Conflict or Coexistence: Human-lion relationships in Kenya's southern Maasailand and beyond



A thesis submitted for the degree of
Doctor of Philosophy

Guy Paul Strum Western

Pembroke College, University of Oxford
Michaelmas Term, 2018

**This thesis is dedicated to all those who have lost their lives,
loved ones, and livestock in the name of coexistence and conservation.
Long may they be remembered.**

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Abstract

Large carnivore populations across the world continue to decline despite concerted efforts to protect them. The range-wide collapse of African lions *(Panthera leo)* epitomizes this decline. Lions are now confined to 8% of their former range, much outside of formally protected areas. Coexistence with, and tolerance of lions, by communities living within the remaining lion range is therefore essential to their conservation. I sought to investigate the socio-economic, political, cultural, and ecological factors which create and allow for human-lion coexistence. My results show that desire to see current lion populations maintained or increased was not ubiquitous or prevalent amongst communities living with lions. Instead, it was predominantly influenced by exposure to personal benefits (tangible and non-tangible) from conservation. These benefits did not always create a desire to see current lion populations maintained because this was heavily influenced by socio-political context and historical narratives of conservation present within a community. Lions living within pastoral rangelands in Kenya's South Rift Valley maintained home ranges comparable in size to those found in prey abundant protected areas and range size was unaffected by seasonal changes in settlement and livestock. Both were influenced by rainfall, pride biomass, cub age and prey dispersion. Pastoralists living in these same areas willingly grazed in areas of known lion presence to attain better pasture. Their use of traditional ecological knowledge and traditional livestock herding helped them to do so. When lion depredations did occur, guarding of livestock at pasture disrupted attacks resulting in reduced mortality. The collective findings of this thesis demonstrate that coexistence between lions and human can be both desirable and achievable.

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Chapter 1

Introduction

Saving Iconic Africa – Large Carnivores and Conservation

Wildlife populations in Africa have been declining slowly since early last century (Craigie et al., 2010). Land-fragmentation and habitat conversion have isolated many of the continents' large protected areas (PA), while others are too small to support wildlife year round and rely on dispersal areas outside the PAs to conserve large free ranging wildlife populations (Western et al., 2009; Ogutu et al., 2016). Wildlife declines have varied across the continent. In the last 30 years populations of large mammals have declined precipitously in West Africa, while those in East Africa have experienced only moderate declines, and Southern Africa's wildlife populations have increased (Caro & Scholte, 2007; Craigie et al., 2010).

The conservation of Africa's large free ranging carnivores such as the African lion (*Panthera leo*) and African wild dog (*Lycaon pictus*), in particular, poses novel challenges because they require large areas and a stable prey base. They also commonly come into conflict with humans (Treves & Karanth, 2003; Macdonald & Loveridge, 2010). Analogous to trends in large mammals, lion populations across Africa have rapidly declined in the last century. Estimates suggest that less than 35,000 lions remain in Africa today, two thirds (approx. 24,000) of which reside in 10 lion strongholds in Eastern and Southern Africa (Riggio et al., 2013; Bauer et al., 2015). Conservation of free ranging lions is now a global priority. Improving management of African protected areas that have large intact lion populations has been suggested as an effective conservation intervention (Packer et al., 2013; Lindsey et al., 2017). Others argue that focusing on conservation in protected areas may be necessary but cannot exist in isolation. They propose that conservation, including lion conservation, requires

engagement with people and communities beyond the boundaries of protected areas (Creel et al., 2013; Dolrenry et al., 2014).

Conservation beyond protected areas means humans and lions must coexist. The focus of this thesis is on how Maasai-lion coexistence is created and maintained in Shompole and Olkiramatian group ranches in Kenya's southern Maasailand. I provide a brief overview of the historical and environmental context and narratives that have shaped conservation within and around Olkiramatian and Shompole as well outline the theoretical framework which forms the foundation of this thesis.

The Emergence of Conservation in Shompole and Olkiramatian, Kenya

The presence of wildlife in Shompole and Olkiramatian is rooted in Maasai culture. Firstly, the concept of caretaking, management, or husbandry embodied in the Maasai word *erematare* captures the interconnectedness between husbandry practices, culture, and natural resources. Livestock and livestock husbandry are the centre piece of the *eramatare* concept, but good care and management extends beyond the realm of livestock, as the Maasai understand that in order to successfully raise livestock, the environment and husbandry practices on which livestock depend must also be conserved, with wildlife species being seen as part of the environment (Godfrey, 2018). Secondly, within Maasai culture the hunting of wild prey for meat was considered taboo except during extreme droughts as noted by (Hollis, 1905), "The Maasai ate the flesh of no wild animals when in olden days they all had cattle" (pg. 319). Wildlife fit into the *eramatare* concept as "second cattle" to be hunted in dire times, which meant they were conserved in good times (Western, 2001). These Maasai cultural concepts of

conservation are the foundation for colonial and post- colonial conservation efforts in Olkiramatian and Shompole.

Precolonial period (pre-1895)

The Maasai are thought to have displaced earlier Cushatic speaking Nilotic peoples who occupied Kenya's southern Rift until approximately 1500 AD (Homewood et al., 2009). The bimodal rainfall in East Africa allows for two livestock calving seasons, enabling the early Maasai to become milk-dependent pastoralists. Despite the predominance of pastoralism, agriculture is common across the wetter regions of Maasailand. Within Olkiramatian and Shompole, for example, early written accounts from Wakefield (1870) and Fischer (1884) describe the Pakase and Ngurumani agricultural settlements which continue to today. As described by Wakefield in his 1870 account of "Routes of Native Caravans from the Coast to the Interior of Eastern Africa":

"To Ngurumani-Sadi says the word "Nguruman" (which is Kikwavi), is synonymous with the swahili verb -"ku lima", to cultivate or till; and that the Wakwavi who inhabit this region cultivate beans, millet, sweet potatoes, &c. These are poor Wakwavi who, having long since been robbed of the cattle by the Masai, were compelled to turn their attention to agricultural pursuits, as a means of obtaining a livelihood…. Sadi thinks the Wakwavi of Ngurumani number 1000 or 1500." (pg 306-307).

Later descriptions of the area by Fischer (1884), the first European visitor to the area, mirror Wakefield's description of an agricultural settlement inhabited by Wakwavi and surrounded by an Acacia woodlands inhabited by Maasai, elephant, and rhino. The distinction of Wakwavi as poor agro-pastoralists in the early literature describing the Maasai is confusing because it is unclear from these descriptions whether the Wakwavi were considered to be Maasai by other Maasai sections (Jacobs, 1968). The first reference to Nguruman Maasai comes from G.E Smith in 1904 expedition:

"On the slopes of the escarpment west of the Magadi lake live the Nguruman Masai. The country is well chosen on a plateau between the main escarpment and the floor of the Rift-valley, and it is well watered by permanent streams from the escarpment. Unlike other Masai, these people cultivate sweet potatoes and millet, and understand a primitive form of irrigation. They keep sheep and goats, but have no cattle; are peaceable and not interfered with by other Masai during intertribal fights. They claim to supply the whole Masai tribe with calabashes. Because of their peaceful habits and from the fact that they live from cultivating the soil, they are rather despised by the rest of the Masai; but they are a definite branch of the main tribe, and send their more important disputes into Nairobi for Lenana to settle. They are not truthful like the other Masai, the effect perhaps of their low esteem among their fellows." (Smith, 1907, pg. 298)

Colonial Period (1895-1963)

The colonial wildlife conservation and game laws in Maasailand and the Kenyan colony in the 19th century emerged with the formation of the Imperial British East Africa Company (IBEAC). They outlawed the commercial hunting of ivory in order to protect what they viewed as a potentially valuable commodity (Kelly, 1978). The formation of the East African Protectorate and the transition of administrative power from the Imperial British East Africa Company (IBEAC) to the British Government in 1895 further cemented the foundation of wildlife conservation laws in Kenya. Game regulations developed by the IBEAC were initially adopted by the Protectorate, but following concerns expressed by Lord Salisbury, these game regulations were reviewed and revised to align with those developed for German East Africa and advocated by colony's governor Dr. Herman von Wiessaman (Anderson & Grove, 1989). The new regulations which entered into force in 1899 outlawed commercial hunting of ivory but allowed for the killing of animals thought to be "vermin" such as lions, leopards, and hyaena (Kelly, 1978).

In 1899, Shompole and Olkiramatian fell within the boundaries of the Ugandan Protectorate and were subject to the game regulation imposed by the Uganda colonial

administration. However, these regulations were closely aligned with those of the East African Protectorate (Parker & Bleazard, 2001). It was not until 1902 when Uganda's Eastern Province—which included Shompole and Olkiramatian—was finally incorporated into British East Africa (Waller, 1976). Between 1897 and 1900 four areas within the Ugandan and British East Africa Protectorate were designated as game preserves. These included the Sugutoa Game Reserve in Uganda, the Southern (Ukamba) Game Reserve, Northern Game Reserve, and the Kenia District in British East Africa (Parker & Bleazard, 2001). Olkiramatian and Shompole, being within the Uganda Protectorate, were adjacent but not included within the initial designation of the Southern Game Reserve.

Despite the inclusion of Maasailand in the Southern Game Reserve, the colonial administration felt the Maasai and their pastoral way of life was not compatible with the vision laid out for the East African Protectorate. These views are clearly articulated by Cranworth (1912) in his book "A Colony in the Making",

"The essence of the problem seems to come to this: here we have a people who, beautiful to look at and in some ways attractive in character, have as far as we know never been of any use to any living soul. Like ravening beasts, they have lived off the weakness of their neighbours, amongst whom they are classed with pestilence, famine, and disease. Have these people any inherent right to be conserved in this condition.? Have we not rather a duty to execute by leading them, or forcing them, to be of some economic use, or perish?" (pg. 37)

This perception of the Maasai paved the way for policies that would shape conservation within Maasailand for the majority of the colonial period. Foremost among them were the Maasai "Moves" of 1904 and 1911. In 1904 the first attempt by the colonial government to settle and control the Maasai led to creation of a Northern and Southern Maasai Reserve. Subsequently, the Northern Reserve was earmarked for European settlement and the Maasai were moved into an enlarged Southern Reserve in 1911

(Sandford, 1919; Hughes, 2008). The boundary of the Southern Maasai Reserve closely conformed with the Southern Game Reserve, which was adjusted in 1906 to mirror the boundaries of the Maasai Reserve (Cranworth, 1912). Given that Maasai did not hunt regularly, pastoralism and wildlife conservation was seen by the colonial government as a compatible land-use within the Southern Game Reserve. Cranworth (1912) provides a description of the Southern Game Reserve as well as its purpose,

"It is to the Southern Game Reserve that most of the attention is directed. The tract of country set aside here runs parallel to the railway line from Nairobi down to Tsavo, and contains about 10,000 square miles. The land comprised in the area varies considerably, but a very large proportion of it is quite unfit for white settlement. With the exception of a small swamp or two and a few waterholes, the only permanent water is that of the Tsavo and Southern Guaso Nyrio rivers, which form the southern and western boundaries, and also the head waters of the Athi." (pg. 312)

"The object of a Game Reserve, it may be presumed is, in addition to the moral obligation to the game itself which I have adduced, is to provide the maximum amount of space to the large and increasing class of those persons who are interested in wild animal life. A further object is to provide an area within which scientific observation and experiment may be carried out, and by this means to provide both benefit and gratification to many who will never be able in person to visit the sanctuary" (pg. 315)

The Guaso Nyiro river described by Cranworth, today known as the Ewaso Nyiro River, bisects the Olkiramatian and Shompole ecosystem, and formed the South Western boundary of the Southern Game Reserve. The Southern Game Reserve was degazetted in 1952 and as a result of the formation of Nairobi National Park and the Ngong Hills Reserve but in the preceding years it afforded a degree of protection for wildlife within the Olkiramatian and Shompole ecosystem(Parker & Bleazard, 2001).

Throughout period between 1920-1963 the perception that Maasai needed to be sedentarized and that their livestock practices led to overstocking and overgrazing, continued to motivate the colonial office to develop tactics to control Maasai pastoralists (Homewood et al., 2009). Principle among them was the African

Development Organisation (Aldev, 1946-1955) and the subsequent Swynnerton Plan 1954-1957 (Swynnerton, 1955; Adlev, 1956). Both the Adlev and Sywnnerton plans aimed to revolutionize and modernize the African agricultural sector. Two main problems which both Adlev and Synnwerton tried to address were noted in the "*Cattle Complex*" and "*African Traditional Form of Land Tenure,*" which are described in Adlev (1956):

"*The cattle complex signifies an attitude towards cattle descending in intensity from the emotional almost religious feeling of the Nilohamatic people...*" *(pg. 5)*

"*African traditional forms of land tenure are often incompatible with good farming…among the pastoral and semi-pastoral tribes. Here the land is owned by the tribe and grazing is free for all. As a result, ten years ago much of this land was badly overgrazed.*" *(pg. 6)*

Grazing schemes such as the Konza and Ilkisongo were set up under Adlev to convert pastoral production systems into western modernized livestock production systems (Adlev, 1956). No projects under either the Adlev or Swynnerton plans were implemented within Olkiramatian and Shompole however this ideology would come to have a lasting effect on views of pastoral production systems and land-tenure in the post-colonial era.

Post-colonial period (1963 to present)

While Kenya's independence in 1963 ushered in a new government, the colonial misperceptions of pastoralism and the Maasai remained. This paved the way for the the group ranch scheme in 1968 (Galaty, 1980). The group ranch was the new administration's solution to the "cattle complex". Implemented by the Kenya Livestock Development Program (KLDP), group ranches were intended to provide freehold titles to small groups (up to 1000 households) of livestock owners which would be governed

by an elected committee of representatives (Rutten, 1992). The belief was that by forcing pastoralists to adopt delineated and legally recognised boundaries and established governance committees the outcome would be the closure of "open access" systems, and lead to a reduction in livestock numbers and overgrazing (Kimani & Pickard, 1998; Mwangi, 2007). Olkiramatian and Shompole were registered as group ranches in 1977 and their members hence forth defined as distinct communities.

Since the degazettement of the Southern Reserve in 1952 no formal protection or protected area for wildlife has existed within the Olkiramatian and Shompole ecosystem. Wildlife persisted largely due to the traditional cultural values for wildlife and husbandry practices described above. The persistence of wildlife within the ecosystem allowed space for small-scale tourism and non-consumptive wildlife utilization until 1991 when the newly established Olkiramatian and Shompole Community Development Project (OSCDP) proposed to mobilize and educate its members about land tenure, livestock disease control and wildlife utilization (Williams et al., 1995). Initiated as part of a community-based tsetse fly control program, ecotourism was encouraged as an alternative livelihood strategy to livestock rearing. The first informal campsites were established in the 1970s but were never adopted as part of the group ranch programmes. The Kenya Wildlife Service was invited to help establish a community wildlife program and four members of Olkiramatian and Shompole were trained in wildlife tourism. By 1993 OSCDP had collapsed due to conflicts between the community, project donors, and NGOs involved in the project (Williams et al., 1995; Brightwell et al., 2001).

Despite its collapse, the formation of OSCDP and focus on wildlife conservation coincided with the establishment of Kenya's community-based conservation (CBC) movement and laid the foundation for future CBC efforts within the ecosystem (Warinda, 2001). Kenya's CBC movement grew out of revenue-sharing agreements established in the 1970s between Amboseli National Park and the surrounding Maasai communities. Subsequently, in 1991, the Kimana Community Conservancy became Kenya's first wildlife conservancy to be operated entirely by the local Maasai community (Meguro & Inoue, 2011). CBC in Kenya was further catalysed in the late 1990s by the Kenya Wildlife Service's (KWS) "Parks Beyond Parks" policy which recognized that its limited staff and budget could not protect the substantial preponderance of wildlife that existed on pastoral lands areas outside protected areas (Western et al., 2009; Western et al., 2015).

After the collapse of OCSDP, the Shompole group ranch leadership sought to reinvent and revive the ecotourism components of the project by creating the Shompole Community Ecotourism Project (SCEDP) (Ole Munge, 2002). Throughout the 1990s, SCEDP continued to charge tourists and campers visiting the area, and developed a relationship with the newly-formed conservation organisation, the African Conservation Centre (ACC), which was established as a national and regional NGO by Wildlife Conservation International (Warinda, 2001). The partnership allowed the community to develop ecotourism plans and invite an investor, Art of Ventures, to construct a tourist lodge within a 300 km^2 area west of the Ewaso Nyiro river which would be designated as a conservation area (Ole Munge, 2002). The area earmarked for conservation had been historically used for dry season grazing. The conversion to a "conservation area" did not change the previous land-use patterns but did create a designated space in which

wildlife-related tourism activities could operate. Following on from the successful establishment of Shompole Lodge and a designated conservation area in 2000, the adjacent group ranch Olkiramatian established its own conservation area and lodge in 2004 (Wariuingi et al., 2005). Today Olkiramatian and Shompole are two of more than 140 community conservancies across Kenya which cover 10.9% of the country as compared to 8% formally designated wildlife areas as national parks under KWS jurisdiction and national reserves under county jurisdiction (Bedelian & Ogutu, 2017; Lalamapaa, 2017).

Conservation, Conflicts, and Culture

A century of conservation in Africa has created new challenges within, surrounding, and separate from Protected Areas. Paramount among them is human-wildlife conflict. Reduction of human-wildlife conflicts is a central focus of many conservation interventions without the recognition that conflict itself is multi-dimensional and dynamic (Dickman and Hazzah, 2016). Human-wildlife conflicts can be categorized as direct and indirect conflicts. Direct conflicts occur when wildlife threatens the livelihood or safety of a person or community (Inskip & Zimmermann, 2009; Dickman & Hazzah, 2016). Indirect conflicts are often driven by underlying human-human conflicts like disagreements over conservation agendas or differing societal values surrounding wildlife (Madden, 2004; Redpath et al., 2013). For example, in Sumatra the creation of multi-use buffer zones around protected areas increased the space available to tigers and elephants but also increased the likelihood of conflict because of the greater likelihood of contact between people and wildlife within in multi-use buffers zones (Nyhus & Tilson, 2004). Tolerance and acceptance of wildlife in these interactions are influenced by a wide variety of tangible and non-tangible factors,

including the costs and benefits of living with wildlife as well cultural beliefs and customs (Kansky et al., 2014).

Tangible economic benefits from conservation have been the principal tool used to improve acceptance of wildlife conservation and to promote tolerance for a range of large carnivores including lions, wolves (*Canis lupis*), and lynx (*Lynx lynx*) (Treves & Bruskotter, 2014). However, the ability of conservation benefits to foster positive perceptions is fickle and can be undermined by socio-political factors. For example, in Great Smoky Mountains National Park, USA, and Podocarpus National Park, Ecuador distrust of the park and park management overshadowed the benefits provided by the park (Stern, 2008). As noted by Kansky and Knight (2014) perceptions about living with wildlife are often more because of intangible costs than tangible benefits. In the context of CBC and CBNRM in Africa, the inability to decentralize power to the community level, flawed economic logic regarding the profitability of wildlife utilization, and failure to establish necessary political and social infrastructures have led to many failures. They have also complicated local perceptions of conservation and even created conflicts between agencies and different human interests (Nelson & Agrawal, 2008; Nkhata & Breen, 2010). The collapse of Zimbabwe's CAMPFIRE program and misappropriation of power in Kimana's Community Sanctuary by the tour operator, African Safari Club, exemplify these shortcomings (Virtanen, 2003; Meguro & Inoue, 2011). CBC has also further compounded conservation conflicts by establishing a new set of elites fostering the perception that conservation groups and governments are acting as neo-colonial hegemonic powers (Singh & van Houtum, 2002; Mbaria & Ogada, 2016). These indirect conflicts and conservation injustices have also been used as a rationale in which killing wildlife becomes political protest (Miller

et al., 2012; Goldman et al., 2013). For example, in the 1970s, Maasai communities adjacent to the new Park boundaries killed lions, rhinos and elephants in response to the creation of Kenya's Amboseli National Park (Western, 1982). More recently restricted livestock access to Amboseli National Park has increased the likelihood and acceptance of lion killing behaviour (Hazzah et al., 2013).

Non-tangible factors such as culture play a critical role in shaping social and ecological relationships between people and wildlife (Sheppard et al., 2010; Waylen et al., 2010; Madden & McQuinn, 2014; Dickman & Hazzah, 2016). Conservation interactions are commonly misunderstood and oversimplified by researchers and conservation practitioners alike, and often ignore non-tangible elements such as culture (Madden & McQuinn, 2014; Dickman & Hazzah, 2016). Men and women in Chitwan, Nepal, have differing opinions of tigers, highlighting the complexity of human-carnivore relationships in that situation. Tolerance in Chitwan was largely predicated on the belief that tigers maintained a healthy ecosystem but women were less likely to believe this and therefore less tolerant of tigers than men (Carter & Allendorf, 2016).

In East Africa, many protected areas, including Serengeti, Maasai Mara, Ngorogoro, and Amboseli, now exist within Maasai tribal lands because the Maasai have had historical coexistence with wildlife (Walpole et al., 2003; Lichtenfeld, 2005). Lions, specifically the majority of East Africa's lion range (Dolrenry et al., 2014), is on Maasai land which makes the continuing coexistence between Maasai and lions both within and beyond East Africa's Protected Areas critical to the long term survival of East Africa's lions. There are different positions about whether coexistence is possible in modern conditions (Goldman et al., 2010). Maasai pastoralists have been vilified by

some for their predisposition towards lion killing (Frank et al., 2006), while others have lauded their ability to coexist with large predators (Lichtenfeld, 2005; Goldman et al., 2013). Debate surrounding Maasai-lion coexistence centers on cultural perceptions of lions and the importance of traditional lion hunts. Lions are often referred to as the 'great predator' by Maasai, *"olowaru kitok*", and killing lions is a symbol of bravery (Spencer, 1988). *Olamayio* hunts involve the killing of male lions to demonstrate the bravery of young warriors during their initiation ceremonies. *Olkiyoi* hunts are a form of retaliatory killing in response to livestock predation. Traditional taboos prohibit the killing of cubs and lionesses during *Olamayio* hunts but is tolerated during *Olkiyoi* hunts (Hollis, 1905; Hazzah et al., 2009). Thus questions that lies at the heart of my research is can human-lion coexistence continue under todays conditions?

Investigating Coexistence

Coexistence between lions and humans is a central concept of this thesis. Following Carter and Linnell (2016), I define coexistence as the sustainable cohabitation of humans and lions within a shared landscape. To investigate human-lion coexistence I propose that coexistence is influenced by two main conditions. Firstly, coexistence requires that individuals and communities living alongside lions have a level of tolerance for them and the associated risk to livestock and people that it brings (Carter & Linnell, 2016). Secondly, human and lion behaviours and decision-making dictate human-lion interactions. This thesis draws on a theoretical framework (Figure 1) which utilizes theories and methods from anthropology, conservation biology, ecology, livestock science, and social psychology to explore the factors that contribute to human-lion interactions and allow humans and lions to coexist.

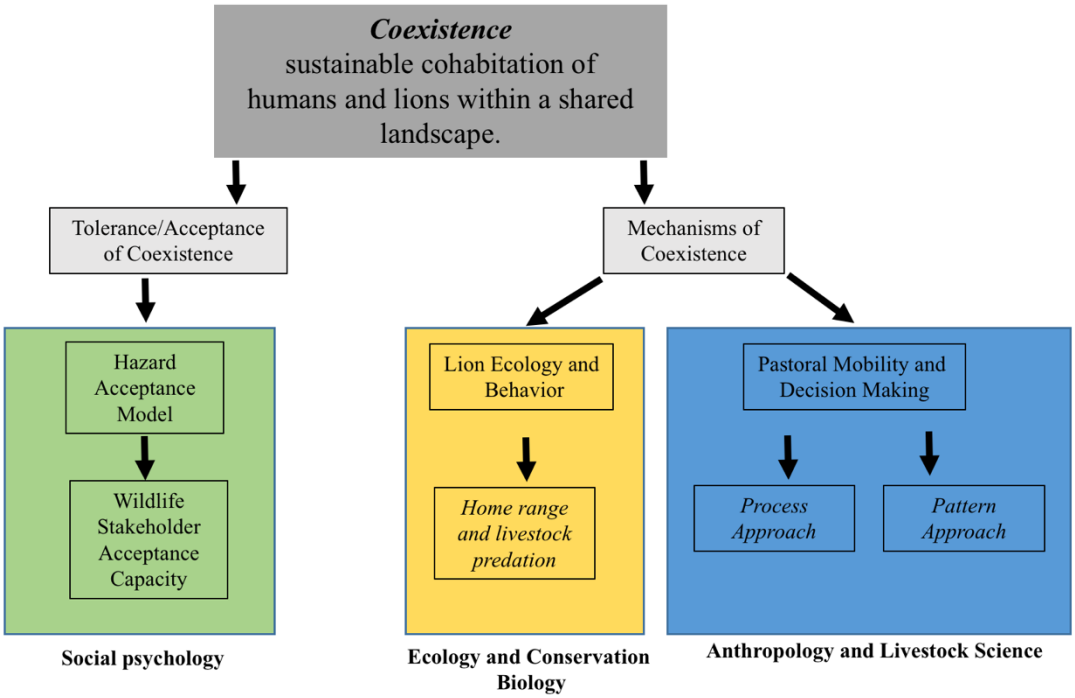


Figure 1: Schematic depicting the theoretical framework used investigate human-lion coexistence

Tolerance and Acceptance of Coexistence

Much of the existing research into human-wildlife interactions has focused on investigating attitudes and specific behaviours that may contribute toward tolerance and coexistence rather than specifically investigating tolerance (Dickman et al., 2013). Borrowing from Albarracín et al. (2005) *attitudes* can be defined as the psychological tendency of an individual to evaluate an entity (person, place, behavior or thing) with a degree of favour or disfavour. Based on the Oxford Dictionary, I define *behaviour* as the way one acts toward others or in response to a specific situation or stimuli. Previous researchers have demonstrated how hard it is to quantify the relationship between attitudes and behaviors (St John et al., 2011; Bruskotter et al., 2015). St John et al. (2011) argue that social psychological theory offers little evidence to support the notion that attitudes predict conservation behaviors. Conversely, lion specific studies

conducted by Hazzah et al. (2017) demonstrated that attitudes towards lions were in fact the best predictors of lion killing behavior.

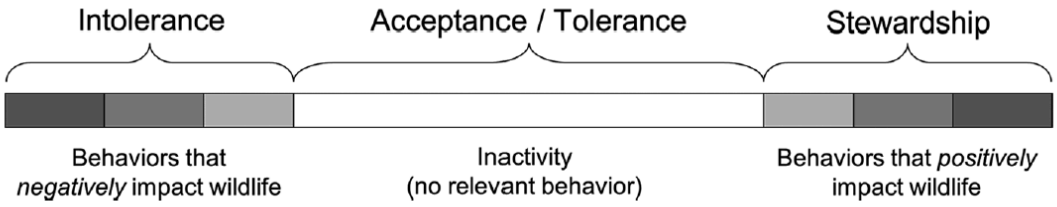


Figure 2: Conceptual model of conservation behavior as proposed by Bruskotter and Fulton (2012)

Whether attitudes predict *behavior* or not, a narrow focus on specific behaviors such as lion killing are not a good measure of tolerance because killing lions is uncommon and the act is an end point rather starting point of intolerance (Bruskotter & Fulton, 2012). Social psychological theories like the "theory of planned behavior" are commonly invoked to explain conservation behaviors and tolerance for wildlife (St John et al., 2011). However, as highlighted by the vibrant debates that exist in the literature (St John et al., 2011; Treves & Martin, 2011; Bruskotter & Fulton, 2012; Treves, 2012; Bruskotter et al., 2015), there is no consensus on how tolerance, intolerance, and stewardship are defined and how they should be applied in understanding conservation. Bruskotter and Fulton (2012) propose a theoretical framework (Figure 2) that marries intolerance, tolerance/acceptance, and stewardship stating that:

"A parsimonious solution is to treat these concepts as representing opposing poles on a continuum of behaviors undertaken to positively impact (stewardship) or negatively impact (intolerance) for a given species. In contrast with stewardship, tolerance/acceptance is a distinctly passive concept—again, tolerating the presence of a species or population of that species requires no involvement nor action on the part of individuals. Conversely, intolerance, like stewardship, implies action. Like stewardship, intolerance can take different forms, such as purposeful killing of individual animals, writing one's congressional representatives, donating to an interest group that opposes a species/ population, or even attending a political rally in opposition to a species/ population." (pg. 99)

Hence, in context of human-lion coexistence I propose the following three definitions: (i) *Intolerance* is active engagement in a behaviour that will negatively impact lions. For example, advocating the degazettement of a national park or conservancy or killing lions; (ii) *Tolerance* is the passive acceptance of living alongside lions, i.e., not engaging in behaviors that will negatively or positively impact lion; (iii) *Stewardship* refers to the active engagement in a behaviour that will positively impact lions for example, Olkiramatian and Shompole communities setting aside conservation areas for the purpose of wildlife conservation.

Within Maasailand people and wildlife have cohabited for several thousand years (Homewood et al., 2009). Coexistence could be a passive acceptance of the status quo rather than an intentional behaviour. My basic assumption in investigating the human-lion coexistence within Maasailand is that it has been a state of inactivity or tolerance rather than the result of a specific behaviour. I therefore align my research with Bruskotter and Wilson (2014) hazard perception model of tolerance and wildlife acceptance capacity (WAC) (Decker & Purdy, 1988; Carpenter et al., 2000; Inskip et al., 2016) and not with the theory of planned behaviours and wildlife tolerance model advocated by St John et al. (2011), Kansky et al. (2016) and others to explain attitudes and behaviours towards wildlife and conservation.

The hazard acceptance model (Figure 3) proposes that *tolerance* is synonymous with acceptance of wildlife and can be best explained by using the psychological theory of hazard acceptance. Bruskotter et al. (2015) suggest that tolerance of wildlife is determined by (i) an individual's perceived control over the threat (wildlife damage),

(ii) societal trust (in the management authorities), (iii) affect for the species, (iv) perceived benefits, and (v) perceived costs.

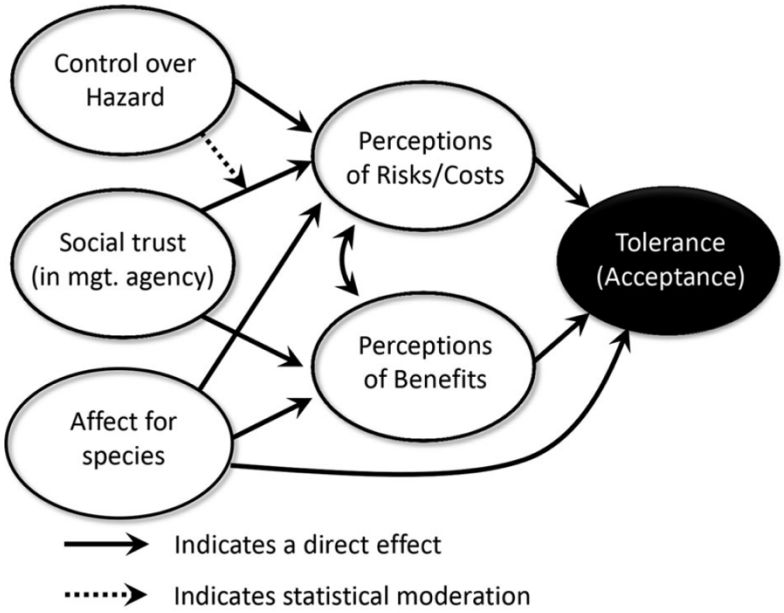


Figure 3: Hazard Acceptance model as proposed by Bruskotter and Wilson (2014)

Pastoral Decision-Making

It is insufficient to ask only why people are willing to coexist with lions to understand coexistence and tolerance. We must go further to examine the mechanisms that allow them do so. I propose that within Maasailand the transhumance nature of Maasai pastoralism is a primary factor influencing human-lion interactions therefore I explore both the patterns of pastoral movement and the decision-making process which are likely to shape human-lion interactions and coexistence (Chapter 4). Analogous to the broad range of methods and theories using social psychology to explain behaviors, anthropologists, geographers and political ecologists have drawn on a diversity of methods and models to understand pastoral movements and decision making (McCabe, 1994; Niamir-Fuller & Turner, 1999; Turner, 1999). Within this body of literature two

predominant approaches have emerged, namely pattern orientated approaches and process orientated approaches.

