys were cited by 56% of respondents to participate in herding cattle, small stock, and donkeys, with 37% herding cattle and small stock, 6% herding only small stock, and 1% herding cattle and donkeys (Table 13). The majority of adults (66%) participate in herding cattle and small stock, 27% in herding cattle, small stock, and donkeys, 7% in herding cattle and donkeys, but none herd small stock alone. However, a combination of young boys and adults were reported to herd cattle and small stock (64%), cattle, small stock, and donkeys (33%), small stock (2%), and cattle and donkeys (1%) (Table 13). Herders' age was significantly associated with herding a particular type of livestock ($\chi^2 = 46.35$, $df = 18$, $P < 0.001$, Table 13).

3.3.5 Effectiveness of livestock husbandry practices

In response to which strategies they considered to be effective for protecting livestock from predators, 98% ($n = 293$) of the respondents scored fortified bomas as 3 (very effective). However, the majority do not use this type of enclosure (Figure 7). Traditional bomas (made either of acacia thorn bush, poles and thorn bush, or planted native trees) were rated as 2 (effective) by 91% ($n = 273$) of respondents. While 71% ($n = 213$) of respondents considered adult herders to be effective in reducing attacks on grazing stock, 51% ($n = 152$) considered young boys to be slightly effective (Table 14). Sixty-seven percent of respondents rated domestic dogs to be "effective" at night (Table 14), but were evenly split (44%/44%) as to their effectiveness during the day. Overall, depredation from traditional bomas was more frequently reported than from fortified bomas (Figure 8). There was a significant association between boma type and number of livestock lost to predators ($\chi^2 = 79.73$, $df = 4$, $P < 0.001$, $n = 1312$, Figure 8).

When asked whether it is possible to avoid livestock depredation, 60% ($n = 181$) of respondents said no while 40% ($n = 119$) said yes. Multiple reasons were offered as to why it is impossible to avoid livestock depredation; for instance, 43% ($n = 103$) were skeptical about using young boys, women, or girls to herd livestock as they gave negative assessments of their competence (Table 15); others (18%, $n = 74$) claimed that because carnivores and livestock live alongside one another, some amount of livestock depredation is inevitable; yet others (8%, $n = 32$) claimed that bomas made of thorn bush branches are not strong enough to keep the predators out. However, 15% ($n = 61$) claimed that it is possible to avoid livestock depredation if herders could always be vigilant during grazing and by strengthening security around bomas during the night. Although 20% ($n = 81$) asserted it is possible to avoid livestock depredation through boma fortification, 14% ($n = 57$) emphasized the importance of using adults rather than young boys as herders to reduce depredation risk.

A majority of respondents (56%, n = 168) were against retaliatory killing of predators versus 44% (n = 132) who thought that killing could be a good strategy (χ^2 = 4.08, df = 1, P = 0.04). Nine percent (n = 26) admitted to having killed a predator due to real or perceived risk of depredation. The major reasons given for not killing predators were because they had not yet come into any conflict (3%, n = 6), they are frightened of killing predators (6%, n = 11), it is unlawful (80%, n = 146), predators do not linger in the vicinity (7%, n = 12), or they are too busy with other tasks (4%, n = 8). Lack of formal education was associated with support for retaliatory or preventative predator killing (χ^2 = 5.03, df = 1, P = 0.025, Figure 9).

3.4 Discussion

We found three main livestock husbandry strategies used by pastoralist communities in the study area to reduce livestock depredation by large carnivores: kraaling stock in bomas at night, herders for daytime grazing, and guard dogs (see also Ogada *et al.,* 2003; Woodroffe *et al.,* 2007). About two-thirds (67%) of respondents perceived domestic dogs to be effective at night, perhaps by alerting people of predators approaching enclosures. An equal number of respondents found dogs to be effective during grazing as those who found them to be not effective. Previous studies by Holmern *et al.* (2007) and Kissui (2008) found that domestic dogs were victims of depredation by leopards and hyenas, which could account for the perception of their lower effectiveness during grazing. Nevertheless, most of the dogs in the surveyed households are not trained as guard dogs to protect livestock, but rather kept as domestic dogs to protect the household (Ogada *et al.,* 2003). Our study did not address whether respondents provided any training to dogs to protect livestock. It is likely that targeted training, combined with careful breeding, would help to increase the effectiveness of dogs for livestock protection (Sims and Dawydiak, 1990; Marker *et al*., 2005).

Boma enclosures and herders were perceived to be effective in reducing attacks at night and during the day, respectively. The type of boma enclosure (traditional or fortified) and the age/gender of herders are perceived to determine their degree of effectiveness in reducing livestock depredation. Specifically, adult herders are perceived to be more effective in reducing depredation than young boys (see also Kolowski and Holekamp, 2006; Ikanda and Packer, 2008). Adult herders may avoid areas where large carnivores are likely to be found (e.g., thick bushes or den sites) and even chase away predators when encountered (Kolowski and Holekamp, 2006; Hemson *et al.,* 2009). There is considerable evidence that the presence of herders of any age can reduce the rate of depredation compared with leaving livestock unattended (Ogada *et al.,* 2003; Breitenmoser *et al.,* 2005). However, a key challenge for herding households is that greater numbers of Maasai children are now going to school, so fewer individuals are available to tend their livestock. Consequently, some households merge their herds and use adult male herders to supervise grazing, or pool their resources to hire people to herd their livestock (Lichtenfeld L. pers. comm. 2014).

We did not test the actual effect of fortified bomas on rates of livestock depredation, but rather relied on respondents' perceptions of relative depredation rates between fortified versus unfortified bomas. Fortified bomas have been previously tested in this ecosystem and found to be effective in mitigating HCC (Lichtenfeld *et al.,* 2014). While fortified bomas are perceived by 98% of respondents to be effective, they are not widely used because of their construction expense. However, it is important to note that, though they are relatively expensive to build, the benefits likely outweigh the costs (Mkonyi *et al.,* 2017b), and the reduction in livestock depredation ensures a good return on investment (Lichtenfeld *et al.,* 2014). Most respondents recognized that fortified bomas accompanied by improved herding practices could help to significantly reduce depredation of livestock in the study area. This perception is supported by evidence showing that fortification of bomas is associated with a reduction of livestock depredation by 90% (Lichtenfeld *et al*., 2014). While fortified bomas are highly effective at preventing livestock depredation at night when properly constructed and regularly maintained, a criticism in the area is that poor maintenance sometimes leads to failure of fortified bomas as effective depredation deterrents (Mkonyi F. pers. obs. 2014).

Despite the greater livestock losses due to depredation and related perceived costs as evaluated in Mkonyi *et al.* (2017b), only 4% of respondents reported using lethal methods (poison or traps) to control predators (cf. Maddox, 2003; Dickman, 2008). The overwhelming reason for using lethal methods area was the perception that carnivores posed a risk to livestock. However, retaliatory or preventative carnivore killing is still a common problem outside PAs. For example, in 2012, six lions were reported to have been killed in a single poisoning incident after killing six cattle in Loibor Siret (Lichtenfeld L. pers. comm. 2014). Our results show that the current reported level of retaliatory or preventative carnivore killing is relatively low. However, there is the possibility of observer bias in this study, with respondents unwilling to report some behaviours (e.g., carnivore killings) to an outsider, particularly one linked to conservation organizations and authorities. Therefore, further work is required through direct monitoring of carnivore mortality to assess the true impact of anthropogenic killing.

Despite the low level of lethal control reported in this area, 99% of respondents clearly stated that wild animals, particularly large carnivores need to be controlled (Mkonyi *et al.,* 2017a). This perception poses the biggest threat to large carnivore species survival in the study area. It is obvious the major reasons for not trapping or poisoning carnivores were practical, in the sense that respondents were unable to access the poisons or traps, moral, in the sense that it is unlawful and wrong, and environmentally unfriendly for posing a threat to other creatures. Generally, most respondents were against retaliatory or preventative carnivore killing because it is illegal and it would not solve the long-term problem as it would be unlikely to stop other predators from preying on livestock. Thus, rigorous law enforcement, stiffer penalties for offenders, education, and awareness campaigns are needed to reinforce the long-term conservation of large carnivores and other wildlife species in the study area.

While compensation for financial losses due to large carnivore livestock depredation was suggested by 85% of respondents, it may be difficult to implement in Tanzania, where there is a lack of funds and management capacity and no chance of verification of depredation. Fifteen percent of respondents were skeptical about the implementation of a compensation scheme, worried that it might be too difficult to determine fair payment and verify losses due to predators. Although there is already a compensation scheme that pays for livestock loss to lions and spotted hyenas in Tanzania (URT, 2011), this is not implemented because of lack of capacity and verification.

3.5 Conclusion and management implications

Despite the efforts by pastoralist communities in improving their livestock husbandry practices, livestock depredation is still a recurring management problem across the TSE. The conflict between livestock and predators will continue as long as carnivore and livestock ranges overlap. Generally, there is no single management option or solution that can entirely resolve HCC problems but rather a combination of strategies. Our study showed that mitigation methods differ depending on the location. Understanding which livestock husbandry practices were perceived as more effective in different contexts facilitates informed decision-making when humans and carnivores come into conflict. In addition, our findings have broader significance to the conservation community involved in mitigating HCC. Our study suggests that livestock depredation by large carnivores could be significantly reduced through boma fortification, herding by adults, vigilant herding, and strengthening the security around bomas during the night.

Although we did not test the actual effect of fortified bomas or improved grazing techniques, their perceived effectiveness as indicated by livestock owners is important in evaluating their impact and determining their potential for conflict mitigation. Naturally, affordability and cultural acceptability by local pastoralists are critical to the success of any conflict mitigation strategy. Fortifying all bomas in the study villages might be perceived as too costly but on an individual basis, the total cost is likely to be lower than that of the depredation (Lichtenfeld *et al.,* 2014). The cost of fortified bomas was cited by the majority of respondents as a prohibitive factor. If this cost can be shared with NGOs or government agencies, then more people may choose to have their bomas fortified. This might ultimately reduce depredation on livestock by carnivores and improve carnivore conservation in the area. The current cost-sharing program gives people a greater sense of fortified boma ownership and encourages their active participation in maintenance responsibilities than when the costs are fully covered by the donors.

Education programmes and training on environmental issues are also important and should be incorporated into village meetings and even in primary and secondary schools curricula. This would raise a greater awareness of the conservation value and role of wildlife, particularly large carnivores, among the youth and local communities and build local capacity in conflict mitigation techniques. Interestingly, some of these recommendations are being implemented in the study area by the TPW (Lichtenfeld L. pers. comm. 2014). Tanzania National Parks (TANAPA)'s outreach programmes should work towards addressing problems such as HCC and involve local communities in conservation initiatives. A very interesting finding of this study was that around 20% of respondents accept carnivores as part of the landscape (Mkonyi *et al.,* 2017a). Improved livestock husbandry practices and access to wildlife-related benefits such as tourism revenue (Parry and Campbell, 1992) may improve the attitude of local people and increase tolerance towards large carnivores. Therefore, financial incentives and better sharing of overall benefits from the national park and promotion of ecotourism should be used in combination with sound livestock management programmes devised to reduce depredation.

This study contributes valuable information for pastoralist communities to adopt acceptable HCC mitigation strategies and promote conservation of large carnivores. It also identifies interventions for further quantitative study in terms of measuring actual effectiveness of different livestock husbandry practices in reducing livestock depredation in the study area. It is therefore important that further research should examine the overlap between actual depredation and people's perceptions of the efficacy of various livestock husbandry practices. In particular, given the perceptions of the important role of domestic dogs at night, additional research is required to test whether providing training to dogs could increase their effectiveness in protecting livestock from predators during the day in the study area.

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Table 13. Percentage and number of respondents on the association between herders' age group and livestock type (number; and % in parentheses).

	Age group						
Livestock type	Young boys	Adults	Young boys and Adults	Women	Girls	Young boys and Women	Young boys and Girls
Cattle and donkeys	1 (1)	7 (7)	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)
Small stock	6 (6)	0 (0)	2 (2)	0 (0)	1 (25)	0 (0)	0 (0)
Cattle, small stock and donkeys	57 (56)	28 (27)	31 (33)	2 (33)	1 (25)	1 (100)	0 (0)
Cattle and small stock	37 (37)	68 (66)	60 (64)	4 (67)	2 (50)	0 (0)	1 (100)

Note: Chi-square test $\chi^2 = 46.35$, $df = 18$, $P < 0.001$

Table 14. Frequency of respondents identifying different strategies perceived to be effective in reducing livestock depredation at night (at bomas) and during the day (in the grazing areas) (N = 300).

Strategies	Very effective		Effective		Slightly effective		Not effective	
	n	%	*n*	%	*n*	%	*n*	%
Guard dogs (day)	0	0	131	44	37	12	132	44
Guard dogs (night)	1	0	202	67	70	23	27	9
Herders (adults)	4	1	213	71	83	28	0	0
Herders (young boys)	0	0	91	30	152	51	57	19
Traditional Bomas	27	9	273	91	0	0	0	0
Fortified Bomas	293	98	7	2	0	0	0	0

Table 15. Summary of reasons given by respondents answering the question: Is it possible to avoid livestock depredation?

Answer	Reason given	Number and % of respondent citing that reason* *n*	%
"No" 60% (*n* = 181)	Difficult in the field because young boys, women or girls are involved in herding the stock.	103	43
	Difficult in the boma because most are constructed of thorn bush branches.	32	8
	We live alongside wild animals and as long as carnivore and livestock ranges overlap livestock depredation is inevitable.	74	18
"Yes" 40% (*n* = 119)	Bomas fortification with Living Walls.	81	20
	Adults to herd the stock.	57	14
	Vigilant herding and strengthening the security around bomas at night.	61	15

*Respondents could cite more than one reason so total percentage may exceed 100%

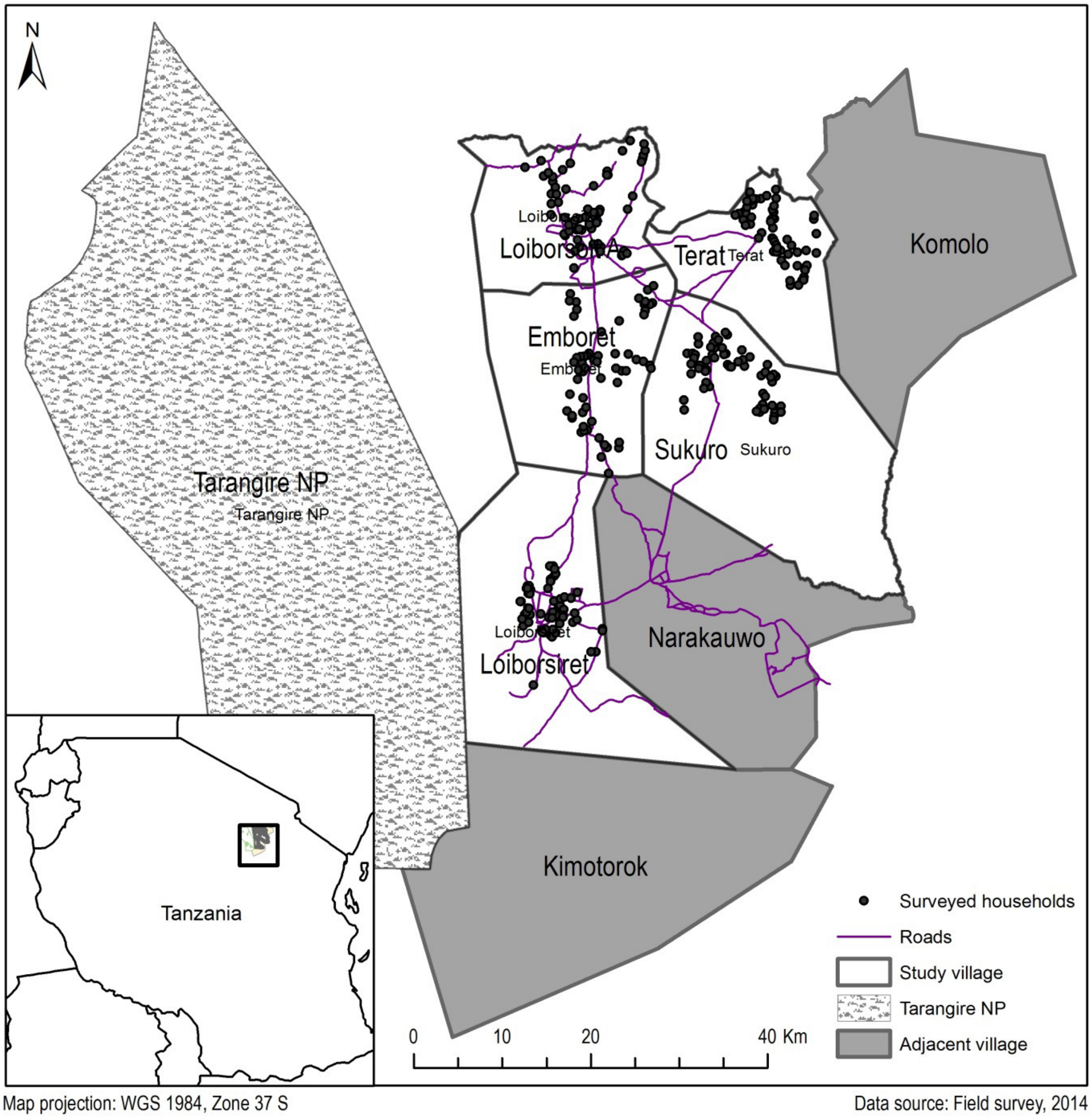

Figure 6. Map showing the location of the studied villages and the households interviewed in the survey

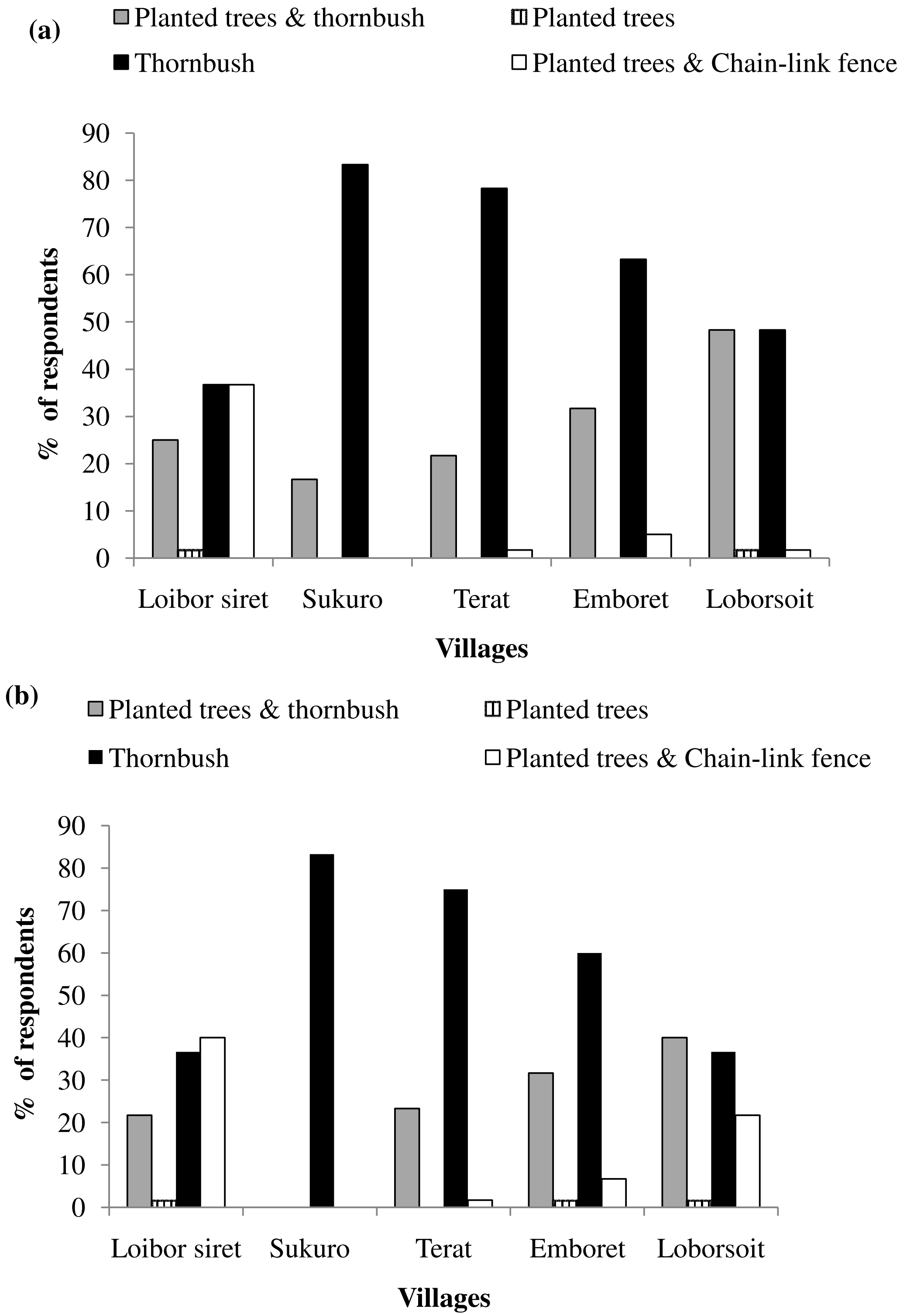

Figure 7. Boma types used by pastoralist communities in the studied villages in Simanjiro district, Tanzania, in 2014 (a) cattle and donkeys, (b) small stock.

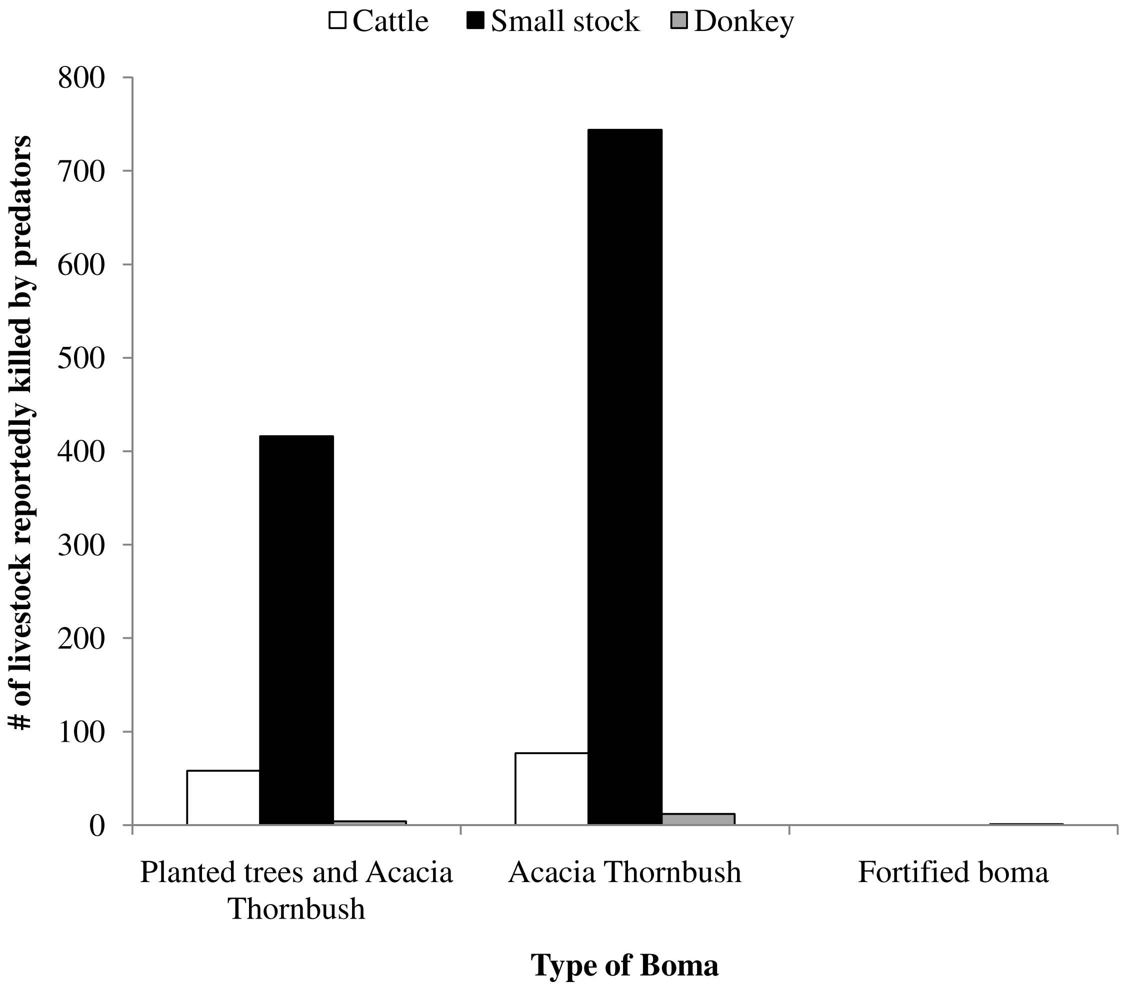

Figure 8. Number of livestock reportedly killed by predators in different types of bomas.

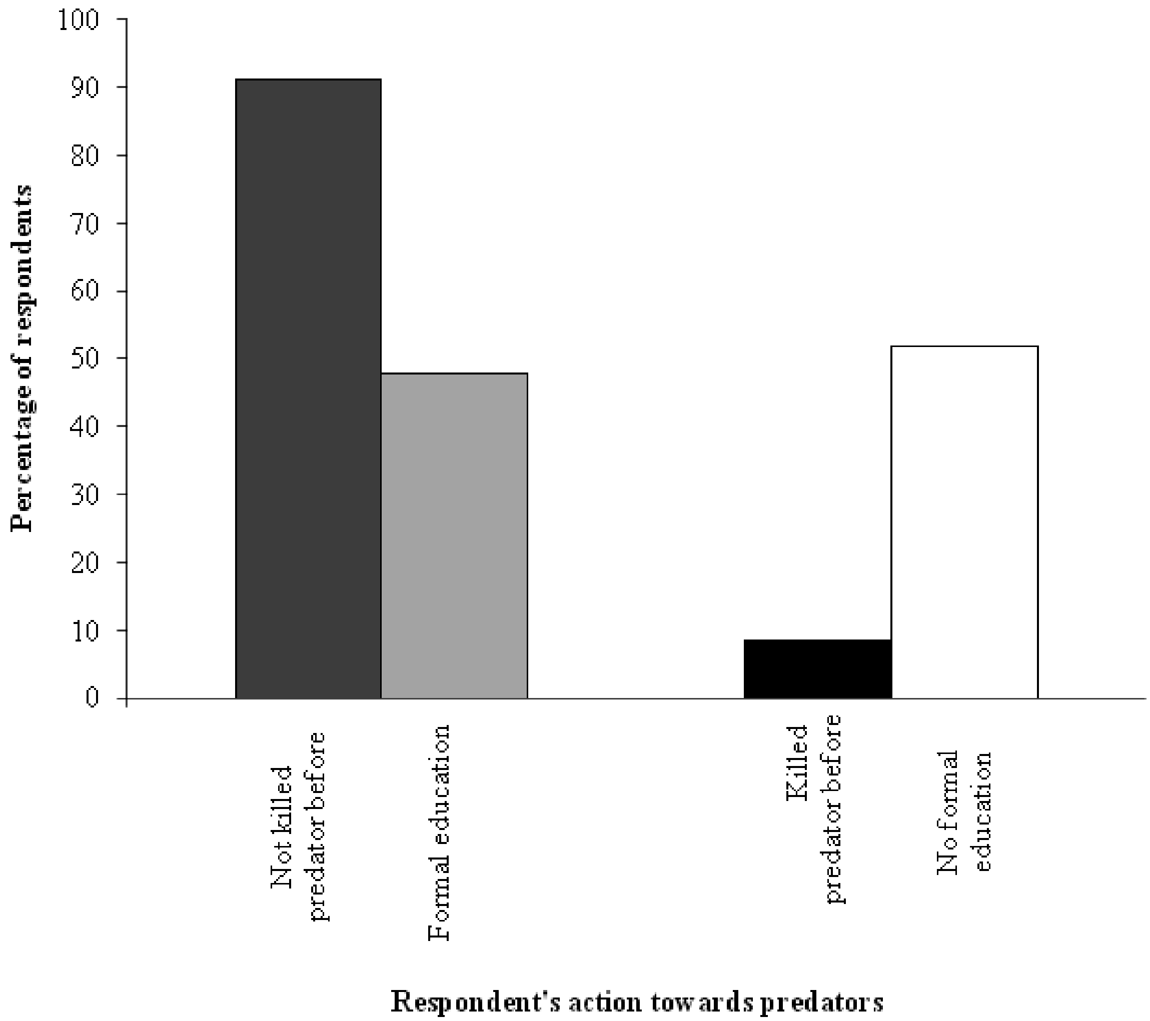

Figure 9. Respondents' anti-depredation measures in relationship to education level.

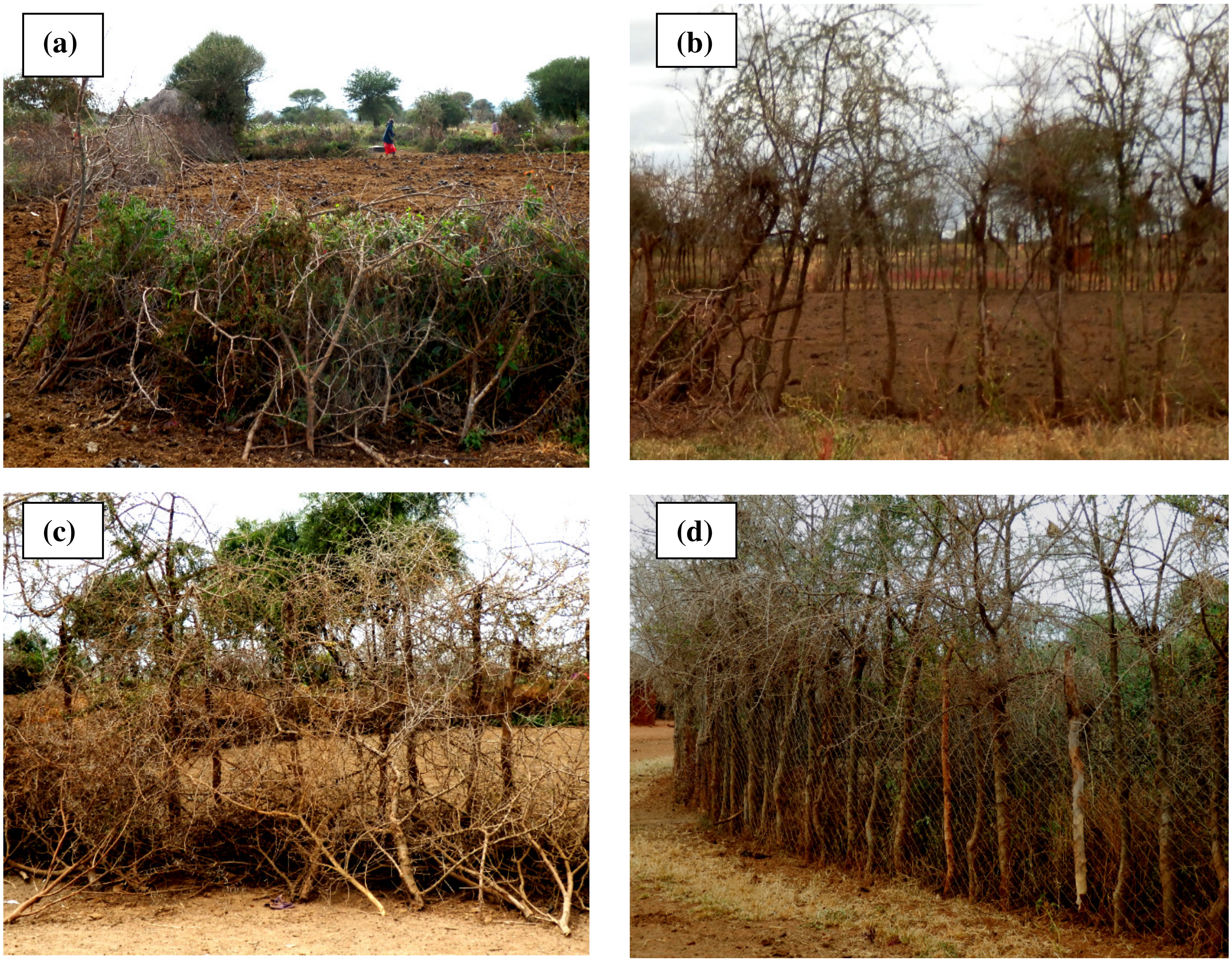

Plate 2. Types of bomas used by pastoralist communities in the studied villages in Simanjiro district, Tanzania (**a**) acacia thorn bush (**b**) planted native trees (**c**) a combination of acacia thorn bush and planted native trees (**d**) a fortified boma with chain link visible.

CHAPTER FOUR

Local Attitudes and Perceptions Towards Large Carnivores in a Human-dominated Landscape of Northern Tanzania[3]

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Running title: Attitudes and perceptions towards large carnivores

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Abstract

We conducted 300 semi-structured interviews with local people adjacent to Tarangire National Park, northern Tanzania, to determine their attitudes and perceptions towards large carnivores. We analysed the relationships between attitudes and age, gender, education, occupation, years at residence, income, distance from protected area, livestock owned, livestock lost to predators and knowledge of carnivores. Three-quarters of respondents (79%) held negative attitudes towards large carnivores, while 20% were generally positive. Three variables were positively associated with attitudes towards different species: formal education (all carnivore species), years at residence (lions and cheetahs) and knowledge of carnivores (cheetahs). Attitudes towards large carnivores were not significantly related to distance from protected area, livestock owned or livestock lost to predators. Findings suggested that interventions aimed at fostering positive attitudes towards large carnivores should focus on improving formal education and securing long-term residency for people in the region.

Keywords: Attitudes, large carnivores, local people, perceptions, Tarangire National Park

4.1 Introduction

Understanding people's attitudes, perceptions of risk associated with large carnivores and the factors that influence these attitudes is critical for developing effective human-carnivore conflict mitigation strategies for carnivore conservation. Large carnivores populations have declined around the world (Ripple *et al.*, 2014). For example, in East Africa, cheetah *Acinonyx jubatus* and African wild dogs *Lycaon pictus* have experienced major contractions in their geographic range, with resident populations now found in only 6% and 7% of their historic ranges (IUCN, 2016). Tanzania has lost 66% of its lion *Panthera leo* population from 1993 to 2014 (IUCN, 2016), and leopard *Panthera pardus* populations have also declined (Packer *et al*., 2011). The major threats facing large carnivores include habitat loss and fragmentation, human population growth, depletion of prey, unsustainable trophy hunting and persecution by humans associated with livestock depredation (IUCN, 2016; Packer *et al.,* 2011). Conflict occurs when people and carnivores live in close proximity (Inskip and Zimmermann, 2009; Sogbohossou *et al.*, 2011).

Human-carnivore conflict typically occurs in association with livestock depredation (Dickman, 2008) and occasionally attacks on humans (Packer *et al.,* 2005).

The large home ranges of large carnivores relative to the size of protected areas (PAs) makes many PAs insufficient to maintain viable carnivore populations (Woodroffe and Ginsberg, 1998). Non-protected and human-dominated landscapes, where large carnivores coexist with humans, may be essential for the persistence of viable populations (Breitenmoser *et al.,* 2005), which presents a challenge to their conservation. Outside PAs, agro-pastoral communities have strong negative attitudes and risk perceptions of large carnivores due to livestock depredation associated with economic loss, which often leads to retaliatory or preventative carnivore killing (Dickman, 2008; Kissui, 2008). This is likely to have potentially severe implications for populations of threatened species that can undermine large carnivore conservation efforts. For example, a study in Namibia attributed 47% of cheetah mortality to persecution by humans on farmland (Thorn *et al*., 2014). Between 2004 and July 2005, 85 lions were killed in retaliation for livestock depredation in the Maasai Steppe, Tanzania (Kissui, 2008). People's tolerance for large carnivores depends on their attitudes and risk perceptions, which may vary by culture, religious beliefs, income, education level and knowledge about carnivores (Dickman, 2010; Mishra, 1997). In Nepal, for example, Buddhists are tolerant of livestock depredation by snow leopards *Panthera uncia* due to their cultural or religious beliefs, killing them is considered a sin (Ale, 1998). Wolves *Canis lupus*, but not snow leopards, are highly persecuted in India even though both species prey on livestock, because of negative cultural beliefs associated with wolves (Mishra, 1997). In Maasai societies, spotted hyenas *Crocuta crocuta* are often viewed with hostility as they are associated with gluttony, stupidity and witchcraft (Maddox, 2003).

The theoretical framework for this article was built on the cognitive hierarchy where human perceptions are shaped by values, value orientations, attitudes and norms, behavioral intentions and behaviors (Fulton *et al.*, 1996). We defined cognitions as "the collection of mental processes (e.g., values, beliefs, attitudes) used in perceiving, remembering, thinking, and understanding, as well as the act of using these processes"(Ashcraft, 2006 p.12). Such cognitions have been arranged in a "hierarchy" where there are connections between fundamental values at the base of a pyramid and overt behavior at the top (Fulton *et al.*, 1996). Values are defined as enduring beliefs that form the foundation of a person's thoughts and actions that lead to specific attitudes and behaviors (Fulton *et al*., 1996). In this article, we examined the relationships between general (fundamental) life values and attitudes towards large carnivores. An attitude was defined as a "psychological tendency that is expressed by evaluating a particular entity with some degree of favorability or unfavorability"(Ajzen, 2001).

Attitudes are commonly seen as people's evaluations of some object or animal (e.g., carnivore) that range from positive to negative (Ajzen, 2001). For example, attitudes towards carnivores can be positive when they are associated with tourist revenue (Dickman *et al.*, 2011), and can be negative where carnivores are perceived as a threat to livestock or human life (Dickman, 2008; Maddox, 2003; Røskaft *et al*., 2007). In this article, we also examined perceptions of carnivore-related risks to understand human-carnivore interactions. Risk perception refers to the innate risk judgments made by citizens as opposed to assessments by experts (Slovic, 1987). There are two constructs to such risk perceptions (a) cognitive risk perception – the perceived probability of encounters with carnivores (e.g., depredation of livestock, attacks on humans), and (b) affective risk perception – the emotional responses to a risk (e.g., concern or worry an individual feels regarding exposure to risks from carnivores) (Sjöberg, 1998).

Resolving human-carnivore conflict requires a better understanding of people's attitudes towards large carnivores and the drivers of these attitudes (Oli *et al.,* 1994). These drivers, however, are often complex and may involve cultural, demographic, ecological, social, and economic components (Dickman *et al*., 2014),which can change over time (Fritts *et al.*, 2003). Variation in people's attitudes towards carnivores is based on the extent to which carnivores conflict with human interests and on inherent human prejudices (Lindsey *et al.,* 2005).

Research has shown that knowledge and understanding of individual species (Lindsey *et al*., 2005), socio-economic characteristics (e.g., income, occupation) (Oli *et al.*, 1994; Dickman, 2008), education (Røskaft *et al.,* 2007), number of livestock owned and livestock lost to predators (Naughton-Treves *et al.*, 2003; Kideghesho *et al.*, 2007) are associated with people's attitudes towards large carnivores. Other factors, such as demographics (e.g., age, gender) (Kellert and Berry, 1987), distance from PAs, experience with carnivores, benefits from conservation (Lindsey *et al*., 2005; Schumann *et al.*, 2008), religious beliefs (Hazzah, 2006) and cultural beliefs (Maddox, 2003) are also influential in shaping people's attitudes towards large carnivores.

The area adjacent to Tarangire National Park (TNP) in northern Tanzania was an ideal site for the current study because of the interactions between people and large carnivores that give rise to human-carnivore conflicts. The current status of the conflict influences attitudes and perceptions of risk associated with large carnivores (Lichtenfeld, 2005; Msuha, 2009). Determinants of attitudes towards large carnivores are poorly known in the region (Lichtenfeld, 2005). This article addressed these gaps. Msuha (2009) indicated that Maasai in the region perceive large carnivores as a threat to livestock and suggested that level of wildlife knowledge, number of small stock lost to predators, number of income sources and density of wild animals near human settlements perceived to be problematic were associated with conflict with carnivores. Lichtenfeld (2005) found that Maasai communities had negative perceptions towards lions due to potential threats they pose to livestock and human life, and they expressed positive perceptions based on utilitarian value (benefits from tourism and sport hunting). Lichtenfeld (2005) also found that dislike of lions varied according to cultural group, with Maasai communities, which were most reliant on livestock, being most likely to dislike lions, while women and wealthier individuals perceived higher level of risk associated with lions.

A sound understanding of people's attitudes and perceptions of risk associated with large carnivores, as well as the factors influencing these attitudes is essential for developing effective human-carnivore conflict mitigation strategies within communities. Specifically, our objectives were to (a) assess people's attitudes and perceptions of risk associated with large carnivores, (b) examine the underlying factors influencing people's attitudes towards large carnivores, and (c) suggest potential interventions that may mitigate conflict and promote human-carnivore coexistence in the region.

4.2 Materials and methods

4.2.1 Study area

This study was conducted in five villages (Loiborsoit, Terat, Emboret, Sukuro, Loibor Siret) of the Simanjiro Plains in Simanjiro district, northern Tanzania (Figure 10). Simanjiro district lies within the Maasai Steppe with a land area of 20,591 km^2. The Maasai Steppe is an important ecosystem in northeastern Tanzania that holds some of the highest diversity of large mammals in the world including populations of Africa's most threatened large carnivore species. On the western part of the Steppe lies the TNP that protects only 15% (2,850 km^2) of the approximately 20,000 km^2 in the Tarangire-Simanjiro Ecosystem (TSE). Large mammalian fauna of the area includes lions, cheetahs, spotted hyenas, striped hyenas *Hyena hyena*, leopards and African wild dogs that may prey upon game and livestock. We focused our study on five large carnivore species existing in the area that are most associated with conflict: lions, cheetahs, leopards, spotted hyenas and African wild dogs. African wild dogs are listed as Endangered, lions, cheetahs and leopard are listed as Vulnerable, whereas spotted hyenas are Least Concern (IUCN, 2016). The major ethnic groups in this area are the Maasai and the Waarusha. Traditionally, the Maasai are semi-nomadic pastoralists and dependent on livestock, although many are now agro-pastoralists, as they are increasingly practicing subsistence agriculture (McCabe, 2003). The Waarusha descended from the Maasai but have a higher frequency of practicing subsistence agriculture. These communities keep a variety of livestock including cattle, goats, sheep, and donkeys.

4.2.2 Questionnaire Design

From June to July 2014, we carried out the social survey using semi-structured interviews (SSIs). The questionnaire was adapted from the format used by Maddox (2003) in northern Tanzania, and by Dickman (2008) in southern Tanzania. The questionnaire was pre-tested on a sample of 15 respondents and revised based on the pre-test. SSIs consisted of both closed and open-ended questions to allow respondents to elaborate on their answers and to express their own ideas and views (Hunter and Brehm, 2003).

A total of 300 face-to-face interviews were conducted. Sixty respondents were selected from each village at random. We chose the household as the sampling unit, following Maddox (2003) and Dickman (2008), and interviews were restricted to one respondent per household. The sample included the head of the family (usually a man), the head's wife, or elder son according to seniority. Women often deferred to men, so respondents were predominantly male. During the interviews, we tested the respondents' knowledge of carnivores using cards with color photographs of the different species. Interviews were divided into two thematic sections: (a) socio-economic and demographic characteristics and (b) knowledge, attitudes and perceptions towards large carnivores.

We explored seven different types of attitudes towards large carnivores: (a) Respondents' attitudes towards large carnivores, (b) Respondents' attitudes towards wild animal presence around their village, (c) Respondents' attitudes towards the desired population change, (d) Respondents' attitudes towards control of wild animals, (e) Perceptions of problem status of large carnivores, (f) Perceived population trends of large carnivores, and (g) Perceptions towards livestock depredation and retaliatory or preventative carnivore killing. We included the following question as a proxy measure for attitudes towards carnivores: i.e., "In general do you like/dislike each of the following carnivore species?" The responses to this question were coded such that 1 = "like" and 0 ="dislike" and used to calculate an attitude index score. The perceived population trends/desired population change questions asked: (a) "What do you think has happened to the number of large carnivores in this area in the time period since you came to this household?" (b) "In your opinion, what would you like to see happening to the number of large carnivores in this area, and why?" The two questions (a) and (b) above were categorized as follows: 1 = "increased/increase"; 2 = "decreased/decrease"; 3 = "disappeared/disappear"; 4 = "stayed/stay the same".

The problematic carnivore species question asked: "Which of the following carnivore species do you think are most problematic? And explain why?" We scored the responses to this question on a 3-point scale, where 0 = "no problem", 1 = "minor problem", 2 = "major problem", and a mean problem/conflict score was calculated for each respondent across all species. We used this score as the main index of conflict where values close to 0 and close to 2 indicated lower and greater perceived conflicts respectively for a particular species. The attitudes towards wildlife question asked: "Do you enjoy seeing wild animals living around your village?" while the control for wildlife question asked: "Would you like someone to control some of the wild animals?" Responses to these questions were therefore coded as 1 = "yes" and 0 = "no".

We recorded the GPS location of each interviewed household. This was used to determine the shortest distance between the interview location and protected area boundary in *ArcGIS v.10.3* (ESRI, Redlands, USA). Interviews were conducted in the Swahili language (with the aid of a translator speaking Maasai where needed) and took approximately one hour to complete.