Pattern orientated approaches seek to explain the patterns of pastoral movement and are traditionally rooted in qualitative anthropological methods (Bernard, 2017; Liao, 2018) such as ethnography and participant observation (see appendix 1 for descriptions). Early pattern orientated models of pastoral movement such as homeostasis (Barth, 1961) and resource maximization (Evans-Pritchard, 1940) proposed that pastoral movement (nomadism) was driven by biological factors. In these models mobility provided a mechanism to either maximize (resource maximization) or maintain constant (homeostasis) access to natural resources such as pasture and water. Evans Prichard and Barth's simplistic models of pastoral mobility have been critiqued and refuted by the other anthropological studies (Stenning, 1959; Dyson-Hudson, 1972; Gulliver, 1975; Dyson-Hudson, 1980), which argue that biological factors such a seasons dictated the general pattern of pastoral movement, while non-biological factors such distance to markets and herd safety usually determined exactly where pastoralists settled and when they moved.

The advent of modern techniques such remote sensing (RS), geographic information systems (GIS), and global positioning systems (GPS) have shifted the focus of pattern orientated research away from qualitative methods into the sphere of quantitative research (Turner, 2003). Many recent studies including those conducted by Coppolillo (2000) in Tanzania, Butt et al. (2009) in Kenya, Akasbi et al. (2012) in Morocco, and Turner et al. (2016) in the Sahel region used GPS tracking and remote sensing to document and explain pastoral movement patterns. These studies demonstrated that

biological factors such as pasture availability, grass greenness, and distance to water best explain patterns of pastoral mobility, but that they often are constrained by non-biological factors such as governance institutions and international boundaries. GIS and GPS technology advanced the ability to accurately track pastoral mobility but Turner (2003) cautions against relying solely on the use of these technologies stating that,

"It is only through such self-reflective uses of these technologies by those familiar with local contexts that the full spatial analytical powers of these technologies can be fully realized in people-environment research" (pg. 273).

Previous studies (Butt et al., 2009; Akasbi et al., 2012; Turner et al., 2016) that used GPS data as a quantitative measure for pastoral mobility have also relied heavily on qualitative methods such as participant observation, ethnography, and semi-structured interviews (Bernard, 2006; Newing et al., 2011) in their interpretation of GPS data.

Process orientated approaches model the pastoral decision-making process rather than patterns of pastoral movement. Process orientated approaches draw heavily on decision making models used in both macro-economics and psychology (Dwyer & Istomin, 2008) and can broadly be categorized as macro-economic or cognitive models.

Macro-economic models emphasize the determinants of pastoral decision-making. For example De Boer and Prins (1989) proposed that herders' decisions followed optimality theory. Their work demonstrated that in Burkina Faso herders' decisions were tried to minimize the daily travel time of livestock herds. By contrast (Moritz et al., 2014a) used agent based modelling to propose that livestock movement in Logone, Cameroon, conforms to an ideal free distribution (IFD). IFD hypothesizes that the number of livestock in an area is predicted by the quality and quantity of resources

within an area and that livestock owners have equal access to these resources (Moritz et al., 2014b). Macro-economic models are often preferred because they produce testable hypotheses however they are based on abstract concepts and make simplistic assumptions (Dwyer & Istomin, 2008). The economic rationale is in question because as St John et al. (2011) suggest, we are not "*homo economicus"* and human decision-making is not always economically rational.

Cognitive models of pastoral movement model the decision-making process rather than determinants of movement and are commonly developed through participant observation as well structured and semi-structured interviews (Bernard, 2006; Bennardo & De Munck, 2014, and appendix 1). One example comes from Mongolia, where Fernandez-Gimenez (2000) demonstrated a hierarchy of decision-making processes. Camp (homestead) and household heads were responsible for selecting camp and seasonal grazing areas while herders were more active role in deciding daily grazing routes. The case-specific nature and heavy reliance on qualitative data of cognitive models limits their broader applicability. Developing a general explanatory model of pastoral decision-making therefore requires an integration of both cognitive and macroeconomic approaches. One such example is the model of "Herd Control" proposed by Dwyer and Istomin (2008). "Herd Control" argues that nomadic movements are a product of the interplay between livestock behavior and the herder's ability to avoid hazards and maintain herd cohesion while minimizing energy and maximizing resources.

As previous studies of pastoral mobility suggest (Dwyer & Istomin, 2008; Butt et al., 2009; Liao, 2018), both qualitative data (gathered from participant observation and

interviews) and quantitative data (from GPS tracking, settlement mapping) are needed to have a robust understanding of pastoral movement and decision making. I therefore investigated both patterns of pastoral movement (pattern approach) and pastoral decision-making processes (process approach) (Figure 3) to understand how pastoral mobility influences Maasai-lion coexistence

Lion Ecology and Behaviour

Africa's largest free-ranging carnivores and one of the continent's most iconic species, lions can weigh upwards of 190kg. They preferentially hunt large wild ungulates ranging between 190-550 kg (Smuts et al., 1980; Hayward & Kerley, 2005; Macdonald et al., 2015). Lions, which show sexual dimorphism in body size and vary behaviourally, are considered social felids. Related females and their offspring live in fission-fusion groups called prides. Communal care of young, cooperative hunting, defence of kills, and the dispersion and abundance of resources have all been proposed as explanations for lion sociality (Schaller, 1972; Kruuk & Macdonald, 1985; Packer et al., 1990; Mosser & Packer, 2009). Female young will generally remain within their natal prides. Pride size and composition varies widely between populations (Van Orsdol et al., 1985). In Kenya, average prides as small as 1.62 sub-adult and adult females have been seen in the Amboseli ecosystem (Dolrenry, 2013), while prides of a mean of 9.2 adult females have been recorded in the Masai Mara (Ogutu & Dublin, 2002). Prey abundance is commonly cited as a principle determinant of pride size (Van Orsdol et al., 1985), but recent studies suggest that small prides sizes could be an adaption used by lions living within human-dominated landscapes (Dolrenry, 2013). Prides establish and defend territories that vary in size depending on resource availability and pride size (Macdonald, 1983; Kruuk & Macdonald, 1985; Loveridge et al., 2009).

Male lions remain in their natal prides until sub-adulthood (approx. 2 years) or sexual maturity (approx. 3 years). Adult males can be solitary but are often in coalitions of 2-4 individuals usually comprised of litter mates of similar ages (Packer & Pusey, 1982). Males including coalitions remain nomadic and can cover several hundred kilometers (often through human-dominated landscapes) as they search for female prides to establish take over (Elliot et al., 2014). Nomadic males must displace incumbent pride males and coalitions to become pride males and gain reproductive access to females. During pride take-overs, males will often kill cubs within the pride to bring their mothers into oestrous early (Packer & Pusey, 1983). Having successfully taken over, a new pride males will establish and expand their territory and may often associate with several groups of females (Mosser & Packer, 2009)

Ethics Approvals and Research Clearance

This research had all the appropriate approvals. The data collection was conducted in accordance with University of Oxfords ethics requirements (R52851/RE001 and Appendix 2). Research clearance was authorized by Zimbabwe Parks and Wildlife Management Authority (Permit numbers: REF:DM/Gen/(T) 25/2010, 06/2011, 12/2012) in Zimbabwe. TAWRI (Number 2012-60-ER-97-2) and Commission for Science and Technology (COSTECH) (permit reference CST/RCA 97/20/2012) in Tanzania, and Kenya Wildlife Service (KWS/BRM/5001) in Kenya. Additionally, data collection in Shompole and Olkiramatian was overseen by the South Rift Association of Land Owners and consent was granted by local governance committees consisting of Maasai elders, group ranch officials and government chiefs.

Thesis Aim and Overview

This study investigates the complexities of human-carnivore interactions within human-dominated landscapes and aims to provide a critical review of whether coexistence is possible and mutually beneficial for carnivores and people. The African lion is a proxy for large free-ranging carnivores in human-dominated landscapes. The study integrates history, ecology, anthropology, and livestock science in six interrelated chapters to quantify the ecological, social, cultural, and economic factors that influence coexistence between lions and people.

Thesis Chapters

Chapter One: An overview of the emergence of conservation and community-based conservation within Olkiramatian and Shompole provides a contextual understanding of the historical factors that have shaped human-lion coexistence within Maasailand. Subsequent sections outline the conceptual framework of the thesis and the key concepts used, namely human-wildlife conflict, human-lion coexistence, wildlife tolerance, pastoral decision-making, and lion ecology.

Chapter Two: Investigates the socio-economic and cultural factors which influence individual and societal desires for coexistence with lions. The focus is on three case studies in Kenya, Tanzania and Zimbabwe that allow comparisons within sites and between sites. Results provide a better understanding of the factors that influence an individual's desire to see lion populations maintained.

Chapter Three: The ecology of lions within a human and livestock dominated landscape, home range size and human disturbance is quantified to assess whether

human disturbance influences lion home range size. The data offers insights about the tenability of coexistence between people and lions as well as ecological adaptions that allow lions to inhabit pastoral rangelands.

Chapter Four: The data focus on pastoral mobility and landscape utilization, particularly whether Maasai in communities southern Kenya actively avoid areas of high lion occupancy. The chapter documents decision-making among pastoral Maasai communities and whether lion presence features in the process of decision-making.

Chapter Five: This chapter explores the social and ecological factors that influence the prevalence and severity of lion depredation. It also examines the role husbandry techniques of livestock guarding have in disrupting lion attacks on livestock.

Chapter Six: Chapter Six is an overview of the thesis. It synthesizes the research findings and proposes a model for coexistence between lion and pastoral communities.

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Appendix 1

Description of social science methods taken from supporting material for: Bennett, N., Roth, R., Klain, S., Chan, K., Christie, P., Clark, D., Cullman, G., Curran, D., Durbin, T., Epstein, G., Greenberg, A., Nelson, P., Sandlos, J, Stedman, R., Teel, T., Thomas, R., Verissimo, D. & Wyborn, C. *Conservation social science: Understanding and integrating human dimensions to improve conservation*. Biological Conservation.

Social science method	Description
Agent-based modeling	Agent based models are a type of **simulation model** used to study the actions and interactions among autonomous agents to determine how they influence a system in its entirety. Agent-based models can be used to study the emergent properties of systems that arise as a result of interactions between sub-components of that system, institutional development and change, and other complex systems, among other topics.
Archival research	Archival research focuses on the analysis of **primary sources**, which were written or created during the period of study (not to be confused with **primary data**, which is data that the researcher collects). Archival researchers seek to gather evidence to construct arguments about historical change. Archival evidence may take the form of letter, historical reports, personal papers, diaries and data. In terms of conservation, archives also may contain immense amounts of historical data about wildlife populations and historical ecological conditions. Where archives permit, documents may be digitized using cameras or scanners, and text made recognizable to computers through optimal character recognition (ocr) software. Practitioners of digital history often use computer programs to analyze large numbers of documents, a process referred to as text mining.
Argument analysis	Argument analysis is the formal process of systematically laying out and then evaluating the accuracy of premises, the validity of inferences, and ultimately the soundness of arguments that underlie any particular ethical claim. Conservation can be described as a set of arguments for why we ought to engage in one action or another, therefore argument analysis can be employed to evaluate the arguments offered to justify those action.
Arts-based research	Researchers can systematically use the process of creating an artistic expression, which can take diverse forms (e.g., paintings, dances, carvings) to understand the people who they study, or apply the arts to understand (art as method) and represent (art as result) a topic of study such as environmental change, water management, or environmental values.
Case analysis	Generally, **case analysis** is an analytical method of problem solving where an issue is divided up into separate cases or sub-issues for consideration. In the context of law, legal researchers read judgments or judicial decisions to clarify legal principles and determine how courts make decisions based on the facts of the case in front of them.
Case study	Case studies involve the use of one or more quantitative, qualitative or mixed method to explore, explain or describe a group, person, decision, project, institution, policy or other system. Researchers use case studies to empirically investigate an issue in its real world context. In **prospective case studies**, researchers define the characteristics of the cases that correspond to the purpose(s) of their research, then select cases when they become available. In **retrospective case studies**, researchers identify inclusion characteristics then select cases from historical records. **Comparative case studies** can illustrate similarities or differences between cultures, countries and contexts. Special attention needs to be paid to the definition of categories and types of data that may vary across case studies when comparing two or more.
Cost-benefit analysis	Cost-benefit analysis is a systematic method for determining and comparing the costs and benefits associated with a policy, decision or project. It provides a framework for comparing alternatives (based on quantitative, monetized values) to inform decision-making. Although traditionally cost-benefit analysis includes few environmental considerations (other than monetized resources), it can be coupled with the economic valuation of ecosystem services to be more relevant for conservation. Since monetary values cannot capture all that matters for decision-making, however, it should never be taken as complete guidance for policy.

Social science method	Description
Discourse analysis	Discourse analysis is the study of the meaning of language beyond the level of a sentence. Given that language is a system of thought and linked to social practices, discourse analysis focuses not just on what is said or written, but how this discourse is embedded in historical, political and social contexts.
Documentation of traditional ecological knowledge (tek)	Berkes (2001) defines tek as "a cumulative body of knowledge, practice and belief, evolving by adaptive processes and handed down through generations by cultural transmission, about the relationship of living beings (including humans) with one another and their environment" (p. 8).* tek researchers record 1) factual observations, such as names and classification systems; 2) management systems that determine access to resources, types of harvest/use etc.; 3) historic and current uses of ecosystem components, often preserved in oral traditions; 4) ethics and values underpinning the management of exploitive capacities as well as appropriate relationships between humans and ecosystems; 5) culture and identity, often embodied in language and cultural landscapes; 6) cosmology and worldview related to beliefs and perceptions of how humans and animals ought to interact and the roles that humans ought to have in their communities.
Economic modeling	Economic modeling involves the identification of key elements of an economic system to determine cause, effect and influence among interacting components. Economists use models to generate different scenarios, often to assess the effects of various policy options or other choices. **Visual models** are graphical representations of an abstracted economy, generally used for teaching. They tend to be visual extensions of **mathematical models**, which are linked systems of simultaneous equations involving multiple variables. **Empirical models** involve the application of data to a mathematical model to estimate the model's values. Computers are critical for economists to build and run **simulation models**, which are mathematical models that the user parameterizes (setting the numerical value of certain variables), then the computer runs the simulation to find solutions to the equations in the model.
Economic valuation (including ecosystem services)	Economic valuation is the assessment of monetary value associated with environmental conditions or ecosystem services (e.g., carbon sequestration, coastal protection from mangroves) that tend to be overlooked in traditional financial valuation. A variety of market and non-market techniques can be used, each with its own assumptions and limitations.
Ethnography	Ethnography is systematic research on people and cultures. Methods can entail **participant observation** as well as generating extensive field notes, **surveys** and **interviews**. Ethnographers strive to be reflexive, that is researchers seek to account for the influence of their presence and personalities within the groups they study.
Focus group	A moderator facilitates a small group discussion among carefully selected people who discuss their perspectives on a specific topic. This method enables researchers to identify the extent to which participants share an understanding of a topic and the influence of individuals on others in the group. Moderators need strong group leadership and interpersonal skills. Focus group facilitators can employ a diversity of social science approaches, such as those listed in this table, and also **delphi methods** (a systematic method of forecasting using a panel of experts), **nominal group processes** (involves developing ranked solutions to a problem) or **structured decision making.**
Free lists	A method to elicit from research participants about all the entities that are related to a particular issue. Particularly useful during initial exploratory research. The benefit of this approach is that it is less leading than direct questions about an issue and is more effective at eliciting participants' views.
Geographic information systems (gis)	**Geographic information systems (gis)** allows for the spatial representation and analysis of attribute data allowing the user to query changes over time and points of co-occurrence, and conflict. It can be used to inform planning, through bridging the social and physical sciences, thus helping to optimize locations for development or conservation. Data sources include **remote sensing** data from satellites and **aerial photos**. Increasingly, gis systems can handle multi-media representations of space/territory allowing for the incorporation of hand drawn sketch maps, photographs, audio and video, allowing for the representation of local knowledge. **Historical geographic information systems (hgis)** allows historians to assess patterns and processes of environmental change over time.

Social science method	Description
Interviews	Interviews seek to identify interviewees' perceptions, opinions, beliefs, and attitudes. The data obtained can be **qualitative** (descriptive data, e.g. Explorations of meaning, asking why and how), **quantitative** (numerical data, e.g., measurements of frequency and magnitude, asking what, when, where, how much) or **mixed**. **Structured** interviews follow a script**. Unstructured** interviews involve questions that are not created in advance, which allows for spontaneity and the developments of new questions over the course of the interview. **Semi-structured** interviews follow a framework of specific topics, but they are flexible, allowing and often enabling new ideas to emerge from the interviewee. **Key informant** interviews focus on the impressions, opinions and experiences of people with a specified expertise. In a **life history interview**, the researcher tends to proceed chronologically and ask open-ended questions to prompt the interviewee to share the story of his or her life. The resulting life-history stories can help researchers understand how people think about and create meaning in their lives and provide insight into other cultures. **Oral history research** involves extensive interviews to assess individual or multi-generational knowledge of environmental change. In aboriginal communities, oral history research might also involve the collection of traditional ecological knowledge (tek).
Lab and field experiments	Lab-based experiments are conducted in closed and controlled settings. Field experiments are conducted in more natural settings with treatment and control groups. Field experiments tend to be associated with greater variability in the data since unanticipated environmental conditions may influence the variables studied. Social scientists can use field experiments and other quasi-experimental methods to identify causal relationships between policy interventions and outcomes.
Meta-analysis	Meta-analysis involves employing statistical methods to combine and/or compare results from previous research to find patterns, disparities or other relationships across multiple studies. Such analysis can collate information to provide greater statistical power pertaining to a metric of interest. Researchers need to be attentive to how they select studies, manage incomplete datasets and deal with publication bias (studies that support the null hypothesis or have inconclusive results are less likely published).
Mixed methods	Mixed method research focuses on understanding the real-world context and cultural influences linked to the topic(s) under investigation. Researchers in mixed methods projects tend to employ quantitative and qualitative methods together integrate the results to provide a more complete picture of the problem being studied and use qualitative research to inform quantitative methods and vice versa. Researchers are also explicit about the philosophy and theory underpinning their inquiries.
Monitoring and evaluation	Monitoring and evaluation is a process for assessing the performance of conservation projects, programs or organizations. Researchers collect, analyze and use data using other methods mentioned here (e.g., surveys, focus groups, interviews, etc) to determine if and to what extent policies, projects and programs are efficient and/or resulting in the intended effect. Such evaluations may include the program's cost per participant, possible ways to improve it, unintended consequences linked to the program, alternatives and insight into whether or not the program's goals are useful and appropriate. Evaluators often work closely with stakeholders in such assessments. Various methods are used to monitor and evaluate the outcomes and effects of conservation programs. A **randomized control trial** is an experimental design that randomly assigns participants into an experimental or a control group to understand the difference between groups relating to an outcome variable being studied. **Most significant change** is a qualitative, participatory approach that involves collecting personal accounts of change from various stakeholders involved in an intervention. These accounts are then systematically discussed to determine which factors are the most significant and why. **Process tracing** is a qualitative data analysis method for testing causal mechanisms within case studies in a theoretically informed way. Process tracing can be used to see if results are consistent with a program's theory of change and examine if alternative explanations can be ruled out. **Realist evaluation** is a qualitative evaluation method, centered on finding not only what outcomes were produced from a given intervention but also how they are produced and affected by the context in which the intervention takes place.

Social science method	Description
Narrative analysis	Researchers use narrative analysis to understand how people create meaning through stories, often based on personal experience. The units of analysis include stories, conversations, journals, autobiographies, letters, interviews, field notes and photos.
Participant observation	The researcher immerses him or herself in a group of people that he/she studies for an extended period of time (months to years). The researcher establishes rapport with the group or community and collects data via **informal interviews**, **life history interviews**, **participating in everyday life** of the group**, observing community discussions**, and **analyzing documents** that individuals and the group create.
Participatory methods	Social scientists work closely with non-academic research partners to co-create research questions and co-produce knowledge relevant to the communities of the research partners and academia. **Participatory action research** involves close collaborations with partners beyond academia aimed at generating social change. There are an array of participatory methods and facilitation techniques.
Participatory spatial analysis	In **community-based mapping,** researchers employ a wide range of tools to facilitate the participation of community members as they map local knowledge (e.g., contaminated sites, sacred sites, sources of water etc.). Such mapping can help communities improve resource management, plan for the future, record and use their local knowledge, make their concerns more visible and improve communication with external organizations (e.g., government agencies). **Transect walks** involve a systematic walk following an established path crossing a project area with locals who create a transect diagram identifying concerns about a particular topic which community members and researchers later discuss.
Physiological evaluation	The response sensorimotor, cognitive and affective response to predesigned marketing stimuli is measured using technologies such as functional magnetic resonance imaging (fmri) and electroencephalography (eeg). This can be used to test a range of reactions, from discomfort and anxiety to excitement and arousal, and aims at understanding some of the biological drivers of decision making. Although many of these techniques, commonly called neuromarketing, are linked to a laboratory setting due to their technological requirements, some such as eye-tracking can be taken to the field and allow for more realistic experiments. By attaching a small camera to plain eye glasses worn by the subject while watching an advertisement or making a purchase decision, it is possible to determine what information the target audiences actually uses in the decision making process.
Pile sort	During a pile sort, the researcher asks a respondent to organize a set of items (specimens, photos of objects, names of things, etc.) Into piles according to criteria that the respondent deems relevant. After the sorting is complete, the researcher asks why the participant sorted in the chosen manner. This method can be less leading that direct questions and effective at eliciting how participants think about the items and how they relate to each other.
Policy analysis	**Analysis *of* policy** tends to be conducted by academics to explain why a policy was developed in a particular context and its intended as well as unintended consequences. Policy makers often commission **analysis *for* policy,** usually conducted on shorter time frames than most academic research. Both entail **case studies, surveys** and **statistical analysis**.
Policy sciences	A high-level approach for integrating multiple methods to comprehensively define a problem in-context, and invent and select alternative courses of action.
Q-method	Q-method enables researchers to quantify the subjective observations, opinions, and worldviews of research participants by asking them to generate a series of statements on a particular topic which they then rank against a fixed distribution. That rank-ordered list is quantitatively analyzed to identify commonalities and differences. In conservation, this approach has proven useful in mapping complex perspectives within groups, enabling them to discover common ground and ameliorate controversies.
Scanner data gathering	The use of data provided by consumers to retailers or service providers, usually as part of loyalty schemes, to track decision making behavior. This is particular powerful as these schemes also often contain demographic data.
Secondary data analysis	Secondary data is information that someone other than the researcher created. Common secondary data sources are census records, records from organizations. Researchers can use this data to reveal aggregate patterns or broad trends and make comparisons over time and across contexts.

Social science method	Description
Secondary document analysis	Secondary document analysis involves the study of documents, often found in libraries and online, containing information originally presented elsewhere, generally in **primary documents**. Secondary document analysts recognize that the authors of secondary documents interpret, evaluate, generalize, synthesize or otherwise alter the original information.
Structured decision making	Structured decision-making (sdm) provides a practical approach to collecting and organizing the knowledge and values of a group working together to identify and evaluate alternatives in the context of a complex decision. With the goals of transparency, rigor and efficiency, sdm clarifies trade-offs and uncertainties while integrating technical information with value-based deliberation.
Surveys/questionnaires	Individuals sampled from a population provide information that can be analyzed statistically. Typically, surveys assess preferences, behavior, factual information and opinions.
Synthetic analysis	Synthetic analysis involves the use of basic conceptual frameworks from ethics (including various ethical theories, environmental ethical theories, and then even some metaphysical ideas) to test people's beliefs with social science methodologies (surveys, focus groups, etc.) To understand not only what people think but why they think it and how this aligns with ethical theories. For example, this might show that people have a variety of opinions about whether or not it is okay to intervene in wilderness, or to hunt large carnivores, etc., but we can also then employ ethical frameworks to understand why – or rather to understand how these various opinions on wilderness and hunting line up with various ethical and environmental ethical predispositions.
Systematic review	A systematic review is a literature review that looks at multiple studies to find, assess, select and compile robust evidence concerning a central research question(s). Reviewers use both quantitative and qualitative methods to synthesize the data.
Textual analysis	Textual analysis is the review of texts to determine some meaning from them. **Statutory interpretation** involves examining the content of texts such as legislation and regulations to interpret their meaning, in particular to determine to what activities the law applies and authorized activities under it. Common principles of statutory interpretation include using the ordinary and plain meaning of words and reading specific provisions within the context of the statute as a whole.

Note: *Berkes, F. (2001). Sacred Ecology. New York, NY: Routledge.

Appendix 2

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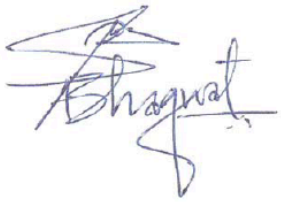
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To Whom It May Concern:

Ref 06 December 2018

During the 2011-2012 academic year Guy Western was enrolled in the MSc/MPhil in Biodiversity, Conservation and Management housed within the University of Oxford, School for Geography and the Environment. In May 2012, Guy Western initiated his research to study human-lion relationships in southern Kenya which contributed towards his Masters thesis entitled 'Buying tolerance or conflict: Conservation and Human-Lion relationships in southern Kenya". His research utilized questionnaire surveys, focus group, discussions, key informant and participant observation interviews to tease out the intricacies of human-predator relationships. As the course director I reviewed his Central University Research Ethics Committee (CUREC 1) form and authorized his research as per the departmental regulations at the time. CUREC approval numbers were not issued by the department at this time and I am hence writing confirm that his research was in accordance with the University of Oxfords ethics requirements and that he was issued with department authorization to conduct his research.

Yours sincerely,



Shonil A Bhagwat, DPhil

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Chapter 2

Creating landscapes of coexistence: Do conservation interventions promote tolerance of lions in human- dominated landscapes?

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Experimental design: GW, AJL, & AJD, Data collection: GW, AJL, & AJD, Data analysis: GW, Writing of 1st draft of manuscript: GW, Improvements to manuscript: GW, DWM, AJL, & AJD

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Abstract

The range-wide decline of lions has led to making their conservation a top priority. Protection of free ranging lion populations is dependent on securing space for lions but also on the ability and desire of local communities to coexist with lions. Our investigation takes a comparative and case study approach to explore the individual and societal desire to maintain current lion populations alongside communities in, or surrounding, Hwange National Park in Zimbabwe, Ruaha National Park in Tanzania, and Kenya's southern Maasailand. Using data from attitudinal questionnaire surveys, we compare and contrast the desire to maintain current lion populations as well as the prevalence and success of conservation interventions aimed at increasing human-lion coexistence. In Maasailand 88% of respondents expressed a desire to see current lion populations maintained. Perceptions of lions were more negative in Ruaha where 42% of respondents wished to see current lion population maintained, while in Hwange only 5% expressed this desire. More respondents reported lion depredation in Maasailand than Hwange, personal benefits from conservation were greatest in Maasailand, while exposure to conservation education was highest in Ruaha. The Hwange findings were confounded by Zimbabwe's political and economic climate. In Ruaha and Maasailand, communal and individual conservation benefit influenced desired changes to lion population. Once variation between sites was controlled for, twinning personal benefits and conservation education together was most likely to increase an individual's desire to see current lion populations maintained.

Introduction

The African lion (*Panthera leo*), an archetypal charismatic felid, has suffered a dramatic reduction in range and concurrent population decrease and now occurs in around 8% of its historic range (Riggio et al., 2013; Bauer et al., 2015a). Countries such as Tanzania, Zimbabwe, and Kenya are vital to maintaining the long term viability of Africa's free ranging lion meta-populations with five of the continent's lion strongholds (contagious areas with over 2000 lions) being fully or partially encompassed within their boundaries (Riggio et al., 2013). Human-lion conflict is ubiquitous across the lion range in Africa and considered to be one of the greatest threats to remaining lion populations, who mostly live within or surrounded by human-dominated landscapes (Lindsey et al., 2017; Loveridge et al., 2017). For viable lion populations to be maintained a degree of tolerance for, and coexistence with, lions is necessary. As defined by Bruskotter and Fulton (2012) tolerance can be considered to be the "passive acceptance of a wildlife population". Borrowing from Carter and Linnell (2016), we consider human-lion coexistence to be the sustainable cohabitation of people and lions within a shared landscape.

Human wildlife conflicts (HWC) occur when wildlife threatens peoples' livelihoods, property, or safety (Inskip & Zimmermann, 2009). Redpath et al. (2013) further identify that a clear distinction is needed between human-wildlife impact and the human to human conflicts created by conservation. Conservation interventions can often create human-human conflicts between communities, non-governmental organizations, and governments who have differing agendas (West et al., 2006; Redpath et al., 2013). Such is the case surrounding Amboseli National Park in Kenya, where Maasai pastoralists living adjacent to

the park where restricted access to grazing in the park leading to a higher stated propensity to kill lions (Hazzah et al., 2013).To understand the current state of lion conservation and human-lion coexistence requires a broader knowledge of how tolerance is created and the effects of conservation efforts aimed at promoting coexistence.

Socio-psychological theories such as the theory of planned behavior can advance our understanding of wildlife tolerance (St John et al., 2011). The wildlife tolerance model (WTM) Kansky et al. (2016) and the human-tiger tolerance model Inskip et al. (2016) are two examples of how psychological models have been used to develop models of human-carnivore tolerance. We propose that tolerance is best explained by Bruskotter and Wilson (2014) hazard acceptance model. The hazard acceptance model suggests that tolerance is determined by the interplay between five components (i) an individual's perceived control over the threat (wildlife damage), (ii) societal trust (in the management authorities), (iii) affect for the species, (iv) perceived benefits, and (v) perceived costs.

Conservation efforts aimed at promoting human-carnivore coexistence and tolerance of carnivores can be grouped into three broad approaches, namely 1) reducing depredation on livestock, 2) providing economic incentives for coexistence, and 3) creating tolerance for carnivores through conservation education.

Reduction in livestock depredation commonly involves targeted interventions that aim to improve livestock husbandry, reduce depredation, or prevent retaliatory carnivore killing (Hazzah et al., 2014; Lichtenfeld et al., 2015). Improving the quality of livestock

enclosures and livestock guarding does reduce the likelihood of lion predation (Ogada et al., 2003; Woodroffe et al., 2007). The use of guarding dogs is another way to deter livestock predation both at pasture and around livestock corals, but the effectiveness of dogs varies according to predator and context (Marker et al., 2005; Eklund et al., 2017). Local participation in lion monitoring has been shown to reduce lion killings, and foster positive perceptions of lions, but its applicability and effectives across a broader range of carnivore species and contexts has not been evaluated (Dolrenry, 2013; Hazzah et al., 2014). Despite the prevalence of initiatives aimed at reducing livestock predation through improved livestock husbandry, there is little consensus about the results or whether reducing rates of livestock depredation leads to greater tolerance of large carnivores (Miller et al., 2016).

Economic incentives for coexistence can be further classified into (i) compensation payments which offset the cost of livestock depredation, and (ii) those that provide economic incentives for coexistence with carnivores (Lindsey et al., 2007; Nelson, 2009). Compensation offsets are commonly used to offset losses incurred by depredation and are a disincentive for retaliatory killing of carnivores, but have been criticized for encouraging bad husbandry and increasing depredation rates (Ravenelle & Nyhus, 2017). In India compensation was shown to be ineffective due to barriers of corruption, wealth, and gender that prevented access (Ogra & Badola, 2008). However, donor funded private compensation schemes in Kenya which incorporated penalties for depredation resulting from poor livestock husbandry have been effective at reducing rates of retaliatory killings (Okello et al., 2014; Bauer et al., 2015b). These examples suggest that compensation

schemes require strong leadership, institutional infrastructure, and verification based on clear guidelines to be effective (Treves et al., 2009).

In countries like Kenya and Namibia community based conservation (CBC) and community based natural resource management (CBNRM) have been used to provide financial incentives which may improve coexistence with wildlife (Jones & Weaver, 2009; Western et al., 2015). This hypothetical direct connection between economic benefits and perceptions of carnivores is often complicated by existing human-human conflicts and the socio-political context (Dickman et al., 2011; Zimmermann, 2014; Inskip et al., 2016). Kleptocracy of leaders or the misappropriation of benefits by elites, and locally perceived wrong-doing by conservation organisations involved in CBC/CBNRM can compound human-wildlife conflict (Nelson et al., 2007; Goldman et al., 2013; Calfucura, 2018).

An alternate approach to providing economic incentives for coexistence are performance payments. Performance payment are made to an individual or group for achieving a predefined conservation indicator (Zabel & Engel, 2010). In Sweden, for example, performance payments fostered coexistence between livestock owners and wolverines (*Gulo gulo*) and wolves (*Canis lupus*), leading to an increase in both populations (Zabel & Holm-Muller, 2008; Persson et al., 2015). The question is whether performance payments are appropriate to the African context given challenges of equity and transparency which CBC and CBNRM have faced (Nelson, 2009; Zabel & Engel, 2010; Dickman et al., 2011).

Conservation education aimed at promoting coexistence is commonly used to increase understanding and acceptance of wildlife (Treves et al., 2006; Gore et al., 2008). Conservation education effectiveness is controversial. Schultz (2011) argues that conservation education and increased knowledge do not change an individual's behaviour which is predominantly driven by individual motivation linked to societal norms and values. For example in the United States, education campaigns were shown to have little effect on reducing bear related impacts (Baruch-Mordo et al., 2011) while, in the Philippines public education campaigns that highlighted the illegality of crocodile killing and the emphasized importance of their protection (van der Ploeg et al., 2011) succeeded in reducing the killing of crocodiles. How information on risks and benefits associated with carnivores are communicated plays a pivotal role in influencing how a species is perceived (Bruskotter & Wilson, 2014). In some cases tolerance of carnivores may actually decrease when information on how to decrease wildlife impact is communicated in isolation (Slagle et al., 2013). Communication of benefits and positive behavioural traits, on the other hand, is likely to lead to positive perceptions of carnivores (Bruskotter & Wilson, 2014). This was the case for coyotes, for which positive perceptions among school children in the United States were created by sharing positive behavioural traits of, and pictures of, coyotes (Draheim et al., 2011).

Previous studies of human-lion conflict in human-dominated landscapes conducted by Dickman (2009); Hazzah et al. (2009); Mkonyi et al. (2017), and others have investigated the drivers of conflict and perceptions of lions at specific sites. This paper aims to build on the existing body of knowledge and enhance our understanding of how different

conservation interventions influence an individual's desire to see current lion populations *maintained* or *increased* in human-dominated landscapes. By taking a comparative case study- base approach across multiple sites we provide an indication of the effectiveness of conservation interventions across three different landscapes in which humans and lions coexist. To do this we use data from attitudinal questionnaire surveys conducted in three study sites across Africa, to compare and contrast the societal and individual desire to maintain current lion populations within human-dominated landscapes. Specifically, we test the following hypotheses:

H1: Across all the three case studies respondents expressed a predominant desire to see lion populations decrease.

H2: Recent exposure to lion depredation t contributes to individual desire to see lion populations *decrease.*

H3: Perceived personal benefit from conservation promotes individual desire to see lion populations *maintained* or *increased*.

H4: Exposure to conservation education influences the desire to see lion populations *maintained* or *increased*.

Methods

Study Sites

Below we discuss case studies from three sites: Hwange National Park, Zimbabwe (Hwange), Ruaha National Park in Tanzania (Ruaha), and Kenya's southern Maasailand (Maasailand). Sites were selected based on the presence of lion populations on communal or private land outside of protected areas and the presence of conservation interventions aimed at (i) reducing livestock depredation, (ii) providing economic incentives for coexistence, and (iii) conservation education efforts.

Hwange, Zimbabwe

Hwange National Park (14,500 km^2) is located in western Zimbabwe. Surveys were conducted in two districts, Tsholotsho and Hwange, which includes 3306 km^2 of land adjacent to the National Park (Loveridge et al., 2017). Ndebele agro-pastoralists are the dominant ethnic group in Tsholotsho and the district is predominantly covered by Kalahari Sands savannah forest. Hwange District is inhabited by predominantly agro-pastoral Nambya, Tonga, Shona and Ndebele. It is made up of *Miombo* and *Mopane* woodland. Rainfall in the region is between 324-1160 mm (Loveridge et al., 2009). Very little wildlife is resident year-round in either location but temporary movement of prey populations and lions in and out of Hwange National Park is common. Hwange National Parks lion density is estimated to be 3.5 lion per 100 km^2. Lions here are part of the larger Okavango-Hwange meta-population (approx. 2300 individuals; (Riggio et al., 2013).

Ruaha, Tanzania

Surveys were conducted on village land associated with the Pawaga-Idodi Wildlife Management Area (PI-WMA), a 750 km^2 area which adjoins the south-eastern border of the Ruaha National Park (RNP) in central Tanzania. The study area is part of the Rungwa-Ruaha region, which covers over 45,000 km^2 and includes the 20,226 km^2 Ruaha National Park and its adjacent Game Reserves as well as the PI-WMA. The PI-WMA is a vital part of the Rungwa-Ruaha ecosystem, as it provides dry season habitat for many of Ruaha National Park's species (Dickman, 2005; Dickman & Marker, 2005). The Ruaha River runs along the border of RNP and is a key resource for wildlife in the area, drawing species towards the park boundary with the PI-WMA. The area is noted for its high biodiversity and species endemism (WCS, 2005). It is situated within one of the World Wide Fund for Nature's 'Global 200' ecoregions (Olson & Dinerstein, 1998), and encompasses two Important Bird Areas (WCS, 2005). The area harbours an intact array of large carnivore fauna, including the continent's third largest population of African wild dogs (*Lycaon pictus*) and is considered a priority 'hotspot' for African carnivore conservation (Mills et al., 2001; WCS, 2005). The Ruaha complex is particularly important for lions since it supports the second largest lion population in the world accounting for nearly 10% of the world's lions (Riggio et al., 2013). The area is also of international ecological significance as it is the only protected area system representing the transition between the East African *Acacia-Commiphora* zone to the Southern African *Brachystegia* or *Miombo* zone (Williams, 1999). The climate is semi-arid to arid, with approximately 500 mm of rainfall annually; rainfall seasons fall in December-January and March-April (Walsh, 2000). The vegetation is a mix of typical East African semi-arid savannah vegetation and *Zambezian*

miombo woodland, with common species including *Acacia, Combretum* and *Commiphora* (Sosovele & Ngwale, 2002).

The area is home to a heterogeneous mix of agriculturalists, agro-pastoralists and pastoralists with at least 35 tribes represented (Dickman, 2009). It is a particularly important area for pastoralists, as it forms a movement corridor linking this pastoralist rangeland with those to the north-east, north-west and south-west of the Rungwa-Ruaha system (Williams, 1999).

Maasailand, Kenya

Kenya's Maasailand is comprised of two southern counties, Kajiado and Narok. Questionnaire surveys took place in adjacent ecosystems within Kajiado County, namely the Greater Amboseli Ecosystem (GAE) (9,000 km^2) and the South Rift Ecosystem (10,000 km^2). Swamps form the ecological foundations of both systems. In the GAE, Nkongo Narok and Lonkinye swamps are key dry season concentration areas for wildlife, while Amboseli National Park covers 392 km^2 surrounding these swamps (Western, 1973). GAE is a semi-arid environment with variable annual rainfall (ranging from 132 mm to 533 mm) and variable pasture (Berger, 1993; Altmann et al., 2002). In the South Rift ecosystem, the seasonal concentration and dispersion of ungulates mirrors that of Amboseli, with ungulates concentrating in the Ewaso Nyiro swamps during the dry season. Unlike Amboseli, no national park exists within the South Rift, but two community conservancies (Olkiramatian and Shompole) have been established to promote wildlife and rangeland

conservation. Rainfall is low and variable, ranging between 200 mm and 600 mm annually (Tyrrell et al., 2017).

Maasailand has Kenya's largest lion population (approx. 800 individuals) (KsNLCT, 2008). Survey locations within each ecosystem reflected the presence of permanent lion populations on communally owned pastoral lands known as group ranches. Group ranches are governed on behalf of their membership by democratically elected group ranch committees. Mbirikani, Eselenkei and Olgulului group ranches cover 2,400 km^2 of the GAE supporting a population density of 1.3 adult lions/100 km^2 (Dolrenry, 2013). Shompole and Olkiramatian group ranches span 890 km^2 of the Southern Rift Ecosystem and sustain a lion population density of 13.6 adult lions/100 km^2 (Schuette et al., 2013). Across all five group-ranches, Maasai are the dominant ethnic group and depend on sheep, goats, and cattle as their main source of livelihood.

Survey Design

Our study is based on the Wildlife Stakeholders Acceptance Capacity (WAC) concept which indicates the "maximum wildlife population level in an area that is acceptable" (Bruskotter et al., 2015). Proposed by Decker and Purdy (1988) the WAC concept has been used across wide range of studies including Inskip et al. (2016) in their model of human-tiger tolerance in the Sundarban region of Bangladesh. Bruskotter et al. (2015) demonstrated that WAC was a reliable indicator of tolerance for wildlife and may explain the prevalence of a species within an area. WAC concepts have commonly been tested by asking individuals whether they would like to see wildlife populations increase, decrease,

or stay the same. In our study we extracted the question "What would you like to see happen to the numbers of lions in this area, and why" to provide a quantitative measure of tolerance from three independently administered and designed questionnaire surveys.

Site-specific questionnaires were designed and administered by AL in Hwange, AD in Ruaha, and by GW in Maasailand. The use of independently designed questionnaires which incorporated common questions allowed the complexity and range of human-wildlife interactions within each site to be captured and ensured that the data being collected in each case study took into account local conservation practices, cultures, and legislation. "Site" was included in fixed effect in cross site comparisons to account for site specific difference in survey administration and human-lion interactions. Surveys in southern Maasailand were adapted by GW from questions used in Hwange and Ruaha for cross-site comparison but focused more specifically on human-lion conflicts. In all sites, questionnaires were piloted on representative members of the community before deployment. Questionnaires at each site included information on (1) desired changes in lion population, (2) livestock depredation, (3) benefits accrued from conservation, (4) exposure to conservation education (Table S1). Complete questionnaires for each site can be found in Appendix S4.

Desired change in lion population

In Hwange and Kenya, responses to the question on desired changes in lion populations were grouped into four categories based on whether respondents were *unsure*, wanted to see local lion populations *decrease*, *stay the same* or *increase*. In Ruaha, responses to this

question were grouped into five categories, i.e., *disappear completely*, *decrease*, *stay the same*, *increase*, and *not sure*. To simplify comparisons, the '*disappear completely'* and '*decrease*' responses from Ruaha were combined into a single group to standardize categories across all three sites (with the final categories being *unsure*, *decrease*, *stay the same*, *increase*).

Of the 757 respondents, 31 who stated they were *unsure* were excluded from subsequent models and calculations, as it could not be ascertained whether they understood the question and the strength of their preference for any change in lion numbers was unclear. Three ordered groups (*decrease*, *stay the same*, *increase*) were created for use in site specific and inter-site cumulative link models. Ordered groups were also converted into a numeric change scale (decrease = - 1, stay same = 0, increase = + 1) to calculate mean desired change in lion populations. In all three sites, respondents were also asked an open-ended question about their reasons with answers categorized by GW based on the predominant theme of the response (Appendix 1 -Table S4).

Livestock Depredation

Data on reported depredation by lions (lion depredation) was collected during interviews. In Maasailand and Hwange respondents were asked to list the number of livestock they had lost to lions in the last year. In Ruaha the time frame for that question was a month. The number of reported lion depredation events was used as an explanatory variable to investigate variation in desired change in lion populations for each case study. For comparisons between case studies a binary (predation, no predation) was created from

reported livestock mortality during the last year in Maasailand and Hwange, and the last month in Ruaha.

Perceived Benefits from Conservation

Perceived benefits from conservation were not predefined in any of the questionnaires but left open to interpretation by the respondent. Hwange respondents were asked whether or not they had received any benefit from Hwange National Park or Communal Areas Management Programme for Indigenous Resources (CAMPFIRE), and the binary responses to each question was combined to create a benefit score (0=No Benefit, 1=CAMPFIRE or Park Benefit, 2=both CAMPFIRE and Park Benefit). To assess the impact of perceived benefits from conservation in Maasailand and Ruaha, we used identical five-point Likert scales: categories ranged from *no benefit* to *very big benefits*. Respondents in Ruaha were asked what level of personal benefit they received from the presence of carnivores. Interviewees in Kenya were asked about perceived personal benefit from lions specifically. Likert scales were converted to numeric benefit scores (*No benefit*=0, *small benefit*=1, *big benefit*=2, *very big benefit*=3). In Ruaha and Maasailand respondents who indicated they were unsure were grouped under the no benefit category. A binary metric of personal benefit from conservation (benefit/ no benefit) was created and used in cumulative link models for comparisons between case studies.

Conservation Education

Exposure to conservation education included engagement with conservation organizations, national park staff, or community conservation officers in which information relating to carnivore conservation was discussed. Respondents in Maasailand were asked if they had ever had someone come and talk to them about lion conservation. Subsequent questions asked to respondent to identify who they had engaged with and the type of engagement. In Hwange the question was phrased as whether representative from the national park had ever come to talk to them about lion conservation. To create a scale of exposure to conservation education in both Hwange and Maasailand cases, respondents who had no engagement with conservation education were scored as 0, conservation education where respondents could not recall the message as 1, and conservation education where respondents were able to recall the conservation message as 2. Interviewees in Ruaha were asked three questions pertaining to conservation education: had they experienced a wildlife video night, received a household visit, or been given any other advice by the Ruaha Carnivore Project (RCP). Responses to each question were coded on a binary scale and summed to create a conservation education exposure scale which ranged from 0 = *no exposure* to 3 = *maximum exposure*. Conservation education exposure scales were only used within case studies, while a binary metric of conservation education (*education, no education*) was used to compare differences in exposure across case studies and included in the combined cumulative link model for data from all sites.

Survey administration and sample selection

In Hwange village heads where first met with to obtain permission for the survey. At each village (24 in Mabale and Gwaai, and 56 in Tsholotsho) we aimed to interview 15% of households in large villages (~ 30-50 households) and 20% in smaller ones as a rule of thumb.

The interviewers started at one side of the village and sampled every 2nd or 3rd household until the required number of interviews had been obtained. The head of household or most senior adult present in each household was interviewed (average age of interviewees was 48 years). We interviewed approximately 15% (n=353) of all the approximately 2300-2400 households in a 30km buffer from the park boundary within our study areas.

In Ruaha, the household or *olmarei* was chosen as the sampling unit, following Maddox (2002), and interviews were restricted to one respondent per household. At each village, the chairman and/or headman was approached, the research explained, and he was then asked for locations of Maasai, Barabaig, Hehe and Bena households around that village. Once a list households and their locations had been created, 20% were randomly selected. Upon arrival at the household the most senior member of the household as asked for permission to conduct the interview and asked to participate. Women deferred to men in seniority, so interviewees were predominantly male, but interviews were conducted with women where they were happy to do so. If no-one respond of appropriate seniority was available then enumerators moved on to another randomly selected household, until the required sample size was reached. As a result, neither the selection of the household, or the individual

respondent, was not influenced in any way by previous interactions with Ruaha Carnivore Project (RCP) staff.

Everyone of appropriate seniority agreed to participate in the survey. All interviewees were adults (≥ 18 years old). Interviews were conducted in Swahili and took approximately one hour to complete with results translated into English by trained enumerators. Approximately 136 Maasai households, 56 Barabaig households, 110 Hehe households, and 68 Bena households where in the study area. Our study sampled 78% of Maasai households, 100% of Barabaig households, 74% of Bena Households, 42% of Hehe.

Questionnaires *in Maasailand* were translated into and conducted in the local language, Maa, by enumerators selected from each study area and trained by GW. Three independent back-translations into English were used to ensure that the translations were accurate. Answers to open-ended questions were recorded in English. Enumerators conducted two trial interviews prior to the commencement of the survey, and were asked to translate respondents' answers from Maa to English to gauge the enumerator's understanding of the questions and translation ability. We used homesteads (bomas) as our sampling unit. . There are approximately 1000-1100 homesteads in the settlement areas of interest. Quota sampling (Newing et al., 2011) was used to select approximately 12% of homesteads from each settlement area found within lion range. Equal numbers of women, young men (age 18-45), and elderly men (age 45+) were chosen at random from a homestead list. In cases where randomly selected respondents were unavailable, we contacted others within each location who matched our selection criteria that were identified by local chiefs. Chiefs

recommended respondents only on the basis of our age and gender criteria and who were available to be interviewed.

Data Analysis.

The Statistical Package R (version 3.3.0) was used to test trends in the data. Data for each case study and comparisons between sites were analysed separately. For each case and across case studies non-parametric Chi squared and Kruskal Wallis tests were used to determine if desired change in lion population varied between individuals with differing exposure to depredation, benefits from conservation, and conservation education. Spearman rank correlations and Pearson product moment correlations were used to assess whether correlations were present ($r > 0.7$) in ordinal and continuous predictors.

The package "*ordinal"* (Christensen, 2015) was used to create cumulative link models (clm) to test the strength of relationship between desired change in lion population and the explanatory variables. All three case studies used the same explanatory variables which were treated as numeric variables; these included personal benefit, livestock mortality, and exposure to education.

To assess the overarching relationship between desired change in lion population and exposure to three key variables (lion depredation, benefits and education) data from all three case studies were combined. Depredation, benefit, and conservation education were converted to a "Yes"/ "No" binary code to account for inter-site variation in sampling methodology and scales. Candidate models were created from a global cumulative link

model in which depredation, benefit and education were included as explanatory variables. Competing models were compared using package *MuMin* in R (Barton, 2016) based on an information theoretic approach "IT" which used Akaike's Information Criterion (AIC) corrected for small sample size (AICc) to identify the best model (Burnham & Anderson, 2004).

Results

A total of 757 surveys were collected from the three study sites (Hwange 353, Ruaha 280, Maasailand 124). *In Hwange* the 353 respondents included Ndebele (267), Nambya (77) and were predominantly male (male=53%, female =47%). The 280 respondents (male=67.5%, female=32.5%) *in Ruaha* were 107 Maasai, 59 Barabaig pastoralists, 49 Bena, and 46 Hehe agro-pastoralists. All 124 respondents *in Maasailand* were Maasai (male=70%, female =30%).

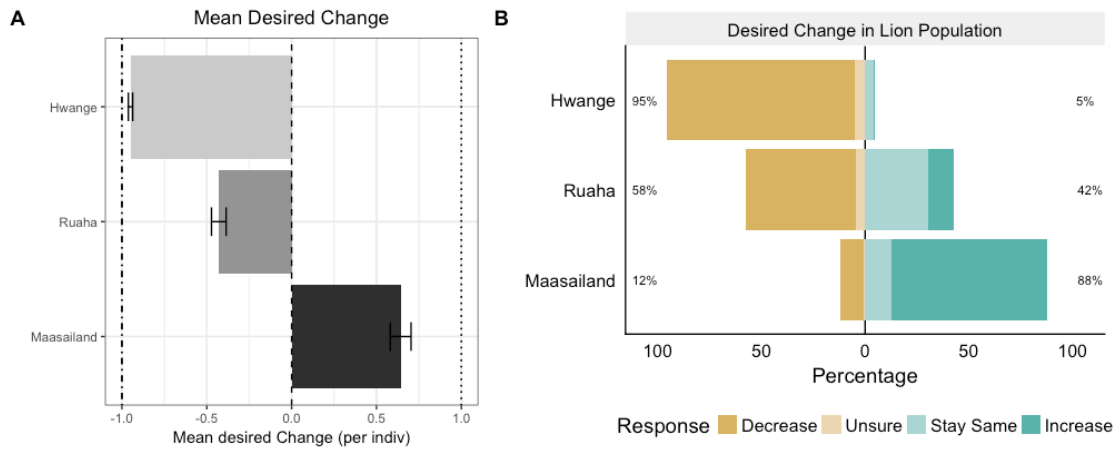


Figure 1: Bar plots depicting variation across sites in (A) reported mean desired change in lion population (-1=decrease, 0=stay the same, 1= increase), (B) Proportion of respondents in each site who wished to see lions *decrease*, *stay the same*, *increase*, or *were unsure*. Percentages on the y-axis indicate the proportion of respondents who desired populations to *stay the same* or *increase* compared to those with who wished to see lion population *decrease* or were *unsure*.

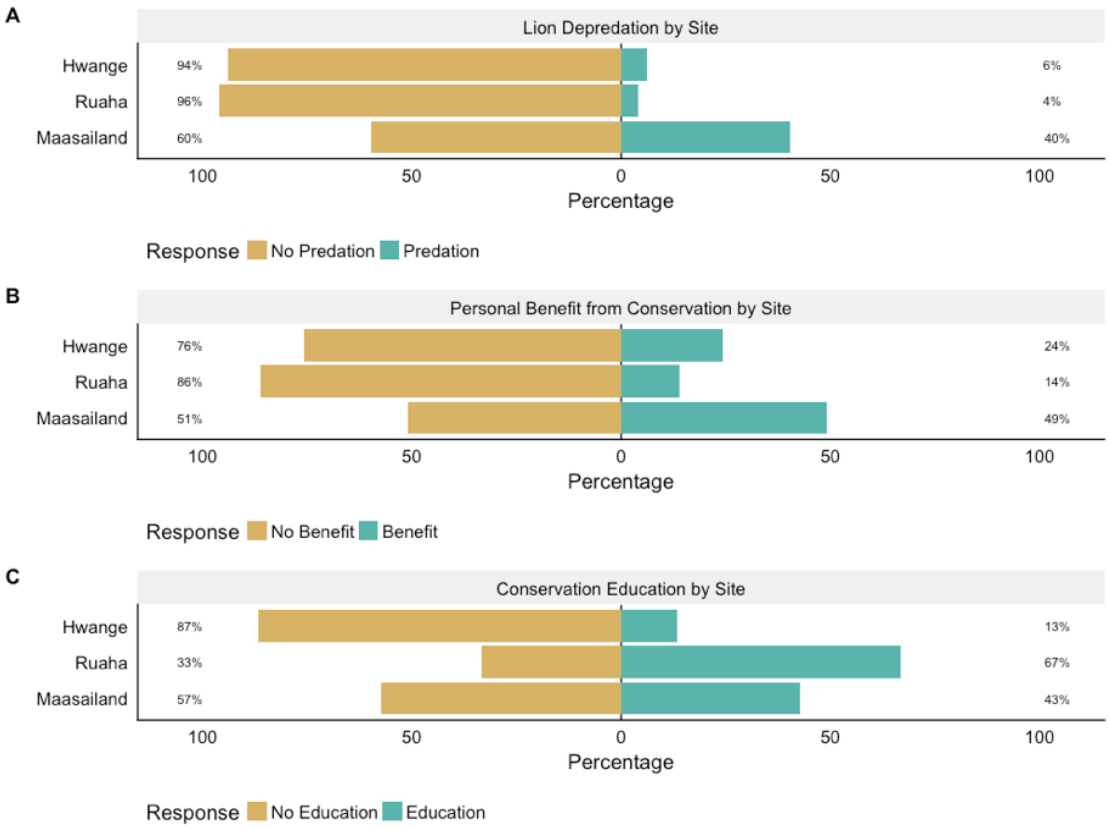


Figure 2 : Bar charts depicting the proportion for respondents who (A) reported losing livestock, (B) received personnel benefiting from conservation, (C) had been exposed to conservation education

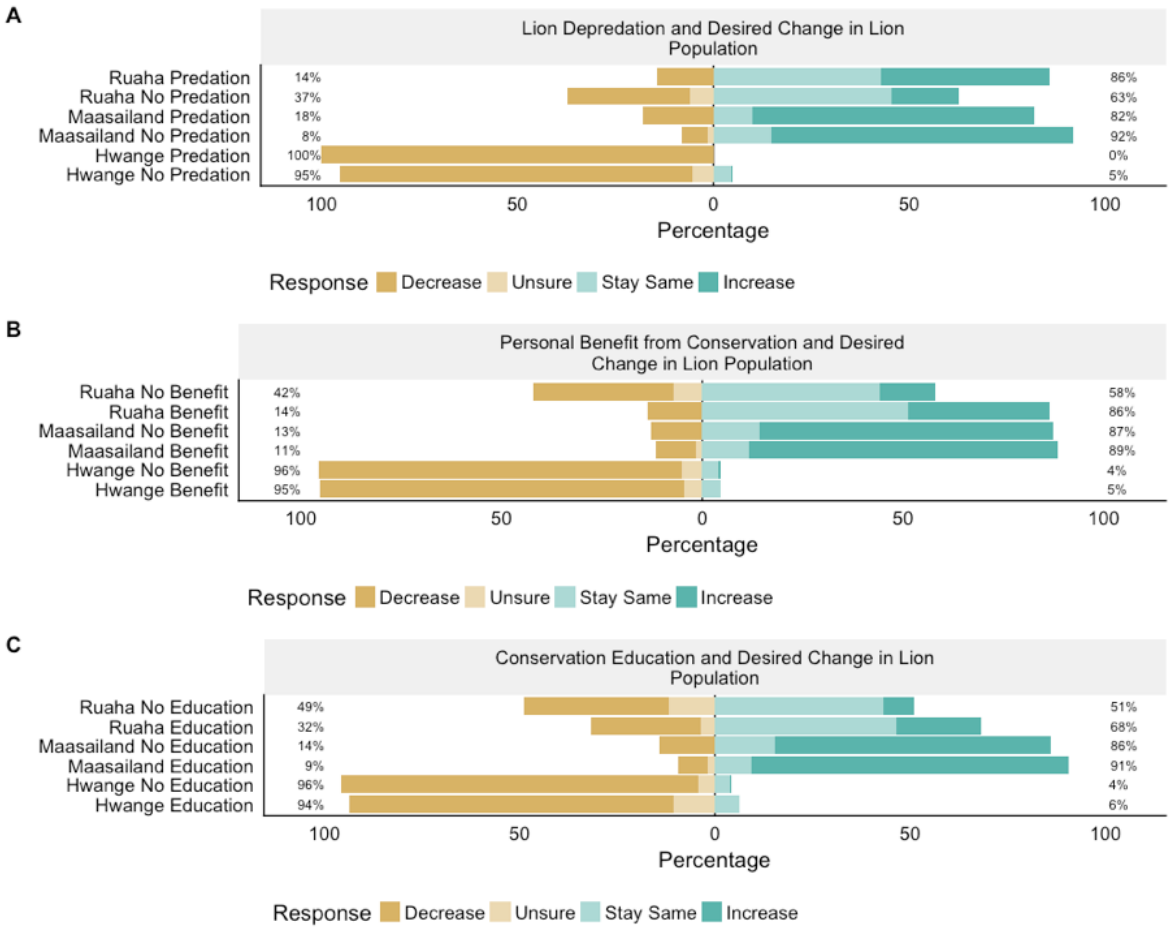


Figure 3: Bar charts depicting cross-site and intra-site variation in desired change in lion population amongst respondents in relation to their reported exposure to (A) Lion Depredation, (B) Personal Benefit from conservation, (C) Conservation Education.

Desired Change in Lion Populations

In Hwange and Ruaha respondents expressed a predominant desire to see lion populations decrease, while in Maasailand respondents primarily wanted to see lion populations increase. The variation in desired change in lion population between case studies was significant (X-squared = 254.77, df = 6, $p < 0.001$). *In Maasailand* 88.0% (n=109) of interviewees expressed a desire to see lion populations either *stay the same* (12.9%, n=16) or *increase* (75.0%, n=93) compared to 42% (n=119) *in Ruaha* and 5% (n=16) *in Hwange* (Figure 1A). In Ruaha 32% (n=91) of respondents wished to see lions *disappear completely*, but data on desired extirpation was not available for Hwange or Maasailand. The average desire of respondents to see lion populations maintained at current levels or higher was significantly (Kruskal-Wallis = 340.62, df = 2, $p < 0.001$) greater in Maasailand (0.64, SE=0.06) than in Ruaha (-0.43, SE=0.04) or Hwange (-0.95, SE=0.01) (Figure 1A).

Inter-Site Variation

Across sites there was significant variation in the proportion of respondents reporting livestock depredations (X-squared = 131.78, df = 2, p-value < 0.001), benefits received from conservation (X-squared = 174.11, df = 2, p-value < 0.001), and exposure to conservation education (X-squared = 191.13, df = 2, p-value < 0.001) (Figure 2).

Table 1: Inter and intra-site variation in the proportion of all respondents desiring to see lion decrease, stay the same or increase among groups with differing exposure to livestock predation, perceived personal benefit, and conservation education.

		Desired Change in Lion Population						
		Unsure	**Decrease**	**Stay Same**	**Increase**	**Sample Size**	**X^2**	**p-value**
Respondents who reported livestock predation								
Maasailand	No Predation	0.81%	4.03%	8.87%	45.97%	124	4.66	0.1981
	Predation	0.00%	7.26%	4.03%	29.03%			
Ruaha	No Predation	3.93%	51.43%	29.64%	11.07%	280	2.78	0.4265
	Predation	0.00%	1.79%	1.07%	1.07%			
Hwange	No Predation	5.10%	84.14%	4.25%	0.28%	353	2.50	0.4752
	Predation	0.00%	6.23%	0.00%	0.00%			
Respondents who perceived personal benefits from lion conservation								
Maasailand	No Benefit	0.00%	6.45%	7.26%	37.10%	124	1.51	0.6789
	Benefit	0.81%	4.84%	5.65%	37.90%			
Ruaha	No Benefit	3.93%	50.71%	23.93%	7.50%	280	33.91	0.025 **
	Benefit	0.00%	2.50%	6.79%	4.64%			
Hwange	No Benefit	3.97%	68.27%	3.12%	0.28%	353	0.41	0.9379
	Benefit	1.13%	22.10%	1.13%	0.00%			
Respondents who received conservation education								
Maasailand	No Education	0.00%	8.06%	8.87%	40.32%	124	3.82	0.2821
	Eduction	0.81%	3.23%	4.03%	34.68%			
Ruaha	No Education	2.14%	21.79%	7.86%	1.43%	280	14.65	0.002147 **
	Eduction	2.14%	31.43%	22.50%	10.71%			
Hwange	No Education	3.68%	79.32%	3.40%	0.28%	353	4.32	0.2285
	Eduction	1.42%	11.05%	0.85%	0.00%			

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’

Recent Exposure to Lion Depredation

Recent exposure to lion depredation influenced respondents desire to see lion populations *decrease* but the relationship was complex being both time scale and site dependent. In Maasailand and Hwange cumulative link models revealed no significant relationship between desired change in lion population expressed by respondents and recent exposure to livestock predation (Table 2). Conversely, the Ruaha cumulative link model showed a strong link and statically significant link between recent the number of livestock lost to predation in the last month and desired change in lion population (Table 2). Respondents in Ruaha who had experienced lion depredation in the last month where more likely (odd ratio =1.32) to state a desire to see lion populations decrease.

Table 2 : Site specific cumulative link models showing factors affecting desired change in lion population by case study**.**

	Desired Change in Lion Population:		
	Maasailand	Ruaha	Hwange
Lion Predation	-0.214 (0.211)	0.274(0.126)	-10.80 (1308)
	z = -1.013	z = 2.176	z= -0.008
	p = 0.196	**p = 0.030***	p = 0.993
Personal Benefit	0.413 (0.260)	0.616 (0.120)	-0.022 (0.259)
	z = 1.586	z = 5.137	z= -0.085
	p = 0.113	**p<0.01****	p = 9.3151
Conservation Education	-0.475 (0.469)	0.262 (0.147)	0.567 (0.675)
	z = -1.013	z = 1.782	z= 0.840
	p = 0.311	**p = 0.075‘’**	p = 0.400
Observations	123	178	335
Log Likelihood	-85.842	-169.878	-65.441

Signif. codes: **p<0.1; *p<0.05; ‘’ 0.10

Across all sites respondents who had not lost livestock to lion predation in the recent past did not express significantly different views from those who had (Table 2). In Hwange and Ruaha reported mean livestock mortality was not significantly higher among respondents than those who desired to see lion populations decrease (Table S1). However, in Maasailand respondents who wanted to see lion populations *increase* or *stay the same* report marginally lower livestock losses than those who wished to see them *decrease* (Kruskal-Wallis chi-squared = 7.1623, df = 3, p-value = 0.06) (Table S1).