4.2.3 Data Analysis

Respondents' attitudes towards large carnivores were compared to socio-demographic attributes, livestock holding, total reported livestock losses and losses attributed to each carnivore species. Chi-square was used to determine whether an association existed between dependent and explanatory variables. Independent-sample *t*-tests were used to compare salience scores between carnivore species. Spearman Rank correlation coefficients (r_s) were used to assess correlation among variables.

To determine which variables were associated with people's attitudes, we used Generalized Linear Models (GLMs) with binomial distribution and logit link function. Our dependent variable was binary, 1 like, 0 dislike for each predator species. GLMs were used to identify which combination of potential explanatory variables (i.e., number of livestock owned, number of livestock lost to all predators and to each predator species, age (years), gender (male or female), occupation (pastoralist or agro-pastoralist), education level (formal or without formal education), number of income sources per household (1 to 5), knowledge score (for attitudes towards cheetahs only), residency time or years at residence (number of years since the respondent had arrived in the area) and distance from protected area (in km)) – best predicted people's attitudes towards large carnivores. We included only knowledge for cheetahs versus leopard in the model since all other carnivore species were exclusively identified by all respondents. The general importance of carnivores in relation to other wildlife was investigated by looking at the relative frequency of mentions and by an index of salience (*S)* measured using an index of 0-1 representing the relative position on each list (*Sj)* and the number of times each animal was mentioned (Borgatti, 1990). Salience index value (*S)* was calculated using the following formula:

$$S = \frac{\sum S_j}{N} \text{ Where } S_j = 1 - \frac{r_j - 1}{n - 1}$$

S = saliency index value, *N* = number of free lists, *rj* = position of item *j* in list, *n* = number of items in list. Spearman Rank correlation coefficients were used to test for multicollinearity between explanatory variables. We selected only one variable as a proxy for the others to use in statistical analysis when two or more explanatory variables significantly correlated with each other. The level of education was negatively correlated with age (r_s = -0.259, $p < 0.001$) and gender (r_s = -0.204, $p < 0.001$), while occupation was positively correlated with income sources (r_s = 0.132, p = 0.022). Therefore, age, gender and occupation were excluded from the model to improve the precision of the estimated model parameters. We ranked candidate models in order of parsimony using Akaike's Information Criterion corrected for small sample size (AICc) and Akaike weights (*wi*) (Burnham and Anderson, 2002). We computed model-averaged coefficients of predictor variables based on top-ranked models with (ΔAICc < 2). All tests were two-tailed and significance was measured at $p < 0.05$.

4.3 Results

4.3.1 Demographic and socio-economic characteristics

Respondents comprised 96% (*n* = 288) Maasai and 4% (*n* = 12) Waarusha. Respondents' age ranged from 18-92 years old, with an overall mean age of 35.85±13.99 (*SD*) years. Overall, 57% (*n* = 170) of respondents were between 18-35 years, 28% (*n* = 84) between 36-50 years, 9% (*n* = 27) between 51-60 years and 6% (*n* = 19) above 60 years. Eighty-eight percent (*n* = 265) of respondents were male and 12%, (*n* = 35) were female. The education level ranged from illiterate (i.e., no formal education) 51% (*n* = 154) to formal education (i.e., 36% (*n* =108) primary, 11% (*n* = 34) secondary and 1% (*n* = 4) tertiary education). On average, women were less educated than men (χ^2 = 12.45, *df* = 1, $p < 0.001$).

Ninety-five percent (*n* = 285) of respondents were agro-pastoralists and 5% (*n* = 15) were pastoralists. The main source of cash income was the sale of livestock (91%, *n* = 272), selling crops (27%, *n* = 82), off-farm activities (35%, *n* = 105) and other income-generating activities (1% i.e., operating a restaurant business, sewing beads, construction and beekeeping).

Nearly all respondents (99%) reported owning cattle with a mean number of 23.13± (*SE* 3.06) cattle per household and a mean number of 38.01± (*SE* 4.67) small stock per household while 89% reported owning donkeys with a mean number of 1.12± (*SE* 0.06) donkeys per household. The overall mean number of livestock holding per household was 62.25± (*SE* 7.60).

4.3.2 Knowledge about wildlife species

Among the five carnivore species, lions, spotted hyenas and African wild dogs were the most well-known and recognized by all respondents. Sixty-three percent (n = 188) of respondents were able to correctly differentiate cheetahs from leopards, while 37% (n = 112) failed to do so. The ability to differentiate between cheetahs and leopards (i.e., knowledge score index) was significantly influenced by the level of education ($\chi^2 = 10.40$, $df = 1$, $p = 0.001$) and gender ($\chi^2 = 26.84$, $df = 1$, $p < 0.001$). We asked the respondents to list all of the wild animals they can think of that live in the area or around their households. The number of wildlife species free-listed was used as an indicator of knowledge. A total of 27 species were listed by the respondents of which seven were carnivores. The number of species listed differed significantly by gender, with men listing more species than women ($\chi^2 = 21.32$, $df = 10$, $p = 0.019$) and by the level of education, with educated respondents listing more species than less educated ($\chi^2 = 33.05$, $df = 10$, $p < 0.001$). Lions, spotted hyenas and leopards were major components of the local people's perception of wildlife, with all recording high salience scores. Cheetahs and wild dogs had lower salience scores (0.06 and 0.12 respectively) in comparison to other carnivore species ($t = 7.82$, $df = 4$, $p = 0.001$).

4.3.3 Attitudes and perceptions of local people towards large carnivores

On average, 20% of respondents liked the focal carnivore species while 79% disliked them and 1% offered no clear opinion. All five carnivore species were disliked by a similar percentage of people ($\chi^2 = 3.82$, $df = 4$, $p = 0.431$, Figure 11). Respondents who showed a negative perception about one species tended to do so about the other species. The main reasons given by respondents for disliking focal carnivores were threats they pose to livestock and human life (81%, n = 298). Respondents expressed positive attitudes towards focal carnivores primarily either because they had no problem with them at present (5%, n = 298) or because they generate revenue through tourism (11%, n = 298). Other reasons given included the perceptions that 'people are used to having these animals around for many years'? (2%, n = 298) and 'proud to see them around'? (1%, $n = 298$). Overall, the mean attitude scores did not differ significantly between focal carnivore species ($\chi^2 = 0.008$, $df = 16$, $p = 1.00$) or between villages ($\chi^2 = 0.008$, $df = 16$, $p = 1.00$).

4.3.4 General attitudes and perceptions towards wildlife

More than half (57%, $n = 172$) of respondents disagreed with the statement 'I enjoy seeing wild animals on my land', while 43% ($n = 128$) were happier to see them on their land. Females expressed more negative attitudes towards wild animals than males ($\chi^2 = 8.32$, $df = 1$, $p = 0.004$). The main reasons given for negative attitudes were that they were a threat to livestock (41%, $n = 123$), followed by threats to livestock and crops (17%, $n = 50$). Conversely, positive attitudes towards wildlife were mainly attributed to expected benefits from ecotourism (16%, $n = 48$) and people considered them part of their natural heritage (10%, $n = 30$). Respondents with less education were less likely to enjoy seeing wild animals on village land ($\chi^2 = 8.81$, $df = 1$, $p = 0.003$). Nearly, 99% ($n = 296$) of respondents stated a desire for wildlife to be controlled in the area while 1% ($n = 4$) were against wildlife control.

4.3.5 General perceptions of problem status of large carnivores

When the respondents were asked to rank carnivore species in terms of how problematic they were, spotted hyena was cited as the single most problematic species, followed by leopards, African wild dogs, lions and cheetahs, in that order ($\chi^2 = 395.82$, $df = 8$, $p < 0.001$, Figure 12). Most respondents agreed that the main problem with large carnivores is perceived risk associated with depredation on livestock. The number of livestock lost to predators correlated positively with the problem score assigned to focal carnivores: cheetahs ($r_s = 0.172$, $p = 0.003$), lions ($r_s = .328$, $p < 0.001$), leopards ($r_s = .330$, $p < 0.001$), spotted hyenas ($r_s = .439$, $p < 0.001$) and wild dogs ($r_s = .286$, $p < 0.001$).

4.3.6 Population trends of large carnivores

On average, two-thirds (65%) of respondents perceived that large carnivore populations had decreased, 30% perceived they had increased, 22% that they had remained constant, and 1% perceived they had completely disappeared from the area ($\chi^2 = 73.07$, $df = 3$, $p < 0.001$, Table 16). This reported decline was most pronounced for lions, cheetahs, leopards and wild dogs while the reported increase was most pronounced for spotted hyenas. The main reasons as to why these carnivore species have declined were attributed primarily to human persecution (40%, n = 119, followed by habitat degradation and fragmentation (18%, n = 55) and increased human settlement (7%, n = 20).

4.3.7 Attitude towards the desired population change of large carnivores

On average, over two-thirds (67%) of respondents wanted large carnivores to decrease, 13% wanted them to disappear, 12% wanted them to increase, 7% wanted them to stay the same, and 1% offered no clear opinion ($\chi^2 = 97.29$, $df = 3$, $p < 0.001$, Table 16). The main reasons given for wanting large carnivore populations to decline or disappear were to reduce carnivore-related risks, particularly livestock depredation, and attacks upon humans. Conversely, the main reasons given for wanting the population of large carnivores to increase was the capacity to generate revenue from tourists (43%, n = 129), lack of genuine problems at current population levels (11%, n = 34) and being valuable for children's education (2%, n = 5).

4.3.8 Perception towards livestock depredation and retaliatory or preventative carnivore killing

Seventy-two percent (n = 218) of the respondents perceived that livestock attacks by carnivores had diminished since they arrived in the area, 25% perceived an increase, 1% perceived no change and 1% had no clear opinion ($\chi^2 = 410.93$, $df = 3$, $p < 0.001$). The main reason given for a perceived decline in depredation was the aforementioned reduction in carnivore populations. Nine percent (n = 26) of the respondents admitted to having killed predators since they arrived in the area.

4.3.9 Factors influencing local people's attitudes towards large carnivores

Respondents with formal education expressed more positive attitudes than those without towards cheetahs ($\chi^2 = 16.49$, $df = 1$, $p < 0.001$), lions ($\chi^2 = 20.32$, $df = 1$, $p < 0.001$), leopards ($\chi^2 = 19.51$, $df = 1$, $p < 0.001$), spotted hyenas ($\chi^2 = 14.27$, $df = 1$, $p < 0.001$) and wild dogs ($\chi^2 = 17.36$, $df = 1$, $p < 0.001$). In addition, respondent's residency time was significantly associated with positive attitude towards cheetahs ($\chi^2 = 49.33$, $df = 30$, $p = 0.015$) and lions ($\chi^2 = 43.76$, $df = 30$, $p = 0.050$) but not wild dogs ($\chi^2 = 44.53$, $df = 30$, $p = 0.063$), leopards ($\chi^2 = 42.04$, $df = 30$, $p = 0.071$) or spotted hyenas ($\chi^2 = 42.59$, $df = 30$, $p = 0.064$). Similarly, attitude towards cheetahs was significantly positively associated with the knowledge score ($\chi^2 = 11.78$, $df = 1$, $p < 0.001$).

Model selection statistics for variables predicting local people's attitudes towards five focal carnivore species are presented in Tables 18-20. Model-averaged coefficient estimates indicated that education and residency time were the most important predictors of attitudes towards lions (Table 17). However, model-averaged coefficients indicated that only education was significantly related to attitudes towards leopards and spotted hyenas. The same trend was found in wild dogs. Attitudes towards cheetahs were positively associated with education, residency time and knowledge score. Overall, attitudes towards large carnivores were positively associated with education level (for all carnivore species), respondent's residency time (for lions and cheetahs) and knowledge of carnivores (cheetahs) (Table 17). Our results showed that attitudes towards large carnivores were not significantly associated with age, gender, number of livestock owned, distance from protected area, number of income sources, number of total stock lost to all predators or stock lost to each predator species.

4.4 Discussion

4.4.1 Attitudes towards large carnivores

Human-carnivore conflict often engenders negative attitudes and low levels of tolerance towards carnivores (Oli *et al*., 1994). We found that attitudes towards large carnivores were not influenced by reported livestock depredation incidents, suggesting that the depredation impact was not significant enough to influence people's attitudes towards large carnivores. This finding contradicts previous studies (Dickman, 2008; Kissui, 2008; Maddox, 2003; Røskaft *et al*., 2007) where negative attitudes towards large carnivores were associated with carnivore-induced livestock losses. In our study, however, livestock depredation was cited as the main reason for antagonism towards large carnivores. The lack of a direct relationship between attitudes towards carnivores and depredation experiences, suggests that underlying drivers of conflict may be more complex and deep-seated than direct depredation. Despite an apparent logical link between stock depredation and human-carnivore conflict (Mishra, 1997), there is not always a simple, consistent relationship between the levels of stock loss and negative perceptions towards large carnivores (Dickman, 2008). In South Africa, on the border of the Kruger National Park, people who experienced depredation were not significantly more hostile towards carnivores than people who did not, due to cultural or aesthetic appreciation of large carnivores (Lagendijk and Gusset, 2008). In Tanzania, around Ruaha National Park, Dickman (2008) found that although people may not have personally experienced livestock depredation by large carnivores, they can still dislike carnivores as they pose a potential threat. By contrast, we found that positive attitudes towards large carnivores were mainly associated with tangible benefits people receive from having them in their area (i.e., revenue from tourism-related activities), as has been shown in other studies (Lindsey *et al.*, 2005; Romañach *et al*., 2007). Contrary to expectations, we did not find any significant difference in attitudes between carnivore species. This could be explained by the 'contagious conflict' where respondents who showed a negative perception about one group of species may do so with other species (Dickman *et al.*, 2014).

4.4.2 Factors influencing local people's attitudes towards large carnivores and other wild animals

Our results showed that respondents with formal education expressed more positive attitudes towards large carnivores than those without any formal education. This finding was in line with previous studies which showed that formal education can improve attitudes and increase tolerance levels for large carnivores (Lindsey *et al.,* 2005; Røskaft *et al.*, 2007; Parker *et al*., 2014; Woodroffe *et al.*, 2005). Oli *et al*. (1994) argued that people with higher levels of education are expected to be relatively more conversant with wildlife protection laws and have greater awareness of the benefits of large carnivores. On the other hand, the level of wildlife knowledge can also influence negative attitudes towards wildlife. For example, Dickman (2008) found that the intensity of reported conflict between people and wildlife increased with people's level of wildlife knowledge around Ruaha National Park in southern Tanzania.

Our findings showed that people who had a long exposure to large carnivore-related risks (i.e., long-term residency) were more likely to express positive attitudes towards them than people with short time exposure. These findings were inconsistent with previous studies in other regions (Arjunan *et al.,* 2006; Newmark *et al.,* 1993), in which increased exposure to wildlife-related risks (i.e., long-term residency) has been associated with negative attitudes. One possible explanation for our findings is that long-term residents might have enough time to develop more effective livestock management strategies (e.g., construction of sturdier enclosures and improved herding practices) to cope with carnivore conflicts than short-term residents. However, an alternative explanation is that prolonged residency is associated with an increased exposure to large carnivores, and this personal experience results in a reduction of negative attitudes. This was suggested by Ericsson and Heberlein (2003) to explain public attitudes to wolves and later demonstrated by Røskaft *et al*. (2003) for members of the public exposed to large carnivores in Norway. Consistent with other studies (Kellert and Berry, 1987, Røskaft *et al.,* 2007; Li *et al.,* 2010), our findings showed that men were more positive towards wildlife and more experienced or knowledgeable about wildlife compared with women.

We found that attitudes towards large carnivores were neither positively associated with number of livestock owned (an index of wealth) nor negatively associated with number of livestock lost to predators. These findings differ from previous studies which have shown that people's attitudes towards carnivores are positively associated with numbers of livestock owned and negatively associated with livestock lost to predators (Kideghesho *et al.*, 2007; Naughton-Treves *et al.*, 2003).

4.4.3 Knowledge of local people about large carnivores

Our results showed that local people had a better knowledge of lions, spotted hyenas and leopards than cheetahs or wild dogs, as evaluated by the salience score indices. This is possibly explained by the commonality of lions, spotted hyenas and leopards around the village. In Pendjari Biosphere Reserve, Benin (Sogbohossou *et al.,* 2011), and in Kruger National Park, South Africa (Lagendijk and Gusset, 2008), better knowledge of species such as lion and spotted hyena was related to their commonality around villages and responsibility for attacks on livestock. Attitude towards cheetahs and knowledge score were significantly associated, which concurs with other studies (Romañach *et al.*, 2007). However, attitudes towards cheetahs and leopards must be treated with due caution, because attitudes and experiences with one species may unintentionally be affecting their responses regarding the other (Dickman, 2008), and our results showed that people had most difficulty distinguishing between these two species.

4.5 Conclusion and management implications

Our findings provide insights and a better understanding of local people's attitudes and perceptions towards large carnivores, as well as factors that influence these attitudes in a human-dominated landscape of northern Tanzania. Education, years at residency and knowledge were the most influential determinants (though dependent on species) of attitudes towards large carnivores than landscape, demographic or economic factors. The differences between our results and previous studies may be explained by the complexity of conflict and its drivers. Our findings suggested that negative attitudes towards large carnivores were driven not only by livestock loss, but by a complexity of other factors not accounted for by this study; such as fear evoked by its very presence (Lichtenfeld, 2005) and deep-seated cultural hostility resulting from past experiences, even if carnivores are not causing present problems (Lagendijk and Gusset, 2008; Røskaft *et al.*, 2007). Dickman (2010) also suggested that conflict is not merely driven by stock losses, but is the result of a complex set of deep-rooted factors such as people's attitudes towards the PAs, autonomy over land which creates limitations on grazing and resource access imposed by nearby PAs and costs imposed by dangerous animals straying out of the park and onto village land. For instance, in Brazil, livestock depredation did not significantly affect local ranchers' attitudes towards jaguars (*Panthera onca*) and pumas (*Puma concolor*) (Conforti and De Azevedo, 2003), whereas in Namibia, cheetah removal from farmland persisted (an average of 14 cheetahs per year) even where they were not thought to cause depredation (Marker *et al.*, 2003). While some studies have shown that decreasing depredation can lead to change in attitudes (Parker *et al.*, 2014), our findings suggested that reducing depredation alone is less likely to produce a substantial change in people's attitudes towards large carnivores. Given these results, further research to understand underlying factors influencing people's attitudes towards large carnivores in the study area is desirable. Our findings suggested that interventions aimed at fostering positive attitudes towards large carnivores should focus on improving formal education and securing long-term residency for people in the region. Although majority of respondents perceived the presence of large carnivores as negative, the impact of the positive attitudes of the minority groups should not be ignored. Securing benefits from large carnivores through ecotourism should be enhanced. Environmental education programs should focus more on people immigrating into the region and women – who are less positive, less educated and least knowledgeable about wildlife. In addition, educational programs aimed at improving knowledge about leopard and cheetah should also be prioritized. Based on our findings, we suggest improving conservation awareness education at all levels of education, as this could help improve attitudes towards wildlife in general and raise community awareness of wildlife conservation (Lindsey *et al.,* 2005). Our findings that the majority of individuals perceived a decline of large carnivore depredation on livestock has implications for future decision-making on the coexistence of people, livestock, and large carnivores in the study area.

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Table 16. Respondents' perceptions of population trends and desired population change for each carnivore species (n = 300) (number, % in parentheses).

	Population trend				Desired population change				
	Increased	Decreased	Disappeared	Stayed the same	Increase	Decrease	Disappear	Stay the same	Don't' know
Lion	38 (12)	254(84)	1(0.3)	10(3)	43(14)	195(65)	33(11)	25(8)	4(1)
Cheetah	32(11)	251(83)	3(1)	17(6)	41(14)	198(66)	33(11)	24(8)	4(1)
Leopard	77(25)	211(69)	1(0.3)	15(5)	33(11)	203(68)	36(12)	24(8)	4(1)
Spotted hyena	220(77)	59(21)	0(0)	6(2)	26(9)	209(70)	46(15)	15(5)	4(1)
African wild dog	73(24)	208(68)	5(2)	19(6)	33(11)	199(66)	43(14)	21(7)	4(1)
Total/ Average	**88(30)**	**196.6(65)**	**2(1)**	**13.4(4)**	**35.2(12)**	**200.8(67)**	**38.2(13)**	**21.8(7)**	**4(1)**

Table 17. Summary statistics of model-averaged coefficients (β), Standard errors (SE) and Wald statistic (which has a χ^2 distribution) calculated for variables explaining variation in attitude of respondents towards large carnivores.

Coefficients	Estimate (β)	SE	Wald χ^2	P value
~Lion~				
(Intercept)	-2.287	0.311	53.92	<0.001
Education_formal[a]	1.286	0.295	19.06	<0.001
Residency time	0.042	0.019	5.14	0.023
~Leopard~				
(Intercept)	-2.424	0.329	53.98	<0.001
Education_formal[a]	1.340	0.315	18.13	<0.001
Residency time	0.032	0.019	2.81	0.094
~Spotted hyena~				
(Intercept)	-2.890	0.382	57.18	<0.001
Education_formal [a]	1.298	0.361	12.92	<0.001
Residency time	0.039	0.021	3.57	0.059
~Wild dog~				
(Intercept)	-2.803	0.376	55.64	<0.001
Education_formal[a]	1.415	0.358	15.67	<0.001
Residency time	0.032	0.021	2.32	0.128
~Cheetah~				
(Intercept)	-1.145	0.565	4.11	0.043
Education_formal[a]	1.077	0.307	12.32	<0.001
Residency time	0.044	0.019	5.32	0.021
Knowledge_correct cheetah ID[b]	0.095	0.347	6.64	0.010

Note.

[a]"without-formal education" was the reference category.

[b]"respondents who failed to correctly differentiate cheetahs from leopards" was the reference category.

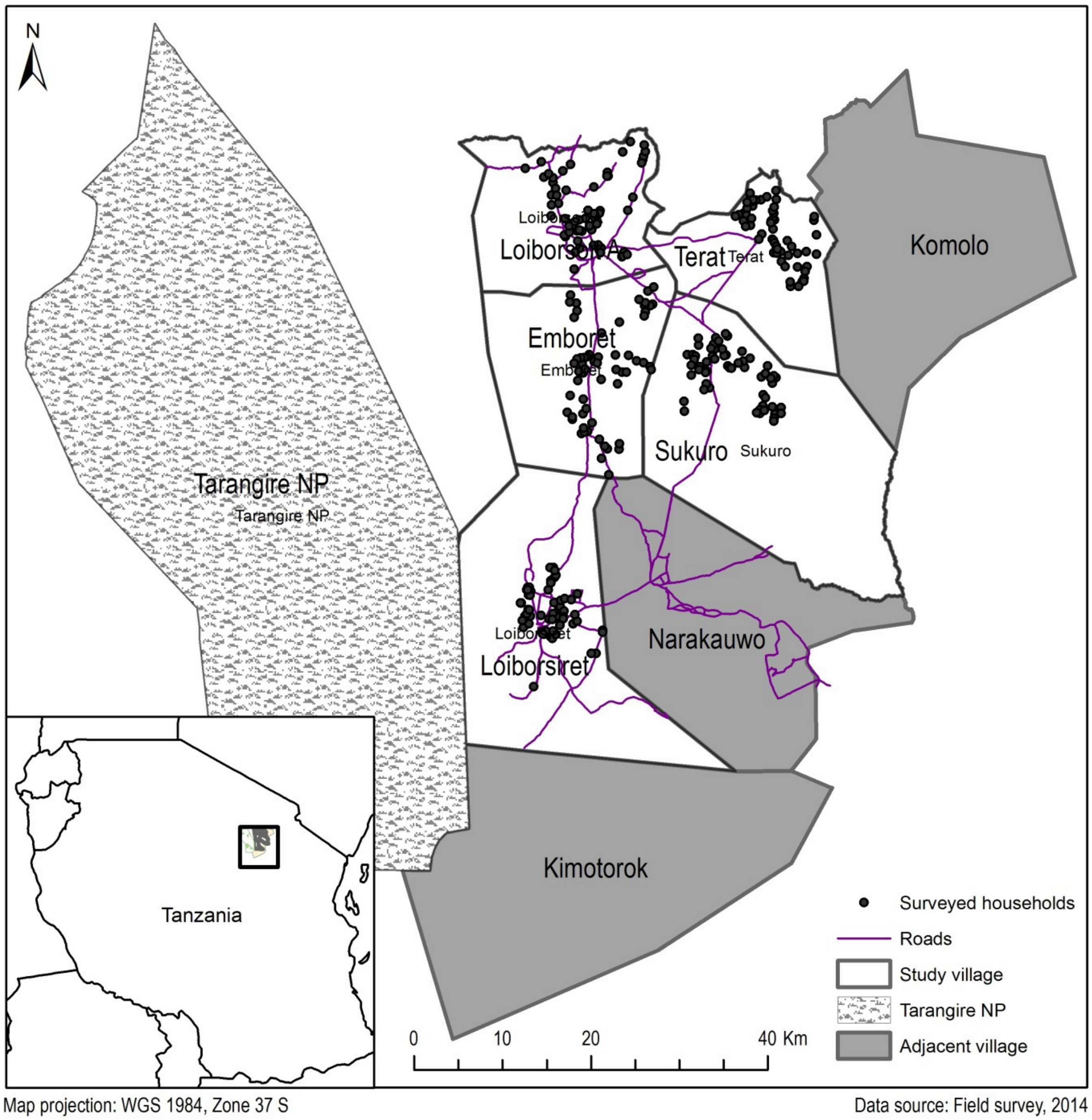

Figure 10. Map showing the location of the studied villages and the households interviewed in the survey

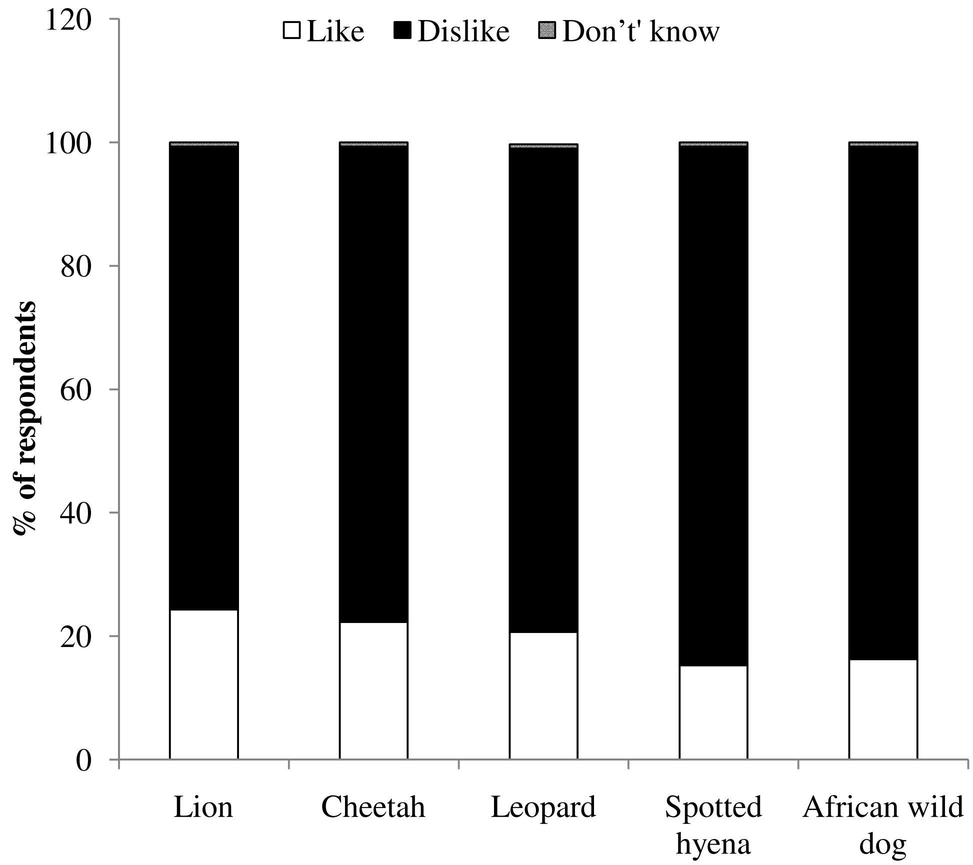

Figure 11. Percentage of respondents claiming that they liked, disliked or did not know how they felt about each of the focal carnivore species.

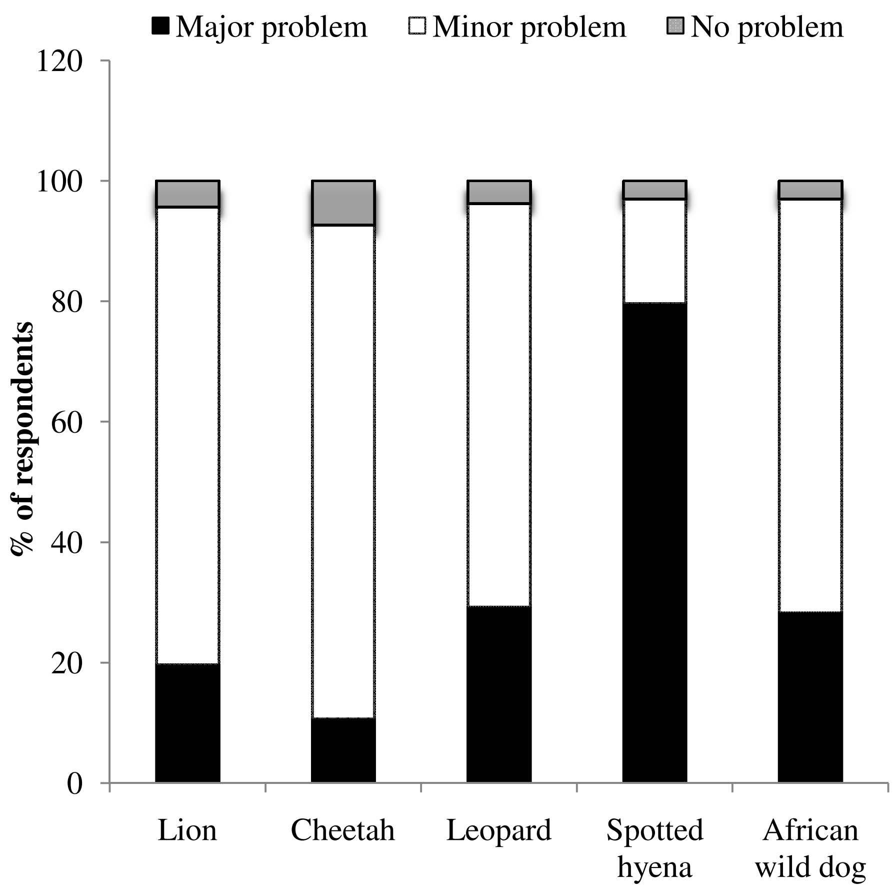

Figure 12. Percentage of respondents ranking carnivore species in terms of how problematic they were around their villages

Supplementary Material

Table 18. A *priori* candidate models for variables predicting local people's attitudes towards lions and leopards. Models were analysed using a generalized linear model with a logit link function and a binomial distribution.

~Lion~						~Leopard~					
Candidate model	-2Log(L)	K	AICc	ΔAICc	ω_i	**Candidate model**	-2Log (L)	K	AICc	ΔAICc	ω_i
Education + Residency time	-152.35	3	310.79	0.00	0.19	Education + Residency time	-141.78	3	289.63	0.00	0.23
Education + Residency time + Income	-151.48	4	311.10	0.31	0.16	Education + Residency time + Income	-141.08	4	290.29	0.66	0.17
Education + Distance + stock owned + Lion Kill + Residency time	-149.68	6	311.65	0.86	0.13	Education	-143.15	2	290.35	0.72	0.16
Education + Lion Kill	-153.07	3	312.22	1.43	0.09	Education + Residency time + Household size	-141.58	4	291.30	2.00	0.08
Education + Distance + Lion Kill + stock owned + Income	-149.12	6	312.62	1.83	0.08	Education + Leopard Kill	-142.87	3	291.82	2.19	0.08
Education + Residency time + Household size	-152.32	4	312.78	1.99	0.07	Education + stock owned	-142.96	3	292.00	2.37	0.07
Education + Distance + Lion Kill + stock owned	-151.50	5	313.21	2.42	0.06	Education + Distance + stock owned + Leopard Kill + Residency time	-140.15	6	292.59	2.96	0.05
Education + Residency time + Household size + Distance + Total Kill + Income	-149.59	7	313.58	2.79	0.05	Education + Distance + Leopard Kill + stock owned	-141.44	5	293.08	3.45	0.04
Education + Distance + Lion Kill + stock owned + Household size	-149.66	6	313.71	2.92	0.04	Education + stock owned + Leopard Kill	-142.64	4	293.41	3.78	0.03
Education	-154.91	2	313.86	3.07	0.04	Education + Distance + Leopard Kill + stock owned + Income	-140.97	6	294.22	4.59	0.02
Education + stock owned + Lion Kill	-152.96	4	314.05	3.26	0.04	Education + Residency time + Household size + Distance + Total Kill + Income	-140.04	7	294.46	4.83	0.02
Education + stock owned	-154.61	3	315.31	4.52	0.02	Education + Distance + Leopard Kill + stock owned + Household size	-141.20	6	294.69	5.06	0.02
Education + Distance + Residency time + stock owned + Household size + Income + Total Kill + Lion Kill	-148.71	9	316.05	5.26	0.01	Education + Household size + Leopard Kill + stock owned	-142.31	5	294.83	5.20	0.02
Education + Household size + Lion Kill + stock owned	-152.96	5	316.12	5.33	0.01	Education + Distance + Residency time + stock owned + Household size + Income + Total Kill + Leopard Kill	-139.02	9	296.67	7.04	0.01
Lion Kill	-163.71	2	331.46	20.67	0.00	Leopard Kill	-153.21	2	310.47	20.84	0.00
Lion Kill + stock owned	-163.28	3	332.64	21.85	0.00	Leopard Kill + stock owned	-152.51	3	311.11	21.48	0.00

Notes: K: number of estimated parameters in the model plus 1 for intercept and error term; -2Log (L): value of the Restricted log-likelihood of the model; AICc: Akaike's Information Criterion corrected for small sample size; ΔAICc: difference in AICc values between the best-performing model and the model of interest; ωi: Akaike model weight; Lion Kill: livestock killed by lion, Leopard Kill: livestock killed by leopard, Total Kill: total livestock killed by all predators, Distance: distance from the park boundary

Table 19. A *priori* candidate models for variables predicting local people's attitudes towards spotted hyena and wild dog. Models were analysed using a generalized linear model with a logit link function and a binominal distribution.

~Spotted hyena~						**~Wild dog~**					
Candidate model	-2Log (L)	K	AICc	ΔAICc	ω_i	**Candidate model**	-2Log (L)	K	AICc	ΔAICc	ω_i
Education + Residency time	-118.74	3	243.56	0.00	0.32	Education + Residency time	-122.64	3	251.36	0.00	0.21
Education + Residency time + Income	-118.35	4	244.83	1.00	0.19	Education	-123.76	2	251.57	0.21	0.19
Education	-120.47	2	244.97	1.41	0.16	Education + Wild dog Kill	-123.05	3	252.19	0.83	0.14
Education + Residency time + Household size	-118.67	4	245.48	1.92	0.12	Education + Residency time + Income	-122.22	4	252.59	1.23	0.12
Education + stock owned	-120.37	3	246.82	3.26	0.06	Education + stock owned	-123.52	3	253.12	1.76	0.09
Education + Hyena Kill	-120.46	3	247.00	3.44	0.06	Education + Distance + Wild dog Kill + stock owned	-121.58	5	253.36	2.00	0.08
Education + Distance + Hyena Kill + stock owned	-119.32	5	248.84	5.28	0.02	Education + stock owned + Wild dog Kill	-122.84	4	253.82	2.46	0.06
Education + stock owned + Hyena Kill	-120.36	4	248.85	5.29	0.02	Education + Distance + Wild dog Kill + stock owned + Income	-121.24	6	254.76	3.40	0.04
Education + Residency time + Household size + Distance + Total Kill + Income	-117.61	7	249.61	6.05	0.02	Education + Household size + Wild dog Kill + stock owned	-122.55	5	255.30	3.94	0.03
Education + Distance + Hyena Kill + stock owned + Income	-119.05	6	250.38	6.82	0.01	Education + Residency time + Household size + Distance + Total Kill + Income	-120.94	7	256.26	4.90	0.02
Education + Household size + Hyena Kill + stock owned	-120.27	5	250.75	7.19	0.01	Education + Residency time + Household size	-122.35	4	252.84	5.13	0.02
Education + Distance + Hyena Kill + stock owned + Household size	-119.28	6	250.84	7.28	0.01	Education + Distance + Residency time + stock owned + Household size + Income + Total Kill + Wild dog Kill	-120.07	9	258.77	7.41	0.01
Education + Distance + Residency time + stock owned + Household size + Income + Total Kill + Hyena Kill	-117.54	9	253.69	10.13	0.00	Distance	-132.05	2	268.14	16.78	0.00
Hyena Kill	-128.19	2	260.41	16.85	0.00	Wild dog Kill	-132.28	2	268.60	17.24	0.00
Hyena Kill + stock owned	-127.81	3	261.69	18.13	0.00	Wild dog Kill + stock owned	-132.26	3	270.60	19.24	0.00

Notes: K: number of estimated parameters in the model plus 1 for intercept and error term; -2Log (L): value of the Restricted log-likelihood of the model; AICc: Akaike's Information Criterion corrected for small sample size; ΔAICc: difference in AICc values between the best-performing model and the model of interest; ωi: Akaike model weight; Hyena Kill: livestock killed by spotted hyena, Wild dog Kill: livestock killed by wild dog, Total Kill: total livestock killed by all predators, Distance: distance from the park boundary

Table 20. A *priori* candidate models for variables predicting local people's attitudes towards cheetahs. Models were analysed using a generalized linear model with a logit link function and a binomial distribution.

Model rank	Candidate model	-2Log (L)	K	AICc	ΔAICc	ω_i
1	Education + Residency time + knowledge score	-142.91	4	293.96	0.00	0.44
2	Education + Residency time + knowledge score + Income	-142.02	5	294.25	0.29	0.38
3	Knowledge score + Education	-145.58	3	297.24	3.28	0.10
4	Knowledge score + Education + stock owned	-144.79	4	297.73	3.77	0.07
5	Education + Residency time + Household size	-146.40	4	300.94	6.98	0.01
6	Education + Residency time + Household size + Distance + Total Kill + Income	-144.46	7	303.29	9.33	0.00
7	Education	-149.89	2	303.83	9.87	0.00
8	Education + stock owned	-149.23	3	304.54	10.58	0.00
9	Education + Distance + Cheetah Kill + stock owned	-144.57	5	305.35	11.39	0.00
10	Education + Distance + Cheetah Kill + stock owned + Income	-146.86	6	306.01	12.05	0.00
11	Education + stock owned + Cheetah Kill	-149.21	4	306.56	12.60	0.00
12	Education + Distance + Residency time + stock owned + Household size + Income + Total Kill + Cheetah Kill	-144.08	9	306.78	12.82	0.00
13	Education + Distance + Cheetah Kill + stock owned + Household size	-147.44	6	307.18	13.22	0.00
14	Education + Household size + Cheetah Kill + stock owned	-148.99	5	308.19	14.23	0.00
15	Knowledge	-152.48	2	309.00	15.04	0.00
16	Residency time	-154.82	2	313.69	19.73	0.00
17	Distance	-157.75	2	319.54	25.58	0.00
18	Cheetah Kill + stock owned	-157.52	3	321.12	27.16	0.00
19	Cheetah Kill	-158.75	2	321.55	27.59	0.00

Notes: K: number of estimated parameters in the model plus 1 for intercept and error term; -2Log (L): value of the Restricted log-likelihood of the model; AICc: Akaike's Information Criterion corrected for small sample size; ΔAICc: difference in AICc values between the best-performing model and the model of interest; ωi: Akaike model weight; Cheetah Kill: livestock killed by cheetah, Total Kill: total livestock killed by all predators, Distance: distance from the park boundary

CHAPTER FIVE

Large Carnivore Distribution in Relationship to Environmental and Anthropogenic Factors in a Multiple-use Landscape of Northern Tanzania[4]

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Abstract

Effective management of threatened wildlife, particularly large carnivores, depends on a sound understanding of their spatial distribution and status in relationship to environmental or anthropogenic impacts. Here we analyse data from spoor surveys to investigate occurrence across a multiple-use landscape in the Tarangire-Simanjiro ecosystem in northern Tanzania for four taxa of African large carnivores: lions (*Panthera leo*), hyenas (spotted hyenas (*Crocuta crocuta)* and striped hyenas *(Hyena hyena*) combined), cheetahs (*Acinonyx jubatus*) and leopards (*Panthera pardus*). We analysed our data using occupancy modelling, explicitly accounting for detectability, to identify associations with environmental and anthropogenic variables. We surveyed 10-km^2 grid cells for hyena and leopard (n = 34), 15-km^2 for lion (n = 20) and 30-km^2 for cheetah (n = 10), and selected 1-km segments within grid cells as spatial replicates. Overall occurrence was estimated at 0.85 (SE = 0.06) for hyena, 0.82 (SE = 0.15) for cheetah, 0.55 (SE = 0.10) for lion and 0.61 (SE = 0.21) for leopard. Lion occurrence was negatively associated with distance to park boundary. Hyena occurrence was positively associated with human population density and negatively associated with bushland, while cheetah and leopard occurrences were positively associated with grassland. These results suggest that lions may be more vulnerable to human impacts than other species, while hyenas may benefit from vicinity to humans. Our study demonstrates the value of spoor-based occupancy surveys for understanding the distribution and habitat-use of secretive large carnivores.

Keywords: African large carnivores, human-wildlife coexistence, multiple-use landscape, occupancy modelling, spatial distribution, spoor surveys

5.1 Introduction

Reliable information regarding species distribution patterns and the factors that influence their occurrence is critical to their effective management and conservation. However, obtaining quantitative information on the distribution and status of rare, elusive and often, nocturnal species, such as large carnivores, can be particularly challenging (Durant *et al.*, 2007; Macdonald and Loveridge, 2010). Because most of the world's large carnivore populations are in rapid decline (Ripple *et al.,* 2014), there is an increasingly urgent need for efficient, practical and cost-effective methods that could be used to determine their population status and distribution across large areas (Funston *et al.*, 2010; Mackenzie *et al.*, 2006). Habitat loss and fragmentation, depletion of prey populations, hunting and illegal trade and persecution by humans, the latter primarily provoked by predation on livestock, are the main drivers of carnivore declines (Inskip and Zimmermann, 2009). Large carnivores are particularly vulnerable to the effects of anthropogenic pressures because they come into conflict with humans; often range over large areas; and occur at relatively low population densities (Woodroffe, 2000).

Indirect sampling methods which rely on spoor counts along transects are often used by wildlife managers to estimate population densities and relative abundances of carnivore species such as cheetah (*Acinonyx jubatus*) (Houser *et al.*, 2009), spotted hyena (*Crocuta crocuta*), leopard (*Panthera pardus*), lions (*Panthera leo*) and African wild dogs (*Lycaon pictus*) (Funston *et al.,* 2010; Stander, 1998). Spoor surveys are an effective non-invasive, inexpensive, repeatable and efficient method for detecting cryptic carnivores (Stander, 1998). Recent advancement in occupancy modeling approach provides a new powerful statistical framework that allows analysis across a landscape, and enables the quantification of environmental and anthropogenic correlates of distribution, while accounting for detection error (Hines *et al.,* 2010; Thorn *et al.*, 2011). This takes the approach way beyond simple spoor density/abundance correlations. Occupancy is defined as the "proportion of area occupied or used by a species (MacKenzie *et al.*, 2006) and it is used to understand distribution and habitat use (MacKenzie and Nichols, 2004). For large carnivores, occupancy modeling approaches are widely used to analyse camera trap data such as in Tanzania's Tarangire ecosystem (Msuha, 2009), in Ghana's Mole National Park (Burton *et al.,* 2011) and in Kenya's Rift Valley (Schuette *et al.*, 2013). Spoor surveys are more easily implemented across much larger areas than camera traps, and are thus particularly useful in generating data on spatial distribution over a relatively large landscape. Thus, there has been a growing interest in the use of spoor in an occupancy survey framework for surveying large carnivores, with recent studies investigating lions in Zambia's Kafue National Park (Midlane *et al.*, 2014) and the W-Arly-Pendjari ecosystem, in the border region of Benin, Burkina Faso, and Niger (Henchel *et al*., 2016), cheetah in Limpopo National Park in Mozambique (Andresen *et al.,* 2014) and leopard in Asia (Steinmetz *et al.,* 2013).

Surveys outside protected areas are becoming increasingly more important due to increasing levels of anthropogenic pressure on large carnivore communities (Durant *et al.*, 2017; Msuha, 2009). In the Tarangire landscape in northern Tanzania, the focus of this study, information on large carnivores is limited to data from non-invasive camera trapping across relatively small areas, and where surveys on unprotected lands were hampered by camera theft (Msuha, 2009). Here we use spoor-based surveys as our detection method in order to estimate the occurrence and detection probabilities of four focal large carnivore taxa (lions, leopards, hyenas and cheetahs) on unprotected and protected land across a multiple-use landscape in the Tarangire-Simanjiro ecosystem. The Tarangire ecosystem supports globally important populations of lions, cheetahs, leopards, hyenas and African wild dogs, even though the National Park itself, encompassing 2,600km^2, is relatively small (TAWIRI, 2009). Because large carnivores range widely, securing their survival beyond, as well as within protected area boundaries is needed to maintain populations that are demographically and genetically viable (Msuha *et al.,* 2012; Woodroffe and Ginsberg, 1998). Thus, understanding the impacts of anthropogenic pressures, including changes in land use outside protected areas on large carnivores, both inside and outside protected areas, is key to securing their long-term viability (Carbone and Gittleman, 2002).