Despite the lack of statistical relationship between lion depredation and desired change in lion population in Hwange and Maasailand, qualitative data suggest that lion predation plays a role in influencing respondents desire to see lion populations *decrease*. In Hwange, among the 90.3% (n=313) respondents who wished to see lions decrease, 52.3% (n=167) cited livestock depredation as the main reason. While the 11.2% (n=14) respondents in Maasailand who indicated that they wanted to see lion populations decrease named livestock depredation (85.7%, n=14) as the primary motivation.

Respondents from all three sites indicated that lions were responsible for substantial levels of livestock predation. *In Hwange*, 6.2% (n=22) of the 353 respondents reported lion depredation in the last year. Mean livestock mortality across all Hwange respondents was 0.23 livestock per individual per year. Of the 280 respondents *in Ruaha* 3.9% (n=11) reported lion depredations in the last month and mean rates depredation were 0.09 head of stock per individual per month. *In Maasailand* 40.3% (n=50) of the 124 respondents reported lion depredation in the last year, mean livestock mortality across all Maasailand

respondents was 0.73 head of livestock per year. Yearly depredation rates and the proportion of respondents reporting depredation were significantly lower in Hwange than in Maasailand (Wilcox Test = 27666, p-value < 0.001, Chi-square = 49.019, df = 7, p-value = < 0.001).

Perceived Benefits from Conservation

Perceived personal benefit did influence respondents desire to see lion populations *maintained* or *increased* but its ability to do so was strongly site and context specific. No relationship between perceived personal benefit and desired change in lion populations existed in Hwange. In Ruaha a strong relationship existed between perceived personal benefit and desired change in lion population, while in Maasailand a weak, non-significant relationship was present (Table 1).

In Hwange, 24.4% (n=86) of all respondents perceived personal benefits from conservation yet the majority (90.69%, n=78) still expressed a desire to see lion populations *decrease* (Figures 1 and 2). Perceived personnel benefit from CAMPFIRE and Hwange Park were closely linked, with all respondents who reported personnel benefit from CAMPFIRE also reporting receiving benefits from Hwange National Park. Of the personal benefits identified in Hwange school improvement was the most common benefit (32%, n=28), followed by borehole creation (19.8 %, n= 17) and CAMPFIRE revenue (19.8 %, n= 17).

In Ruaha, the cumulative link model (Table 2) revealed a strong positive relationship between desired change in lion population and personal benefits (Personal benefit clm: z

=5.14, $p < 0.01$; Table 3A). Those who perceived personal benefit (13.9%, n=39) from conservation were more likely (odds ratio = 1.87) to express a desire to see the lion population *maintained* or *increased*. Chi-square tests further revealed the proportion of respondents in Ruaha who desired to see lion populations *increase* was greater among respondents perceived personal benefits from conservation compared to who did not (Figure 3, Table 1). Perceived benefit from conservation in Ruaha was predominantly attributed to revenue generation from tourism (35. 9 %, n=14) and the value of being able to see lions (28.2%, n=11). However, the level of perceived benefit was low. Mean personal benefit scores for respondents in Ruaha were 0.25 per individual (Benefit scale: *No benefit*=0, *small benefit*=1, *big benefit*=2, *very big benefit*=3).

In Maasailand, 49.2% (n = 61) of all respondents perceived personal benefit from conservation. Yet the cumulative link model revealed no relationship was present between receiving personal benefit and desired change in lion population (Table 2). Respondents did associate an increase in lions with a greater potential to generate tourism revenue. When asked why they would like to see lion populations change, of the 75% (n=93) of Maasailand respondents who wanted to see lion populations *increase*, 68.8% (n=64) cited increased personal and communal benefits from wildlife as the predominant reason and 15.1% (n=14) of respondents felt lions increased tourism. Respondents in Maasailand perceived substantial benefit was accrued from conservation. Mean personal benefit scores reported by all respondents in Maasailand was 1.90 per individual (Benefit scale: *No benefit*=0, *small benefit*=1, *big benefit*=2, *very big benefit*=3). Perceived personal benefit in

Maasailand was primarily from student scholarships (40.3%, n=23), tourism revenue generation (29.0%, n=18), and employment (24.1%, n=15).

Exposure to Conservation Education

Exposure to conservation education did not create a desire to see lion populations *maintained* or *increased*. Cumulative link models revealed that in all three sites no statistically significant relationship existed between exposure to conservation education and desired change in lion populations expressed by respondents in Hwange and Maasailand, but a weak relationship existed in Ruaha (Table 2). Mean exposure to conservation education was also marginally higher (Kruskal-Wallis = 7.57, df = 3, p-value = 0.056) among respondents in Ruaha who desired to see lion populations increase (Table S1). Across the site the prevalence of conservation education varied substantially. *In Hwange* only 13.3% (n=47) of all respondents reported being exposed to conservation education compared to 66.8% (n=187) *in Ruaha,* and 42.7% (n=53) *in Maasailand* (Figure 2).

Cross-Site Predictors of Desired Lion Change

Analysis of inter-site variation (Table S3) revealed significant variation between depredation, benefit and education across sites, hence "site" was subsequently included in all cross-site candidate models as a fixed effect. Cumulative link models which included site as fixed effect and combined responses from Hwange, Ruaha, and Maasailand revealed that desired change in lion population was best predicted by a benefit and education model

(Table 3). The full model, which included exposure to depredation, personal benefit from conservation, and conservation education as binary variables, could be considered (ΔAICc= 1.89) a top model contender (ΔAICc< 2) but the AICc weight was considerably lower, indicating the model held less explanatory power than the more parsimonious benefit and education model. None of the three variables, treated in isolation, proved good predictors of the respondent's desire to see a change in lion populations.

Table 3 : Model comparison showing predictive models of desired changed in lion population across all three sites.

Model	K	logLik	AICc	AICc delta	AICc weight
Change ~ Ben + Edu	6	-342.21	696.54	0.00	0.501
Change ~ Ben + Dep + Edu	7	-342.13	698.43	1.89	0.195
Change ~ Edu	5	-344.75	699.6	3.06	0.109
Change ~ Ben	5	-344.83	699.75	3.20	0.101
Change ~ Dep + Edu	6	-344.67	701.48	4.94	0.042
Change ~ Ben + Dep	6	-344.69	701.52	4.98	0.042
Change ~ Null Model	4	-348.44	704.94	8.39	0.008
Change ~ Dep	5	-348.29	706.67	10.13	0.003

Ben=Personal and or communal benefit
Edu=Exposure to conservation education
Dep=Exposure to livestock Depredation
Null Model= Change ~ Site

Discussion

Across all three case studies respondents did not express a predominant desire to see lions decrease. Contrary to our hypothesis significant numbers of respondents in Ruaha (42%) and Kenya (88%) actually desired to see population *maintained* or *increased.* A potential limitation of our research findings are that they draw from three case studies that used three different questionnaires, that are administered in three ways and in three different study sites. The use of different questionnaires limits the ability to compare across sites but we feel this is countered by the benefit of site specific questionnaires. Use of site specific questionnaires allowed them to be designed and administered in a manner that best captured the complexity of human-lion relationships within each study site. Wildlife stakeholder acceptance capacity formed the common foundation which linked all three questionnaires in all case studies and as highlighted by Inskip et al. (2016):

"Although tolerance and its antecedents are complex, methods used to build an understanding of tolerance need not be. Simple, reliable measures of tolerance can be especially useful for large carnivore conservation as the most pressing conservation challenges associated with these species often occur in areas where illiteracy is high and numeracy is low. We show how a simple measure of tolerance based on the Wildlife Stakeholder Acceptance Capacity concept can be used to improve understanding of tolerance". (pg. 2)

In comparing across case studies our intention was to investigate whether, at its broadest scale, exposure to livestock predation, benefits from conservation, and conservation education influenced the desired change in lion population stated by respondents.

Despite lion predation being prevalent across all three cases studies, it proved to be a good predictor of an individual's desired change in lion population in only one of the three case studies. This suggests that livestock loss to lions is not the principal factor influencing the

desired change in lion population so that simply decreasing the level of livestock depredation does not necessarily reverse perceptions of lions.

Perceived benefits from conservation and conservation education played a role in fostering a desire to see populations maintained at current levels or higher but their ability to do so was also highly sites specific. This suggests that these interventions can improve tolerance of lion presence but their effects may can be confounded by a variety of factors including national wildlife and conservation policies, and pre-existing cultural beliefs, economic factors, as we explain below.

Hwange and Zimbabwe

In the case of Hwange respondents wished to see lion populations decrease. Similar attitudes towards lions were also present among respondents living around Zimbabwe's Gonarenzhou National Park (Gandiwa et al., 2013), suggesting that negative perceptions of lion may be widespread across the country. Applying Bruskotter and Wilson (2014) hazard acceptance model of tolerance to Hwange we suggest that the failure of CAMPFIRE and Zimbabwe's current political and economic state is likely to play a major part in shaping local perceptions of lions by (i) lowering social trust in wildlife management authorities, (ii) reducing the perceived and actual benefits from lions, (iii) increasing the risk/costs associated with lions.

CAMPFIRE emerged in the 1980's to cultivate the sustainable use of wildlife as an economic incentive for conservation (Alexander & McGregor, 2000; Taylor, 2009).

Though it had some initial success, CAMPFIRE has not achieved its intended aim of devolving wildlife management or generating substantial revenue from conservation (Sibanda, 2014). Sanctions placed on Zimbabwe since 2000 further stifled CAMPFIRE, decreasing its donor support from US $35 million between 1989 and 2003 to less than US $600,000 from 2003 to 2009 (Taylor, 2009). Following the 2000 sanctions revenue received by CAMPFIRE communities dropped significantly; Gandiwa et al. (2013) report that the revenue from CAMPFIRE received by Chibwedziva community (~11,000 people) adjacent to Gonarezhou National Park dropped from US $109,000 in 2001 to almost zero in 2010. The failure of CAMPFIRE is likely to have played a major role in lowering the societal trust placed in rural district councils and wildlife management authorities to deliver benefits from conservation and mitigate lion depredation.

World Bank statistics indicate that between 1997 and 2008 Zimbabwe's GDP dropped from US $8.5 billion to $4.4 billion. Surveys in Hwange were conducted in 2010. Against this back drop of economic and political hardship our results show that livestock depredation was considered a major risk to respondents around Hwange, with the majority citing predation as the principal reason for wanting lion numbers to decrease. Actual monetary losses to lion predation among these same communities totalled US $49,843 per year, leading to an average household cost of lion predation of US $79 per year (Loveridge et al., 2017). During this period of economic hardship respondent's perceptions of costs associated lion predation may have been heightened and contributing to the predominant desire to see lion populations decrease.

Ruaha and Tanzania

In Ruaha, our findings showed that just over half of respondents 53% (n=119) wanted to see lion populations decrease, indicating more tolerance of lion presence than in Hwange, but less than in Maasailand. Unlike in Hwange and Maasailand, in Ruaha, the desired change in lion populations was related to lion depredation during the last month suggesting that very recent exposure to livestock depredation influences a respondent's stated tolerance in the short term but may not have a lasting effect. As the cumulative link model for Ruaha demonstrates perceived personal benefits from conservation was the most important factor influencing the desired change in lion populations stated by respondents. Interpreting these results through the lens of the hazard acceptance model once again provides useful insight (Bruskotter & Wilson, 2014). Tanzania's political and environmental policies appears to have created a situation where respondents in Ruaha perceived very little benefit from conservation and have been disenfranchised by state centric wildlife management policies.

Tanzania's communities like those surrounding Ruaha have been alienated from their land and their resources by colonial and post-colonial government policies (Nelson et al., 2007). Starting with the creation of National Parks in the 1940's, local communities across Tanzania were repeatedly evicted to make space for protected areas (Igoe & Brockington, 1999). During the 1970's President Nyere's socialist policy known as "Ujamaa", nearly five million Tanzanians were resettled into consolidated villages leaving a lasting legacy of failed land-reform, resettlement and increased conflicts over resources such as grazing (Homewood & Rodgers, 2004). The Wildlife Conservation Act of 1974 further vested

rights over wildlife utilization to the central government, village land continued to be annexed for the expansion of national parks (Nelson, 2010). Despite the formation of wildlife management areas (WMA's) areas under the Wildlife Policy of 1998, ownership and management of wildlife in Tanzania remains focused on the State (new Wildlife Policy of 2008 and Wildlife Conservation Act of 2008). As recently as 2008 local communities were evicted from the nearby Usangu Game Reserve to allow for its inclusion in the newly expanded Ruaha National Park, continuing the legacy of evictions to create space for conservation (Benjaminsen et al., 2013; Kiwango et al., 2017).

Wildlife Management Areas (WMA) have been beset by issues such as poor governance and perceived inequalities. Communities like those around Ruaha were not actively engaged in the creation or management of WMAs, and these have not delivered significant economic benefits to the communities, thereby devaluing the importance of conservation as a livelihood and land-use option (Kiwango et al., 2017). Given this long history of elite capture and state centric management there is a strong need to increase the perceived benefits from conservation and societal trust placed in government and conservation institutions. The evidence from this study suggests that even communities like those in Ruaha who have relatively little ownership of their wildlife or natural resources can still be positive about wildlife presence if benefits are directly linked to wildlife presence. This requires benefits to reach communities directly and equitably allowing for societal trust to be generated.

Maasailand and Kenya

Viewing the Maasailand context through the hazard acceptance model reveals a possible explanation for why Maasailand was the only site where desire to see lion populations increase was the norm rather than the exception. High level perceived benefits documented in Maasailand are also complemented by a degree of social trust, affect for lions (see below), formal compensation programs and informal societal safety nets.

In Maasailand, an individual's desire for lion's populations to increase was predominantly attributed to increasing tourism revenue. This strong link between benefits from tourism and lion conservation although not statistically significant is exemplified by an interviewee who stated *"It was the community that made the decision to stop killing lions so they could reap the benefits of tourism".* In other parts of the lion range the relationship between conservation, tourism benefit, and personal benefit is not as tangible. For example, Hemson et al. (2009) showed in Botswana, tourism revenue did not accrue at the individual level and very few respondents valued tourism.

In Kenya, conservancies and community-based conservation initiatives have grown organically since the creation of the Kimana conservancy in 1997, which set a precedent for CBC in Kenya and paved the way for over 150 community conservancies that exist in Kenya today (Bedelian & Ogutu, 2017). Western (2012) demonstrated in Maasailand communities perceived ownership of lions living within their landscapes. In combination with our findings these results suggest that CBC and community conservancies in Maasailand have effectively succeeded in building societal trust in conservation by

allowing communities to both benefit from and perceive ownership of wildlife. In Hwange and Ruaha respectively, the ability of CAMPFIRE and WMA initiatives to create similar results to those seen in Maasailand may have been constrained by state-centric wildlife management and government policies which undermined societal trust. We propose more research is needed to investigate whether this interplay between perceived ownership, individual benefit, and societal trust does in fact promote a desire to see lion populations increased.

Affect has been shown to play a large part in determining tolerance for wildlife and is defined by (Bruskotter & Wilson, 2014) as "one's instinctual and emotive response to a species". In the case of Maasailand a pre-existing affect for lions may have been shaped by cultural practices and values. Among the Maasai lions are both both feared and respected often being referred to as the 'great predator', *olowaru kitok*"(Spencer, 1988). Across Maasailand lions are an important part of cultural ceremonies and male lions are actively killed during *Olamayio* hunts to demonstrate the bravery of young warriors (*illmurran)* (Goldman et al., 2013). Positive portrayals of lions are also present in Maasai folk stories in which lions protect and escort women back to their homesteads (Goldman et al., 2010). Maasai affect for lions is however difficult to categorize as demonstrated by previous ethnographic studies of Maasai which offer both positive and negative portrayals of Maasai lion-relationships (Roque de Pinho, 2009; Goldman et al., 2010). In contrast to our results from Kenya's Maasailand in the adjacent Maasai Steppe region of Northern Tanzania, 76% of Maasai respondents wished to see lions decrease or disappear completely (Mkonyi et al.,

2017), providing further evidence that Maasai affect for lions cannot be generalized and varies across political and economic landscapes.

The strong desire to see lion populations increase by respondents in Maasailand is surprising given the prevalence of livestock depredation. However, previous studies have also shown that recent livestock depredation does not necessarily influence perceptions of carnivores. One case comes from the Sunderbans region of Bangladesh where tolerance of tigers was not linked to an individual's personal experience with tigers (Inskip et al., 2016).

Formal compensation schemes for loss of livestock operated on two (Mbirikani and Olgulului) of the five group ranches. Compensation schemes on Mbirikani and Olgulului have reduced retaliatory lion killing but further research is needed to determine whether they have also influenced individuals' desire to see lions increase (Hazzah et al., 2009; Maclennan et al., 2009; Okello et al., 2014). In Maasailand the impact of livestock losses, including those from lion predation, is still commonly offset by informal and reciprocal insurance schemes known as '*stock associateship*'. Stock associates are members of your extended family or friends within the broader social network who can be called upon to donate livestock to replenish your herd after loss to drought, disease, or predation (Spencer, 1988; Galvin, 2008).

Conclusions

Although there is no single solution to resolving human-wildlife conflicts, this study suggests that positive attitudes towards lions can be maintained and promoted even

amongst those who suffer the direct costs of wildlife presence. Our results show that an individual's desire to see current lion populations maintained varied by sites and was highly context dependent. In the absence of context specific constraints, we suggest that multi-pronged efforts that provide tangible personal benefits from conservation and incorporate conservation education are more likely to foster coexistence than targeted initiatives which only utilize a single conservation tool, particularly those initiatives focused merely on reducing the carnivore depredation.

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Appendix 1

Table S1: Comparison of questions asked in the three case studies to access desired change in lion population, recent exposure to livestock depredation, and exposure to conservation education

Question	Site
Desired Change in Lion Populations	
What would you like to see happen to the numbers of the following animals (lions) in the area around your village, and why?	Hwange
What would you like to see happen to the numbers of the following animals (lions) in this area, and why?	Ruaha
What would you like to see happen to the numbers of lions in this area, and why?	Maasailand
Livestock Depredation	
How many livestock have you lost to each of the following causes (predators) in the last 12 months?	Hwange
Can you tell me a bit about the animals you lost to predators? Which Predator?	Hwange
Please fill in this information for stock at this household, for the last month: No. Lost to Large carnviores, which carnviore?	Ruaha
Please give the following information about the carnivore (lion) attacks on your livestock that occurred in the last year:	Maasailand
Benefit from Conservation	
Do you benefit from the presence of Hwange National Park? If yes, when/how?	Hwange
Have you ever benefited from the CAMPFIRE scheme? If yes, when/how?	Hwange
How much personal benefit do you receive from the presence of large carnivores in this area?	Ruaha
How much personal benefit do you receive from the presence of lions in this area?	Maasailand
Exposure to Conservation Education	
Have you ever had someone from Hwange National Park come and talk to you about the Park?	Hwange
Have you ever experienced any of the following: Wildlife video night, household visit, other depredation advice?	Ruaha
Have you ever had someone come and talk to you about lion conservation?	Maasailand

Table S2: Inter and intra-site variation in mean rates of livestock predation, personal benefit, communal benefit and exposure to conservation education amongst groups with differing desires to see lions change.

	Desired Change in Lion Population							
	Unsure	Decrease	Stay Same	Increase	Sample Size	Range	p-value	
Mean number of livestock reported killed by lions								
Maasiland	-	1.36	0.56	0.67	124	0-10	0.067	.
Ruaha	0.00	0.05	0.07	0.32	280	0-5	0.397	
Hwange	0.11	0.25	0.00	0.00	353	0-5	0.462	
Mean personal benefits received from lion conservation								
Maasiland	-	1.64	1.37	2.01	124	0-4	0.131	
Ruaha	0.00	0.14	0.40	0.74	280	0-4	< 0.001	**
Hwange	0.44	0.49	0.53	-	353	0-2	0.938	
Mean communal benefits received from lion conservation								
Maasiland	-	2.64	2.81	2.88	124	0-4	0.439	
Ruaha	0.45	0.66	0.86	1.65	280	0-4	< 0.001	**
Mean exposure to conservation education								
Maasiland	-	1.29	1.31	1.46	124	0-3	0.2856	
Ruaha	0.73	0.94	1.12	1.29	280	0-3	0.056	*
Hwange	1.28	1.12	1.20	-	353	0-3	0.2297	

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' '

Table S3: Ordinal regression results showing the interaction effect of site on education, benefit, depredation and the desire to see lions increase

Coefficients	Estimate	SE	Z-value	p-value	
BenBenefit	1.18	0.75	1.57	0.12	
DepPred	-0.41	0.43	-0.93	0.35	
EduEdu	0.65	0.46	1.42	0.15	
SiteTZ	-3.12	0.80	-3.89	0.00	***
SiteZIM	-4.66	0.82	-5.70	0.00	***
BenBenefit:SiteTZ	0.39	0.79	0.49	0.62	
BenBenefit:SiteZIM	-1.20	0.96	-1.25	0.21	
EduEdu:SiteTZ	0.11	0.54	0.21	0.83	
EduEdu:SiteZIM	-0.08	0.81	-0.10	0.92	
DepPred:SiteTZ	1.34	0.73	1.82	0.07	**
DepPred:SiteZIM	-12.66	0.00	-12145200.00	0.00	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

TZ=Ruaha

ZIM=Hwange

Table S4: List of higher order codes used to categorize responses to (i) What would you like to see happen to the numbers of lions in this area, and why? (ii) Personal benefit received from conservation (iii) Whether a clear message from conservation education engagement could be recalled.

	Desired change in lion numbers	**Example from Data**
1	General Benefit	They provide enough income
2	Employment	I am employed at the lodge
3	Livestock Depredation	They eat livestock
4	Human-Wildlife Conflict Broadly	If they increase the problem will be higher
5	Desire to See	I would like children to see
6	Ecological Balance	They help balance hyaena
7	Fear	Very dangerous
8	Park Benefit	It have benefit in the park
9	Religious	They are all created by god so they have to live like other animals
10	Tourism	If they disappear we will lack tourist attraction
11	Community Benefit Generally	To bring more benefit to the community
12	Personal Benefit/Employment	Because then my children can have jobs
	Type of benefit received	**Example from Data**
1	Tourism Revenue	Tourists are paying foreign currency when visiting the park
2	Increase Tourism	To have more tourists
3	Employment	I am employed as community scout
4	Conservation Fee/research Fees	Researchers pay to study them
5	School fees/bursaries	KWS provide school bursaries for the children
6	To see wildlife	Only to see them
7	Compensation	We get compensation when our cows are eaten
8	Building Bomas	RCP help to build my boma
9	Creation of lodges	A lodge has been built for tourists
10	Clinics	Because he is getting treatment from the dispensary that was builded by the park
11	Schools Improvement	In school premises construction
12	CAMPFIRE	Through campfire
13	Boreholes	We get a borehole in our village
	Conservation Education	**Example from Data**
1	Could not recall message of the encounter	they only where interested in looking for poachers
2	Could recall the message of the encounter	we talked about the coexistence if humans and wildlife amongst other things.

Appendix 2

Hwange Questionnaire

[All instructions to interviewer are given within square brackets]

[Introduce the study and the questionnaire. Refer to separate notes.]

Interviewer name: _____Date of interview:
SECTION 1: Personal information

1a.What is your name? _____
1b. What is your position in the household? _____
1c. What is your age? _____
1d. What is the name of the village? _____
1e. How long have you lived here? _____
1f. What is your first language? _____
1g. Level of education [None, Primary, Secondary, Tertiary]_____
1h. Record names of all people present at interview:
_____
[Record GPS location of household: _____

2a. How many people are in your household?

Position in household	Age	Sex	Living at home?
1			
2			
3			
4			
5			
6			
7			
8			
9			
10			

2b. How many houses make up the household? _____
3a. How many of the children attend school? _____
3b. How many meals does the household usually eat per day? _____
3c. How many times per week does the household eat meat? _____

4. What are the household's sources of livelihood? Please list all, giving the largest/most important first.
[List responses in code, using key below]

_____
_____
_____

1 = Livestock 2 = farming of crops 3 = Regular employment (please specify) 4 = Casual labour (please specify)	5 = Arts and crafts 6 = Other small business (please specify) 7 = hunting 8 = photographic tourism	9 = money sent home from abroad 10 = Other (please specify)

5. What do you think is the greatest threat to your livelihood?
[code using key below]

1 = Crop raiding 2 = Predators killing livestock 3 = Disease of livestock 4 = Natural deaths of livestock	5 = Accidental deaths of livestock 6 = Drought 7 = Lack of government assistance 8 = Theft of livestock	9 = Malnutrition of family 10 = Disease of family 11 = Other (specify)

SECTION 2: Crop husbandry
[ignore this section if crops not listed as source of income in question 4]

6a. Which crops do you grow?
[List all in the table below, using key below]

1 = Maize 2 = Cotton	3 = Millet 4 = Vegetables (specify which)	5 = Other (specify)

6b. What quantities of each crop do you grow? **[use information to complete table below]**
6c. When do you plant each crop? [use information to complete table below]
6d. When do you harvest each crop? **[use information to complete table below]**
6e. What measures do you take to protect each crop?
[List all in the table below, using key below]

1 = Fences 2 = Children guarding	3 = Adults guarding 4 = Repellents (specify)	5 = Other (specify)

Response grid

a. Crop	b. Amount (bags)	c. When planted	d. When harvest	e. Steps to protect	Comments [use if code 5 appears in grid]

7. In what months is it most important to protect your crops?

_____

_____

8a. How do you till your land?

Tractor		Hand hoe		Plough		Other (specify):	
- own		- own		- own		- own	
- hire		- hire		- hire		-hire	

8b. Who is responsible for tilling the land? _____

SECTION 3: Livestock husbandry
[ignore this section if livestock not listed as source of income in question 4]

9. What livestock does your household own?
Cattle: _____ Oxen: _____ Donkeys: _____ Goats: _____ Sheep: _____
Poultry: _____ Dogs: _____Other (specify): _____

10. What livestock has the household acquired in the last 12 months, and how was it acquired?

	Bought	Born	Traded	Gifts	Other (specify)
Cattle					
Oxen					
Donkeys					
Goats					
Sheep					
Dogs					
Poultry					
Other (specify):					

11a. What do you do to protect your livestock? [encourage respondent to list all measures]

_____

_____

11b. Where do livestock drink? [include distance from homestead] _____

12a. How do your livestock usually graze: [use code below to record response for each type of livestock kept]

Cattle		Goats		Poultry	
Oxen		Sheep		Other (specify):	
Donkeys		Dogs			

1 = Unattended 2 = Herded by children (go to Q12b)

3 = Herded by adults (go to Q12b) 4 = Guarded by dogs (go to Q12c)

12b. Are the guards armed in any way? [circle appropriate answer]
No / Yes If yes, what are they armed with _____

12c. If guarded by dogs, how many? _____

12d. If guarded by dogs, do you use your dogs for any other purpose?
No / Yes If yes, what purpose(s) _____

13. Do you have a boma?
No (go to Q17) Yes (go to Q14)

14a. What livestock do you put into your boma? [circle all that apply]
1 = Cattle 2 = Oxen 3 = Donkeys 4 = Goats
5 = Sheep 6 = Dogs 7 = Other
(specify)_____

14b. What are the reasons for using your boma in the wet season? [list all reasons in order of importance]

_____
_____

14c. What are the reasons for using your boma in the dry season? [list all reasons in order of importance]

_____
_____

15a. Do you use your boma more: [circle appropriate answer]
1= in the wet season than in the dry season
2= in the dry season than in the wet season
3= use same amount in wet and dry season

15b. How often do you put your livestock into your boma in the wet season? [circle appropriate answer]
5 = Every night (Go to Q16)
4 = More than once a week
3 = Less than once a week
2 = Rarely
1 = Never

15c. How often do you put your livestock into your boma in the dry season? [circle appropriate answer]
5 = Every night (Go to Q16)
4 = More than once a week
3 = Less than once a week

2 = Rarely
1 = Never

16. Can we see the boma?
[Inspect boma and complete all sections of Q16 – do not ask respondent]

16a. What is the distance to the nearest human habitation in meters? _____
16b. Where is the boma situated in relation to village? _____
16c. What is the boma made of?
1 = Poles 2 = Thorn bushes 3 = Piles of sticks
4 = Wire 5 = Other
(specify)_____

16d. Write a brief description of the boma, detailing how it is constructed and mentioning the complexity of the design.
_____
_____
_____
_____

16e. How big is the boma, in terms of internal area? **[circle closest answer]**
Small (5 x 5m) Medium (10m x 10m) Large (20m x 20m)
16f. Are there gaps in the boma?
No If no, go to Q16f
Yes If yes, go to Q16e

16g. Approximately what size are these gaps?
Small (10 cm – 20 cm) Medium (20 cm – 50 cm) Large (50 cm – 100 cm)

16h. How tall is the boma at its lowest point (in meters)? _____
16i. How thick are the boma walls on average (in meters)? _____
16j. What is the visibility through boma? **[circle closest answer]**
5 = No visibility
4 = 25% vis
3 = 50% vis
2 = 75% vis
1 = 75%+vis

16k. Which of the descriptions below best matches the construction of the boma?
5 = Strong poles
4 = Thick branches
3 = Medium branches
2 = Small branches
1 = Small hedge

16l. What is the condition of the poles? [circle as appropriate]
Treated / Untreated
Brittle / Strong

16m. How stable are the poles? [circle as appropriate]
Stable / Unstable

16n. If constructed of wire, please specify construction:
1 = Diamond mesh on poles
2 = Barbed wire (specify number of strands)_____
3 = Other (please specify) _____
[questions below to be directed to respondent]

17. If you don't bring livestock home at night, do you have: [circle appropriate answer]
1 = Armed adults sleeping with them
2 = Unarmed adults sleeping with them
3 = Armed children sleeping with them
4 = Unarmed children sleeping with them
5 = Dogs guarding them
6 = Satellite bomas
7 = No protection (left to roam)
8 = Other (specify) _____

18a. What is the furthest distance from your homestead that you graze the following livestock in the wet season? (km)
Cattle _____Oxen _____Donkeys _____ Goats
Sheep _____Other (specify) _____

18b. What is the furthest distance you graze the following livestock in the dry season? (km)
Cattle _____Oxen _____Donkeys _____ Goats _____
Sheep _____Other (specify)

18c. Do you graze your livestock in wildlife areas?
No / Yes If yes, which livestock? _____
In what months? _____
And, where and how far? [distance from homestead] _____

19. Do you graze all your livestock in one herd?
No / Yes

20. Do you group your livestock with other people's livestock?
No / Yes If yes, with how many livestock? _____

21. Do you dip your livestock?
No / Yes If yes, which livestock? _____
How frequently? _____

22. Do you vaccinate your livestock?
No / Yes If yes, which livestock?
_____
How frequently? ____ And, against what? _____

23. Do you collect and dry maize/grass for winter stock feed?
No / Yes

24. How often do you count/take stock of your livestock?

5 = every day	4 = More than once a week	3 = Less than once a week	2 = Rarely	1 = Never

25. Do any of your livestock wear bells?
No / Yes If yes, what livestock and how many?
_____
_____
26. How did your forefathers look after their livestock?
_____
_____
_____
_____

27. Do you think that practices have changed?
No / Yes If yes, why?
_____
_____
_____
SECTION 4: Wildlife in the area

28. Please tell me all of the wild animals that live in this area that you can think of:

1	**2**	**3**	**4**	**5**
6	**7**	**8**	**9**	**10**
11	**12**	**13**	**14**	**15**

[Show each animal picture card and ask the following questions:]

29a. What animal is this? [If identified incorrectly, record response]
29b. How regularly do you see this animal in your village?

29c. When was the last time you saw it?

[Use the table below to record responses]

Species	**ID?**	**X response**	**1= Daily**	**2= Weekly**	**3= Monthly**	**4 = Rarely**	**5= Never**	**Last seen**
Hyaena								
Elephant								
Lion								
Leopard								
Baboon								
Bushpig								
Genet								
Serval								
Caracal								
Python								
Wild dog								
Jackal								
Cheetah								
Kudu								
Buffalo								
Tiger								
Vervet								
Porcupine								

[Show each spoor picture card and ask the following questions:]

30a. What animal spoor is this? [If identified incorrectly, record response]

30b. How regularly do you see the spoor of this animal in this village?

2**9c. When was the last time you saw it?**

[Use the table below to record ALL responses]

Species	**ID?**	**X response**	**1= Daily**	**2= Weekly**	**3= Monthly**	**4 = Rarely**	**5= Never**	**Last seen**
Hyaena								
Elephant								
Lion								
Leopard								
Baboon								
Bushpig								
Genet								
Serval								
Caracal								
Python								
Wild dog								
Jackal								
Cheetah								
Kudu								
Buffalo								
Tiger								

Vervet								
Porcupine								

31. How much do you like the following animals, and why?

Species	5 = strongly like	4 = quite like	3 = neither like nor dislike	2 = quite dislike	1 = strongly dislike	Why?
Hyaena						
Elephant						
Lion						
Leopard						
Baboon						
Bushpig						
Genet						
Serval						
Caracal						
Python						
Wild dog						
Jackal						
Cheetah						
Kudu						
Buffalo						
Vervet						
Porcupine						

32. What would you like to see happen to the numbers of the following animals in the area around your village, and why?

Species	Increase	Decrease	Stay the same	Don't know	Why?
Hyaena					
Elephant					
Lion					
Leopard					
Baboon					
Bushpig					
Genet					
Serval					
Caracal					
Python					
Wild dog					
Jackal					
Cheetah					
Kudu					

Buffalo					

33. How important do you think it is to protect wildlife in Hwange National Park?

5 = very important	4 = quite important	3 = neither impt or unimpt	2 = quite unimportant	1 = very unimportant

34. How important do you think it is to protect wildlife in the communal lands?

5 = very important	4 = quite important	3 = neither impt or unimpt	2 = quite unimportant	1 = very unimportant

35. How do you feel about having predators in your area?

5 = very positive	4 = quite positive	3 = indifferent	2 = quite negative	1 = very negative

36. Why do you feel this way?

_____

_____

37. How often are you bothered by each of the following?
37a. When was the last time you were bothered by each of the following?

Species	**1=Daily**	**2=Weekly**	**3=Monthly**	**4 = Rarely**	**5= Never**	**Last bothered**
Hyaena						
Elephant						
Lion						
Leopard						
Baboon						
Bushpig						
Genet						
Serval						
Caracal						
Python						
Wild dog						
Jackal						
Cheetah						
Kudu						
Buffalo						

38a. Can you tell me all the ways that each animal bothers you? [record answers in table below]

38b. Is the problem better in the wet season or dry season? [record answers in table below]

Species	Destroys crops	Kills livestock	Disrupts humans	Scavenges food	Damages property	Injures humans	Other (specify)	Wet vs Dry
Hyaena								
Elephant								
Lion								
Leopard								
Baboon								
Bushpig								
Genet								
Serval								
Caracal								
Python								
Wild dog								
Jackal								
Cheetah								
Kudu								
Buffalo								

SECTION 5: Livestock losses

39a. How many livestock have you lost to each of the following causes in the last 12 months? [for each loss reported, please record which month loss occurred]

Species	Cattle	Oxen	Donkeys	Goats	Sheep	Dogs	Poultry	Month(s)
Predators								
Disease								
Natural deaths								
Accidental deaths								
Slaughter								
Sold								
Used in transaction								
Stolen								
Given as gift								
Other (specify								

39b. Can you tell me a bit about the animals you lost to predators?
[please complete table below – one row for each animal lost to a predator:]

Animal lost	Age of animal	Sex of animal	Predator	Month of loss	GPS of incident
1					
2					
3					
4					
5					
6					
7					
8					
9					

40. Do you think that killing of livestock by predators has increased, decreased or stayed the same over the past 12 months?

Increased	Decreased	Stayed the same

41. How many of each animal would you be willing to lose to predators in a year before you would take action against the predator responsible?

Cattle	Oxen	Donkeys	Goats	Sheep	Dogs	Poultry

42. Who do you think is responsible for your losses to predation, and why?

_____
_____

43. How do you think livestock can be better protected against predation?

_____
_____

44. Do you use these methods?
No / Yes **If no, why not?**
_____

45. What action do you think should be taken after livestock predation has occurred? Who do you think should take such action?

_____
_____

Section 6: Human injury

46. Has anyone in your household ever been attacked by a wild animal?
No / Yes If yes, please give details.

[please try to record the following information: name of person attacked, age of person attacked, when and where the attack happened, what the person was doing at the time, nature of the injury, type of predator, what happened to the predator]

_____
_____
_____
_____
_____
_____
_____
_____
_____
_____

47. Do you think that attacks of humans by wild animals has increased, decreased or stayed the same over the past 5 years?

Increased	Decreased	Stayed the same

SECTION 7: Crop losses

48a. How much of each crop have you lost to each of the following causes in the last 12 months (in bags)? [for each loss reported, please record which month loss occurred]

Crop	Maize	Millet	Cotton	Veg	Other (specify)	Month(s)
Trampled by animals						
Eaten by animals						
Disease						
Drought						
Theft						
Other (specify)						

48b. Can you tell me a bit more about the crops you lost to animals, through being eaten or trampled?
[please complete table below – one row for each crop (or part of crop) lost:]

Crop	Amount Damaged	Trampled or eaten	Animal responsible	Month of loss	GPS of incident
1					
2					
3					
4					
5					
6					
7					
8					
9					

49. Do you think that the number of crops lost to animals has increased, decreased or stayed the same over the past 12 months?

Increased	Decreased	Stayed the same

50. How much of each crop would you be willing to lose to animals in a year before you would take action against the animal responsible?

Maize	Millet	Cotton	Veg	Other (specify)

51. Who do you think is responsible for your crop losses to animals, and why?

_____

_____

52. How do you think crops can be better protected against animals?

_____

_____

53. Do you use these methods?
No / Yes **If no, why not?** _____

54. What action do you think should be taken after crops are lost to animals? Who do you think should take such action?

_____

_____

SECTION 8: Conservation

55a. Are you aware of the existence of Hwange National Park?
No / Yes If yes, what do you think of it?

5=Strongly like	**4=quite like**	**3=neither like nor dislike**	**2=quite dislike**	**1=strongly dislike**

55b. Why?

_____
_____
_____

56. What is the purpose of Hwange National Park? Why does it exist?

_____
_____
_____

57. Have you ever had someone from Hwange National Park come and talk to you about the Park?

No / Yes **If yes, describe the encounter:**

_____
_____
_____

58. Do you benefit from the presence of Hwange National Park?
No / Yes If yes, how? _____
59. Have you heard of the CAMPFIRE scheme?
No / Yes
60. What is the function of this scheme?

_____
_____
_____
_____

61. Have you ever benefited from the CAMPFIRE scheme?
No / Yes
If yes, when/how often: _____
How: [select from options below]

	Amount	When? [Year]	Where?
Financial (specify when & amount)			
Meat (specify when & amount)			
Building schools (When? Where?)			

Building roads (When? Where?)			
Drilling boreholes (When? Where?)			
Other (specify, include amount, when & where)			

62. Have you ever received compensation for the loss of livestock?
No / Yes
If yes, from whom?: _____
When?: _____
How much?: _____
For what loss?: _____

63. How much compensation (in US $) do you think is appropriate for the loss of a:

Cattle	Oxen	Donkey	Goat	Sheep	Dog	Poultry

64. Have you ever received compensation for the loss of crops?
No / Yes
If yes, from whom?: _____
When?: _____
How much?: _____
For what loss?: _____

65. How much compensation (in US $) do you think is appropriate for the loss of an acre of:

Maize	Millet	Cotton	Vegetables	Other (specify

66. In your opinion, are there any positive aspects of having wild animals in your area?
No / Yes
If yes, what?
_____
_____

67. In your opinion, are there any negative aspects of having wild animals in your area?
No / Yes
If yes, what?
_____
_____

68. Do you feel the benefits of having predators in your area outweigh the negative aspects?
No / Yes
Why?
_____

69. Do you think it is necessary to control the predation of livestock by wild animals?
No / Yes **If yes, which of the following methods do you think are appropriate?**
[if more than one, please rank your choices, 1 for the most preferred and so on]

Method	Rank
Improving methods for protecting livestock	
Avoiding areas with high risks	
Financial compensation	
Removing problem animals	
Eradication of predators	
Fencing the Park	
Other (specify):	

70. Do people in this household ever need to take action to control wild animals?
No / Yes
If yes, what action? _____
How often? _____
If no, why not? _____

71. Have you ever killed a wild animal yourself?
No / Yes
If yes, what kind? _____
How many? _____
When? _____
Where? _____

72. Has anyone else in the household ever killed a wild animal?
No / Yes
If yes, what kind? _____
How many? _____
When? _____
Where? _____

Ruaha Questionnaire

Boma (mzee) name _____Respondent name _____

1. Survey number	2. Date (day, month, year)	3. Interviewer(s)	4. Village	5. Subvillage

6. GPS S	7. GPS E	8. Waypoint	9. GPS used

10. Age (years)	11. Sex	12. Ethnic group	13. When did you settle at this household?	14. Religion	15. No. people at this household	16. No. adult dogs at this household

17. Have you been interviewed by this project before? Yes / No

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

	Yes	No	Rank (if needed)	Notes
Selling/exchanging livestock				
Selling crops/vegetables/grain				
Trophy hunting				
Photographic tourism				
Other (specify)				

19. How many livestock do you own? Cattle/calves _____ Smallstock _____ Donkeys _____ Other

20. Please fill in this information for stock at this household, for the last month? Month

	No. at start	No. sold	No. slaughtered	No. given away	No. stolen	No. killed by large carnivores	Large carnivores responsible	No. died from disease	No. died from other causes	What were other causes
Cattle										
Smallstock										
Donkeys										
Other										

21. Is it a good or bad thing for you, to have large carnivores living in this area (within 1 day's walk of boma)?

Very bad	Bad	Not sure	Good	Very good

Why?

_____

_____

_____

_____

22. Is it a good or bad thing for you, to have the Ruaha Carnivore Project working in this village? (select one)

Very bad	Bad	Not sure	Good	Very good

Why?_____
_____
_____
_____

23. Is the presence of Ruaha National Park good or bad for you? (select one)

Very bad	Bad	Not sure	Good	Very good

Why?_____
_____
_____
_____

24. Have you ever experienced any of the following? (circle the appropriate response)

Wildlife DVD night from RCP? Yes / No When?
_____
Household visit from RCP? Yes / No When?
_____
Gone on a Park visit with RCP? Yes / No When?
_____
Given noisemaker from RCP? Yes / No When?
_____
Had a wire boma made by RCP? Yes / No When?
_____
If yes, how useful do you think it has been? Useful / Not useful / Don't know
Other help or input from RCP? Yes / No Details if yes
_____
_____
Have you heard of the Lion Guardians programme? Yes / No
Any involvement with Lion Guardians? Yes / No Details if yes
_____
If yes, how do you feel about the Lion Guardian programme? Like / Dislike / Don't know

25. How much <u>personal</u> benefit do you receive from the presence of large carnivores in this area?

No benefits	Small benefits	Not sure	Big benefits	Very big benefits

What are these benefits (if there are any)?
_____
_____
_____
_____

26. How much benefit does your <u>household</u> receive from the presence of large carnivores in this area?

No benefits	Small benefits	Not sure	Big benefits	Very big benefits

What are these benefits (if there are any)?
_____
_____
_____
_____
_____

27. How much benefit do you think your <u>village</u> receives from the presence of large carnivores in this area?

No benefits	Small benefits	Not sure	Big benefits	Very big benefits

What are these benefits (if there are any)?

_____
_____
_____
_____
_____

28. Do you think the benefits of large carnivores to local people in this village have increased, decreased or stayed the same over the past 5 years?

Increased / Decreased / Stayed the same / Don't know

Why? What has changed?

_____
_____
_____
_____
_____
_____

29. Do you think the problems caused by large carnivores in this village have increased, decreased or stayed the same over the past 5 years?

Increased / Decreased / Stayed the same / Don't know

Why? What has changed?

_____
_____
_____
_____
_____

30. Overall, how much of a problem do you think large carnivores pose to you?

A big problem / A small problem / No problem / Don't know

Attitudes and knowledge

31. Can you sort these pictures into animals that are a big problem, small problem or no problem to you, and explain why? *(show picture cards):*

	Identification		Do you know the animal?	Does species occur here? (1 days walk?)	Problem?			Why is it a problem?
	Right Y/N	Species confused with			Big	Small	No problem	
Giraffe								
Elephant								
Hippo								
Lion								
Leopard								
Cheetah								
African wild dog								
Spotted hyaena								
Striped hyaena								
Impala								
Tiger								
Serval								
Rhino								
Crocodile								
Snake								
Buffalo								
Jackal								
Wildebeest								
Warthog								
Zebra								

32. Which animal (even if it has not been mentioned so far) causes the biggest problems to you in this area? Why (if it hasn't been explained above)?

_____
_____
_____
_____
_____
_____

33. What do you think has happened to the numbers of the following animals in this area (1 day's walk), in the time period since you came to this boma?

	Increased	Decreased	Stayed the same	Don't know
Lion				
Cheetah				
Leopard				
Spotted hyaena				
African wild dog				

34. What would you like to see happen to the numbers of the following animals in this area, and why?

	Increase	Decrease	Disappear completely	Stay the same	Don't know	Why?
Lion						
Cheetah						
Leopard						
Spotted hyaena						
African wild dog						

35. Please give the following information about the most recent carnivore attacks on your livestock:

	Lion	Cheetah	Leopard	Spotted hyaena	African wild dog
When (year and month if possible)					
Season (dry/wet)					
In bush, or at boma?					
GPS location					
Time of day					
Livestock type					
No. livestock present					
No killed					
No. injured but not killed					
Who was with the livestock?					
Was there a dog with the stock?					
Were any adults present?					
Did anyone see the attack?					
Number of predators					
Sex/age of predators					
What happened to the predator					

36. Has there ever been a large carnivore attack on a human at your household? Yes / No
37. Year of attack _____ Species of carnivore _____ Age of person attacked _____
38. No. of people killed _____ 39. No. of people injured _____

40. If your livestock is killed by a predator what is your normal response? (allow to respond, do not suggest – then circle response)?
Report to game scout (0) Hunt/kill animal (1) Poison animal (2) Scare animal (3)
Build fence (4) Change husbandry techniques (5) Leave area (6) Do nothing (7)
Other (8)

41. Attitudes (circle one response)	Strongly disagree	Disagree	Neutral	Agree	Strongly agree
a. I feel lions have the same rights as livestock to live on this land					
b. I would be happier if there were no lions					
c. I feel that lions are beautiful animals					
d. God would want me to protect all the wildlife					
e. Lions deserve protection					
f. Lions have a right to exist					
g. It is important to me that my grandchildren see lions					
h. I think there are too many lions					

42. Killing Attitudes/Subjective Norms/Behavioral Intentions	Strongly disagree	Disagree	Neutral	Agree	Strongly agree
a. Killing a lion for prestige/status is acceptable?					
b. If lions are a problem, it is acceptable to use poison on them?					
c. Most people important to me think that killing lions is admirable?					
d. Among my majarani, most would agree that it is a good to kill lions?					
e. Many people important to me would disapprove of me killing lions?					
f. If my cow was killed by a lion I will kill the lion?					
g. I will kill a lion to defend my property?					
h. If a family member was injured by a lion I would kill it?					
i. If a lion entered my boma I would kill it?					
j. When I see a lion in the bush I will kill it?					

43. Have you ever killed a large carnivore? Yes / No

44. How many have you killed? Lions _____ Cheetahs _____ Hyaenas_____ Wild dogs_____ Leopards _____

45. When was the last time you killed a large carnivore? _____

46. Why did you kill it? _____
47. How did you kill it? _____

48. Would you be willing to engage in monthly monitoring with us? Yes / No

Thank you for your participation!

Maasailand Questionnaire

I. Respondent Information:

Respondent Name:	Interviewer Name:

Survey number	Date (day, month, year)	Group Ranch	Sub location

Age (years)	Age Set	Sex	Community (Tribe)	Clan

Marital Status	Main Occupation	Main Source of Household Income	Religion	Education*

(*Education level completed - none, primary, secondary, or tertiary.)

II. Introduction

1. How long have you lived in this group ranch?

0-5 years	6-10 years	10-20 years	21-30 years	30+ years

2. Where did you come from when you came to this group ranch?

3. Why did you move?

4. Do you know what conservation is?

Yes	No

Define:

5. Who does conservation? (Tick which applies and list any others mentioned in the blank spaces)?

Communities	Government	KWS	Researchers	Tourists	Conservation organizations		

II. Lion Conservation

6. Tell us a personal story about Maasai and lions.

7. Have lion numbers in your group ranch decreased, increased, or stayed the same over the last ten years and why (indicate which one)?

Increased	Decreased	Stayed the same	Don't know	Haven't been here for 10 years

Why:

8. Are lions protected in your group ranch (if yes, list the people and organizations that help protect them)?

Yes	No

List:

9. How important do you think it is to protect lions in Kenya's National Parks (Tick which applies)?

Very important	Quite Important	neither important or unimportant	quite unimportant	very unimportant

10. How important do you think it is to protect lions on community lands (Tick which applies)?

Very important	Quite Important	neither important or unimportant	quite unimportant	very unimportant

11. Name all the groups that benefit from lions in Kenya (List all below).

12. Have you ever had someone come and talk to you about lion conservation?

Yes	No

If yes who, when, where and what was the message (for where 1=community meeting/baraza, 2= school visit, 3= Boma visit, 4 =Visit following conflict, 5=Other)

Who	**When**	**Where**	**Message**

13. How much benefit do you think **your group ranch** receives from the presence of lions in this area?

No benefits	Small benefits	Not sure	Big benefits	Very big benefits

14. Who gets the benefits from lions in **your group ranch** (list all groups and type of benefit and from whom it came)?

Group	Benefit	Whom

15. How much **personal benefit** do you receive from the presence of lions in this area**?**

No benefits	Small benefits	Not sure	Big benefits	Very big benefits

16. What types of benefit have **you** received and from whom (list all groups and type of benefit and from whom it came)?

Group	Benefit	Whom

17. What are the disadvantages of lion conservation in your area (list below)?

IV. Human-Lion Interactions

18. Have **you** ever seen a lion?

Yes	No

19. Under what circumstances have you seen lions (tick all that apply)?

Never	
When herding livestock	
Visits to national parks or conservancies	
Around the Boma at night	
When walking in the bush	
Other:	

20. How do you protect yourself from lions?

21. How do you protect your livestock from lions?

22. Do you think the problems caused by lions in this group ranch have increased, decreased or stayed the same over the past 10 years? (Tick which applies.)

Increased	Decreased	Stayed the same	Don't know	Haven't been here for 10 years

23. Why? What has changed?

24. Please give the following information about the carnivore attacks on **your** livestock that occurred in the last year:

	Lion	Cheetah	Leopard	Hyaena	African wild dog
Was it at this household or elsewhere?					
When (year and month if possible)					
Season (dry/wet)					
In bush, or at boma?					
Time of day					
Livestock type					
No. livestock present					
No killed					
No. injured but not killed					
Who was with the livestock?					
Was there a dog with the stock?					
Were any adults present?					
Did anyone see the attack?					
Number of predators					
Sex/age of predators					
What happened to the predator					

25.
26.

27. When was the last time lions were killed on this group ranch (give details of killings when it occurred, the number of lions, how they were killed)?

28. What would you like to see happen to the numbers of lions in this area, and why?

Increase	Decrease	Disappear completely	Stay the same	Don't know	Why?

29. Who do the lions in your area belong to?

30. When lions cause problems, who responds and what help is provided (List all)?

Response by who	Help provided

31. When lions cause problems who should respond and how (list all)?

Response by who	Help provided

32. Are there any questions you have for us? Any comments? (Write them below.)

Chapter 3

Ghosts in the dust: Determinants of African lion (*Panthera leo*) home range size in a human and livestock-dominated landscape

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Author contributions

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Abstract

Almost half the remaining wild lion range is outside formally protected areas as space for conservation continues to be lost. Coexistence between wildlife and people around and outside of protected areas is increasingly becoming an essential part of species conservation. Home range is useful to identify the space an animal needs, to define the area required to maintain access to food resources and ensure reproductive success. Lion home ranges are helpful to lion conservation efforts. Existing studies of lion home range have predominantly focused on lions in protected areas which are free of human disturbance. Our study assesses variation in lion home range by looking at the principal factors which dictate lion home range size in a human-dominated landscape and in response to human and livestock disturbance, as well as season. The results demonstrate that home range size for both male and female lions remained uniform despite changes in human settlement and season. Mean monthly home range size for males was 87.2 km^2 and for females was 38.6 km^2. Rainfall, cub age, and pride biomass exerted the greatest influence on female home range and prey dispersion and pride biomass dictated female core home range. Female home range was largest during periods of low rainfall, prior to cubs being weaned, when pride biomass was lowest, and during times of prey dispersion. Males' core and universal home range size was driven by changes in prey abundance and were largest during times of peak prey abundance.

Introduction

Pastoralists and wildlife have co-habited Eastern Africa's rangelands for several thousand years (Saitoti, 1978; Marshall, 1990). Starting in the early part of the 20th century the creation of Protected Areas (PA) such as the Serengeti National Park decoupled this coexistence in many domains and created a perception that wildlife and people should occupy different spheres (Adams & McShane, 1992). Over the last 50 years, however, conservation in Africa has once again undergone a major paradigm change, shifting from a singular focus on strict PAs towards initiatives like community based conservation (CBC) that strive to conserve wildlife and habitat around and outside of PA networks (Adams & Hulme, 2001; Berkes, 2004). This emergence of conservation beyond PAs parallels a broader paradigm shift in ecology. Traditional views that define "nature" and "wilderness" landscapes without people are increasingly being challenged by notions that anthropogenic disturbance has manipulated "nature" for thousands of years (Cronon, 1996; Jackson & Hobbs, 2009; Pickett et al., 2010). Many ecological studies now seek to investigate ecological processes within human-dominated landscapes and examine how large carnivores, such as tigers (*Panthera tigris),* grey wolves (*Canis lupus*), and lions (*Panthera leo*), can coexist alongside humans in shared spaces (Nyhus & Tilson, 2004; Chapron et al., 2014; Oriol-Cotterill et al., 2015).

Large iconic carnivores such as African lions are at the forefront of ecological research and conservation agendas alike (Sergio et al., 2006; Macdonald et al., 2015). Analogous to the debate over fortress protection versus community-based conservation, the precipitous decline in lion populations across Africa has catalysed differing opinions over how to prioritize their conservation. Large fenced protected areas have been

proposed by some conservationists as the only way to safeguard lion populations while others argue for maintaining unfenced meta-populations (Creel et al., 2013; Packer et al., 2013; Lindsey et al., 2014). In reality, almost half the remaining wild lion range is outside formally protected areas, so understanding how lions and people coexist is vitally important for the success of future conservation strategies (Bauer et al., 2015).

Coexistence between lions and people is contested in the literature and pastoral communities like the Maasai have been labelled both as lion killers and conservationists (Frank et al., 2006; Goldman et al., 2010; Hazzah et al., 2017). Perceptions of Maasai as lion killers emerge from the central role that ritual lion hunts play in Maasai society (Lichtenfeld, 2005; Goldman et al., 2010). Two types of lion hunts exist in Maasai culture, namely *Olamayio* and *Olkiyoi*. *Olamayio* ritual hunts are conducted by young warriors (*illmurran*) as part of male initiation. *Olkiyoi* killings are carried out in response to any lion attacks on people or livestock (Hazzah et al., 2009; Goldman et al., 2013b).

The long history of overlap between Maasai and lions is likely to have shaped lion behaviour within pastoral rangelands. Today, lions living within Eastern Africa rangelands face greater ecological perturbations than in the past such as the decline of wildlife populations against a backdrop of a growing human population and the switch from cattle to more sheep and goat livestock (Ogutu et al., 2016; Mtui et al., 2017).

Studies of lion ecology and demography within human-dominated landscapes have shown that lions use a variety of coping mechanisms, including small pride sizes and avoidance of areas of high human disturbance (Dolrenry, 2013; Schuette et al., 2013a;

Oriol-Cotterill et al., 2015). However, few studies have investigated the determinants of lion home range size within human-dominated landscapes. 'Home range' is an ecological concept which describes an animal's patterns of space use and can be considered as the area required to maintain access to food resources and ensure reproductive success (Mattisson et al., 2013). Determinants of home range size vary widely between species and contexts which is useful in ecological understanding of a species. In lions, home range size is influenced by a variety of social and ecological factors. Ranging behaviours in lions are sexually dimorphic; when males reach sexual maturity, they are forced out of their natal prides. By contrast, females remain in their natal group. Male home ranges tend to be larger than female and are predominantly driven by access to females and prey (Loveridge et al., 2009). Pride home range size is influenced by a variety of factors both social and ecological. For example, Loveridge et al. (2009) demonstrated that group size (as measured by pride biomass) was a key determinant of lioness home range size in Hwange National Park in Zimbabwe. In contrast, studies from Kruger in South Africa and Manyara National Park in Tanzania showed home range size was predominately driven by lean season prey abundance (Van Orsdol et al., 1985).

This study expands on earlier investigations within protected areas to better understand the ecological and anthropogenic determinants of lion home range within a human- and livestock-dominated landscape. To do so our study centres on three principle objectives:

1. Assess variation in lion home range size in response to increased human and livestock presence.
2. Assess seasonal variation in lion home range.

3. Ascertain the most important anthropogenic, environmental, and demographic factors influencing lion home range size. Specifically, home range size was examined in relation to settlement abundance, livestock ranging distance, rainfall, prey abundance and dispersion, cub age and pride size.

This investigation focuses on a landscape in southern Kenya where lions are still abundant within pastoral rangelands but subject to no formal protection. By doing so we hope to help guide future conservation management strategies for lions in unprotected areas which are a critically important component of their remaining range.

Methods

Study Area

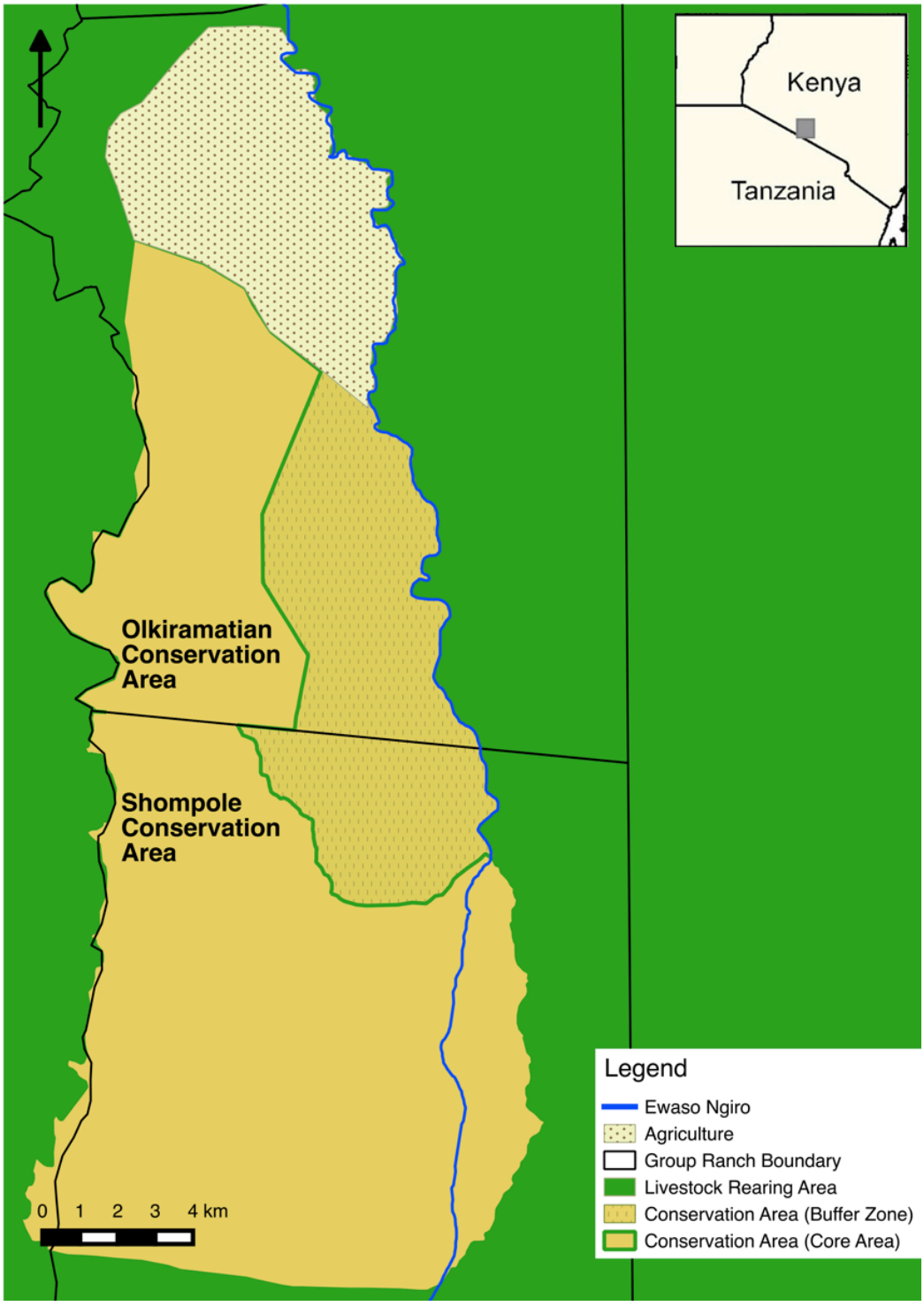


Figure 1: Map of the study area showing Olkiramatian and Shompole conservation areas, core conservancies, buffer zones, agricultural areas, and the Ewaso Nyiro River.

Research was conducted in two Maasai group ranches, Olkiramatian (270 km^2) and Shompole (620 km^2), located in southern Kenya (1°58 S, 36° 21 E). Collectively the two communities encompass a wide variety of habitats ranging from open grasslands to *Salvidora purscia* thickets. Flowing through the study area, the Ewaso Nyiro river provides a source of permanent water in what is otherwise a semi-arid region (rainfall = 200-600 mm per year) (Schuette et al., 2013a).

Land ownership in these group ranches is communal and governed by local group ranch committees who dictate settlement and grazing rules. Communal ownership and management have kept the land open, maintaining mobility and nomadic practices (Tyrrell et al., 2017). On both group ranches, Maasai communities have traditionally coexisted with wildlife. More recently they have established two adjacent conservation areas (Olkiramatian 150 km^2, Shompole 300 km^2) to further promote conservation and tourism within the area (Figure 1).

Both conservation areas are comprised of a core conservancy area and buffer zone (Figure 1). Temporary settlement is permitted in the buffer zone and was also tolerated in the core conservation area during parts of the study period (September 2014 to May 2015). Seasonal grazing occurs within the conservation areas (core conservancy and buffer) during dry months (September to March) but is tightly coordinated and controlled by local governance committees. Ordinarily during the wet months (April to August), settlement is not permitted within the core conservancy or buffer areas. Wet season settlement is confined to permanent homesteads in seven areas within the livestock rearing zone on the eastern side of the Ewaso Nyiro river (Figure 1).

Five species of large carnivore, namely African wild dog (*Lycaon pictus*), striped hyaena (*Hyaena hyaena*), spotted hyaena (*Crocuta crocuta*), cheetah (*Acinonyx jubatus*), lion and leopard (*Panthera pardus)* have been documented within the ecosystem (Schuette et al., 2013b). The ecosystem supports a significant lion population (13.6 individuals/ 100 km^2) which adapts to seasonal increases in human and livestock presence by taking refuge in the core conservation areas and denser habitat within the ecosystem (Schuette et al., 2013a).

Table 1: List of anthropogenic, environmental, and demographic variables used in model formulation.