Our specific objectives were to 1) estimate the probability of occurrence (ψ) and detection (p) of focal large carnivore species across the study area; 2) evaluate environmental correlates of the distribution of the focal large carnivores; 3) evaluate how distributions of focal large carnivores are modified by key anthropogenic variables.

5.2 Materials and Methods

5.2.1 Study Area

This study was conducted in the Simanjiro Plains and Tarangire National Park (TNP) across the Tarangire-Simanjiro ecosystem (TSE) of northern Tanzania and lies between 3°52´ to 4°24´ S and 36°05´ to 36°39´ E (Figure 13). This region is characterized by bimodal rainfall averaging 650 mm per annum, with short rains from (November-December) and the long rains from (March-May). The TSE is a mosaic of habitats comprised primarily of grassland (*Digitaria macroblephara* and *Panicum coloratum)*, woodland (*Acacia tortillis* and *Commiphora schimperi)*, bushland (*Acacia stuhlmannii* and *A. drepanolobium)* and seasonally water-logged bushed grassland (*Pennisetum mezianum* and *Acacia stuhlmannii)* (Kahurananga, 1979).

We used the Land-use/Land-cover (LULC) maps of Tarangire-Manyara ecosystem for 2015. These were extracted from Landsat imageries i.e., Landsat-8 OLI (Operational Land Imager), captured during the dry season, 2015; with 30 m × 30 m spatial resolution. We used the supervised object-oriented image classification technique to reclassify LULC types into eight broad classes: woodland, wetland, grassland, bushland, forest, agricultural land, bareland and other lands (Figure 13).

We divided the study area into three sample blocks based on an assessment of primary type of land use i.e. TNP/protected area (337 km^2), communal grazing land (414 km^2) and village land (468 km^2) (Figure 13). Transects were conducted in defined sampling units (grid cells) delineated in each respective survey blocks. The Tarangire National Park is the core protected area where no human settlement or hunting is allowed, and land uses are primarily restricted to wildlife-based tourism. The village land incorporates a wide variety of land uses including permanent human settlement, livestock grazing and cultivation. The communal grazing land is generally an open semiarid savanna with short grass plains and wooded grassland, encompassing the Simanjiro Game Controlled Areas which are administered by the Wildlife Division for licensed wildlife hunting and livestock grazing (Kahurananga and Silkiluwasha, 1997). The Simanjiro plains are the main dispersal areas for wildlife during the wet season (November - May) and grazing for pastoralists during the dry season (June – October). During the rainy season, most migratory wildlife species such as wildebeest (*Connochaetes taurinus*), zebra (*Equus burchellii*), hartebeest (*Alcelaphus buselaphus*) and fringe-eared oryx (*Oryx beisacallotis)* disperse away from TNP to areas in the east (Simanjiro plains), or north (Lakes Manyara and Natron) in search of better grazing and calving grounds. They eventually return to TNP during the dry season (Kahurananga and Silkiluwasha, 1997). The large carnivore community in the area includes lions*,* cheetahs, leopards, African wild dogs, spotted and striped hyenas (*Hyena hyena*). The IUCN Red List threat assessment lists African wild dogs as Endangered; lions, cheetahs and leopard as Vulnerable; striped hyenas as Near Threatened; and spotted hyenas as of Least Concern (IUCN 2016). The flood plains contain black cotton soils while the well-drained areas contain the dark red, sandy clay loam (Kahurananga and Silkiluwasha, 1997).

5.2.2 Sampling design and field methods

We used a grid-based sampling approach to define sampling units (grid cells) for the study species as 15 x 15-km for lion, 30 x 30-km for cheetah and 10 x 10-km for leopard and hyena based on their home range sizes (Figure 13). We selected 1-km segments within grid cells as spatial replicates (Hines *et al.*, 2010; Karanth *et al.,* 2011) to conduct detection, non-detection surveys. We considered that the grid cells should be larger than the home range size of focal species to minimize the risk of spatial autocorrelation between neighbouring grid cells, but conservative enough to assume that if carnivore species were detected within a grid cell, the entire unit could be assumed to be used or occupied (Karanth *et al*., 2011; MacKenzie *et al.*, 2006). The 15 x 15-km (225 km^2) unit size was chosen for lion based on an estimated annual home range of approximately 209 km^2 in the study area (Laizer *et al.,* 2014). Studies from other regions have estimated home range for cheetah to be 800 km^2 for non-territorial males and females in the Serengeti National Park (SNP) (Caro, 1994; Laver, 2005); for striped hyenas 44 km^2 for males and 72 km^2 for females in the SNP (Kruuk, 1976); for spotted hyenas 24.5km^2 (ranging from 9-40 km^2) in Ngorongoro crater (Höner *et al.*, 2005; Kruuk, 1976); and for male leopards 57.5 km^2 and for females 50 km^2 in the SNP (Schaller, 1972; Sunquist, 1983). Because our grid cells may have been smaller than the likely home range sizes of the focal large carnivore species, we used occupancy as a measure of their habitat use instead of "true occupancy" (Mackenzie *et al.*, 2002). We overlaid our grid cells on the land-cover matrix of the study area (Figure 13) using *ArcGIS v10.3* (ESRI, Redlands, California).

5.2.3 Spoor surveys

We established spoor transects along the pre-existing road network and heavily-used cattle trails. We assessed the suitability of roads and trails in terms of substrate quality, accessibility and traffic. We conducted spoor counts across two sampling occasions from August to November 2014 (dry season) and April to May 2015 (wet season) with the help of the experienced Hadza trackers. Hadzabe live in traditional hunter-gatherer communities and are well known for the reliability and high accuracy of their tracking skills, in particular, their ability to recognize individual animals from spoor, have been described in detail (Lichtenfeld, 2005). We systematically drove transects on a four-wheel-drive vehicle travelling at a slow speed of 10 to 15km/hour (Funston *et al.*, 2010) to maximize the likelihood of spoor detection and to minimize the likelihood of 'false absences' (MacKenzie *et al.*, 2006). The total mean length of transects sampled was 11.09 ± (SE 1.13) (n = 41, range 2 – 28km) providing a total distance of 433 km.

Two experienced observers sat on the bonnet/bumper and scanned for tracks directly ahead of the vehicle. When a fresh spoor (< 24 hours old) was encountered, the vehicle stopped and the spoor was assessed for species, group size, sex, age class, the GPS location, transect number, date, time, number of individuals and vegetation type. The spoor of new individuals were followed on foot to retrack the path they walked in order to reduce the likelihood of that individual being counted twice on a given transect. We drove each transect repeatedly in a random order in six replicates (i.e. 3 times wet season, 3 times dry season), with at least 48 hours between temporal replicates to minimize double counting. During the dry season, roads and trails outside protected area were prepared 12 hours before sampling by dragging thorn bushes behind the observation vehicle.

We postponed sampling on roads disturbed by rain in the previous 24 hours and ended if rain occurred at any stage during sampling. Spoor surveys were conducted in the early morning hours (generally between 05:30 and 11:00 hours) to take advantage of the low angle of the sun and prior to the disturbance of the track by livestock and people. Spoor were recorded as individual spoor, not as a family group, that is five spoor found together were counted as five individual spoor. We merged the detection histories for striped and spotted hyenas because it was extremely difficult to differentiate their tracks using our survey protocol.

5.2.4 Data Analysis

We used single-season, single-species occupancy models in the program PRESENCE v. 11.5 (Hines, 2006) to estimate the probability of occurrence and detection for each species. We analysed our data according to separate surveys, and thus, we assume that sites were closed to changes in occupancy during each survey. During our survey, we avoided any misidentifications. Although the Hadzabe are experienced and reliable trackers, spoor identification was also always checked by the lead author. Due to the wide-ranging behaviour of focal carnivore species, the assumption that detecting a species at one site is independent of detecting at all other sites (MacKenzie *et al*., 2002) may have been violated. Thus, data could not be used to estimate overall abundance, but focused on the Proportion of Area Used (PAU) by each species and the probability of occurrence. Occupancy models also assume that both detection and occupancy probabilities remain constant across survey sites (Mackenzie *et al.*, 2002). Spatial variation in abundance may induce heterogeneity in both parameters in our study area, hence we overcame this violation by including relevant covariates in the occupancy analysis (Royle and Nichols, 2003). We analysed each focal carnivore species separately, since differences in ecology and behavior were expected to affect habitat use and detection probability. Detection of an individual species was assigned a binary value of "1" for detection and "0" as non-detection on each 1-km segment (MacKenzie *et al.*, 2006).

5.2.5 Model covariates

The PAU by the focal carnivore species and the probability of detecting them (p) are functions of environmental and anthropogenic covariates. We extracted environmental and anthropogenic covariates likely to influence carnivore occurrence and detection probabilities from GIS layers using *ArcGIS v10.3* (ESRI, Redlands, California). We identified fourteen predictor variables (covariates) expected to influence large carnivore occurrence in the study area: *environmental variables* [i.e., elevation, slope, distance to permanent water, proportions of woodland, grassland, bushland, forest, wetland, agricultural land, bareland and other lands], *anthropogenic variables* [i.e., distance to nearest village, distance to park boundary and human population density as proxy for human influence] (Table 21). We calculated distance to villages and park boundary by taking the distance of the center of each grid cell to the nearest village/park boundary. We also expected that carnivore detectability (p) varies with season (dry, August – November, versus wet, April-May) and proportion of habitat available within each grid cell (woodland, grassland, bushland, forest, wetland, agricultural land, bareland and other lands), so we included both as covariates in detection models. We assumed that large carnivore occurrence would be influenced by environmental and anthropogenic variables affecting species presence, while detection of large carnivores would be influenced primarily by variables affecting spoor detectability on roads, primarily habitat (which may influence road use) and season (which affects spoor visibility). We expected the focal large carnivore species to equally use roads between the three sampling blocks and seasons.

We selected covariates for occupancy modelling based on *a priori* knowledge of habitat preferences of the focal carnivore species. We first ran all models without additional covariates to allow comparisons of occupancy and probability of detection across species, sites and seasons using the null model $\psi(.)$, $p(.)$, where occupancy and detection probability are held constant. Next, we followed a two-step process to model parameters of interest. First, we constructed models for each species to examine the effect of habitat and season covariates on detection probability p through univariate and multivariate analyses while holding ψ constant i.e. $\psi(.)p(\text{covariate})$ (Karanth *et al.*, 2011). Second, we modeled the effect of site covariates on occupancy probability ψ while holding p constant i.e. $\psi(\text{covariate})p(.)$ (Karanth *et al.*, 2011). We constructed models where both occupancy and probability of detection were allowed to vary with individual or additive combination of the covariates. We scaled and/or standardized all continuous covariates to *z*-scores prior to analysis to optimize model convergence (Cooch and White, 2005). We eliminated non-convergent models from the candidate models list and from further analysis. We treated categorical covariates as dummy variables with values of 0 or 1. We calculated a naïve estimate of occupancy (ψ) simply as the proportion of sites within an area where a species is detected i.e. $\psi = x / s$; where x = number of cells in which a species was detected, and s = the number of plausible cells within which a species might occur. We used a Spearman's correlation matrix in program SPSS *v.22.0* (SPSS Inc., Chicago, Illinois, USA) to test for multi-collinearity (i.e. pair-wise correlation) between continuous covariates using a cut-off of ($r \geq |0.80|$) (see Tables 27-29, Supporting information). If two covariates were highly correlated with one another (i.e., $r \geq 0.80$), we dropped one of the highly correlated covariates from the analysis.

5.2.6 Model selection and assessment of model fit

We selected the best-performing models based on the Akaike Information Criterion (AIC) corrected for small sample sizes (AICc) and model weights (ωi) (Burnham and Anderson, 2002; MacKenzie *et al.*, 2006). We considered models with highest AIC weights (ωi) and the lowest AIC values ($\Delta AICc < 2$) as having the best fit to the data and considered variables from these models important in predicting species occupancy and detectability (Burnham and

Anderson 2002). We assessed model fit using chi-square test based upon 1000 parametric bootstraps and found the estimated overdispersion parameter ($\hat{c}$) to be approximately 1 for all models (Tables 23-25), suggesting that the models adequately explain the variation in the observed data (Donovan and Hines, 2007). To avoid overparameterization, we included only single- and additive double-factor models in our candidate model set. We used model-averaging for competing models (i.e., models within 2 ΔAICc to estimate ψ, *p*, and covariate coefficients) (Burnham and Anderson, 2002). We calculated variable importance weights, which are the sum of the model weights of all models that contain a given variable. The effect of covariates on ψ and *p* was assessed using a logistic regression approach (using the logit link functions) and described using covariates' coefficient values. The sign of the untransformed *β*-coefficients for each covariate represented the direction of influence of the covariate (*i.e.* positive or negative).

5.3 Results

We detected a total of 932 spoor incidents, 56 for cheetahs (group size: 6), 136 for lions (group size: 8), 24 for leopards (group size: 2) and 716 for hyenas (group size: 10) over 41 transects representing 433 1-km replicates across 34 surveyed cells for hyena and leopard, 20 cells for lion and 10 cells for cheetah. We did not detect African wild dogs.

5.3.1 Detection probability

The probability of carnivore detection varied greatly between species and seasons (Table 22). For cheetah and leopard, the probability of detection was highest during the dry season, while hyena had the highest probability of detection in the wet season p = 0.73 (SE= 0.06). For lion, the probability of detection was not significantly different between wet and dry seasons. Hyena had the highest overall probability of detection p = 0.64 (SE = 0.04), while leopard had the lowest overall detection p = 0.10 (SE= 0.05).

5.3.2 Occurrence probability

Overall occurrence (ψ) estimates from models with no covariates varied significantly between species. Hyena showed highest overall occurrence (ψ = 0.85 (SE = 0.06), using 85% or approximately 3400 km^2 of potential habitat, followed closely by cheetah (ψ = 0.84 (SE = 0.14) and leopard (ψ = 0.70 (SE = 0.33, 38% increase from the naïve estimate), while lion had the lowest overall occurrence (ψ = 0.56 (SE = 0.11) (Table 22). Occurrences for lion, cheetah and hyena were higher during the dry season than in the wet season.

(i) Hyena

During the dry season, hyena had the highest probability of occurrence on village land, followed closely by the park and then communal grazing land in that order (t = 20.89, df = 2, p = 0.002), but the reverse was true in the wet season (t = 8.34, df = 2, p = 0.014, Figure 14). The probability of detection (p) for hyena was highest in the village land compared to other habitats during the wet season (t = 7.93, df = 2, p = 0.015) and in the communal grazing land during the dry season (t = 5.56, df = 2, p = 0.031, Figure 15). The best fit model for detection was the null model $\Psi(.),p(.)$, indicating that covariates had no effect on detection probability (Table 23). Hyena occurrence was strongly positively associated with human population density (β = 2.03, SE = 0.81; $\sum$w = 0.65), and strongly negatively associated with the proportion of bushland cover (β = -11.10, SE = 4.96; $\sum$w = 0.68) (Table 26). The averaged models for overall estimated occurrence and detection probabilities were $\hat{\hat{\Psi}}$ = 0.85 (SE = 0.06) and $\hat{\hat{p}}$ = 0.63 (SE = 0.04) respectively.

(ii) Cheetah

Cheetah had the highest probability of occurrence in the village and communal grazing lands during the dry season (t = 22.07, df = 2, p = 0.002), while in the wet season there was no significant difference in occurrence between different land use types (p > 0.05, Figure 14). The probability of detection (p) for cheetah was highest on village land during both seasons (Figure 15). Grassland (β = 17.75, SE = 11.18) was an important positive predictor of cheetah occurrence (Table 26). Cheetah detection was higher in the dry season than in the wet season (β = -1.17, SE = 0.48). The averaged models for overall estimated occurrence and detection probabilities were $\hat{\hat{\Psi}}$ = 0.82 (SE = 0.15) and $\hat{\hat{p}}$ = 0.38 (SE = 0.07) respectively (Table 23).

(iii) Lion

The probability of occurrence (ψ) estimate from the model with no covariates showed that lion had the highest occurrence estimates on village land, followed closely by the park during the dry season (Figure 14). We failed to detect lions on communal grazing land over the entire sampling period. After adjusting for imperfect detection, lion occurrence across the entire landscape was lower near water sources (β = 1.35, SE = 0.97) and greater closer to or within protected area (β = -3.16, SE = 1.66; Table 26). The model-averaged estimate of lion detectability was <1 ($\hat{p}$ = 0.49, SE = 0.06) and the overall estimate of occurrence was $\widehat{\Psi}$ = 0.55 (SE = 0.10) (Table 24). However, within the National Park, lion occurrence was negatively associated with (1) distance to permanent water and (2) distance to village (Table 24). In the village land, lion occurrence was positively associated with distance to permanent water (β = 6.93, SE = 18.40), and negatively associated with distance to park boundary (Table 24).

(iv) Leopard

Leopard had the highest occurrence on village and communal grazing lands than in the park during the dry season when all covariates were excluded (t = 7.82, df = 2, p = 0.016, Figure 14). There was no difference in the occurrence estimates between village land, communal grazing land and the park during the wet season (t = 2.00, df = 2, p = 0.183). Rather surprisingly, leopard occurrence was associated with a higher proportion of grassland (β = 3.40, SE = 3.50) (Table 26). The top-ranked detection model contained the parameters bushland and season, with higher detections in the dry season than in the wet season (β = -2.19, SE = 0.76) and more detections in bushland cover (β = 3.57, SE = 1.24) (Table 26). The model-averaged estimate of leopard detectability was <1 ($\hat{p}$ = 0.11, SE = 0.04) and the overall estimate of occurrence was $\widehat{\Psi}$ = 0.61 (SE = 0.21) (Table 25).

Human population density had the strongest anthropogenic influence on occurrences across species (∑w = 1.00), followed by distance to park boundary (∑w = 0.69) and distance to village (∑w = 0.13). On the other hand, grassland cover had the strongest environmental influence on occurrences across species (∑w = 1.03), followed by bushland cover (∑w = 0.95), distance to permanent water (∑w = 0.50), woodland cover (∑w = 0.33), agricultural land cover (∑w = 0.29), slope (∑w = 0.14) and bareland cover (∑w = 0.11).

5.4 Discussion

This study provides a detailed analysis of large carnivore occurrence from spoor count data across a multiple-use landscape in northern Tanzania. We were able to explore the distribution of a diverse carnivore guild across a broader landscape compared with previous studies (Lichtenfeld, 2005; Msuha, 2009). The overall results uphold our predictions that anthropogenic and environmental variables influence the probability of occurrence of large carnivores in the Tarangire landscape. However, the influence of these variables on habitat use and occurrence were species-specific, likely due to the differences in ecology and behavior of the focal large carnivores. Lion and hyena occurrences showed the strongest relationship with anthropogenic factors. As previous studies have shown (Table 21), the probability of lion occurrence declined with increasing distance from the park boundary, suggesting that lions may be more vulnerable to human impacts than other species. This finding corroborates the importance of full protection within the National Park for lions, and is consistent with a previous study showing that lion density is higher in the TNP as compared to areas outside its boundaries (Lichtenfeld, 2005). We also found that lions avoided agricultural landscapes, providing evidence that habitat conversion to agriculture could have serious implications for lion distribution due to their particular sensitivity to anthropogenic influences (Loveridge *et al.,* 2010b, Valeix *et al.,* 2012). In the National Park, where areas surrounding water bodies are protected, lions were strongly associated with permanent water. This is consistent with patterns observed by Hayward and Kerley, (2005, 2008), who found that close proximity to water increases the likelihood of use by lions, where encounter rates with water-dependent herbivores may be higher. In contrast, in the village land, lions strongly selected sites that were farther from permanent water, suggesting that lions were possibly avoiding encounters with people around water bodies, likely because water acts as a proxy for human activities (cf. Sunarto *et al.,* 2012). We did not detect any lions in the communal grazing land, suggesting that there may be strong avoidance of these areas, perhaps due to persecution in form of poisoning and preventative or retaliatory killing (Kissui, 2008).

Contrary to our predictions, higher hyena occurrence was associated with greater human population density across the study area, suggesting that they may be finding benefits from vicinity to humans, such as scavenging thrown away food or carcasses (Kolowski and Holekamp, 2007; Yirga *et al.,* 2015). Hyenas avoided bushland habitat and appeared to prefer open grassland habitats, where it might be easier to find scavenged food (Hayward, 2006). Of all carnivore species surveyed, hyena had the highest overall estimated occurrence and detection probability across habitat types and seasons, possibly due to their adaptability, wide ranging habits and resilient behaviour (Van Meter *et al.,* 2009). Overall results showed that occurrence and detection probability estimates for hyenas were statistically robust and were highest on village land and communal grazing land than inside the park.

Contrary to our expectations, leopard occurrence was unrelated to proportions of forest and woodland cover, but was positively related to the proportion of grassland cover. However, this result should be interpreted cautiously, as leopards usually avoid grassland habitat (Durant *et al*., 2010). We suspect this may be an artifact of wet season concentration of migratory prey in these areas. Alternatively, the small sample size of leopard in this study (n = 24) could have led to potentially spurious results due to overfitting of complex models (Stockwell and Peterson, 2002). On the other hand, leopards are unlikely to be found in open areas in the dry season which may have induced a substantial amount of bias in our results. In addition, we found that the leopard used village and communal grazing lands considerably more often and the park considerably less during both dry and wet seasons. Previous studies have shown that leopards exhibit remarkable behavioral plasticity in terms of habitat selection and they can do better in human-dominated landscapes (Nowell and Jackson, 1996).

Consistent with our predictions, cheetah occurrence was positively associated with grassland in the study area. This result concurs with previous studies showing that cheetahs prefer open grasslands (Caro, 1994; Durant *et al.,* 1988), although they can also inhabit a wide range of bush, scrub and woodland habitats (Myers, 1975; Nowell and Jackson, 1996; Purchase and du Toit, 2000). Therefore, our results should be interpreted with caution, as like leopard, this association may be an artifact of wet season concentration of migratory prey in these areas or may be a spurious result due to the low number of cheetah detections in this study (n = 56).

5.5 Conclusion and management implications

This study demonstrates the efficacy of spoor-based occupancy models in establishing the distribution of a guild of large carnivores across a multiple-use landscape. However, further survey effort would increase confidence in our results for cheetah and leopard. Our findings highlight the importance of protected areas, water availability, grassland habitat availability and the remaining natural habitats outside of formal protected area network for large carnivore conservation in the region. Hence, in order to achieve conservation targets for large carnivores, wildlife managers should consider maintaining habitat connectivity between existing protected areas and areas outside of formal protected area networks. In addition, further studies would be useful to understand the mechanisms of human-wildlife interactions in relation to anthropogenic land modification in order to achieve coexistence with large carnivores. From a conservation perspective, it is vitally important to conserve protected areas and create buffers for wildlife, such as wildlife corridors in communal and village lands.

Combining several different methods such as call-up surveys (for lions and hyenas), spoor surveys, camera trapping and radio tracking (for lions, hyenas, cheetah and leopards) would most likely result in an increase of their detection probabilities. Our study has demonstrated that a spoor-based occupancy survey is a valuable approach for assessing the distribution and habitat-use patterns of wide-ranging carnivore species across a wider landscape.