Variable	Time Frame	Metric	Source of Data
Anthropogenic			
Settlement abundance	Monthly	Number of occupied settlements	Field data collection
Cattle ranging distance	Monthly	Maximum distance from homestead	Field data collection
Environmental			
Rainfall	Monthly	Total recorded rainfall	Field data collection
Prey Abundance	Monthly	NDVI	https://lpdaac.usgs.gov
Prey Dispersion	Monthly	Pasture biomass	Field data collection
Demographic			
Pride size	Monthly	Pride biomass	Field Data collection
Cub age	Monthly	Cub stage	Field Data collection

Lion Movements and Home Range

Between December 2011 and February 2016 African Wildlife Tracking (www.awt.co.ze) Iridium GPS radio-collars were deployed on 8 lions (4 females and 4 males) within the Shompole and Olkiramatian group ranches. Based on previous studies which demonstrated that lion prides operate as cohesive groups we considered individual movements of pride members or male coalitions to be representative of group movement (Schaller, 1972; Oriol-Cotterill et al., 2015). The number of known

resident prides within the study area fluctuated between 4 and 6, while the number of coalitions varied between 2 and 4. Due to the small number of prides occupying this study site, we were limited in the number of lions we could collar without risking pseudo replication of data. We collared 66% (n=4) of available prides and 100% (n=4) of male coalitions. Similar sample sizes have been used by Oriol-Cotterill et al. (2015); Schuette et al. (2013a); and Valeix et al. (2012) to investigate lion behaviour in human-dominated landscapes. Data from three collars were unusable either due to collar failures or lion mortality hence only data from 5 collars (2 females and 3 males) were used for analysis.

Collars were programmed to take between 4 and 6 locations within a day (24h) to optimize data quality and battery life. Spatial locations were consolidated using the statistical package *adehabtiatHR* (Calenge, 2011) in R version 3.3.4 to produce three monthly home range metrics: Brownian bridge movement models (BRB), minimum convex polygons (MCPs), and kernel density estimates (KUD). Months with less than 70 data points were removed from the data set. Brownian bridge parameters were Tmax 48hours, Lmin 50, Hmin 20. HRef values were auto-selected for KUDs, bivariate normal kernel density.

Home range was investigated at two spatial scales. Core home range was defined as the 50% isopleth, and the total (or universal) home range as the 95% isopleth (Campos et al., 2014). Brownian Bridge models (BRB) were used preferentially to KUD and MCP as they effectively address spatial auto-correlation issues by using time-ordered locations to calculate sets of nearest neighbour points (Benhamou, 2011).

Lion Demography

Data on the identity, age and sex of lions present, kills, and any other behaviours such as inter-pride encounters, and mating were collected during set weekly observations by GW and a team of four research assistants. Un-collared individuals and prides were monitored using weekly spoor surveys, spotlight transects, and opportunistic sightings (Thorn et al., 2010; Midlane et al., 2014). Whisker patterns and ear notches provided the basis for identification of un-collared lions and a database of known individuals was created and maintained to track changes in population demography and pride turnover (Pennycuick & Rudnai, 1970).

Field observations of collared and un-collared prides revealed similar pride structures (Table S5) to those documented by (Dolrenry, 2013). For each collared lioness, a monthly index of cub age was created. Cubs (less than one year) and sub-adults (>1 year and less than 24 months) were grouped into six sequential numerical categories based on age and life stage (Table S6).

Group Biomass

Lions in this study could not be weighed during the collaring, hence mean weight recorded by Loveridge et al. (2009) was used to estimate the total weight of adult lions within a pride. Cub and sub-adults weights were calculated based on Smuts et al. (1980) growth equation in which female body mass (kg) = 3.31 x age (months) + 6.64, and male body mass (kg) = 4.21x age (months) + 5.29. We calculated a 'monthly pride composition' as most common pride composition from the weekly observations over that period (Loveridge et al., 2009). Monthly pride composition was then used to

estimate the total monthly pride biomass (kg) for prides associated with each collared animal (Van Orsdol et al., 1985).

Climatic Variables

Monthly rainfall was aggregated from daily rainfall measurements recorded using HOBO UB30 automated weather station (http://www.onsetcomp.com). Median monthly rainfall (26.80mm) was further used to categorize months into two seasons (wet and dry). Dry months were defined as months with less than 28.60 mm of rainfall, and wet those receiving more than 28.60mm (approx. 3-6 a year).

Prey Abundance and Dispersion

Lions within the study areas frequently kill zebra (*Equus quagga*) and wildebeest (*Connochaetes taurinus*) (Creel et al., 2014). Drawing on these findings, prey abundance was based on zebra and wildebeest abundance. Pasture and prey abundance were monitored by Tyrrell et al. (2017) using monthly point counts and vegetation plots.

Data from Tyrrell el al., 2017 were analysed using Jolly's method 2 (Jolly, 1969) to create monthly estimates of prey abundance, but were only available from Nov 2014. Further analysis demonstrated a clear correlation (r_p=0.71, $p < 0.01$) between prey abundance (zebra and wildebeest) and grass greenness, which allowed normalized difference vegetation index (NDVI) to be used as a surrogate for prey abundance across the whole study period. To create an index of prey dispersion NDVI was extracted from

20 sites within the ecosystem using 16-day composites, and at 250m resolution, using MODIS tools in R and averaged to a create monthly estimate.

Similar to many savannah ecosystems grazer dispersion within the study area is driven by pasture abundance (Tyrrell et al., 2017; Russell et al., submitted). Herd dispersion occurring during times of peak pasture and herd concentration at low pasture (Tyrrell et al., 2017). Based on these findings biomass (grams/m^2) was used as a proxy for prey dispersion. Monthly vegetation biomass estimates were produced using a general additive model (GAM) fitted with thin plate splines, and the maximum available degrees of freedom in the package *mgcv* (Wood & Scheipl, 2017).

Human Settlement and Livestock Presence

Settlement mapping and livestock tracking were employed to ascertain the degree of human presence and likelihood of human-lion interaction. Given the highly migratory nature of pastoral communities in the study area, monthly settlement mapping identified the presence of human settlement within the core conservancy area, buffer, and wet season grazing areas. Lion presence within Olkiramatian and Shompole is predominantly limited to the core conservation areas and buffer zone (Figure 1) (Schuette et al., 2013a). Consequently, we defined these areas as core lion areas and monthly presence of settlement within them was used as a proxy for human presence. A numeric scale of monthly human presence was created based on the specific definitions. If there was any settlement in the core lion areas, the whole month were indexed as 2 while months without any settlement for part of the month were indexed as 1. Months with no human or livestock presence indexed as 0.

Livestock tracking was used to quantify the maximum daily distance from settlement that cattle travelled which provides a metric of human sphere of influence and potential livestock-lion interactions. Between April 2012 and March 2014 herders or paid observers accompanied cattle herds and tracked them for 3-6 days a month using Garmin Etrex 10 GPS units. To ensure ranging patterns across the whole study area were captured, twenty-four livestock herds were selected from seven permanent settlement areas. Because strict settlement and grazing regulations within the group ranches create considerable homogeneity in grazing patterns and spatial movements of livestock herds from specific settlement areas, movements of individual herds were considered representative of livestock patterns within a given settlement area.

Exploratory spatial analysis in QGIS version 2.8.4 was used to determine which of the study herds' movements overlapped with the seasonal and monthly ranges of collared lions or core lion areas (Figure S1). Herds failing to meet this criterion were not considered representative of livestock movement within core lion areas and excluded from further analysis. For the remaining herds, monthly ranging distance was standardized as a proportion of the herd's maximum distance from the *boma* (livestock enclosure) during the study period using the equation: *mean daily maximum distance from boma (m)/ maximum distance from boma.* Monthly ranging distances of each herd were then averaged to create a single monthly metric of cattle ranging distance.

Statistical Analysis and Model Formulation

Monthly lion home range data were grouped by sex and individual. ANOVA and t-tests were used to compare mean monthly home range as well as home range across seasons, between sexes, and collared individuals. These same statistical tests were also used to

compare mean home range during periods when settlement was present within core lion areas compared to when settlement was absent.

Linear Mixed Models (LMM) were created separately for males and females to ascertain the most important anthropogenic, environmental, and demographic factors influencing lion core and total home range size (Table 1). Female explanatory variables included rainfall, cattle ranging distance, settlement presence, pride biomass, cub age, prey abundance and prey dispersal. Male explanatory variables were rainfall, cattle ranging distance, settlement presence, prey abundance, prey dispersal, and group biomass. The number of prides collared males consorted with was not included as variables as we were unable to collect reliable on data on monthly interactions between collared males and un-collared prides.

Linear Mixed Models (LMM) explored the most important anthropogenic, environmental, and demographic factors influencing lion core and total home range size (Table 1). A subset of monthly core and total Bownian Bridge home range (BRB) estimates (June 2012 to March 2014) were extracted from the full dataset for inclusion in the models. Use of this smaller subset was necessary as livestock ranging data was only available for this period. Inter-sex variation in lion ranging behaviour necessitated monthly home range data to be grouped by sex and separate LMM were fitted to both male and female datasets using the R package *lme4* (Bates et al., 2009). Datasets were visually inspected for normality using density plots and log transformation was deemed unnecessary. For all models BRB home range was classified as the response variable, with lion identity included as random factor to account for repeated observation (Börger et al., 2006). Square root number of locations was used as a fixed effect to address the

relationship between home range size and sampling effort (Campos et al., 2014). Explanatory variables for both sexes were selected *a priori* based on the findings of Loveridge et al. (2009); Schuette et al. (2013a); Tuqa et al. (2014), and our collective experience.

Prior to inclusion in the models, all explanatory variables were assessed for multi-collinearity using variance inflation factors (VIF) in the statistical package R. Collinearity was considered to be present for any explanatory variable in which VIF > 3 (Zuur et al., 2010). Explanatory variables below the VIF threshold were then standardized using unitless Z-scores. Separate sets of male and female candidate models were created and compared using the *MuMin* package in R (Barton 2016).

Information theory "IT" based model selection using AICc and model averaging was preferentially chosen over null hypothesis theory testing by several recent home range studies by Drabik-Hamshare and Downs (2017), Bengsen et al. (2016), and Aronsson et al. (2016). To determine whether model averaging was appropriate we used posterior inclusion probabilities (PIPs) from averaged posterior plots (MAP plots) created using the *MApp* package (Banner & Higgs, 2017) as a diagnostic tool. Model ranking was subsequently based on Akaike's Information Criterion (AICc) values and the top models (ΔAICc < 2) subjected to model averaging based on partial standard deviations to determine the relative importance of explanatory variables (Cade, 2015). To calculate the amount of variation (r^2) explained by the models we used the package *r.squaredGLMM* (Nakagawa & Schielzeth, 2013).

Results

A total of 98 monthly home ranges (68 for females, 30 for males) were calculated from an average of 116 locations per month (Table S1). Male monthly universal home range (BRB95) were significantly larger than female monthly home ranges (Males 87.2 km^2 SE=9.59 km^2, range=24.4-210.8 km^2; Females 38.6 km^2 SE=1.94 km^2, range=5.35-88.5 km^2; t-test, df = 120.97, p-value = 0.01359) (Figure 2B). Similarly, average core monthly home ranges of males (mean= 14.08 km^2, SE=1.33 km^2, range=4.09-27.95 km^2) were significantly larger (t-test, df = 34.265, p-value <0.001) than those of females (mean= 7.63 km^2, SE=0.44 km^2, range=0.98-17.02 km^2).

We observed the average number of adult lionesses within collared prides was 1.38 (Table S5), demonstrating that females regularly operated as solitary individuals and cub rearing by collared females was largely the responsibility of the mother with little or no assistance from a pride. The number of prides with which collared males consorted varied between 2 and 6, but each male was only observed to consort with one of the collared prides. Hence reliable estimates of pride biomass or distribution of females associated with collared males could not be made due to the fission-fission structure of prides and cryptic nature of non-collared individuals in this population.

Table 2: Variation in monthly lion home range size by sex and (A) rainfall season, (B) settlement presence.

(A)

Season	Sex	Home Range	n	Mean	SE	Min	Max	t	p-value
Wet	F	BRB 95	25	38.62	2.61	5.35	59.19	0.02	0.98
Dry	F	BRB 95	42	38.71	12.70	13.64	88.55		
Wet	M	BRB 95	10	78.78	2.83	26.45	153.22	0.68	0.51
Dry	M	BRB 95	19	91.69	14.29	24.42	210.80		
Wet	F	BRB 50	25	8.10	0.68	0.98	16.94	-0.84	0.41
Dry	F	BRB 50	42	7.35	0.57	1.70	17.02		
Wet	M	BRB 50	10	13.94	2.54	4.84	26.72	0.68	0.95
Dry	M	BRB 50	19	14.15	1.58	4.09	27.95		

(B)

Settlement	Sex	Home Range	n	Mean	SE	Min	Max	t	p value
Absent	F	BRB 95	6	38.80	7.93	19.02	64.41	0.16	0.99
Present	F	BRB 95	61	38.66	2.00	5.35	88.55		
Absent	M	BRB 95	6	118.35	22.74	44.61	194.45	1.58	0.16
Present	M	BRB 95	23	79.12	10.12	24.42	210.80		
Absent	F	BRB 50	6	38.80	7.93	19.02	64.41	-0.64	0.55
Present	F	BRB 50	61	38.66	2.00	5.35	88.55		
Absent	M	BRB 50	6	118.35	22.74	44.61	194.45	1.00	0.34
Present	M	BRB 50	23	79.12	10.12	24.42	210.80		

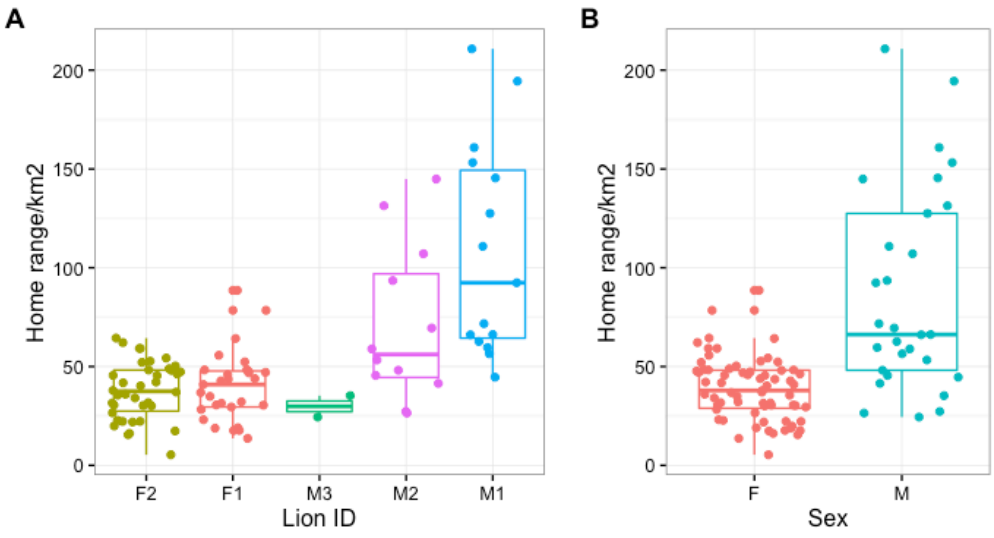


Figure 2: Variation in monthly universal Brownian bridge home range (BRB 95%) by (A) Individual (F1=yellow, F2= Red, M3=Green, M2= Purple, M1=Blue), and by (B) sex (Female= Red, Male= Green).

Variation in Home Range

For both male and female lions, mean universal home range (BRB 95) did not vary significantly between months in which human settlement was present compared to those in which settlement was absent (Table 2A; Figure 3B). Neither was there significant change in mean universal home range between wet and dry months for either sex (Table 2B; Figure 3A). Changes in male and female core home range (BRB 50) also remained relatively constant across season and changes in settlement presence (Table 2).

Female Home Range Variation

Rainfall, cattle ranging distance, settlement presence, pride biomass, cub age, prey abundance and prey dispersal were all included as explanatory variables in the linear mixed models of female home range (core and universal). VIF tests indicated that no statistically significant multicollinearity was present between explanatory variables.

Model averaging (Figure 4, Table S3) incorporated the effect of lion identity and sampling effort in all models and demonstrated that prey dispersion, followed by pride biomass were the most important variables in predicting core home range size (Figure 4). The prey dispersion model (BRB50~D) accounted for 23.1% of variance in core home range. Prey dispersion exerted a negative influence on core home range, with females' core home ranges smaller during times of prey concentration and larger during periods of prey dispersion. The pride biomass model (BRB50~P) was a poor predictor of core home range, explaining 9.4% of variance. Cub age and settlement presence were also weak determinants of core home range.

Rainfall was the most important influence on total home range size (Figure 4), with cub age and pride biomass of minor importance (Table S2). Combined with lion identity and effects of sampling effort, the rainfall model (BRB95~R) explained 22.6% of variation home range. The cub age model (BRB95~C) age explained 20.0% of variance and pride biomass model (BRB95~P) a mere 10.0% of variation. A positive relationship between pride biomass and universal home range was present, indicating that larger prides required larger home ranges. Rainfall and cub age exhibited negative relationships to universal home range, so home ranges were largest during periods of low rainfall and when young cubs were present.

Male Home Range Variation

Prey Abundance was the only factor found to determine both core and universal home ranges for males. Model selection revealed the prey abundance model (BRB95~Prey Abundance; BRB50~Prey Abundance) to be a significantly better predictor (ΔAICc < 2) of core and universal home-range than any other model (Table S3). The model explained 36.1% of variance in core home range size and 42.0% in universal home range size. Prey abundance drove the expansion of male home ranges, with largest home ranges being found during times of high prey abundance.

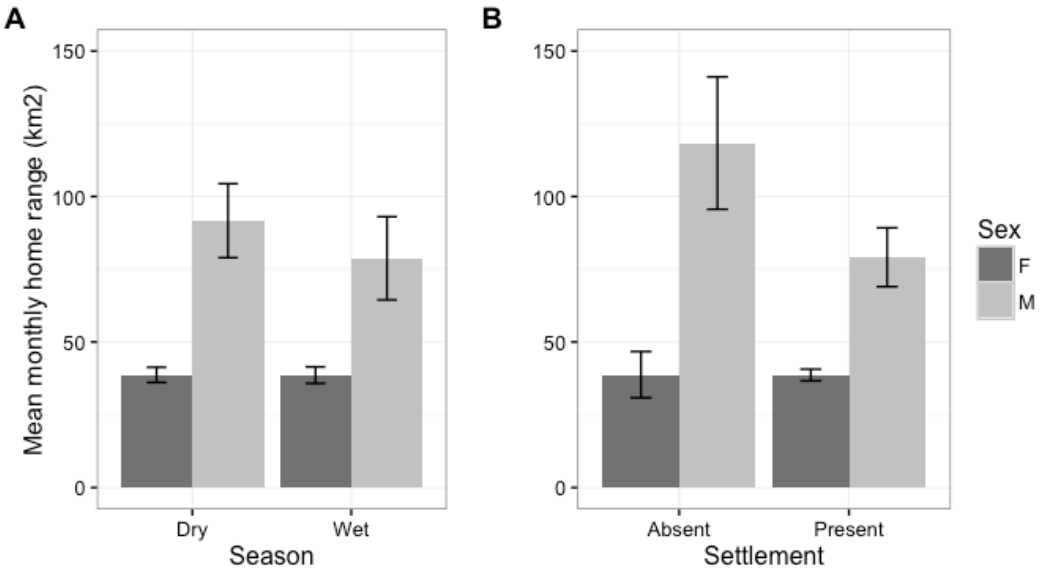


Figure 3: Variation in monthly universal brownian bridge home range (BRB 95%) by (A) season, and (B) presence of human settlement.



Figure 4: Model-averaged regression coefficients and relative variable importance for linear mixed models of lioness monthly core (BRB 50%) and universal home (BRB 95%) range size. Box width indicates 95% confidence intervals of predictor variables. Relative importance of each variable was calculated using the sum of Akaike weights for each of the candidate models in which the variable was included.

Discussion

Mean monthly universal home range sizes of prides (38.6 km^2) and coalitions (87.2 km^2) within the study area were markedly smaller than those reported for other lion populations within human dominated landscapes, namely Valeix et al. (2012a) in Botswana (monthly LoCoH estimates: Female 88km^2, Male=531km^2) and by Dolrenry (2013) in Amboseli (Annual MCP estimates: Female 375 km^2, Male 744 km^2).

Early studies by Van Orsdol et al. (1985) showed that lion home range size in Serengeti National Park was negatively correlated to lean season prey abundance. Based on this relationship between range size and prey abundance, we propose the small size of average monthly home ranges found in our study are likely a consequence of comparatively higher prey abundance found in the ecosystem as compared to home range studies that have been carried out in other human-dominated landscapes. In Olkiramatian and Shompole conservation areas, zebra (*Equus quagga*) and Grants gazelle (*Nanger granti*) densities (zebra: 11.2 individuals km^2, Grant's gazelle: 10.11 individuals km^2) are comparable to prey abundance in East African protected areas such as Maasai Mara (zebra: 10.4 individuals km^2, Grant's gazelle: 0.8 individuals km^2) and Ngorogoro (zebra: 3.2 individuals km^2, Grant's gazelle: 4.1 individuals km^2) (Schuette et al., 2016).

These small lion home ranges are consistent with small seasonal home-ranges observed in East Africa prey-abundant Protected Areas. For example, in the Mara ecosystem total pride home ranges were 23.3 km^2 (Mogensen et al. 2011), while Blackburn et al. (2016) reported mean pride home ranges between 59.5 km^2 to 149.12 km^2. In Ngorogoro Crater average pride ranges were of 87.4 km^2 (Elliott & Cowan, 1978). Similar to these

parks our study area was located in nutrient rich eutrophic or mesotrophic savannahs (high or medium nutrient soils). Nutrient rich savannahs which occur in Africa's double rainfall zones are able to support high prey densities that make smaller lion ranges possible. Conversely, southern Africa's single rainfall dystrophic savannahs with low nutrient soils such as in Hwange National Park support low prey densities which require lions to have large home ranges (KDE Home range: Female=388 km^2; Male=478 km^2) (Loveridge et al., 2009) .

Determinants of Home Range Size

Another similarity to lion populations in protected areas, is that lion home range in this study was influenced by social and ecological factors. Female universal home range was influenced by cub age, by rainfall, and marginally by pride biomass. Female core home range responded to prey dispersion and secondarily to pride biomass. By contrast, prey abundance was the sole factor affecting male core and universal home ranges. Core and universal home range sizes for males and females were unaffected by changes in livestock and human presence or livestock ranging distance.

For female lions, cub age and pride biomass were both key determinants of core and universal home range. Within our study, collared prides had one or two adult females, therefore the benefits of communal cub rearing reported by Schaller (1972) and Packer and Pusey (1983a) were largely absent. Small pride sizes (1.62 sub-adult and adult females) were also recorded by Dolrenry (2013) in the adjacent Amboseli ecosystem and appear to be typical of lion populations within pastoral landscapes. Home range size slowly decreased up to independence as young become more mobile and able to

accompany their mothers. Therefore, in the absence of communal cub rearing, cub age became a fundamental determinant of home range size.

Biomass of study prides increased slowly through time as cubs matured to independence. As young cubs grew they required more calories to meet their metabolic needs, thereby necessitating larger home ranges. The same is true elsewhere. Pride biomass has been shown to be a key determinant of range size in Hwange National Park (Loveridge et al., 2009), although pride biomass does not always dictate home range as noted by Van Orsdol et al. (1985). However, the relationship between pride biomass and range size is consistent with the broader ecological principles of expansionism proposed by Macdonald (1983) and Kruuk and Macdonald (1985).

Prey dispersion was the most important determinant of a lioness' core home range but was of little importance in determining universal home range. Expansion of core range during periods of prey dispersion in this study is consistent with the findings from West and Southern African Parks (Bauer & Iongh, 2005; Loveridge et al., 2009). The discrepancy in importance of prey dispersion as a determinant of home range at differing scales indicates that home range size maybe dictated more by the dispersion of patches of available resources than by their overall abundance (Macdonald, 1983; Carr & Macdonald, 1986). Hence pride universal home ranges were sufficiently large to maintain access to prey but prey dispersion was still a key determinant of fine-scale movement. Spatial clustering of home ranges around resource rich patches such as waterholes was also observed in Hwange (Loveridge et al., 2009; Valeix et al., 2012b). The importance of rainfall as a determinant of a lioness' universal home range within the study system lends supports to the Resource Dispersion Hypothesis (Macdonald,

1983; Macdonald & Johnson, 2015). Key resources such as prey, water, and good cover are most abundant and homogeneous during periods of high rainfall. Then, lionesses are able to maintain access to all their key resources within a small universal home range. Pasture, prey and, water resources become less abundant and unevenly distributed across the study area as rainfall decreases (Tyrrell et al., 2017). Under conditions of resource scarcity and heterogeneity, lionesses are likely to have to travel larger distance between resource patches.

Prey abundance was the sole factor affecting male home ranges. Male lion home ranges are commonly based around the need to secure food and acquire and maintain female prides (Schaller, 1972; Bygott et al., 1979). Within our study two of the collared males began to expand their territories north of the study area; while it was never confirmed we suspect they were consorting with prides that were present in this area. These periods of expansion coincided with, and were possibly facilitated by, periods of peak prey abundance when prey was readily available across the study area.

Core and universal home range sizes for males and females remained constant across dry and wet seasons, and periods of human and livestock settlement or absence. Previous studies by Schuette et al. (2013a) revealed that during periods of human settlement in the buffer zones, lions were more likely to occupy the conservation areas and increased their use of denser habitat. Where other studies have demonstrated that lions can show fine scale spatio-temporal avoidance of human locations (Oriol-Cotterill et al. 2015), and are able to modulate this further by selecting for habitat structures that offer more concealment (Schuette et al., 2013a, Oriol-Cotterill et al., 2015), our findings suggest that changes in human settlement and livestock grazing patterns can

have little effect on lions' overall access to resources on the larger home range scale. Uniform home range sizes across periods of varying human settlement observed in our study suggests that the spatial avoidance of human settlement, as demonstrated by Schuette et al. (2013a) (and also observed anecdotally in this study) did not compromise an individual lion's ability to access key resources (prey, water, vegetation cover) within the ecosystem.

Conclusions

Contrary to expectations, seasonality and anthropogenic effects such as cattle ranging distance and settlement presence had little or no effect on lion home range size. Our results demonstrate that the home range sizes of lions within the livestock- and human-dominated landscape of the Olkiramatian and Shompole are influenced by the same social and environmental factors as in protected areas (Loveridge et al., 2009). Although lions in the same area studied by Schuette et al. (2013a) avoid human settlements through an increased utilization of the conservation areas, we find that avoidance does not alter the overall home range sizes for lions. The reason is the concentration of prey species into the core conservation areas during periods of high human presence observed by Schuette et al. (2016) and Tyrrell et al. (2017) allowed lions to access prey-rich areas while simultaneously avoiding areas of high human settlement. Prides within our study system, like those in Northern Kenya, therefore seemed able to adjust their spatio-temporal patterns in ways that minimize interaction with people and maximize access to resources (Oriol-Cotterill et al., 2015).

Today in Africa, much of the lion population is outside protected areas. This creates concerns over the impact of growing human and livestock pressures. Our findings

suggest that in multi-use landscapes lion home range size is unaffected by changes in settlement and grazing patterns so long as there is sufficient year-round prey and rainfall. Therefore, establishment of conservation areas within pastoral landscapes can create key refugia for wildlife and lions extending their viability beyond protected areas. This suggests that land-use planning and conservation management needs a better understanding of ecological dynamics in order to maintain high prey and pasture abundance within multi-use landscapes.

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Appendix

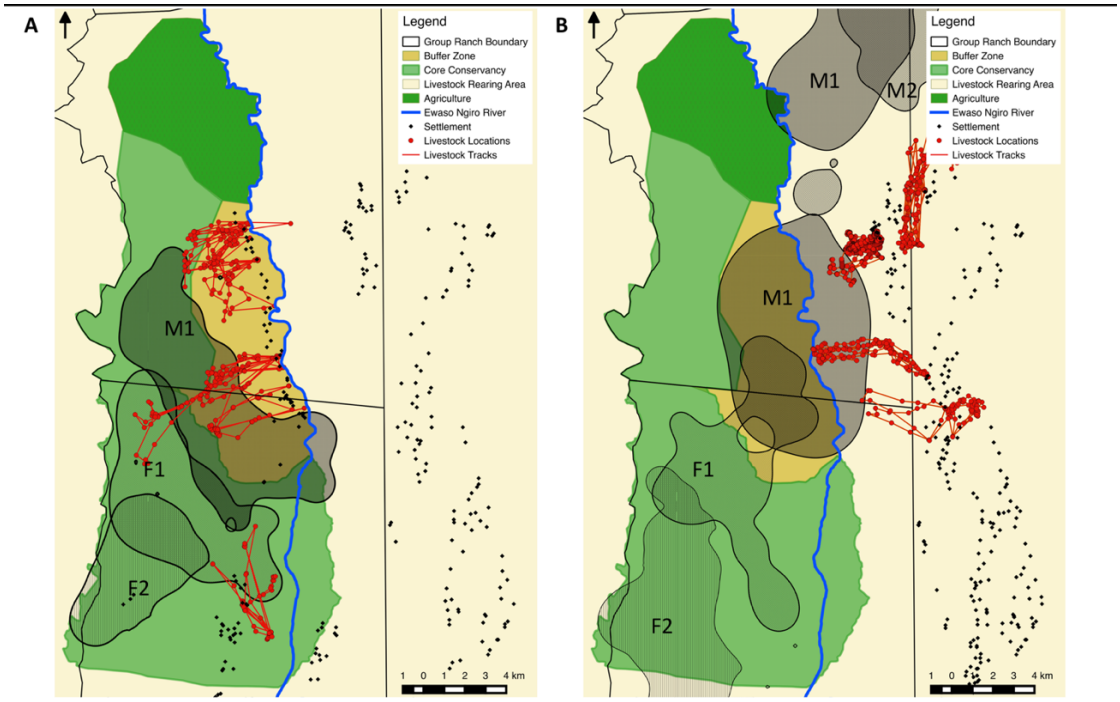


Figure S1: Maps depicting changes in lion monthly universal home range (BRB 95%) for individual lions (M1, M2, F1, F2) and livestock ranging patterns when settlement is present in the conservancies (A) and when it is absent (B).

Table S1: Summary of monthly home range estimates by sex and lion ID.

	Number of Months	Fixes Per Month	Diffusion Speed	Mean Monthly Home Range (Km2)					
				BRB .95	MCP.95	KUD.95	BRB .50	MCP.50	KUD.50
Average	98	116.1	44.5	52.5	45.9	112.3	9.4	13.4	24.5
Females	68	117.2	36.2	38.6	29.8	59.4	7.6	8.7	13.9
Males	30	113.7	63.5	87.2	82.3	232.2	14.1	23.9	48.6
Female 1	39	116.0	31.7	37.2	29.2	60.7	7.4	9.0	14.6
Female 2	29	118.9	42.2	39.9	30.5	57.7	7.8	8.4	12.8
Male 1	15	121.7	79.9	108.2	100.8	306.7	15.9	29.7	62.4
Male 2	12	114.4	53.5	70.6	75.3	185.2	13.1	21.5	40.6
Male 3	3	70.7	21.0	22.7	18.0	47.6	4.3	4.1	11.6

Table S2: Model comparison showing (A) predictive models of lioness universal home range (BRB95), and (B) variable importance calculated from model averaging using partial standard deviations.

(A) Female Universal Home Range

Model	K	logLik	AICc	delta	weight
BRB95 ~ C + R + P	7.00	-132.26	282.68	0.00	0.44
BRB95 ~ R	5.00	-136.11	284.28	1.60	0.20
BRB95 ~ D + C + R + P	8.00	-131.42	284.39	1.71	0.19
BRB95 ~ C + R	6.00	-134.74	284.48	1.80	0.18

C= Cub Stage

R= Monthly Rainfall

P= Pride Biomass

D = Prey Dispersion

S= Settlement

(B) Female Universal Home Range Variable Importance

Variable	Importance	Mean	Standard Error	Z-value	Pr(>|z|)
Rain	1.00	-4.56	2.01	2.18	0.03
Cub Age	0.80	-4.56	2.03	2.16	0.03
Pride Biomass	0.62	6.05	1.90	3.04	0.00
Prey Dispersion	0.19	-2.48	1.89	1.25	0.21

Table S3: Model comparison showing (A) predictive models of lioness core home range (BRB50), and (B) variable importance calculated from model averaging using partial standard deviations.