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Table 21. Description of environmental and anthropogenic covariates used for occupancy modeling and *a priori* predictions about their influence on the probabilities of occurrence and detection by focal carnivore species in the Tarangire-Simanjiro ecosystem, northern Tanzania. 2014-2015

Variables	Code	Variable description	Expected influence on occurrence probability	Expected influence on detection probability	Supporting citation(s)
Occupancy probability model					
Distance to park boundary (km)	Dist_PA	The NEAR tool was used to measure distance (km) between grid cell centres and Tarangire National Park boundary (km)[1]	**Negative effect on lion, leopard and hyena**, as the probability of occurrence is expected to decline with increasing distance from the park boundary, but the opposite situation will apply to cheetahs.	-	**Lion** (Hemson, 2003; Lichtenfeld, 2005; Valeix *et al.,* 2012); **Leopard** (Balme *et al.,* 2010); **Hyena** (Mills and Hofer, 1998); **Cheetah** (Marker *et al.,* 2003);
Elevation (m)	Elv	Mean elevation in meters above sea level in each grid cell. Transformed by dividing by maximum elevation and multiplying by 10. Range of values between 0 and 10. Digital elevation data were extracted at a 30 m x 30 m resolution[2].	Low to Mid elevations are favored by lions, leopard, cheetah and hyenas while higher elevations are avoided by all species	-	Cristescu *et al.,* 2013 Durant *et al.,* 2010 Abade *et al.,* 2014
Slope (°)	Slo	Mean slope in degrees in each grid cell. Slope was calculated from elevation using the Surface analysis option in Spatial Analyst toolbox[3].	Flat slopes are favored by all species, steep slopes are avoided by all species	-	
Distance to village (km)	Dist_Vill	The NEAR tool was used to measure distance (km) between grid cell centres and nearest village[4].	**Negative effect on lion, leopard and cheetah**, as their probabilities of occurrence are expected to decline with increasing levels of human influence (measured as distance to nearest village). **Positive effect on hyena,** as its occurrence probability is expected to increase with increasing levels of human influence (measured as distance to nearest village).	-	**Lion** (Valeix *et al.,* 2012); **Leopard** (Henschel *et al.,* 2011; Ngoprasert *et al.,* 2007); **Cheetah** (Andresen *et al*., 2014) **Hyena** (Hofer and East, 1993; Kolowski and Holekamp, 2011)

[1] **Source:** Derived from Tanzania Ministry of Natural Resources and Tourism Data

[2] **Source:** Extracted from Shuttle Radar Topography Mission ((USGS, 2000), http://www.landcover.org/data/srtm/

[3] **Source:** Derived from digital elevation model, http://www.landcover.org/data/srtm/

[4] **Source:** Derived from Tanzania National Bureau of Statistics, 2012

Table 21. continued

Distance to permanent water (km)	Dist_water	The NEAR tool was used to measure distance (km) between grid cell centres and nearest water source (permanent rivers and drainage lines)[5].	**Negative effect on all focal carnivore species**, as their probabilities of occurrence are expected to decline with increasing distance from permanent water.	-	**Lion** (Hayward and Kerley 2005; 2008; Loveridge *et al.,* 2009; Valeix *et al.*, 2010) **Cheetah** (Rostro-García *et al.,* 2015); **Leopard** (Balme *et al.,* 2013; Simcharoen *et al.,* 2008; Steyn and Funston, 2009); **Hyena** (Abade *et al.,* 2014)
Human population density	Hpd	Total number of people for every grid cell. Log transformation was used. Hpd was used as a measure of 'human influence'[6].	**Negative effect on all focal carnivore species**, as their probabilities of occurrence are expected to decline with increasing levels of human influence (measured as human population density)	-	**Lion** (Valeix *et al.,* 2012); **Leopard** (Henschel *et al.,* 2011); **Cheetah** (Andresen *et al.*, 2014) **Hyena** (Mills and Hofer, 1998)
Proportion of woodland	Wdl	The TABULATE AREA tool was used to calculate the proportion within each grid cell covered by woodland.	Woodland cover is expected to have a strong positive effect on leopard occurrence which provide cover for hunting and resting, but also favored by lions, cheetahs and hyenas	-	**Leopard** (Hunter *et al.,* 2013); **Lion** (Boitani, 1998; Druce *et al*., 2004; Nowell and Jackson, 1996); **Cheetah** (Durant, 1998; Mills *et al.*, 2004; Purchase and du Toit, 2000); **Hyena** (East and Hofer, 2013)
Proportion of grassland	Gr	The TABULATE AREA tool was used to calculate the proportion within each grid cell covered by grassland	Grassland cover is expected to have a strong positive effect on cheetah occurrence which promote ease for prey chase, as well as positive effect on lion and hyena occurrence, but negative effect on leopard occurrence	-	**Cheetah** (Caro, 1994; Durant *et al.,* 1988); **Lion** (Boitani, 1998; Druce *et al*., 2004; Nowell and Jackson, 1996). **Hyena** (East and Hofer, 2013); **Leopard** (Durant *et al*., 2010)
Proportion of bushland	Bushl	The TABULATE AREA tool was used to calculate the proportion within each grid cell covered by bushland	Bushland cover favors all focal carnivore species	-	**Cheetah** (Durant *et al.,* 2010); **Leopard** (Hayward *et al.,* 2006); **Hyena** (Kolowski and Holekamp, 2011); **Lions** (Mudumba *et al.,* 2015)
Proportion of forest	For	The TABULATE AREA tool was used to calculate the proportion within each grid cell covered by forest	Forest cover is expected to have a strong positive effect on leopard occurrence	-	Hunter *et al.,* 2013.

[5] **Source:** Derived from Tanzania National Bureau of Statistics, 2012

[6] **Source:** Derived from Tanzania National Bureau of Statistics, 2012

Table 21. continued

Proportion of wetland	Wl	The TABULATE AREA tool was used to calculate the proportion within each grid cell covered by wetland	-	-	
Proportion of bareland	Bl	The TABULATE AREA tool was used to calculate the proportion within each grid cell covered by bareland	-	-	
Proportion of agriculture	Agr	The TABULATE AREA tool was used to calculate the proportion within each grid cell covered by agriculture	**Negative effect on lions**, as increasing agriculture is expected to be associated with lower levels of lion occurrence due to their particular sensitivity to anthropogenic influences **Positive effect on hyenas and leopard** as they are more adapted to anthropogenic activities (e.g., agriculture), agricultural land also favor cheetah	-	**Lion** (Valeix *et al.,* 2012); **Hyena** (Boydston *et al.*, 2003); **Leopard** (Woodroffe, 2000; Marker and Dickman, 2004); **Cheetah** (Marker-Kraus *et al.,* 1996)
Proportion of other lands	Other	The TABULATE AREA tool was used to calculate the proportion within each grid cell covered by other lands	-	-	
Detection probability model					
Season	Season	The effect of season on detection probability was tested by assigning a score of "1" to dry season (August-November) and a score of "0" to wet season (April-May) sampling occasions	-	Negative effect on detectability since focal carnivore species are expected to be more detected (likely to use roads more often) in the wet season than dry season due to high vegetation growth	
Proportion of the habitat available per cell	Wdl, Gr, Bushl, For, Wl, Bl, Agr, Other	Proportion within each grid cell covered by woodland, grassland, bushland, forest, wetland, bareland, agriculture and other lands.	-	Positive effect on focal carnivore species detection as increase in land cover is expected to be correlated with higher probability of detecting the spoor	

Table 22. Occurrence probability (ψ), naïve estimates (ψ), probability of detection (p) as well as the overall occurrence (Ψ *overall*) and detection probabilities (p *overall*) of focal carnivore species combined for dry and wet seasons based on spoor data collected between August-November 2014 and April-May 2015 in the Tarangire-Simanjiro ecosystem, northern Tanzania.

Dry				Wet			Overall occurrence and detection probabilities		
Species	Naïve ψ	ψ(SE)	p(SE)	Naïve ψ	ψ(SE)	p(SE)	Naïve ψ	Ψ *overall* (SE)	p *overall* (SE)
Cheetah	0.80	0.96(0.20)	0.45(0.13)	0.40	0.52(0.25)	0.38(0.19)	0.80	0.84(0.14)	0.37(0.08)
Lion	0.70	0.80(0.13)	0.50(0.09)	0.35	0.40(0.13)	0.50(0.14)	0.55	0.56(0.11)	0.46(0.06)
Leopard	0.29	0.66(0.37)	0.18(0.11)	0.06	1.00(0.00)	0.02(0.01)	0.32	0.70(0.33)	0.10(0.05)
Hyena	0.85	0.91(0.07)	0.60(0.06)	0.74	0.75(0.08)	0.73(0.06)	0.85	0.85(0.06)	0.64(0.04)

Table 23. Model selection statistics derived from occurrence (Ψ) and detection probabilities (*p*) of hyena and cheetah in the Tarangire-Simanjiro ecosystem, northern Tanzania based on spoor data collected between August-November 2014 and April-May 2015. Models are ranked according to AICc. No. of sites: hyena = 34, cheetah = 10.

Model	AICc	ΔAICc	ωi	Model Likeli-hood	K	-2LL	$\hat{\Psi}$ (SE)	$\hat{p}$ *(SE)*	ĉ
Hyena									
Detection models (*p*) ~									
Ψ(.),p(.)	258.92	0.00	0.5853	1.0000	2	254.92	0.85(0.06)	0.64(0.04)	1.09
Ψ(.),p(Bl)	260.77	1.85	0.2321	0.3965	2	256.77	0.86(0.06))	0.60(0.03)	1.10
Occupancy models (*Ψ*) ~									
Ψ (Hpd+Bushl),p(.)	251.85	0.00	0.5480	1.0000	3	245.85	0.85(0.07)	0.64(0.04)	1.10
Ψ(.),p(.)	258.92	7.07	0.0160	0.0292	2	254.92	0.85(0.06)	0.64(0.04))	0.99
Averaged model							***0.85(0.06)***	***0.63(0.04)***	
Cheetah									
Detection models (*p*) ~									
Ψ(.),p(Season)	73.38	0.00	0.8894	1.0000	2	69.38	0.85(0.13)	0.37(0.04)	1.20
Ψ(.),p(.)	77.55	4.17	0.1106	0.1243	2	73.55	0.85(0.14)	0.37(0.08)	0.93
Occupancy models (*Ψ*) ~									
Ψ(Gr),p(.)	77.34	0.00	0.1470	1.000	2	73.34	0.84(0.13)	0.37(0.08)	0.94
Ψ(Hpd),p(.)	77.52	0.18	0.1344	0.9139	2	73.52	0.85(0.14)	0.37(0.08)	0.94
Ψ(.),p(.)	77.55	0.21	0.1324	0.9003	2	73.55	0.85(0.14)	0.37(0.08)	0.94
Ψ(Wdl),p(.)	77.97	0.63	0.1073	0.7298	2	73.97	0.78(0.12)	0.38(0.07)	1.00
Ψ(Bushl),p(.)	78.10	0.76	0.1006	0.6839	2	74.10	0.82(0.14)	0.37(0.08)	0.97
Ψ(Dist_Vill+Hpd),p(.)	78.50	1.16	0.0823	0.5599	3	72.50	0.83(0.13)	0.38(0.07)	0.92
Ψ(Slo+Gr),p(.)	78.61	1.27	0.0779	0.5299	3	72.61	0.80(0.17)	0.38(0.07)	0.94
Ψ(Dist_water+Gr),p(.)	78.62	1.28	0.0775	0.5273	3	72.62	0.82(0.15)	0.38(0.07)	0.94
Ψ(Hpd+Agr),p(.)	78.70	1.36	0.0745	0.5066	3	72.70	0.83(0.17)	0.38(0.07)	0.91
Ψ(Gr+Agr),p(.)	78.94	1.60	0.0661	0.4493	3	72.94	0.82(0.17)	0.38(0.07)	0.93
Averaged model							***0.82(0.15)***	***0.38(0.07)***	

Notes: All models with ΔAICc <,2.0, plus the constant-only models, are reported. K is the number of estimated parameters; ΔAICc is the difference between the AICc of the model and the lowest-AICc model; ωi is the Akaike's model weight; ($\hat{\Psi}$) is the estimated overall occurrence probability; ($\hat{p}$) is the estimated overall detection probability; (SE) is the associated standard error for the estimate; –2LL is the negative value of twice the log likelihood and ĉ is the estimated overdispersion parameter. Covariate abbreviations: Dist_water = distance to permanent water; Dist_vill = distance to nearest village; Slo = slope; Hpd = Human population density; Gr = proportion of grassland; Bushl = proportion of bushland; Agr = proportion of agriculture; Bl = proportion of bareland; Wdl = proportion of woodland; season = wet versus dry seasons.

Table 24. Model selection statistics derived from occurrence (Ψ) and detection probabilities (*p)* of lion across the entire landscape, and occurrence probability (Ψ) within Tarangire National Park and village land based on spoor data collected between August-November 2014 and April-May 2015. Models are ranked according to AICc. No. of sites = 20.

Model	AICc	ΔAICc	ωi	Model Likeli-hood	K	-2LL	$\hat{\Psi}$ (SE)	$\hat{p}$ *(SE)*	$\hat{c}$
Landscape-scale models									
Detection models (*p*) ~									
Ψ(.),p(Bl+Season)	116.35	0.00	0.9503	1.0000	3	110.35	0.56(0.11)	0.60(0.06)	1.10
Ψ(.),p(.)	122.25	5.90	0.0497	0.0523	2	118.25	0.56(0.11)	0.46(0.06)	1.09
Occupancy models (*Ψ*) ~									
Ψ (Dist_water+Dist_PA),p(.)	113.30	0.00	0.4556	1.0000	3	107.30	0.54(0.11)	0.45(0.06)	1.20
Ψ(Dist_PA),p(.)	114.64	1.34	0.2331	0.5117	2	110.64	0.55(0.08)	0.46(0.06)	0.99
Ψ(.),p(.)	122.25	8.95	0.0052	0.0114	2	118.25	0.56(0.11)	0.46(0.06)	1.20
Averaged model							***0.55(0.10)***	***0.49(0.06)***	

Model	AICc	ΔAICc	ωi	Model Likeli-hood	K	$\hat{\Psi}$ (SE)	$\hat{p}$ *(SE)*	β (SE)
Occupancy models within Tarangire National Park								
Ψ (Dist_vill),p(.)	51.35	0.00	0.2065	1.0000	2	0.69(0.13)	0.53(0.09)	-2.85(2.14)
Ψ(Gr),p(.)	52.79	1.44	0.1005	0.4868	2	0.76(0.14)	0.53(0.09)	20.12(15.29)
Ψ(Bushl+Gr),p(.)	52.80	1.45	0.1000	0.4843	3	0.67(0.18)	0.53(0.09)	-49.15(38.63); 56.22(38.63)
Ψ(Dist_vill+Wdl),p(.)	52.91	1.56	0.0947	0.4584	3	0.70(0.14)	0.53(0.09)	-2.11(1.96); 7.93(18.02)
Ψ(Bl),p(.)	52.97	1.62	0.0919	0.4449	2	0.74(0.14)	0.53(0.09)	19.08(15.26)
Ψ(Dist_water+Dist_villl),p(.)	53.12	1.77	0.0852	0.4127	3	0.72(0.16)	0.53(0.09)	-0.84(1.42); -1.73(1.92)
Ψ(.),p(.)	53.72	2.37	0.0632	0.3057	2	0.72(0.17)	0.53(0.09)	0.96(0.86)
Averaged model						***0.71(0.15)***	***0.53(0.09)***	
Occupancy models within village land								
Ψ (Dist_water),p(.)	56.90	0.00	0.2358	1.0000	2	0.82(0.09)	0.41(0.08)	6.93 (18.40)
Ψ(Wdl),p(.)	57.59	0.69	0.1670	0.7082	2	0.80(0.07)	0.41(0.08)	187.22(237.96)
Ψ(Hpd),p(.)	58.08	1.18	0.1307	0.5543	2	0.90(0.14)	0.40(0.09)	0.54(0.39)
Ψ(.),p(.)	58.11	1.21	0.1288	0.5461	2	0.90(0.14)	0.40(0.09)	2.20(1.62)
Ψ(Gr),p(.)	58.14	1.24	0.1268	0.5379	2	0.89(0.14)	0.40(0.09)	53.41(40.21)
Ψ(Bushl),p(.)	58.36	1.46	0.1136	0.4819	2	0.89(0.15)	0.40(0.09)	33.70(26.67)
Ψ(Dist_water+Dist_PA),p(.)	58.67	1.77	0.0973	0.4127	3	0.87(0.14)	0.41(0.08)	4.32(8.06); -0.97(2.09)
Averaged model						***0.87(0.12)***	***0.40(0.09)***	

Notes: All models with ΔAICc <,2.0, plus the constant-only models, are reported. K is the number of estimated parameters; ΔAICc is the difference between the AICc of the model and the lowest-AICc model; ωi is the Akaike's model weight; ($\hat{\Psi}$) is the estimated overall occurrence probability; ($\hat{p}$) is the estimated overall detection probability; (SE) is the associated standard error for the estimate; –2LL is the negative value of twice the log likelihood; $\hat{c}$ is the estimated overdispersion parameter and β is the untransformed estimate of coefficient for covariates. Covariate abbreviations: Dist_water = distance to permanent water; Dist_vill = distance to nearest village; Dist_PA = distance to park boundary; Hpd = Human population density; Gr = proportion of grassland; Bushl = proportion of bushland; Bl = proportion of bareland; Wdl = proportion of woodland; season = wet versus dry seasons.

Table 25. Model selection statistics derived from occurrence (Ψ) and detection probabilities (*p)* of leopard in the Tarangire-Simanjiro ecosystem, northern Tanzania based on spoor data collected between August-November 2014 and April-May 2015. Models are ranked according to AICc. No. of sites = 34.

Model	AICc	ΔAICc	ωi	Model Likeli-hood	K	-2LL	$\hat{\Psi}$ (SE)	$\hat{p}$ *(SE)*	ĉ
Detection models (*p*) ~									
Ψ(.),p(Bushl+Season)	97.93	0.00	0.7386	1.0000	3	91.93	0.77(0.30)	0.17(0.06)	0.64
Ψ(.),p(.)	105.56	7.63	0.0163	0.0220	2	101.56	0.70(0.33)	0.09(0.05)	1.20
Occupancymodels (*Ψ*) ~									
Ψ (Gr),p(.)	104.03	0.00	0.1288	1.0000	2	100.03	0.72(0.18)	0.10(0.03)	1.10
Ψ(Bushl+Gr),p(.)	104.60	0.57	0.0969	0.7520	3	98.60	0.55(0.21)	0.12(0.05)	0.92
Ψ(Gr+Wdl),p(.)	105.06	1.03	0.0770	0.5975	3	99.06	0.70(0.33)	0.10(0.04)	1.01
Ψ(Hpd+Bushl),p(.)	105.12	1.09	0.0747	0.5798	3	99.12	0.56(0.21)	0.12(0.05)	0.95
Ψ(Bl),p(.)	105.21	1.18	0.0714	0.5543	2	101.21	0.63(0.16)	0.11(0.04)	1.03
Ψ(Hpd),p(.)	105.55	1.52	0.0602	0.4677	2	101.55	0.68(0.33)	0.10(0.05)	1.10
Ψ(.),p(.)	105.56	1.53	0.0599	0.4653	2	101.56	0.70(0.33)	0.10(0.05)	1.10
Ψ(Slo),p(.)	105.69	1.66	0.0562	0.4360	2	101.69	0.68(0.34)	0.10(0.05)	1.00
Ψ(Wdl),p(.)	105.70	1.67	0.0559	0.4339	2	101.70	0.47(0.03)	0.13(0.04)	0.95
Ψ(Dist_water),p(.)	105.73	1.70	0.0551	0.4274	2	101.73	0.50(0.10)	0.13(0.04)	0.76
Ψ(Dist_Vill),p(.)	105.98	1.95	0.0486	0.3772	2	101.98	0.51(0.12)	0.13(0.04)	0.93
Averaged model							***0.61(0.21)***	***0.11(0.04)***	

Notes: All models with ΔAICc <,2.0, plus the constant-only models are reported. K is the number of estimated parameters; ΔAICc is the difference between the AICc of the model and the lowest-AICc model; ωi is the Akaike's model weight; ($\hat{\Psi}$) is the estimated overall occurrence probability; ($\hat{p}$) is the estimated overall detection probability; (SE) is the associated standard error for the estimate; –2LL is the negative value of twice the log likelihood and ĉ is the estimated overdispersion parameter. Covariate abbreviations: Dist_water = distance to permanent water; Dist_vill = distance to nearest village; Hpd = Human population density; Slo = slope; Gr = proportion of grassland; Bushl = proportion of bushland; Bl = proportion of bareland; Wdl = proportion of woodland; season = wet versus dry seasons.

Table 26. Relative summed variable importance weights (∑w) for predictors of occurrence (*Ψ*) of focal carnivore species based on spoor data collected from 2014 – 2015 in the Tarangire-Simanjiro ecosystem. Untransformed β coefficients and associated standard errors (SE) are reported for the top occupancy models according to AICc. Note: +/- sign indicates direction of influence

Hyena			**Cheetah**			**Lion**			**Leopard**		
Covariate	**∑w**	**β (SE)**	**Covariate**	**∑w**	**β (SE)**	**Covariate**	**∑w**	**β (SE)**	**Covariate**	**∑w**	**β (SE)**
Bushland	0.68	-11.10(4.96)	Grassland	0.37	17.75(11.18)	Distance to park boundary	0.69	-3.16 (1.66)	Grassland	0.30	3.40 (3.50)
Human population density	0.65	2.03(0.81)	Human population density	0.22	0.43(0.27)	Distance to permanent water	0.45	1.35 (0.97)	Bushland	0.17	0.46 (1.28)
Grassland	0.36	7.74(2.30)	Agriculture	0.14	4.86(5.79)	Agriculture	0.15	-12.53(8.72)	Woodland	0.13	-131.46 (255.01).
Bareland	0.04	13.73(5.02)	Bushland	0.10	16.08(11.07)	Woodland	0.06	7.71(7.94)	Human population density	0.13	0.21(0.39)
Woodland	0.03	15.90(6.20)	Woodland	0.11	16.29(12.10)				Bareland	0.07	3.47(4.83)
			Distance to village	0.08	0.28(0.72)				Slope	0.06	0.28(0.60)
			Slope	0.08	0.53(0.45)				Distance to village	0.05	0.23(0.53)
									Distance to permanent water	0.05	-0.33(0.50)

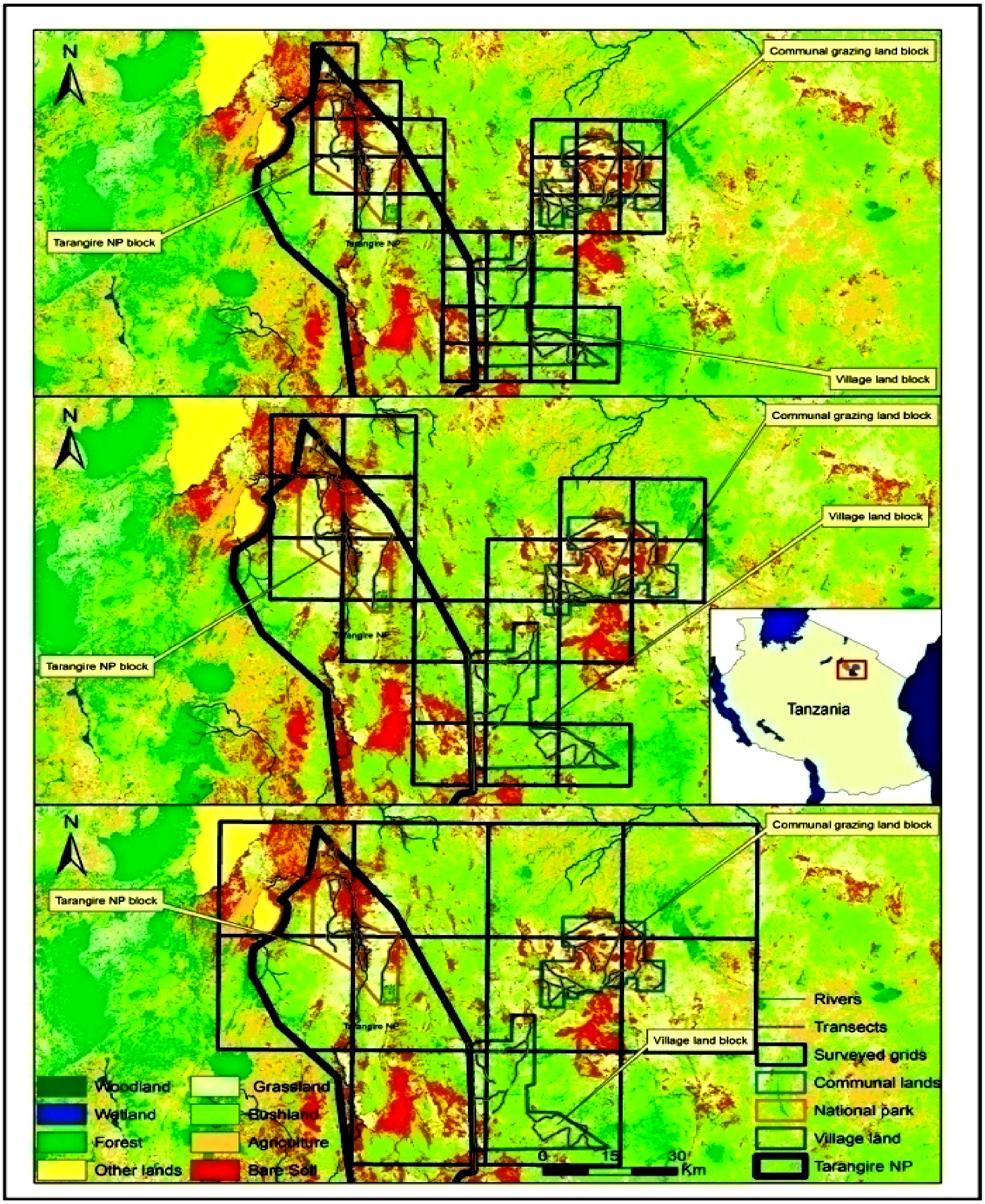

Figure 13. Study area in the Tarangire-Simanjiro ecosystem of northern Tanzania showing the survey design, transects and surveyed grids for (A) hyena and leopard, 10-km^2 (B) lion, 15-km^2 (C) cheetah, 30-km^2. Inset: map of Tanzania showing a location of the study area.

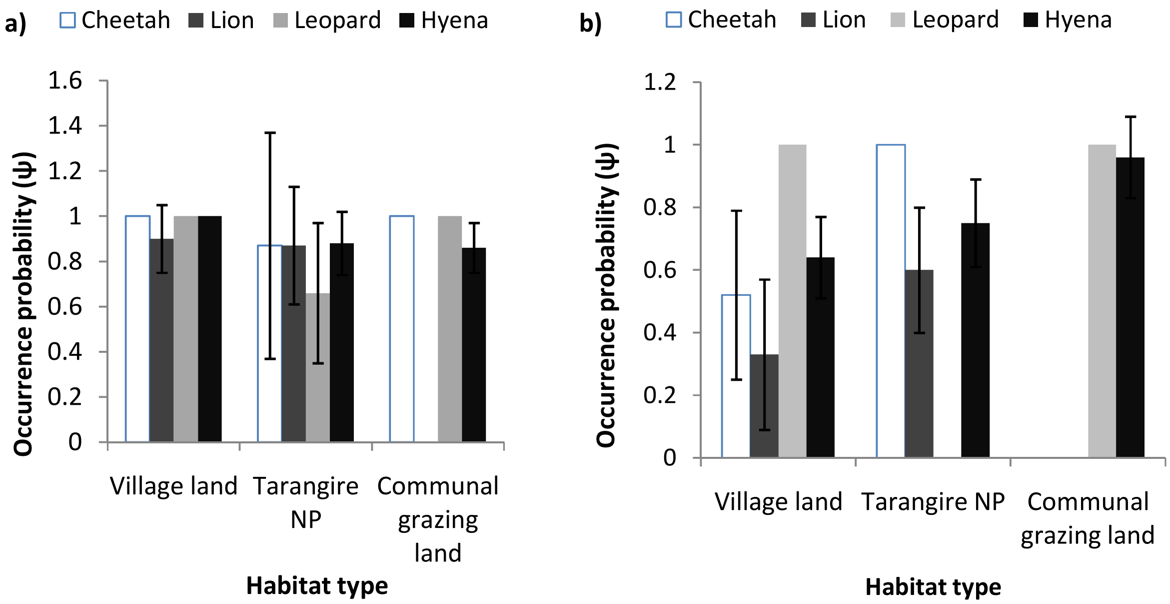

Figure 14. Occurrence probabilities (ψ) of focal carnivore species during (a) the dry and (b) wet seasons across habitat categories in the Tarangire-Simanjiro ecosystem, northern Tanzania, 2014-2015. Bars represent ± standard errors.

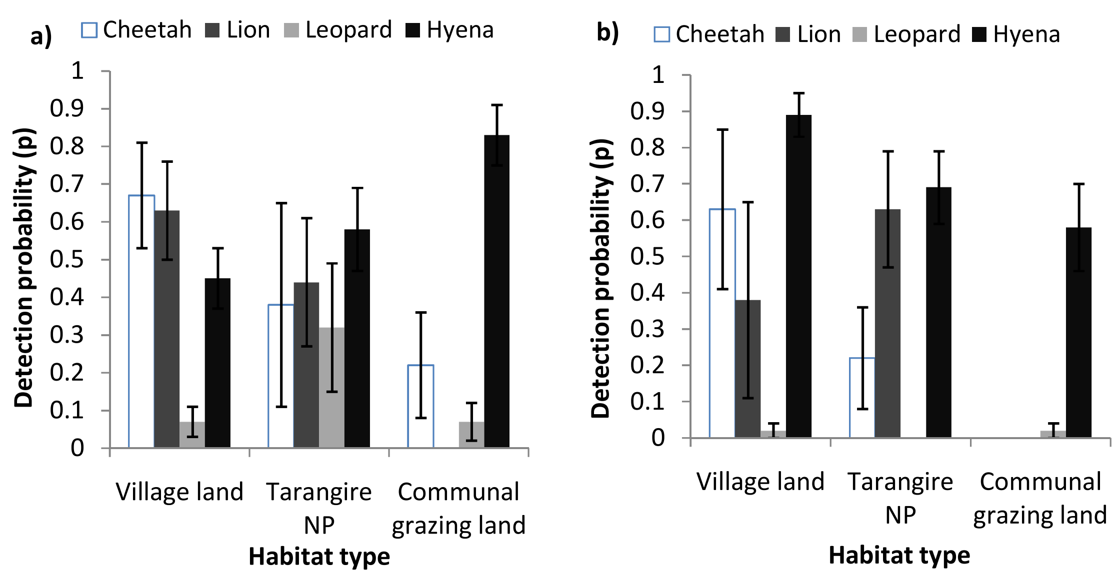

Figure 15. Detection probabilities of focal carnivore species (*p)* during (c) the dry and (d) wet seasons across habitat categories in the Tarangire-Simanjiro ecosystem, northern Tanzania, 2014-2015. Bars represent ± standard errors.

Supporting information

Table 27. Spearman's correlation coefficients matrix of site-specific covariates (r-values) for hyena and leopard at 10 × 10 km grid level. Dist_Vill: distance to nearest village; Dist_PA: Distance to park boundary; Dist_water: Distance to water; Hpd: Human population density; Slo: Slope; Elv: Elevation; Wld: proportion of woodland; Gr: proportion of grassland; Bushl: proportion of bushland; For: proportion of forest; Wl: proportion of wetland; Agr: proportion of agriculture; Bl: proportion of bareland; Other: proportion of other lands; + missing covariate; Bold type indicates statistically significant correlation ($p < 0.05$). 'Elevation' and 'distance to park boundary' were strongly positively correlated (r = 0.757), so "elevation' was removed from further analysis.

Variable	Dist_Vill	Dist_PA	Dist_water	Hpd	Slo	Elv	Wld	Gr	Bushl	For	Wl	Agr	Bl	Other
Dist_Vill	1													
Dist_PA	0.001	1												
Dist_water	0.196	**0.467**	1											
Hpd	-0.003	-0.278	0.303	1										
Slo	-0.259	**-0.380**	**-0.390**	0.103	1									
Elv	-0.186	**0.757**	**0.433**	-0.279	-0.088	1								
Wld	0.160	-0.227	-0.050	0.059	-0.325	-0.174	1							
Gr	0.009	-0.234	**-0.350**	0.086	0.170	-0.032	0.057	1						
Bushl	-0.038	0.044	**0.620**	0.139	-0.021	0.119	-0.072	**-0.651**	1					
For	0.193	**0.517**	**0.652**	0.064	-0.014	**0.505**	0.045	-0.286	**0.498**	1				
Wl	+	+	+	+	+	+	+	+	+	+	1			
Agr	-0.044	**0.718**	0.018	**-0.394**	**-0.362**	**0.451**	-0.099	-0.134	-0.263	0.077	+	1		
Bl	0.095	-0.197	**-0.457**	-0.230	-0.201	-0.267	0.125	0.140	**-0.650**	**-0.639**	+	0.048	1	
Other	-0.168	-0.289	-0.208	0.165	0.005	-0.293	0.275	-0.031	-0.069	-0.280	+	-0.013	0.207	1

Table 28. Spearman's correlation coefficients matrix of site-specific covariates (r-values) for cheetah at 30 × 30 km grid level. Dist_Vill: distance to nearest village; Dist_PA: Distance to park boundary; Dist_water: Distance to water; Hpd: Human population density; Slo: Slope; Elv: Elevation; Wld: proportion of woodland; Gr: proportion of grassland; Bushl: proportion of bushland; For: proportion of forest; Wl: proportion of wetland; Agr: proportion of agriculture; Bl: proportion of bareland; Other: proportion of other lands; Bold type indicates statistically significant correlation ($p < 0.05$). 'Other lands' and 'elevation' were strongly negatively correlated (r = -0.803), as it was for 'bare land' and 'forest' (r = -0.827), so 'other lands' and 'bareland' were removed from further analysis.

Variable	Dist_Vill	Dist_PA	Dist_water	Hpd	Slo	Elv	Wld	Gr	Bushl	For	Wl	Agr	Bl	Other
Dist_Vill	1													
Dist_PA	-0.309	1												
Dist_water	-0.214	0.422	1											
Hpd	0.522	-0.304	0.037	1										
Slo	-0.522	0.226	-0.276	-0.515	1									
Elv	-0.406	**0.666**	0.589	-0.588	0.297	1								
Wld	0.290	-0.356	-0.544	**0.685**	-0.297	**-0.745**	1							
Gr	-0.349	0.084	0.501	-0.036	0.146	0.401	-0.195	1						
Bushl	-0.058	-0.058	-0.007	-0.103	0.127	0.115	-0.067	-0.067	1					
For	-0.349	0.551	0.142	-0.267	0.547	0.255	-0.401	-0.122	0.055	1				
Wl	-0.111	-0.309	-0.214	0.174	-0.406	-0.522	0.406	-0.349	-0.522	-0.349	1			
Agr	-0.406	**0.666**	0.007	-0.358	0.576	0.358	-0.285	-0.116	-0.467	0.578	0.058	1		
Bl	0.406	-0.601	-0.022	0.382	**-0.745**	-0.370	0.370	0.097	-0.382	**-0.827**	0.522	-0.576	1	
Other	0.360	-0.161	-0.425	0.571	-0.295	**-0.803**	**0.709**	-0.349	-0.477	-0.016	0.541	0.069	0.232	1

Table 29. Spearman's correlation coefficients matrix of site-specific covariates (r-values) for lion at 15 × 15 km grid level. Dist_Vill: distance to nearest village; Dist_PA: Distance to park boundary; Dist_water: Distance to water; Hpd: Human population density; Slo: Slope; Elv: Elevation; Wld: proportion of woodland; Gr: proportion of grassland; Bushl: proportion of bushland; For: proportion of forest; Wl: proportion of wetland; Agr: proportion of agriculture; Bl: proportion of bareland; Other: proportion of other lands; + missing covariate; Bold type indicates statistically significant correlation ($p < 0.05$). No covariates had Spearman correlation values ≥ 0.80, so no covariates were removed from occupancy modelling analysis.

Variable	Dist_Vill	Dist_PA	Dist_water	Hpd	Slo	Elv	Wld	Gr	Bushl	For	Wl	Agr	Bl	Other
Dist_Vill	1													
Dist_PA	0.112	1												
Dist_water	0.285	**0.509**	1											
Hpd	-0.132	-0.322	0.049	1										
Slo	-0.301	0.134	-0.349	0.219	1									
Elv	0.115	**0.740**	**0.607**	-0.318	0.051	1								
Wld	0.156	-0.288	-0.350	0.067	-0.102	**-0.47**	1							
Gr	0.035	-0.289	-0.306	0.063	0.158	0.032	-0.163	1						
Bushl	-0.071	-0.091	0.302	0.158	0.118	-0.044	0.049	**-0.517**	1					
For	0.278	**0.607**	**0.593**	0.037	0.160	**0.620**	-0.051	-0.395	**0.468**	1				
Wl	+	+	+	+	+	+	+	+	+	+	1			
Agr	-0.176	**0.707**	-0.002	**-0.522**	-0.035	0.416	-0.140	-0.255	-0.266	0.162	+	1		
Bl	0.132	-0.254	-0.235	-0.211	-0.384	-0.259	0.219	0.130	**-0.685**	**-0.590**	+	-0.023	1	
Other	-0.114	-0.198	-0.237	0.152	-0.026	-0.287	**0.601**	-0.219	0.176	0.072	+	-0.070	0.105	1

CHAPTER SIX

Synthesis and General discussion

6.1 Introduction

The aim of this dissertation was to understand human-carnivore conflict over depredation on livestock in the Tarangire-Simanjiro ecosystem, and to assess the key drivers of any such conflict, by integrating ecological, socio-economic and livestock husbandry factors and to identify which strategy was most likely to be effective at reducing human and large-carnivore conflict. More specifically, this study investigated the reported patterns and extent of conflict with large carnivores, and to assess the key drivers of any such conflict, as well as the financial livestock losses to local communities due to the perceived large carnivore depredation on livestock in relationship to other causes (Chapter 2), livestock husbandry practices and their perceived effectiveness at reducing livestock depredation (Chapter 3), local attitudes and perceptions towards large carnivores (Chapter 4), and large carnivore distribution in relationship to environmental and anthropogenic factors (Chapter 5). The present study is intended to bridge the gap between conservation research and policy-making for enhanced well-being of wildlife (particularly large carnivores), environment and the local people in the study area. The results and recommendations of this study may be critical to policy makers for making informed management decisions or revising the existing conservation policies and programmes to mitigate human-carnivore conflicts, reducing anthropogenic pressure on wildlife (particularly large carnivores) and their associated habitats, and improving local livelihoods in the studied region. The Tarangire-Simanjiro ecosystem was chosen as an ideal setting for this research because it represents an interface between human, livestock and wildlife (particularly large carnivores). In this chapter, the key findings of this research including their broad implications for conservation are summarized and discussed. Management recommendations and directions for future research are given, and general conclusions are drawn.

6.2 Socio-economic correlates of livestock depredation by large carnivores

In Chapter 2, the extent and reported patterns of livestock depredation, factors influencing livestock depredation, as well as the financial loss to local communities due to the perceived large carnivore depredation on livestock in relationship to other causes were examined.

Results indicated that three-quarters (75%) of the interviewed people reported carnivore attacks in their households, which is equivalent to an average loss of 1.4% of the total herd per annum and 8.5 livestock per household worthing US$ 633. This figure is within the range of the 0.02-2.6% worldwide losses to large carnivores reported by Graham *et al*., (2004) and is less compared to 2.4% reported by Patterson *et al*., (2004) around Tsavo National Park in Kenya and is far more than 0.26% of the total herd reported in Ruaha National Park (Dickman, 2008). Livestock depredation imposes substantial economic and cultural costs to local households. Total estimated financial loss due to large carnivores over the 19-months of the study was US$141,847, of which spotted hyenas accounted for 70.3% of the total herd and 57.7% of the financial loss. Furthermore, this study indicated that livestock depredation, particularly by lions, cheetahs, wild dogs, leopards and spotted hyenas peaked during the wet season in response to seasonal migration of wild prey from national parks into communal village lands (Kahurananga and Silkiluwasha 1977). Similar findings have been reported for hyenas and lions in the Maasai Steppe of northern Tanzania (Kissui, 2008; Mponzi *et al*., 2014) and for lions in Tsavo National Park in Kenya (Patterson *et al*., 2004).

Chapter 2 also showed that disease was responsible for higher livestock losses than any other cause within and among villages over a one month preceding the survey. This was closely followed by depredation, theft and other causes (snake bites, accidents and buffalo assaults). Disease accounted for 90.8% of all stock losses initially reported per household during the one month preceding the interview survey, which is equivalent to an average loss of US$ 147,235 (US$ 491 per household) in the study villages. The cost per household/month due to depredation and theft was US$27 and US$6 respectively. This concurs with other studies conducted in Tanzania, in which disease was found to be the leading cause of livestock loss (Dickman, 2008; Holmern *et al.*, 2007; Kissui, 2008; Nyahongo and Røskaft, 2012).

Overall results in Chapter 2 also showed that reported levels of livestock depredation were explained by a combination of several factors. Number of livestock owned, respondent's residency time, distance from the park boundary, level of education, number of herders and fortified boma for cattle were the most important factors influencing the reported levels of livestock depredation. Overall, reported depredation frequency by all large carnivore species increased significantly with increasing number of livestock owned, respondent's residency time, distance from the park boundary and declined significantly with increasing level of education, number of herders and improved fortified boma for cattle. These findings are consistent with other studies that have also identified education level (Holmern *et al*., 2007), number of herders (Ogada *et al*., 2003) and distance from the protected area (Holmern *et al.,* 2007; Patterson *et al.,* 2004) as determinants of reported livestock depredation by large carnivores. In addition, livestock depredation by lions and spotted hyenas declined significantly with improved boma for cattle. However, contrary to other studies, my results indicated that households that are closer to the park experienced less depredation of livestock than those located further away. This unexpected result may be explained by improved fortified bomas in households closest to the park (i.e. around 42% of the traditional bomas in Loibor Siret were fortified); while in more distant households such as Sukuro lacked fortified bomas. However, this trend varied by species. For example, reported lion and leopard attacks declined with increasing distance from the protected area, although the reverse was true for spotted hyenas. These findings support other studies (Hofer and East, 1993; Holmern *et al*., 2007) suggesting that lions are more likely to attack livestock in households that are closer to the protected areas, due to the fact that lions usually stay close to their natural habitat whereas spotted hyenas often move far from the park. This study revealed important findings about the potential utility of integrating ecological, socio-economic and livestock husbandry data for use in predicting the occurrence of large carnivore depredation.

Finally, results in Chapter 2 showed that most attacks on livestock were reported to occur at night at bomas than during the day in the grazing areas. However, this again varied by species depending on their behaviour. Spotted hyenas and leopards are mostly nocturnal, with most of the attacks occurring at night (at bomas) while cheetahs and wild dogs are diurnal in nature, and thus attack livestock only during the day (in the grazing areas). This concurs with other studies (Kissui, 2008; Maddox, 2003). However, lions were reported to attack grazing livestock during the daytime and livestock enclosed in bomas at night in the same proportion. This is contrary to Ogada *et al*. (2003) and Hemson (2003) who found the majority of lion depredation occurring at night in the bomas. Furthermore, Bauer (2003) found that attacks by lions near Waza National Park in Cameroon, occurred mainly during the day because at night herds are kept in enclosures inside villages. Carnivore species were found to prey selectively upon different livestock species corresponding to the size of the predator and in accordance with the size of their prey, prey preference and abundance. Cheetah, spotted hyena, leopard and African wild dog preyed mostly on small stock (goats, sheep) and calves reflecting their preference for small prey, while lions depredated mostly on cattle and donkey reflecting their preference for large prey. However, small stock were the most preferred prey by cheetah, spotted hyena, leopard and wild dog, probably related to their relative abundance in comparison to other livestock. These results are consistent with previous findings that livestock species selection corresponds to the size of the predator (Patterson *et al*., 2004) and in accordance with the size of their prey (Hayward, 2006). In addition, it is assumed that retaliatory killing and also the culturally motivated killing of lions by humans in response to damages caused by lions is negatively affecting lion populations in this ecosystem (Kissui, 2008; Lichtenfeld L. pers. comm. 2014). Based on this evidence, it is also likely that retaliatory killing is taking place for other species.

6.3 Livestock husbandry practices and conflict mitigation

Chapter 3 showed that three main livestock husbandry strategies were used by pastoralist communities to reduce livestock depredation by large carnivores: kraaling stock in bomas at night, herders for daytime grazing, and guard dogs. More than 97% of the respondents perceived fortified bomas to be very effective to reduce nighttime depredations, while adult herders were perceived to be effective (71%) to reduce daytime depredations. However, most of the respondents did not use fortified bomas citing cost as being a prohibitive factor. Fortified bomas can be costly to implement, in terms of both time and money, which means that carnivores are still imposing significant costs on local pastoralists. Furthermore, Chapter 3 indicated that about two-thirds (67%) of respondents perceived domestic dogs to be effective at night, perhaps by alerting people of predators approaching enclosures. However, an equal number of people found dogs to be effective during herding as those who found them to be not effective. Previous studies by Holmern *et al.* (2007) and Kissui (2008) found that domestic dogs were victims of depredation by leopards and hyenas, which could possibly account for the perception of their lower effectiveness during grazing. This is contrary to Ogada *et al*. (2003), Woodroffe *et al.* (2007) and Hemson (2003) who revealed that the presence of dogs can reduce depredation risk at bomas and in the grazing areas. Nevertheless, most of the dogs in the surveyed households are likely domestic dogs, and are not trained as guards, as highlighted in other studies (Ogada *et al.,* 2003). Overall, depredation from traditional bomas was more frequently reported than from fortified bomas. The present study also indicated that a lack of formal education was associated with support for retaliatory or preventative predator killing.