(A) Female Core Home Range

Model	K	logLik	AICc	delta	weight
BRB50 ~ D	5.00	-84.32	180.72	0.00	0.38
BRB50 ~ D+ P	6.00	-83.18	181.36	0.65	0.28
BRB50 ~ D+ C + P	7.00	-82.02	182.20	1.48	0.18
BRB50 ~ D+ S + P	7.00	-82.18	182.51	1.80	0.16

C= Cub Stage

R= Monthly Rainfall

P= Pride Biomass

D= Prey Dispersion

S= Settlement

(B) Female Core Home Range Variable Importance

Variable	Importance	Mean	Standard Error	Z-value	Pr(>|z|)
Prey Dispersion	1.00	-1.16	0.46	2.40	0.02
Cub Age	0.18	-0.70	0.45	1.48	0.14
Settlement Presence	0.16	-0.65	0.45	1.37	0.17
Pride Biomass	0.62	0.98	0.46	2.01	0.04

Table S4: Model comparison showing predictive models of male lion (A) universal home range (BRB95), and (B) core home range (BRB 50).

(A)

Model	K	logLik	AICc	delta	weight
BRB95 ~ Prey Abundance	5	-119.75	252.82	0	0.597
BRB95 ~ Catttle Ranging Dist + Prey Abundance	6	-119.69	256.32	3.497	0.104
BRB95 ~ Prey Abundance + Settlement	6	-119.71	256.37	3.542	0.102
BRB95 ~ Prey Dispersion + Prey Abundance	6	-119.74	256.42	3.596	0.099
BRB95 ~ Prey Abundance + Rain	6	-119.74	256.42	3.6	0.099

(B)

Model	K	logLik	AICc	delta	weight
BRB50 ~ Prey Abundance	5	-75.66	164.66	0	0.605
BRB50 ~ Prey Abundance + Settlement	6	-75.17	167.28	2.625	0.163
BRB50 ~ Catttle Ranging Dist + Prey Abundance	6	-75.41	167.76	3.107	0.128
BRB50 ~ Prey Dispersion + Prey Abundance	6	-75.61	168.17	3.51	0.105

Table S5: Monthly pride and coalition composition associated with collared lions, young under 1 year (Cubs), sub-adult females (SAF), sub-adult (SAM), adult female (AF), adult male offspring that are not yet independent (AM).

Collar ID	Month	Pride Size	Cubs	SAM	SAF	AF	AM
F2	Dec-11	8	1	5	1	1	0
F2	Jan-12	12	5	5	1	1	0
F2	Feb-12	11	4	5	1	1	0
F2	Mar-12	11	3	6	1	1	0
F2	Apr-12	11	3	6	1	1	0
F2	May-12	10	2	6	1	1	0
F1	Jun-12	9	2	1	0	1	5
F2	Jun-12	8	0	6	1	1	0
M1	Jun-12	1	0	0	0	0	1
M2	Jun-12	1	0	0	0	0	1
F1	Jul-12	9	2	1	0	1	5
F2	Jul-12	1	0	0	1	0	0
M1	Jul-12	1	0	0	0	0	1
M2	Jul-12	1	0	0	0	0	1
F1	Aug-12	3	1	1	0	0	1
F2	Aug-12	7	0	6	1	0	0
M1	Aug-12	1	0	0	0	0	1
M2	Aug-12	1	0	0	0	0	1
F1	Sep-12	3	1	1	0	0	1
F2	Sep-12	1	0	0	1	0	0
M1	Sep-12	1	0	0	0	0	1
M2	Sep-12	1	0	0	0	0	1
F1	Oct-12	3	1	1	0	0	1
F2	Oct-12	1	0	0	1	0	0
M1	Oct-12	1	0	0	0	0	1
M2	Oct-12	1	0	0	0	0	1
F1	Nov-12	3	1	1	0	0	1
F2	Nov-12	1	0	0	0	1	0
M1	Nov-12	1	0	0	0	0	1
M2	Nov-12	1	0	0	0	0	1
F1	Dec-12	3	1	1	0	0	1
F2	Dec-12	4	3	0	0	1	0
M1	Dec-12	1	0	0	0	0	1
M2	Dec-12	1	0	0	0	0	1
M4	Dec-12	1	0	0	0	0	1
F1	Jan-13	3	0	2	0	0	1
F2	Jan-13	4	3	0	0	1	0
M1	Jan-13	1	0	0	0	0	1
M2	Jan-13	1	0	0	0	0	1
M4	Jan-13	1	0	0	0	0	1
F1	Feb-13	3	0	2	0	0	1
F2	Feb-13	4	3	0	0	1	0
M1	Feb-13	1	0	0	0	0	1
M2	Feb-13	1	0	0	0	0	1
M4	Feb-13	1	0	0	0	0	1
F1	Mar-13	4	1	2	0	0	1
F2	Mar-13	4	3	0	0	1	0
M1	Mar-13	1	0	0	0	0	1

Table S5 continued

Collar ID	Month	Pride Size	Cubs	SAM	SAF	AF	AM
F1	Apr-13	3	1	0	0	0	2
F2	Apr-13	4	3	0	0	1	0
M1	Apr-13	1	0	0	0	0	1
M2	Apr-13	1	0	0	0	0	1
F1	May-13	2	0	1	0	0	1
F2	May-13	4	3	0	0	1	0
M1	May-13	1	0	0	0	0	1
M2	May-13	1	0	0	0	0	1
F1	Jun-13	2	0	1	0	0	1
F2	Jun-13	7	6	0	0	1	0
M1	Jun-13	1	0	0	0	0	1
M2	Jun-13	1	0	0	0	0	1
F1	Jul-13	2	0	1	0	0	1
F2	Jul-13	7	6	0	0	1	0
M1	Jul-13	1	0	0	0	0	1
M2	Jul-13	1	0	0	0	0	1
F1	Aug-13	2	0	1	0	0	1
F2	Aug-13	7	6	0	0	1	0
M1	Aug-13	1	0	0	0	0	1
M2	Aug-13	1	0	0	0	0	1
F1	Sep-13	2	0	1	0	0	1
F2	Sep-13	7	6	0	0	1	0
F1	Oct-13	2	0	1	0	0	1
F2	Oct-13	7	6	0	0	1	0
F1	Nov-13	2	0	1	0	0	1
F2	Nov-13	7	6	0	0	1	0
F1	Dec-13	2	0	1	0	0	1
F2	Dec-13	7	6	0	0	1	0
F1	Jan-14	2	0	1	0	0	1
F2	Jan-14	7	3	2	1	1	0
F1	Feb-14	2	0	1	0	0	1
F2	Feb-14	7	3	2	1	1	0
F1	Mar-14	2	0	1	0	0	1
F2	Mar-14	7	3	2	1	1	0
F1	Apr-14	3	3	0	0	0	0
F2	Apr-14	7	3	2	1	1	0
F1	May-14	3	3	0	0	0	0
F2	May-14	7	3	2	1	1	0
F1	Jun-14	3	3	0	0	0	0
F2	Jun-14	7	0	5	1	1	0
F1	Jul-14	3	3	0	0	0	0
F2	Jul-14	7	0	5	1	1	0
F1	Aug-14	3	3	0	0	0	0
F2	Aug-14	7	0	5	1	1	0
F1	Sep-14	3	3	0	0	0	0
F2	Sep-14	7	0	5	1	1	0
F1	Oct-14	3	3	0	0	0	0
F2	Oct-14	7	0	5	1	1	0
F1	Nov-14	3	3	0	0	0	0
F2	Nov-14	10	3	5	1	1	0

Table S5 continued

Collar ID	Month	Pride Size	Cubs	SAM	SAF	AF	AM
F1	Dec-14	3	3	0	0	0	0
F2	Dec-14	10	3	5	1	1	0
F1	Jan-15	3	3	0	0	0	0
F2	Jan-15	10	3	5	1	1	0
F1	Feb-15	3	3	0	0	0	0
F2	Feb-15	10	3	5	1	1	0
F1	Mar-15	3	3	0	0	0	0
F2	Mar-15	9	3	4	1	1	0
F1	Apr-15	3	0	0	3	0	0
F2	Apr-15	9	3	4	1	1	0
F1	May-15	3	0	0	3	0	0
F2	May-15	9	3	4	1	1	0
F1	Jun-15	3	0	0	3	0	0
F2	Jun-15	9	3	4	1	1	0
M3	Jun-15	1	0	0	0	0	1
F1	Jul-15	3	0	0	3	0	0
F2	Jul-15	9	3	4	1	1	0
M3	Jul-15	1	0	0	0	0	1
F1	Aug-15	3	0	0	3	0	0
F2	Aug-15	9	3	4	1	1	0
M3	Aug-15	1	0	0	0	0	1
F1	Sep-15	2	0	0	2	0	0
F2	Sep-15	9	3	4	1	1	0
M3	Sep-15	1	0	0	0	0	1
F1	Oct-15	2	0	0	2	0	0
F2	Oct-15	9	3	4	1	1	0
M3	Oct-15	1	0	0	0	0	1
F1	Nov-15	2	0	0	2	0	0
F2	Nov-15	4	0	1	2	1	0
F1	Dec-15	2	0	0	2	0	0
F2	Dec-15	8	3	1	2	2	0
F1	Jan-16	2	0	0	2	0	0
F2	Jan-16	8	3	1	2	2	0
F1	Feb-16	1	0	0	1	0	0

Table S6: Numeric index of cub stage categorization based on age and activity.

Code	Age (months)	Description
1	0-2	Cubs unable to accompany their mothers
2	2-8	Cubs once had begun to accompany the adults but had yet to be weaned (approx. 8 months)
3	8-12	Cubs weaned and accompany adults but not partake in hunts
4	12-16	Sub-adults begin to accompany adults and during hunts
5	16-20	Sub-adults take part and initiate hunts
6	20+	Sub-adults fully capable of independence and begin to spend time independent of their mothers

Chapter 4

To move or not to move: Changes in rangeland occupancy and livestock patterns within a lion landscape

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Abstract

East Africa's rangelands are critically important for both people and wildlife. They are home to pastoral communities like the Maasai and also support a high diversity and abundance of large mammals including threatened large carnivores like lions (*Pathera Leo*). However, rangelands are under severe threat from fragmentation and agricultural conversion which are reducing the space for both pastoralists and wildlife. If pastoral communities and wildlife populations are to be maintained within the rangeland, people and wildlife must continue to coexist as they had in the past. This study investigates two pastoral Maasai communities in southern Kenya who continue to coexist with wildlife, including lions. We assess whether pastoral mobility affects proximity to large carnivores and if the presence of carnivores within rangelands influences pastoral decision-making. We found that individual decision-making was constrained by communal governance in the form of grazing and settlement regulations which dictated where households grazed and settled. Livestock owners were aware of lion presence but gave little consideration to lions in the decision-making process. Proximity of pastoralist and their herds to lions was greatest during times of low pasture quality and quantity. During these periods, the number of settlements within the conservation areas was highest and livestock were travelling furthest from their homesteads. Only 6 of the 24 cattle herds studied spent time in areas of high lion presence to feed on pasture but this came with higher predation risk. Livestock owners used mechanisms to offset the risk of increased predation. Resource tracking, known as *Ele'enore,* was used to monitor changes in lion occupancy, water and pasture. Active guarding of livestock was used to protect them at pasture.

Introduction

East Africa's bimodal pattern of rainfall provides optimal conditions for year round milk production which allowed the emergence of milk-based pastoralism nearly 2000 years ago (Marshall, 1990). The Maasai peoples, traditionally milk-based pastoralists, are more recent immigrants to East African rangelands. Arriving around the 17th Century, they are believed to have displaced earlier Cushatic peoples and still occupy much of Kenya's rangelands (Hanotte et al., 2002; Smith, 2005; Homewood et al., 2009). A long history of co-evolution with their environment has allowed the Maasai to acquire a wealth of traditional knowledge about livestock husbandry and rangeland management (Spear & Waller, 1993; BurnSilver et al., 2004). East Africa's rangelands are also home to the highest diversity of ungulates on the planet which in turn supports a broad guild of large carnivores (Du Toit & Cumming, 1999).

Kenya's rangelands have undergone significant changes in land tenure and policy over the last 100 years but until recently remained open and communal, allowing for mobility and nomadic practices to continue (Spencer, 1988; Galvin, 2008). Starting with the formation of the Maasai Reserve in 1904, there were concerted efforts by the colonial administration to restrict pastoralists movements and replace traditional systems with livestock practices that were considered to be more productive (Sindiga, 1984; Mwangi & Ostrom, 2009). Shortly after independence, communal pastoral rangelands were granted new legal standing under the Group Ranch Act of 1968 which assigned land titles to predefined communities (Government of Kenya, Act. 237,1968). Group ranch committees, composed of elected group ranch members, act as a form of local governance, dictating land-use within the

ranch (Western & Nightingale, 2004; Mwangi, 2007). Despite the Group Ranch Act there has been continual and increasing political and economic pressure for pastoralists to settle. Beginning of the late 1970s, government policy again actively sought to privatize communally owned rangeland as a mechanism for improving and commercializing livestock production (Kimani & Pickard, 1998). Pressure to subdivide communal rangelands continued to build in the 1980's when World Bank structural adjustment programs in Kenya began a country-wide push for individual land titles. Over the last 20 years economic and urban growth has also led to land subdivision, privatisation, and agricultural conversion, reducing and fragmenting existing rangelands and decreasing the space for both pastoralists and wildlife (Mwangi, 2007; Herrera et al., 2014).

Within Kenya's remaining southern rangelands, Maasai livestock practices along with their cultural perceptions of the value of wildlife are thought to create an individual and societal tolerance for coexistence with wildlife including large carnivores (Lichtenfeld, 2005; Goldman et al., 2010). Perceptions of a wildlife species are created through cultural models defined by Bennardo and De Munck (2014) as "mental representations shared by members of a culture". These mental representations function both to make sense of and interpret sensory input andalso to produce and shape purposive and communicative behaviors". Cultural models of wildlife develop over time based on a combination of personal experiences, traditional societal conceptions, and cultural values (Decker & Purdy, 1988; Inskip et al., 2016). For Maasai pastoralists, their cultural models of mobility and livestock husbandry influence decision making and affect livestock health and predation risk, as well as human well-being (Western & Finch, 1986).

Like other pastoral groups the Maasai use a wide variety of strategies to maintain mobility and maximize livestock health (Niamir-Fuller & Turner, 1999). One such method is the use of "*scouts"*, members of the community who are dispatched to assess availability and quality of key resources such as water and pasture as well as collecting information on risks associated to livestock health and security prior to a move. The information brought back by the *scouts* helps herd-owners decide where and how to graze their livestock (Hollis, 1905; Butt, 2010).

Among the Maasai, as in many other livestock cultures, husbandry and herding decisions and risk management are influenced by an array of social and environmental considerations. Pastoralists in Mali planned their daily grazing to diversify forage intake, while simultaneously minimizing drought stress on livestock and maximizing social interactions with other herders (Turner, 1999). Among Fulani pastoralists in West Africa, herd movements were based on accessing water and pasture while avoiding teste fly areas (Bassett, 1986). Maasai pastoral mobility, decision-making and landscape utilisation have been extensively studied by Homewood et al. (1987), Niamir-Fuller and Turner (1999), and Butt (2010). Maasai-lion interactions have also been investigated by Goldman et al. (2010), Roque de Pinho (2009), and Lichtenfeld (2005). These studies have focused more specifically on Maasai perception of lions and on the prevalence of lion killing within Maasai society.

None of the previous studies of either pastoral mobility or Maasai-lion interactions have evaluated how mobility within pastoral systems affects proximity to large carnivores, or whether the presence of carnivores within rangelands influences pastoral decision-making and livestock ranging patterns. Our research aims to fill this gap with a case study of pastoral decision-making and human-lion proximity in two intact group ranches in Kenya's Maasailand. Here lions and other large carnivores still overlap with transhumance pastoralism. We seek to understand whether lion presence influences pastoral decision-making and livestock ranging patterns as well as what factors bring pastoralists into proximity with lions. Drawing on a mixed method approach, the case study focuses on three key questions:

1. How do Maasai pastoralists decide where to settle and graze within an ecosystem?
2. Is lion presence an important consideration in the pastoralists decision-making process about where to settle and graze?
3. What circumstances bring pastoralists into closer proximity with lions, and how do pastoralists then actively respond to the presence of lions?

Methods

Study Area

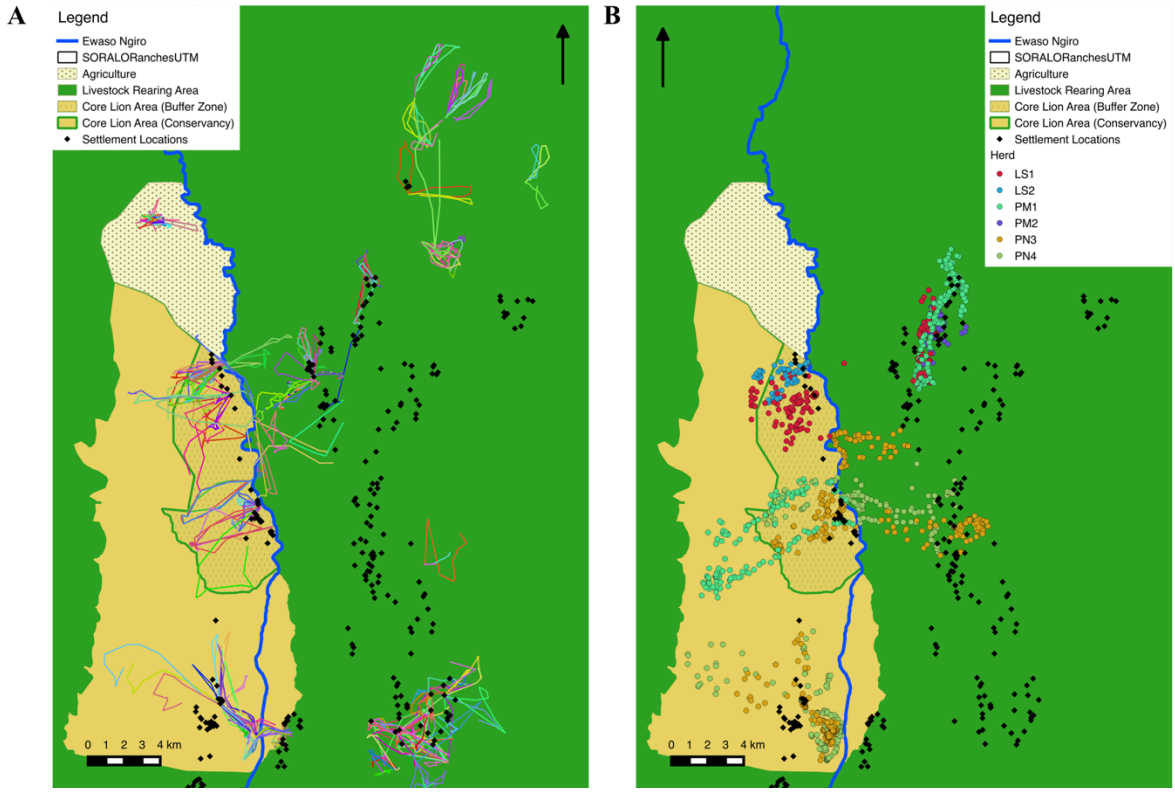


Figure 1: Map showing cattle ranging patterns (A) for all 24 study herds during the dry season, and (B) for the 6 study herds which spent time in areas of high lion presence during dry season and wet season.

The study was situated on Olkiramatian and Shompole Group Ranches in south western Kajiado county, Kenya. The two communities share a single ecosystem and have similar governance systems but are considered distinct entities. Situated at the base of the western Rift Valley escarpment, the group ranches together are inhabited by approximately 30,000 people and cover an area of 890 km^2 (Schuette, 2012). The group ranches also support high

livestock and wildlife ungulate densities (52.2 sheep and goat per km^2, 6.23 cattle per km^2, 6.65 zebra per km^2, and 3.26 wildebeest per km^2 (Russell et al., 2018). Lion densities are also high (13.1 adult lions per 100 km^2) but occupancy is largely confined to the conservation area and buffer zones (Schuette et al., 2016).

The region receives 200-600 mm of rainfall annually and is classified as semi-arid (Tyrrell et al., 2017). Five permanent rivers flow off the Rift Valley escarpment bisecting the area, the largest of which is the Ewaso Nyiro. Small scale irrigated agriculture within the study site is supported by the smaller Olibortoto, Pakase, and Entasopia rivers.

The presence of permanent water within a semi-arid lowland area (altitude 600m) has created a novel agro-pastoral system that has existed for several centuries (Jacobs, 1968). As early as the 1700s, the area is described as inhabited by the Nguruman and Lodokalani Maasai. The incorporation of irrigated agriculture into their pastoral way of life has made the Nguruman Maasai culturally distinct from other Maasai sections (Wakefield, 1870; Jacobs, 1968).

Over the last 50 years, the area has been subjected to considerable changes in land status. It was designated as a Maasai Reserve (1904) under the colonial administration, became group ranches under the Group Ranch Act 1968, and is now classified as Community Land under the Community Land Act of 2016. Despite these changes in policy and substantial external and internal pressure to subdivide into individual private parcels, the two communities have effectively transitioned traditional land-use and settlement patterns into

normative practices under the governance of group ranch committees. The establishment of community conservation areas (also referred to as "grass banks") are the most recent step in this transition process. The Shompole group ranch set aside 300 km^2 to the west of the Ewaso Nyiro river as a conservation area in 2000. Olkiramatian set aside an area of 150 km^2 in 2004.

Prior to their designation as conservation areas, the land had been used for dry season grazing. The conversion to "conservation area" did not change previous land-use patterns but provided an additional mechanism to regulate grazing and settlement. It also created a space in which wildlife related tourism activities could operate. Seasonal grazing is allowed within the conservation areas but is tightly controlled by the group ranch committees (Tyrrell et al., 2017). No permanent settlement is allowed within the conservation area but an adjacent buffer zone was created where temporary settlements (*bomas*) can be established for grazing in the conservation areas.

In conjunction with the creation of the conservation areas, land-use was further designated as agricultural and livestock rearing zones (Figure 1). Agricultural areas are predominately farmed using flood irrigation and provide an alternative food production system for pastoral families and a drought refuge for livestock. Permanent settlement is only permitted within the agricultural and livestock rearing zones. During the dry months (September to March) group ranch members can settle anywhere within designated permanent or temporary settlement areas, but in wet months (April to August) grazing and settlement is confined to the permanent settlement areas.

Contextual Information and Research Design

The methodological framework for this research (Figure 2) included an in-depth literature review, first had observation, and examination of group ranch records that outlined land-use and grazing plans within the two group ranches. Previous studies of pastoral mobility and decision making (Turner, 2003; Butt, 2010) advocate for a mixed methods (qualitative and quantitative data collection) approach to the study of pastoral mobility and decision making. Advances in remote sensing (RS) and Global Positioning System (GPS) tracking means that pastoral mobility can be recorded with greater precision however robust interpretation of tracking data requires an understanding of pastoral systems that is best captured by interviews, participant observation and other ethnographic methods (Turner, 2003; Bernard, 2006; Liao, 2018). A baseline understanding of the pastoral mobility within Olkiramatian and Shompole was developed between August 2010 and September 2011 when GW spent 9 months living in the two group ranches and observing changes in wildlife and livestock movements. During this time group ranches records such as group ranch constitutions and minutes from leadership meetings contributed to an understanding of land-use and grazing management in the study area. Based on this contextual information pastoral mobility and decision-making seemed to be governed at two levels: at the community level and at an individual (household level). A mixed methods approach was subsequently used to design the study's methodological framework (Figure 2) that focused on both the pattern and process (see Chapter 1, pg.18) of individual and communal decision making and mobility.

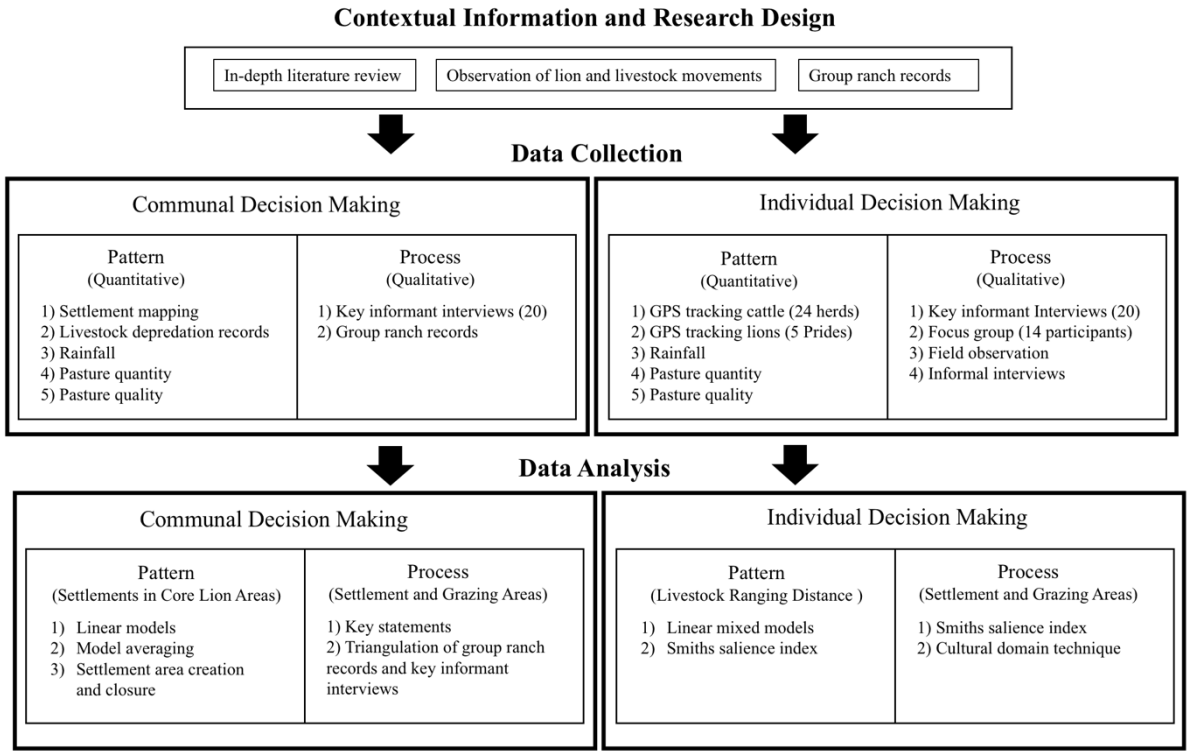


Figure 2: Schematic depicting methodological framework used to investigate pastoral mobility and decision making adapted from Oteros-Rozas et al. (2013).

Communal Decision-Making Pattern

Monthly settlement mapping, livestock depredation records, rainfall, pasture quality, and pasture quantity were recorded and used to create predictive models (linear models) of settlement occupancy within areas of high lion presence (conservation areas).

Settlement mapping captured changes in both settlement and livestock occupancy within the ecosystem. Between September 2014 and November 2016 settlement mapping conducted by the South Rift Association of Landowners (SORALO) identified, catalogued, and geo-referenced the homesteads (*bomas*) within the conservation area, buffer zone, and livestock rearing zone. *Bomas* were categorized as either permanent or temporary

depending on their location. Permanent *bomas* were those within the permanent settlement zone and were the primary base of the family and herd. Temporary *bomas* were defined as those within the buffer zone areas used seasonally to gain access to grazing or water resources. Whether a *boma* was occupied or unoccupied, and the type of livestock present were also recorded.

Livestock predation by lions was recorded on a monthly basis (from September 2014 through November 2016). Community members were encouraged to report incidents of wildlife attacks on livestock to game scouts, Kenya Wildlife Service (KWS), or our research team. Reported incidents were subsequently investigated and verified by our research team. The total number of lion attacks on livestock from the previous month was used to provide a measure of predation risk for a given calendar month. Livestock predation events were frequently discussed within the community and information on lion depredation shared between livestock owners. Consequently, it was assumed that our livestock predation records were reflective of the communities' knowledge of livestock predation.

Rainfall, pasture quantity, and pasture quality have been shown to influence landscape utilisation by livestock and wildlife within pastoral systems (Western & Finch, 1986; Homewood et al., 1987; Turner et al., 2016). Monthly r*ainfall* was the sum of daily rainfall measurements recorded by a HOBO UB30 automated weather station located centrally within the study area. *Pasture quantity* was calculated using total vegetation biomass estimates produced by Russell et al. (2018). Vegetation biomass estimates were

interpolated into monthly estimates of pasture biomass by fitting a general additive model (GAM) with thin splines and maximum degrees of freedom using package *mgcv* in R. *Pasture quality* was measured using Normalized Distance Vegetation Index (NDVI) (Butt et al., 2009; Turner et al., 2016). Monthly NDVI estimates were created using *MODIS* tools in R to extract 16 day composites at 250 m resolution from 20 randomly selected sites across the ecosystem.

Communal Decision Making Pattern

Key informant interviews and group ranch records were used to investigate the communal decision making process (Newing et al., 2011). Olkiramatian and Shompole had four broad leadership groups (i) group ranch officials, (ii) traditional leaders (*legwinak*), (iii) community elders, (iv) administrative chiefs (*viangozi*) (Appendix S3). Five key informants (Appendix 4- Table S1) were selected from each leadership group and semi-structured interviews (Appendix 4- Table S2) used to gather information on grazing and land use management in the two group ranches. Key informants were selected opportunistically based on availability (convenience sampling) with emphasis placed on trying to interview the most senior and/or respected leaders first. Interviews conducted by GW in either Swahili, English or Maa. A translator was used for any interviews conducted in Maa. Due to the difficulties of translating concepts from Maa to English these translations were considered to be semantic translations (the focus of the translation is to convey the meaning of the phrase and sentence; Newmark, 1988). Interviews where recorded using either notebooks and/or audio recordings (Appendix 4- Table S1).

Publicly available group ranch records such as minutes from group ranch meetings and group ranch constitutions were also used in the research (Appendix 2).

Individual Decision Making Pattern

Cattle movements, lion movements, rainfall, pasture quantity, and pasture quality were recorded monthly to create predictive models (LMM) of cattle ranging distance.

Cattle movements of 24 herds were tracked between October 2011 and March 2014 using Garmin etrex handheld global positioning system (GPS) (Butt, 2010). To maximize spatial coverage and provide a representative indicator of livestock ranging patterns across the 1000 km^2 study area, GPS units were provided to cover a total of 24 cattle herds selected from 7 of the 9 areas of permanent settlement areas within the two group ranches. Selection of herds from permanent settlement zones (livestock rearing zones and agricultural zones, Appendix 2) rather than temporary settlement areas was based on the assumption that these settlements were the epicentre of livestock movement. Herds always returned to permanent *bomas* during wet periods whereas utilisation of and selection of temporary *bomas* locations changed seasonally depending on availability of resources. Study herds in each of the 7 settlement areas were selected by identifying livestock owners who understood the goals of the project and were willing to participate in the study. Cattle tracking was conducted for 3 consecutive days every two weeks. GPS units were preprogramed to take fixes at 5 minute intervals and provided to either herders or research assistants who accompanied the herd. Cattle tracking ceased in March 2014 when persistent drought

forced a large proportion of livestock (including the study herds) to migrate to Tanzania in search of grazing.

Lion movements were recorded between (December 2011 and August 2014) using African Wildlife Tracking Iridium GPS collars (www.awt.co.za) fitted on five lions (2 females, 3 males). Collars recorded between 4 and 6 locations per day (24h). Monthly Rainfall, pasture quantity, and pasture quality were used along with lion movements and recorded as described previously.