6.4 Local attitudes and perceptions towards large carnivores

Chapter 4 showed that the majority of respondents (79%) held negative attitudes towards large carnivores, with perceived threats to livestock cited as the main source of antagonism towards large carnivores. This study revealed no significant relationship between attitudes and reported livestock depredation, suggesting that conflict is driven by numerous factors, rather than livestock depredation alone. These results are inconsistent with other studies (Bagchi and Mishra, 2006; Dickman, 2008; Maddox, 2003; Ogada *et al.*, 2003; Røskaft *et al.*, 2007) which demonstrate that negative attitudes towards large carnivores are influenced by carnivore-induced livestock losses. The tolerance levels towards wildlife were generally low, with more than half of the respondents disagreeing with the statement 'I enjoy seeing wild animals on my land'. Spotted hyenas were cited as the single most problematic species, followed by leopards, African wild dogs and lions in that order. Cheetahs were considered to pose the smallest problem. Very few people (20%) expressed positive attitudes towards large carnivores linked to direct and potential benefits of ecotourism.

Results from Chapter 4 also indicated that attitudes towards large carnivores were influenced by education level (for all carnivore species), residency time of respondents (for lions and cheetahs) and knowledge of carnivores (cheetahs) rather than by landscape (distance from the park boundary) or economic factors (livestock owned or depredation losses). These variables have been identified as determinants of human attitudes towards large carnivores in many other areas (Røskaft *et al.*, 2007; Selebatso *et al*., 2008). It is most likely that the negative attitudes towards large carnivores are driven not only by livestock loss, but by a complexity of other factors not accounted for by this study; such as cultural beliefs and perhaps past experiences, people's attitudes towards the PAs, autonomy over land which creates limitations on grazing and resource access imposed by nearby PAs, and costs imposed by dangerous animals straying out of the park and onto village land (Dickman, 2010). However, this deserves further investigation.

6.5 Large carnivore distribution in relationship to environmental and anthropogenic factors

Chapter 5 showed that hyenas had the highest overall estimated occurrence and detection probabilities in the study area. This finding is not surprising, as it could be due to their adaptability, wide ranging habits and resilient behaviour (Hofer and East, 1993).

Furthermore, Chapter 5 showed that lion occurrence was negatively associated with distance to park boundary i.e., decreasing in occurrence as distance to park boundary increased. This finding corroborates the importance of full protection within the National Park for lions, and is consistent with a previous study showing that lion density is higher in the TNP as compared to areas outside its boundaries (Lichtenfeld, 2005). It is most likely that favorable ecological conditions inside the park e.g., increased prey availability and diversity of habitat types might have influenced habitat used by lions, as the survival of any predator is related to appropriate habitat conditions and prey availability (Ramesh, 2010; Sunquist and Sunquist, 2002). There was also substantial evidence that lions were strongly associated with permanent water in the National Park, consistent with patterns observed by Hayward and Kerley, (2005, 2008), who found that close proximity to water increases the likelihood of use by lions, where encounter rates with water-dependent herbivores may be higher. However, in the village land, lions strongly selected sites that were farther from permanent water, suggesting that lions were possibly avoiding encounters with people around water bodies (cf. Surnato *et al.,* 2012). No lion spoor were detected in the communal grazing land over the entire sampling period. This suggests that lions may be suffering from persecution in form of poisoning and preventative or retaliatory killing (Kissui, 2008) or habitat loss (Msoffe *et al*., 2011). Moreover, leopard and cheetah were poorly sampled in the communal grazing land. These results have important implications for lion, leopard and cheetah conservation in the Tarangire ecosystem given the increasing trend in rangeland conversion for agriculture. As expected, lions avoided agricultural landscapes, providing evidence that habitat conversion to agriculture could have serious implications for lion distribution.

Chapter 5 also showed that hyena occurrence associated positively with human population density across the study area, suggesting that they may be finding benefits from the vicinity to humans, such as scavenging thrown away food or carcasses (Kolowski and Holekamp, 2007; Yirga *et al.,* 2015). However, this study indicated an avoidance of bushland by hyenas, and preference for open grassland habitats, where it might be easier to find scavenged food (Hayward, 2006). Chapter 5 also showed that leopard occurrence was positively associated with the proportion of grassland cover, contrary to earlier prediction. The sample size for leopard was considerably low (n = 24), which could have led to potentially spurious results. Chapter 5 also showed that cheetah occurrence was positively associated with grassland in the study area. This result is in agreement with previous studies indicating that cheetahs prefer open grasslands, which promote ease for prey chase (Caro, 1994; Durant *et al.,* 1988). However, these results should be interpreted with caution, as the association of cheetah or leopard occurrence and grassland might be an artifact of wet season concentration of migratory prey in these areas. Overall results suggest the need for caution when interpreting results from occurrence estimates for species with low sample sizes and low detection rates.

Given the high survey effort, the lack of detections for wild dog during the sampling period might more appropriately reflect its true rarity in the study area.

6.6 Management recommendations

Mitigation of carnivore conflict includes interventions that minimize the amount of livestock lost and those that increase tolerance for those losses (Macdonald and Sillero-Zubiri, 2004). Due to the complexities of human-carnivore conflict, there is no panacea for the management of this conflict. The only solution is to find mechanisms to best manage human and large carnivore coexistence, by minimizing livestock depredation. Studies are also needed to examine how best to generate benefits from wildlife for local communities. When communities can benefit from large carnivores economically, socially and culturally, it will be easier to foster sustainable coexistence.

A variety of livestock management techniques should be combined in order to minimize the risk of large carnivores becoming used to any single method. Because it is difficult to modify the behavior of large carnivores, efforts should be focused on modification of human behaviors. Based on the results of this study, the following recommendations (if implemented) may contribute to reducing the current levels of livestock depredation by large carnivores across the study area. Firstly, improving formal and conservation awareness education at all levels of education (i.e. during primary, secondary and tertiary school education). Secondly, improving livestock husbandry by (i) use of fortified bomas and strengthening the security around bomas at night (ii) improving supervision of grazing livestock such as increasing the number of herders (particularly adults) and finding out high and low-risk areas where livestock is more or less susceptible while grazing, and eventually educating herders to avoid grazing their livestock in high-risk areas (predator hotspots) or always be vigilant while grazing in such areas. Community involvement in conservation activities and incentive programmes for conservation, like sharing of wildlife-related benefits with local communities should be put in place to offset costs of livestock losses and increase tolerance of carnivores from livestock keepers. As disease was perceived to be a greater cause of livestock loss than livestock depredation in the surveyed villages, there is a need for control and management of livestock diseases through preventive vaccinations and increased access to veterinary services. Nevertheless, multi-scale studies are needed to understand the epidemiology of livestock diseases and how to control or prevent the transmission of these diseases between livestock and wildlife or among livestock in the studied region.

Generally, this study suggests that interventions aimed at fostering positive attitudes towards large carnivores should focus on improving formal education and securing long-term residency for people in the region. Environmental education programs should focus more on people immigrating into the region, as they are likely to have the most negative attitudes towards large carnivores and women - who are less positive, less educated and least knowledgeable about wildlife. In addition, as leopards are often mistakenly for cheetahs and vice versa, resulting in unintended persecution, educational programs aimed at improving knowledge about leopard and cheetah should also be prioritized. In order to engender more positive attitudes towards large carnivores, there is a need for institutions like TANAPA to involve local communities in conservation initiatives and to have clear strategies in place to address human-carnivore conflict. Environmental education programs should be added to primary and secondary school curricula and develop a greater awareness of conservation value of carnivores among the youth. The school children are more likely to embrace this knowledge and eventually engender future support for large carnivore conservation in the region. Moreover, environmental education programs should also be initiated targeting local communities, focusing on the importance of PAs and benefits of wildlife, particularly large carnivores in the study area. These programmes might gradually bring about a local change in attitude towards large carnivore conservation in the region. Increased knowledge about predators could also help people correctly identify species causing livestock losses and decide upon the most effective techniques for preventing livestock depredation.

Due to the low literacy level of the respondents, this study suggests that improvement of education in rural communities with emphasis on wildlife conservation and awareness programmes may reduce the human-carnivore conflict and increase local people's tolerance of large carnivores (Sillero-Zubiri *et al.,* 2007). This may also help to minimize the ill effects of socio-economic and ecological constraints in the study area. One example of a successful conservation non-governmental organization is the Tanzania People and Wildlife Fund (TPW), which has been successful in increasing local community tolerance for wildlife through environmental education programmes, raising awareness of wildlife conservation, and implementing improved livestock management techniques. Conservation efforts should focus more on women and those with less education and knowledge. To improve people's attitudes, there may be a need to complement educational programs with financial incentives such as realized revenue from park's ecotourism and insurance plans. Financial incentive-based schemes can be used to ameliorate negative attitudes and facilitate human-carnivore coexistence, and this could help local people perceive tangible economic benefits from tolerating large carnivores (Dickman *et al.*, 2011). Direct performance payments to livestock owners where farmers are rewarded for the presence of carnivores on their land, or if they manage land in a way that is likely to conserve threatened populations could be worth implementing in the Tanzanian context. However, this incentive scheme has been found to be more feasible and beneficial at the community level than at an individual level (Nyhus *et al.*, 2005). Another alternative approach may be the initiation of a community-based livestock insurance programme, where farmers pay a premium for cover against a defined risk, such as predation of livestock (Mishra *et al*., 2003). Based on the results of this study, livestock keepers should use fortified bomas as a long-term solution to prevent nocturnal livestock loss and adult herders for livestock during the day.

Although spoor counts were most appropriate for estimating occurrence and detection probabilities for lions, cheetahs, leopards and hyenas, this method failed to detect the presence of rare and elusive carnivore species such as wild dogs. Therefore, additional monitoring methods may be needed to effectively detect the presence of wild dogs. Whenever possible, spoor count surveys should be augmented by other techniques such as call-up surveys (for lions and hyenas), camera trapping and radio tracking. It is important that future research efforts should maintain the use of these techniques in tandem as part of a comprehensive large carnivore community study. This study recommends that future monitoring of large carnivore populations should be implemented across the study area following the survey protocol of this baseline survey. Spoor-based occupancy surveys are most reliable, easy to implement and inexpensive methods for future large-scale, multiple species monitoring.

6.7 Further research

This study focused on understanding the perceived rather than actual levels of livestock depredation because verification of each depredation event would have required substantial additional time and resources. Furthermore, perceptions of conflict often matter more in terms of attitudes to large carnivores than actual rates of loss. In the case of large carnivores, the perceived levels of conflict may be at odds with the reality of actual levels of conflict (Dickman, 2008), due to the mistaken attribution of livestock deaths to wild predators. Therefore, further research should address the actual levels of livestock depredation and compare them with the perceived levels. This might help in understanding the ‘conflict hotspots’ or sites predisposed to livestock depredation across the village land, allowing herders and wildlife managers to concentrate livestock protection and conservation education programs in such areas. Additionally, future work should expand on the information presented in this study to disentangle the multiple factors influencing people's attitudes towards the main carnivore conflict species. Further research should also explore attitudes of local people towards the Tarangire National Park which was explicitly not covered in this study.

As long as this study focused on people's perceptions on the effectiveness of livestock husbandry practices, further research should examine the overlap between reality (actual depredation) and people's perceptions of the efficacy of various livestock husbandry practices. In addition, given the perceptions of the important role of domestic dogs at night, additional research is required to test whether providing training to dogs could increase their effectiveness in protecting livestock from predators during the day in the study area. In view of the fact that large carnivores are limited by prey populations (Hayward *et al.,* 2007; Carbone *et al.*, 2011), a future work focusing more specifically on carnivore species and their prey is therefore needed. A long-term telemetry study focusing on threatened carnivore species, potentially cheetahs, given its sensitivity to human impacts is recommended. This would provide information about habitat use, home range and movement patterns of this species and guide wildlife managers to develop a sound conservation and management plan in the region.

6.8 General conclusion

This dissertation focused on understanding the extent of and patterns of reported conflict with large carnivores over depredation on livestock, as well as factors influencing livestock depredation by large carnivores in the Tarangire-Simanjiro ecosystem, northern Tanzania. Overall, this study provides valuable insight into the intensity and complexity in patterns of livestock depredation and factors influencing these patterns, local attitudes and perceptions towards large carnivores and possible mitigation measures for reducing livestock depredation in this landscape. This study has integrated landscape, livestock husbandry and socio-economic factors to understand the factors influencing livestock depredation and local perceptions of large carnivores. This information can be used as a model for future studies regarding human-carnivore conflict and perceptions of large carnivores across different geographical locations. This study has shown that the reported frequencies of livestock depredation are influenced by several factors. Number of livestock owned, respondent's residency time, distance from the park boundary, level of education, number of herders and boma type for cattle were the key factors influencing livestock depredation. Attitudes towards large carnivores were influenced by education level (for all carnivore species), respondent's residency time (for lions and cheetahs) and knowledge of carnivores (cheetahs) rather than by landscape (distance from the park boundary) or economic factors (livestock lost to predators, number of livestock owned). Therefore, reducing depredation alone is less likely to produce a substantial change in people's attitudes towards large carnivores in the region, as attitudes could be influenced by the complexity of other factors than livestock depredation. This indicates that all the factors influencing people's attitudes towards large carnivores may never be fully understood, but the key determinants of attitudes towards large carnivores can be identified and addressed. This study has also contributed to filling the gap in knowledge on habitat use and distribution patterns of large carnivores in the studied region. This study has provided baseline information which could be useful in guiding future conservation efforts and monitoring of large carnivore populations in the region. An integrated approach combining formal education and securing long-term residency for people in the region may help improve people's attitudes towards large carnivores and maintain human-carnivore coexistence in the region. Furthermore, improving formal education, fortifying boma enclosures and improving herding practices such as increasing the number of herders per herd could be used as potential measures to mitigate current and future human-carnivore conflict.

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SUPPLEMENTARY MATERIAL

APPENDIX I. Interview schedule (QUESTIONNAIRE) used in this survey

1.Date (day/month/year)	2. Survey no.	3.Respondent Individual ID	4.Interviewer (s) name	5. Other people present at start of interview? (describe)
6. Household GPS:			7. Village and sub village:	
S: E:				

PART I: DEMOGRAPHIC AND SOCIO-ECONOMIC CHARACTERISTICS:

								16. Size of Household		
8. Name (Actual optional)	9. Age (years)	10. Age class	11. Gender (M/F)	12. Ethnic group	13. Religion	14. Education 1 = illiterate, 2 = Primary, 3 = Secondary, 4 = Tertiary	15. Length of time lived in this household	Men	Women	Children

17. Livestock owned	Cattle	Smallstock (sheep and Goats)	Donkeys	Dogs	Poultry	18. Occupation 1 = Farmer, 2 = pastoralist, 3 = agro Pastoralist, 4 = other	19. Do you grow any crops?		20. Is your harvest usually enough to feed your family?	
							Yes	No	Yes	No
Total #										

21. **During the last year, have you or anyone in your family at this household received any income from:**

	"Yes"	"No"	Notes
Selling/exchanging livestock?			
Selling crops/vegetables/grain?			
Trophy hunting?			
Photographic tourism?			
Off-farm activities (Business/salaried employment/casual labor)			
Other (specify)			

22. **How many cattle/small stock/donkeys/poultry have you gained over the past one month?**

	Born	Bought	Gifts	Other (specify)
Cattle				
Small stock (sheep and goats)				
Donkeys				
Poultry				

23. How many cattle/small stock/donkeys/poultry have you lost over the past one month?

	Sold	Died	Slaughtered	Given away	Stolen	killed by Predators (specify)	Other (specify)	Unit value (Tsh)
Cattle								
Small stock (sheep and goats)								
Donkeys								
Poultry								

PART II: ATTITUDES, KNOWLEDGE AND PERCEPTION:

24. Please tell me of all the wild animals that are found in this area/ around this household (within 1 day's walk) you can think of:

1.	2.	3.
4.	5.	6.
7.	8.	9.
10.	11.	12.

25. According to you, among the five species, which are the most problematic? And explain why?? Give a score 0 to 2 where : 0 = no problem, 1 = minor problem, 2 = major problem (*Show picture cards*)

	ID		Problem?					
	Right Y/N	Species Confused with	[2] big problem	[1] small problem	[0] No problem	Don't know animal	Does not occur here	Why?
Lion								
Cheetah								
Leopard								
Spotted hyena								
African wild dogs								

26. Which animal (*even if it has not been mentioned so far*) **causes the biggest problems in the area around your village or household (within 1 day's walk)? Why?**

……

27. Do you enjoy having wild animals living around your village?

Yes □ No □………Why?…………………………………………………

28. . Would you like somebody to come and control some of the wild animals?

Yes □ No □……………………………………………………………………………

29. Have you had any experience with the National Park or with people related to it? (Briefly describe encounter)

Yes □ No □……………………………………………………………………………

30. Check if the respondent could identify cheetah and leopard on pictures (*Show pictures of cheetah and leopard*)

Right ID: Cheetah vs Leopard… Yes □ No □……………………………………………
…………………………………………………

31. Please indicate your attitude towards the following animals?

	[1] Like them	[2] Dislike them	Don't know	Why?
Lion				
Cheetah				
Leopard				
Spotted hyena				
African wild dogs				

32. What do you think has happened to the numbers of the following animals in this area, in the time period since you came to this household?

	[1] Increased	[2] Decreased	[3] Disappeared completely	[4] Stayed the same	Don't know	Why?
Lion						
Cheetah						
Leopard						
Spotted hyena						
African wild dogs						

33. In your opinion, what would you like to see happening to the numbers of the following animals in this area, and why?

	Increase [1]	Decrease [2]	Disappear completely [3]	Stay the same [4]	Don't know	Why?
Lion						
Cheetah						
Leopard						
Spotted hyena						
African wild dogs						

PART III: FREQUENCY OF SIGHTINGS:

	Lion	Cheetah	Leopard	Spotted hyena	African wild dog
When did you last see…around this household?					
34. Season of sighting (dry/wet)?					
35. Where (location of sighting)?					
36. When (yr/month)?					
37. Time of day?					
38. How many(adults) observed?					
39. How many(cubs) observed?					
40. Age/sex of predator if known?					
41. What were they doing?					

PART IV: LIVESTOCK DEPREDATION AND HUMAN ATTACKS:

Has anyone ever had livestock attacked by …?	**Lion**	**Cheetah**	**Leopard**	**Spotted hyena**	**African wild dog**
42. ***Year/month of attack?***					
43. Season of attack (dry/wet)?					
44. Where/location of attack?					
45. Time of day of attack?					
46. Livestock type attacked?					
47. No. of livestock injured?					
48. No. of livestock killed in attack?					
49. Who was with the livestock?					
50. Was there a dog with the stock at the time of attack?					
51. Were any adults present at the time of attack?					
52. Did anyone see the attack?					
53. No. of predators involved?					
54. Age/sex of predators involved?					
55. What happened to the predator?					
Has anyone ever been attacked by…..?					
56. Age when attacked?					
57. Location of attack (place)?					
58. When (yr/month)?					
59. Season of attack?					
60. What was the person doing?					
61. Was the person Injured or /killed?					
62. What happened to the predator?					

63. According to you, what is the trend of livestock depredationsince you arrived in this area? a. Increasing □ b. Decreasing □ c. Stable □ d. I don't know □

PART V: ACTIONS: ANTI-PREDATION MEASURES:

Lethal:

	"Yes"	**If yes, poison ("P")? Traps ("T") ? how often?**	**"No"**	**If no, why not?**
64. Do people around this boma use poison ("P") or traps ("T") to control predators?				
		If yes, what kinds, how many, and when?		
65. Have you ever killed cheetah or any other predator before?				
66. Has anyone else in this boma ever killed a predator?				

	"Yes/ No "	Why/why not?	What kinds?	How often?
67. Do you ever hunt any other kinds of animals?				
68. Does anyone in this boma ever hunt other kinds of animals?				

Non-Lethal:

69. Which method do you use to reduce your livestock depredation? (a) Guard Dogs □ (b) Protective Enclosures □ (c) Human Guards/shepherds □ (d) Other □

PART VI: LIVESTOCK HUSBANDRY TECHNIQUES AND CONFLICT MITIGATION:

70. Who herds/look after your stock at this household (e.g., layon, moran, elders etc.)?

Cattle	Small stock (sheep and goats	Donkeys

71. How are livestock in this household kept/tended at night?

	In Boma made of planted trees for enclosure	In Boma enclosure made of bricks	In Boma made of poles and thorn bush	In Boma made of poles	In Boma made of thorn bush	In Boma made of poles and chain-link fence	Other (specify)
Cattle							
Small stock							
Donkeys							
Poultry							

72. Do you keep a guard dog with the stock when herding your

Cattle? Yes □/No□/NA□ Small stock (sheep and goats)? Yes□/No/□NA□ Donkeys? Yes□/No/□NA □

73. Do you think it is possible to avoid livestock depredation? Yes □….How? ………………… No□. Why?..

74. Which of the following methods do you think are appropriate in controlling predation of livestock by large carnivores?

	Day	Night	Effectiveness
(a) Guard Dogs			
(b) Traditional boma Enclosures			
(c) Fortified Bomas			
(d) Herders			
Moran			
Layon			
(e) Other (specify)			

Scale: [0]- Not effective, [1]- slightly effective, [2]- effective,[3]- very effective

75. Do you think financial compensation for livestock depredation could be me a good mitigation method?Yes □……
No □………………………Why?.......................................

76. Do you think carnivore killing could be a good method to reduce livestock depredation? Yes □..No □…..

THANK YOU FOR TAKING PART IN THIS INTERVIEW!

APPENDIX II. Photographs used to identify carnivore species

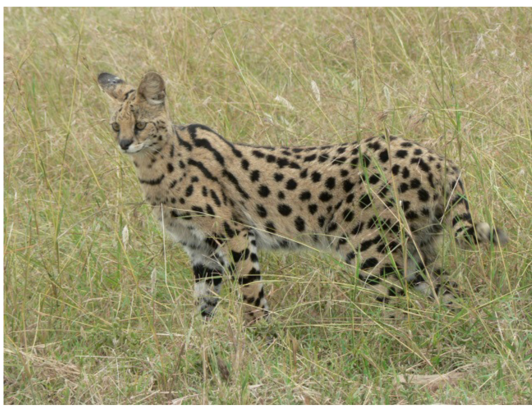
Cheetah African wild dog

Leopard Spotted hyena

Striped hyena Tiger

Black-backed jackal

Side-striped jackal



Serval

Lion