Individual decision-making process

Key informant interviews and informal conversations were used to capture information on the process of individual decision making. Information provided by interviews was subsequently validated and augmented using a focus group discussion. During key informant interviews the same 20 participants involved in interviews on communal decision making were asked a subset of questions relating to individual decision making (Appendix 4)

Focus group discussions were conducted with 14 resource assessors employed by the South Rift Association of Landowners (SORALO), a Maasai community land trust. These resource assessors function as modern-day *"scouts"* to track and monitor changes in resource availability within the two group ranches. Trained in both the traditional Maasai practices of resource tracking and empirical ecological monitoring, resource assessors were selected as participants based on their ability to convey and articulate traditional knowledge

in a clear and concise manner. Freelisting was conducted by splitting participants into three groups and asking each group to list (free-list) most important factors they consider when assessing where to graze and settle. This helped to identify the most important factors affecting individual decision making (Bernard, 2006; Newing et al., 2011). Each group was then asked to identify the sub factors which constituted the higher level factors they had listed in the previous activity. Subsequently, an open forum discussion about the decision-making process and factors which influence it was conducted with focus group participants of to provide greater insight into the decision-making process

Communal Decision Making Analysis

Linear models were used to determine effects of rainfall (R), pasture quality (NDVI), pasture biomass (P) and livestock predation (Pred) on the number of settlements (S) within areas of high lion presence. Home range analysis conducted in Chapter 2 supported the findings of Schuette (2012), who demonstrated lions predominantly occupied the conservation area and buffer zone. Consequently, the area to the west of Ewaso Nyiro River, comprising conservation and buffer zones, was considered an area of high lion presence (core lion area).

Prior to their inclusion, the four explanatory variables (R, NDVI, P, Pred) were tested for multi-collinearity using variance inflation factors (VIF); those exceeding three (VIF > 3) were excluded from model formulation (Zuur et al., 2010). Variables included in candidate models were further standardized using unitless z-scores (REF). Interactions between all three predictor variables were included. Linear models were created and compared with the

package *Mumin* (Barton, 2016) in the statistical program R version 3.3.0. Model selection and ranking was based on Akaike's Information Criterion (AICc) values (Burnham & Anderson, 2004). Models within ΔAICc < 2 of the highest ranking model were considered contenders for the top model. Additionally, R^2 values were calculated to provide an indication of the variance explained by the fixed and random effects included within each model. Model averaging using the package *relaimpo* (Grömping, 2006) was used to provide a visual representation (*lmg*, bootstrapping =1000) of variance (R^2) of specific explanatory variables from within the top set of linear models (ΔAICc < 2).

Key quotes and information relating to communal management collected during key informant interviews was indexed by interview number and question number (transcribed by GW). Sections from group ranch records that reference communal management were similarly indexed by document name and page number and key quotes were extracted. The consistency of information from key informant interviews and group ranch records was cross referenced (a process known as triangulation, see Appendix 2 and 3) and consolidated into a communal decision-making framework by GW. The decision making framework was subsequently validated by the chairman of each group ranch.

Individual Decision Making Analysis

Linear mixed models were used to predict whether pasture abundance (P), and pasture quality (NDVI), and lion presence (HR) influenced changes in livestock ranging distance.

Daily locations from lion GPS collars were consolidated into monthly total home ranges using Brownian bridge movement models (Tmax 48hours, Lmin 50, Hmin 20) (Benhamou, 2011). Subsequently spatio-temporal overlap between cattle and lions was assessed using QGIS version 2.8.4 to overlay lion monthly home ranges with livestock ranging locations. Cattle herds which used areas of high lion presence and/or exhibited spatial-temporal overlap with home ranges of collared lions were extracted for further analysis. For each specific cattle herd included in that analysis, monthly estimates of lion home range size (HR) were assigned based on the home range size of the individual lion with the largest amount of home range overlap with the specific cattle herds. The home range size of the closest lioness was used as a surrogate for herds within core lion areas but whose range did not overlap with collared individuals.

Maximum daily ranging distances (Max Distance) for each herd which used areas of high lion presence was calculated using the straight line distance from the homestead to furthest GPS location (Butt et al., 2009). The maximum daily ranging distance a herd was able to travel varied by season and location. Proportional Max Distance (PMD) from settlement was calculated for each herd on a monthly basis using the following equation: *PMD=Mean (Max Distance)/ Max Distance during the Study Period.*

The package *lme4* (Bates et al., 2015) was used to create linear mixed models. Once again VIF scores were used to assess multicollinearity between predictor variables. Pasture biomass, NDVI, and lion home range (HR) were included as explanatory variables with

interactions and livestock herd identity as random effects. *Mumin* was used to compare highest ranking models based on AICc values.

Key quotes and information relating to individual management collected during key informant interviews was indexed by interview number and question number transcribed by GW (Appendix 2 and 3). Focus group discussions used free listing to identify the factors such as pasture and water which influence individual decision making. To rank the importance of these factors a smith's Salience Index (Smith & Borgatti, 1997) was created using the package *anthrotools* (Purzycki & Jamieson-Lane, 2017) based on the free listing response of all three groups (Newing et al., 2011). Focus group discussions also identified the sub-factors within higher level factors. To visualize and understand how focus group participants conceptualized higher level factors influencing decision making and and their constituent sub-factors a folk taxonomy (a hierarchical taxonomic graph) was created by GW (Bernard, 2017). Information from folk taxonomies and key informant interviews were used by GW to create a framework of individual decision which was reviewed by focus group participants.

Results

Communal decisions relating to settlement and grazing

Ecosystem management and communal decision making rested in the hands of the group ranch committees (11 members), elected by the registered members of each group ranch (generally male household heads). Group ranch committees were given legal and societal mandates to dictate where settlement and grazing was permitted thereby parametrizing individual decision making (Appendix 2). Deliberations about areas in which grazing was permitted extended beyond the group ranch committee and involved a broader decision-making body known as the leadership forum comprised of an elected conservation sub-committee and *legwinak* (traditional elders) (Appendix 3-Olkiramatian Constitution (2018) Article 4, pg. 12). Seasonal grazing and settlement areas located within the group ranch were not opened up to livestock arbitrarily. Lack of pasture within the permanent settlement areas catalysed grazing meetings which sanctioned the change in grazing and settlement (Appendix 3- Olkiramatian Constitution (2018) Article 2.4.1, pg.6). During meetings leaders within the decision-making body would take turns describing the current environmental and political context. Based on a combination of past experience, knowledge of current environmental and political contexts, and self-interest, members of the decision-making body would give an opinion on whether or not to open up new areas to grazing. The decision-making process was one of consensus; only once there was agreement by all present was a decision taken and new settlement and grazing restrictions agreed upon (Fieldnotes, 2013).

Consideration of lion presence in communal decision making

Lion presence was seldom taken into consideration by the leadership forum when planning grazing and settlement. During the study period (2011-2016) there were eight major alterations in permitted settlement areas within the study system (Table 1). All the changes eight alternations in settlement took place in areas of high lion presence but were primarily motivated by a desire to minimize grazing pressure and maximize the duration that pasture was available. A Shompole group ranch committee member explained:

"We have chosen to close off settlements such as those in conservation area (referring to Olirishi and Kikuru) as we have learned from the last drought that we should not have the community living in the middle of their drought refuge. Now that people have to walk from distant settlements to access these areas they cannot graze for as long and the pasture will last the community longer."

Semantic translation from Maa -Interview K02-Q4 (48m:37s-49m:11s)

This closing off of 75 *boma* sites in the two settlement areas of Olorishi and Kikuru was facilitated by the opening up of a new area in Oremit-Olkeriyan, widely known to be frequented by lions (Table 1, Appendix 2-Figure S3).

Individual decisions relating to settlement and grazing

Individual livestock owners were free to choose where to settle and graze so long as it was within those areas permitted by the group ranch leadership. Although livestock ownership was individual, husbandry and decision-making was most commonly made collectively at the household level and the process involved many members of the extended family. A system of age graded status still existed within Maasai society and elders in society were considered to possess the greatest knowledge of livestock husbandry. Heads of households were predominantly elders who commonly owned the largest proportion of livestock and

exerted the greatest influence in the decision-making process. Younger family members who might own cattle within the same herd often did not make the decisions on where their livestock grazed or the family settled, deferring to the elders. As one explained,

"I own 7 cows within my family herd, but it is my father who decides where and how we should graze, sometimes the decisions he makes are difficult for me and my family but we respect them."

Literal Translation from Swahili -*Field Notes- Notebook 2-18/3/2013*

Focus group discussions revealed livestock owners used a process of resource tracking known as *Ele'enore* (meaning the process of scouting to assess and evaluate resources) to compare their current personal, environmental, and political contexts against that of alternative sites. Household heads would commonly send herders and younger members of the household out on *Lalenerai* (a derivative of *Ele'enore* referring to scouting trips themselves*)*. Household heads and elders would also conduct their own *Lalenerai,* especially when it was felt that younger members of the household could not be trusted to provide all the crucial information necessary such as during times of drought, or when considering a move to areas outside of their usual settlement and grazing areas.

Information from *Lalenerai* was brought back to the wider family where individuals deliberated over the environmental conditions and their capacities to adapt to the challenges and risks present in each potential site prior to making a decision (Figure 3). During the decision-making process, households would consider whether to move their sheep and goats separately from their cattle and whether to combine herds with extended family or close friends known as "stock associates'. Polygamy is still practiced in the study area which allowed households to split their livestock herds between multiple wives and

children. In many instances, sheep and goat would remain in permanent *bomas* closest to schools and amenities to allow children (overseen by one wife) to attend school, while the rest of the household migrated to temporary *bomas* with the cattle (Fieldnotes, 2013).

Table 1: Summary of alterations to settlement areas during the study period, whether or not the settlements where in an area of high lion presence, and the reason for alteration.

Area Name	Date	Change	Number of Bomas	High Lion Presence	Reason
Lengungu	August 2012	New Bomas	5	Yes	Greater access to pasture
Shompole Water Hole	August 2014	New Bomas	9	Yes	Greater access to pasture/water
Naijotir	August 2014	New Bomas	2	Yes	Greater access to pasture/water
Shompole Water Hole	May 2015	Boma Closure	9	Yes	Control access to dry season pasture
Naijotir	May 2015	Boma Closure	2	Yes	Control access to dry season pasture
Kikuru- Olorishi	May 2015	Boma Closure	75	No	Control access to dry season pasture
Olkeriyan- Oremit	August 2015	New Bomas	8	Yes	Control access to dry season pasture

Table 2: Summary statistics and ranking based on AICc for candidate models predicting the maximum livestock ranging distance (PMD) of livestock herds utilizing core lion areas of Shompole and Olkiramatian group ranch**.**

Model	K	logLik	AICc	delta	weight	R^2
PMD ~ NDVI	4	19.38	-29.87	0.00	0.39	0.35
PMD ~ P + NDVI	5	20.12	-28.88	0.99	0.24	0.37
PMD ~ HR + NDVI	5	19.4	-27.44	2.44	0.12	0.35
PMD ~ P + NDVI + P*NDVI	6	20.22	-26.48	3.40	0.07	0.37
PMD ~ P + HR + NDVI	6	20.15	-26.35	3.53	0.07	0.37
PMD ~ HR + NDVI + HR*NDVI	6	19.42	-24.89	4.99	0.03	0.35
PMD ~ P + HR + NDVI + P*HR	7	20.61	-24.55	5.33	0.03	0.38
PMD ~ P + HR + NDVI + P*NDVI	7	20.26	-23.86	6.02	0.02	0.37
PMD ~ P + HR + NDVI + HR*NDVI	7	20.16	-23.65	6.23	0.02	0.37
PMD ~ P + HR + NDVI + P*HR + P*NDVI	8	20.62	-21.73	8.14	0.01	0.38
PMD ~ P + HR + NDVI + P*HR + HR*NDVI	8	20.61	-21.71	8.17	0.01	0.38
PMD ~ P + HR + NDVI + P*NDVI + HR*NDVI	8	20.26	-21.02	8.86	0.01	0.37
PMD ~ P + HR + NDVI + P*HR + P*NDVI + HR*NDV	9	20.62	-18.75	11.13	0.00	0.38
PMD ~ (1 | Herd)	3	10.51	-14.51	15.37	0.00	0.07
PMD ~ P	4	10.56	-12.23	17.64	0.00	0.07
PMD ~ HR	4	10.55	-12.2	17.67	0.00	0.07
PMD ~ P + HR	5	10.59	-9.82	20.06	0.00	0.07
PMD ~ P + HR + P*HR	6	11.73	-9.51	20.36	0.00	0.11

PMD= Monthly mean ranging distance from Homestead (proportion of greatest distance)
P=Mean Monthly Pasture abundance (g/m^2)
R=Monthly Rainfall (mm)
HR= Lion home range size with livestock ranging areas (km^2)

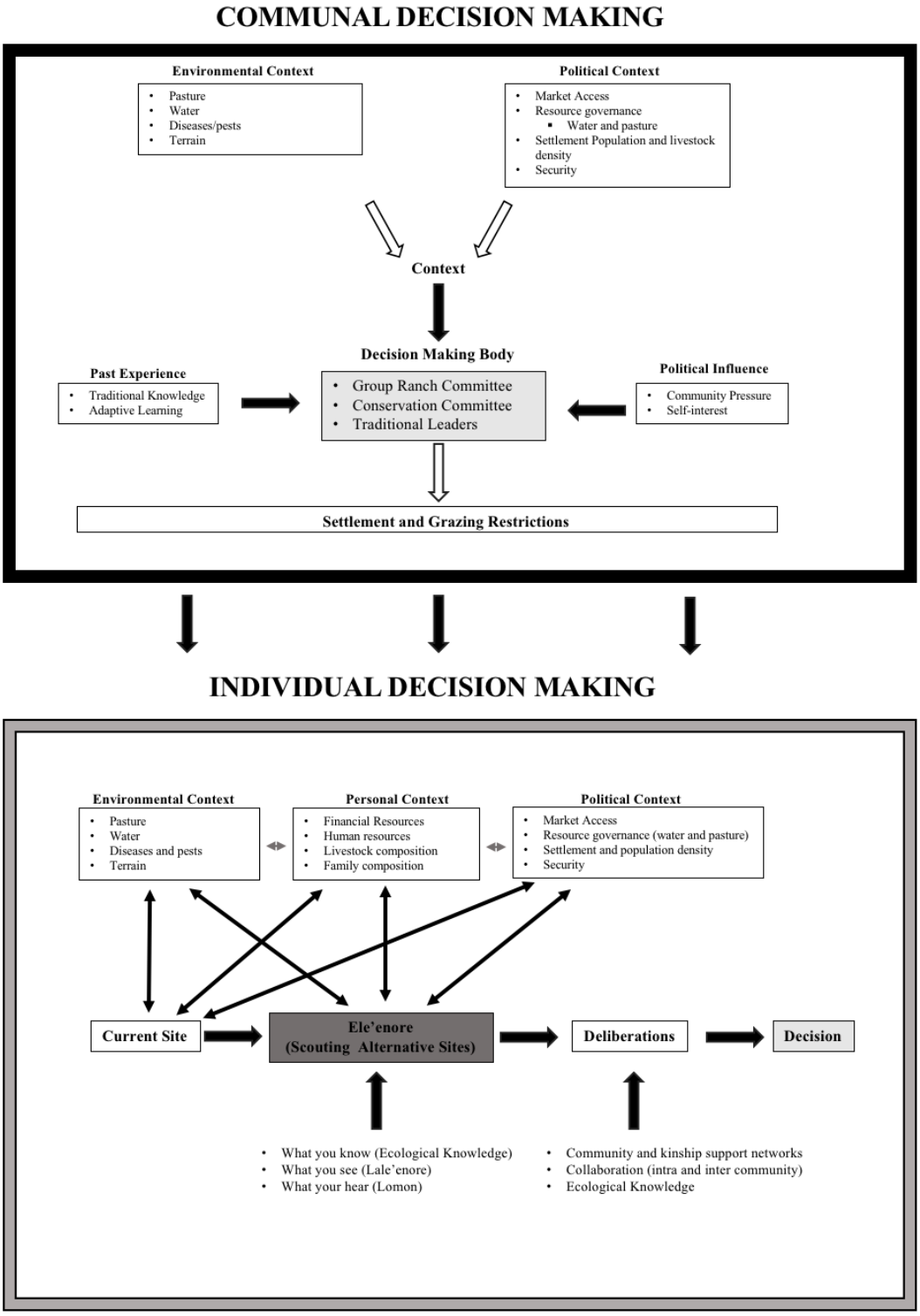


Figure 3: Schematic depicting how grazing and settlement decision are made at the communal and individual levels within the Olkiramatian and Shompole communities.

Rank	Factor	Subfactors		
		Level 1	*Level 2*	Level 3
1	***Pasture***	**Type of grasses**		
		Size of nearest town		
		Quantity of grass		
		Grass greenness		
		Presence of poisonous grasses		
		Distance from homestead		
		Proximity to water		
2	***Water***	**Quality of water**		
		Quantity of water		
		Type of watering point		
		Distance from homestead		
3	***Security***	**Livestock**	*At night*	Proximity to other settlement
			During day	Dangerous animals
				Risk of Theft
		Human	*Household safety*	Proximity to other settlement
				Tribe and clan of adjacent settlement
			Herder safety	Prevalence of livestock theft
				Dangerous animals
				Vegetation and cover
4	***Disease/pests***	**Diseases**	*Presence*	
			Type	
			Livestock affected	
			Last outbreak	
		Pests	*Tsetse*	
			Ticks	
			Dangerous wildlife	***Predators***
				Buffalo/Elephant
5	***Land and Terrain Suitability***	**Terrain Type**	*Topography*	
			Substrate	
		Number of settlement		
		Livestock condition		
6	***Market Access***	**Distance to town**		
		Size of nearest town		
		Avalibiltiy of markert commidites	*Livestock drugs*	
			Food	
7	***Grazing Management***	**Governance systems**	*Restrictions*	
			Fines/Penalties	
8	***Reasources***	**Means of transport**		
		Family demography	*Number of people moving*	
			Number of wives	
			Number and age of children	
		Avalibiltiy of herders		
		Will livestock herds be split		
9	***Settlement***	**Are there boma to move into**		
		Governance systems		
		Access to water	*Livestock*	
			Household	
		Desntiy of Settlment		
		Who will move	*Will livestock herds be split herds*	
			Are there young livestock	

Figure 4: Taxonomy of factors and sub-factors influencing an individual or household's decision on where to settle and graze their livestock.

Lion presence and individual decision making

Lion presence was of very little importance in individual pastoral decision making. Free-listing during focus group discussions revealed that basic husbandry considerations like livestock pasture (food) and water, were the most salient elements influencing decisions about settlement and grazing (Appendix 5-Table S3). Folk taxonomies created from focus group discussions further demonstrated that lion presence was grouped by participants with leopard, hyaena, wilddog as predator presence more generally. Predator presence itself was sub-factor (level 3) within the broader categories of security and wildlife/pests (Figure 4).

Key informant interviews further corroborated that shortage of pasture motivated individual livestock owners to live and graze within areas of high lion presence. During time of pasture shortage lion depredation was a minor and a potentially avoidable threat compared to lack of pasture (drought). Key informants described drought as a major threat to livestock survival and was driven beyond one's control often using statements such as *"there is not much we can do but hope that the rains come soon"* or *"God will bring the rain*". Lion predation by contrast was seen as more minor and mitigatable threat:

"I would rather lose a few cows to lions then my whole herd to drought"
English- Interview K04-QU13

"The Maasai know how to live with lions; we do not need to separate people and wildlife for we have learned how to move around one another."
Literal translation from Swahili- Interview K19-QU13

Settlement Within Areas of High Lion Presence

Settlement mapping was conducted 22 times between October 2014 and November 2016 and revealed that pasture availability was the predominant factor that induced settlement in proximity to areas of high lion presence. The number of occupied settlement within areas of high lion presences ranged between 0 and 86.

Multicollinearity was present between NDVI and other response explanatory variables (rainfall, predation, pasture quantity) in linear models. NDVI was subsequently removed from model formulation and pasture quantity was used as a surrogate for both pasture quality and quantity based on its correlation with NDVI (r_p=0.84, $p < 0.01$). Model selection (supplementary information- Table S2) revealed that the pasture model (S ~ P) was the best predictor of whether people settled in areas of high lion presence outperforming the model that included livestock predation and pasture (S ~ Pred + P) model by ΔAICc =3.02. The pasture model explained 51% of variance in settlement presence within areas of high lion presence with lowest settlement presence occurring during times of peak pasture quantity and quality (Figure 6). These findings support descriptions of movements collected from key informant interviews and field observations (Appendix 3).

Rainfall as represented by the model S~R was a relatively unimportant factor in predicting settlement patterns, explaining only 8% of variance. Livestock predation (Pred) and the interaction effect between rainfall and pasture quality (R:P) proved the worst predictors of settlement presence (Figure 5).

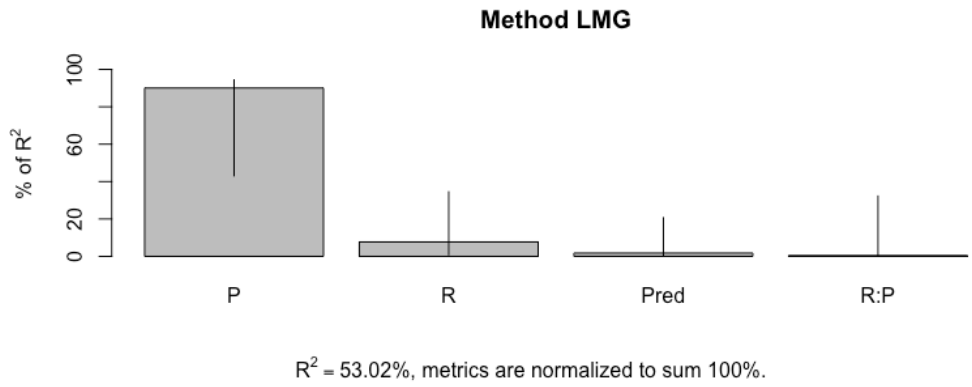


Figure 5: Bar plot of model averaging results with 95% bootstrapping confidence intervals. Variable importance is indicated on the y-axis by the percentage of variance (R^2) in monthly *boma* occupancy explained by changes in pasture (P), monthly rainfall (R), predation (Pred), and the interaction of rainfall and pasture (R:P).

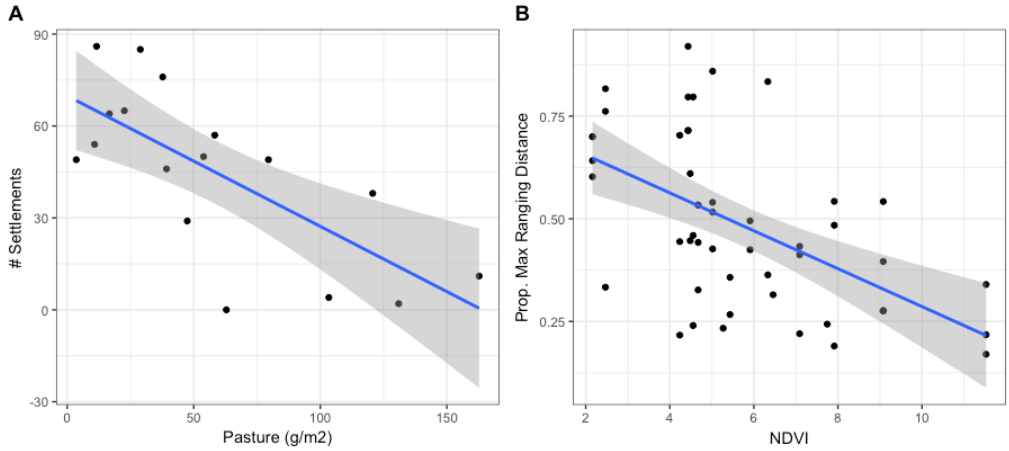


Figure 6: The actual relationship (black points) and fitted linear models (blue lines) with 95% confidence intervals (grey shading) between (A) the number of settlements with core lion areas and grass quantity as measured by pasture biomass (g/m^2), (B) livestock ranging distance (prop. max ranging distance- PMD) and grass quality (NDVI).

Grazing Within Areas of High Lion Presence

Proximity between livestock grazing herds and grazing in areas of high lion presence was largely determined by the herds permanent settlement location. Only 6 of the 24 study herds spent time in core lion areas. Study herds selected from the permanent settlement areas of Oloika, Shompole and Oldorko and Nguruman did not exhibit any overlap with core lion areas, while herds from Nkonyoro, Diggia, and Lengobai spent considerable amounts of time in areas of high lion presence (Figure 1, Appendix 2- Figure S1 and S2).

Between October 2011 and March 2014, a total 256 livestock tracks from six herds were used to determine the drivers of variation in maximum livestock ranging distance within areas, which ranged from 1.2 to 10.5 km per day. No collinearity was present between pasture abundance (P), pasture quality (NDVI), and lion presence (HR), hence all three were included as explanatory variables in linear mixed model of livestock ranging distance (PMD). Model selection (Table 3) revealed two competing models of PMD. The NDVI model of grass quality (PMD~NDVI) was a marginally (ΔAICc= 0.99) better predictor of livestock ranging distance than pasture quantity and NDVI pasture quality (PMD~P+NDVI) model. Grass quality explained 35% of variance in ranging distance. Greatest ranging distance occurred when grass quality (as expressed by NDVI) was lowest (Figure 6). Likelihood of human-lion interaction, as measured by lion home range size, proved a poor predictor of livestock ranging distance (ΔAICc = 17.67) explaining a mere 7% of variance (Table 3). The aualitative data (Appendix S3) further validates our model and demonstrates that livestock owners are willing to graze in areas where lions are known to be in order to access high quality or quantity forage.

Discussion

Within Olkiramatian and Shompole, areas of high lion presence were contiguous with areas reserved for late dry season grazing. Living and grazing in areas these high lion presences came at the expense of higher predation risk but allowed for spatio-temporal adaption to resource scarcity and greater resource access. We observed that communal and individual decisions were informed primarily by traditional ecological knowledge and resource tracking and influenced by a broad range of socio-political, economic, and environmental factors. A diverse array of grazing and settlement strategies were employed by livestock owners aimed at maximizing accesses to resources.

Decision Making, Mobility, and Resource Tracking

Seasonal grazing and settlement within Olkiramatian and Shompole were predominantly governed by communal decision-making to maintain pasture availability during the dry season. Traditional leaders (*Leginwinak*) and elected group ranch officials were responsible for developing and enforcing grazing and settlement management. The presence of governance structures that promote communal landscape utilization and management through mobility are also common in other pastoral societies (Herrera et al., 2014). For example, the Himba in Namibia believed "By not moving you kill an area". Like the Maasai in this study, the Himba close off areas to grazing and move between established settlement sites to preserve grazing (Behnke Jr, 1999). Among the Maldahri communities living in India's Gir Forest, the benefits of greater resource access for herders living in the National Park also offset the increased risk of lion predation. Government compensation

for livestock loss to lions further decreased the costs of livestock predation and facilitating settlement and grazing within the park (Banerjee et al., 2013).

Members of Shompole and Olkiramatian knew that the conservation areas had more lions but still choose to settle and graze there because the importance of access to resources such as pasture and water far outweighed the risk of predation. Unlike in the Indian Gir Forest, the cost of lion depredation in Shompole and Olkiramatian was not offset by compensation, but by knowledge based decisions acquired in a large part through resource tracking. Resource tracking in Shompole and Olkiramatian (*Ele'enore)* was central to the communal and household decision-making processes. Tracking wildlife movements meant that herders could adapt and avoid areas of lion presence on a daily basis as described by an elder in Shompole:

"Even as an old man I know where lions, leopards and all manner of wildlife can be found. When my livestock go to pasture, I go ahead to survey the area to ensure that there is nothing that will bring them harm…If I find lion tracks, I show them to my children in order to teach them the areas that are dangerous for livestock".

Semantic translation from Maa -Interview K12-Q4 (56m:11s-56m:49s)

In the nearby Maasai Mara ecosystem, Butt (2010) similarly recorded how pre-selected grazing locations changed during the day based on information provided by other herders about forage, water and carnivores. In this study, ability to track carnivore movements created a perception that lion predation was a relatively minor risk that could be managed and mitigated compared to the array of other factors involved in individual decision-making. Predation risk has not featured in other studies on Maasai mobility (Homewood et al., 1987; Butt et al., 2009), resource governance (Bekure 1991, Potkanski 1994) and settlement patterns (Western & Dunne, 1979), suggesting that Maasai herders are aware of

carnivore presence but that it has little influence on Maasai seasonal settlement and land-use patterns.

Pastoralist Proximity to Lions

Key informant interviews as well as predictive models of settlement presence and livestock ranging distance indicate that pasture quality and quantity were the main drivers that brought pastoralists into proximity with lions. Respondents did not express concern or reluctance to graze in areas of high lion presence. Moreover, neither prevalence of human-wildlife conflict nor lion presence was a key determinant in our predictive models of settlement or ranging distance.

Pasture quantity and quality proved the best predictor of settlement within areas of high lion presence while grass quality dictated livestock ranging distances. There were fewest settlements in areas of high lion presence when pasture was abundant and livestock herds were closest to the homestead (*boma*) when grass quality was highest. As quality decreased livestock travelled further from the homestead, often travelling upwards of 20 km through areas of high lion presence. Surrounding Hwange National Park in Zimbabwe, distance from homestead also changed seasonally and influenced the vulnerability of livestock to predation. During the wet season in Hwange, herds were pushed away from homesteads and into denser habitats increasing the risk of predation, while during the dry season livestock were encouraged to graze on fallow fields adjacent to homesteads decreasing the risk of predation (Kuiper et al., 2015). Ranging distance within our study were considerably further than those reported in Boone et al. (2008) (12.5 km) for Amboseli and

in the Maasai Mara by Butt et al. (2009) (16.57 km), suggesting that greater ranging distances were possible and/or required in Olkiramatian and Shompole to access patches of high quantity and quality pasture during dry periods.

Analogous to our findings, pasture quality was shown to be a critical determinant of pastoral mobility in the adjacent Amboseli ecosystem where herders preferentially targeted patches of highest grass quality (BurnSilver et al., 2004; Boone et al., 2008; BurnSilver et al., 2008). While we did not specifically investigate whether herders target resource rich patches within the ecosystem, both pasture quantity and quality-quantity models were good predictors of livestock ranging distance, similar to findings in Amboseli. Livestock owners in this study had a diverse set of grazing and settlement strategies to maximize access to pasture and water. As a result, the majority of study herds (18 of 24) avoided areas of high lion presence completely.

Livestock owners and herders who did choose to spend considerable time in areas of high lion presence relied heavily on the process of *Ele'enore* to track the movements of lions within the ecosystem. Livestock guarding was also a technique to minimize the risk of predation, theft, and livestock lost associated with greater ranging distances. Guarding helped to enable access to high risk areas. Families would often combine their cattle herds during periods of greatest ranging distances and ensure herders accompanied livestock but this was not always the case when cattle were grazing close to home or outside of areas high lion presence. Even though households owned both small stock (sheep and goats) and cattle, the two were seldom herded together. Elders, women and children were

predominantly responsible for herding small stock and young men were left with the responsibility of safeguarding cattle.

Conclusions

The management of natural resources among the Olkiramatian and Shompole Maasai remains communal and is governed by complex user rights intended to maximize access to resources and reduce vulnerability to resource scarcity. Households and livestock herds within the study system moved frequently between temporary and permanent settlements. Despite the increased risk of lion predation where pasture was abundant we show that, analogous to pastoral systems elsewhere, a large portion of the variation in settlement and grazing patterns can be explained by pasture quality and quantity. Furthermore, we show that little consideration is given lion presence during the decision-making process of where to settle or where to graze.

There is a growing acceptance that pastoralism can be ecologically compatible with modern conservation agendas (Schuette et al., 2016; Kimuyu et al., 2017; Tyrrell et al., 2017). Our results show that coexistence with lions uses the same mechanisms employed to reduce vulnerability to resource scarcity. This includes mobility of people and herds, resource tracking, and livestock herding and guarding, which also reduce vulnerability to lion predation. Together they allow for resource access even in areas of high lion occupancy and predation risk. While these pastoral practices still exist in the traditional communities of Olkiramatian and Shompole, they are disappearing elsewhere among pastoralists in African rangelands (Sternberg & Chatty, 2013).

Large felids and pastoral communities are facing similar threats today from land-subdivision and fragmentation, yet our research suggests that carnivore conservation and development agendas can be made complementary. This requires a focus on fostering pastoralist resilience and improving integrity and health of pastoral rangelands for the benefit of people and wildlife. Maasai pastoralism, as illustrated in Olkiramatian and Shompole, is a complex social-ecological system that relies on both communal institutions and individual knowledge and skills to negotiate variable resource availability, livestock needs, and predation risks. This research illustrates how important traditional institutions and traditional knowledge are to human-wildlife coexistence as well as to coping with a variable environment, which climate change will only make more capricious.

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Appendix 1

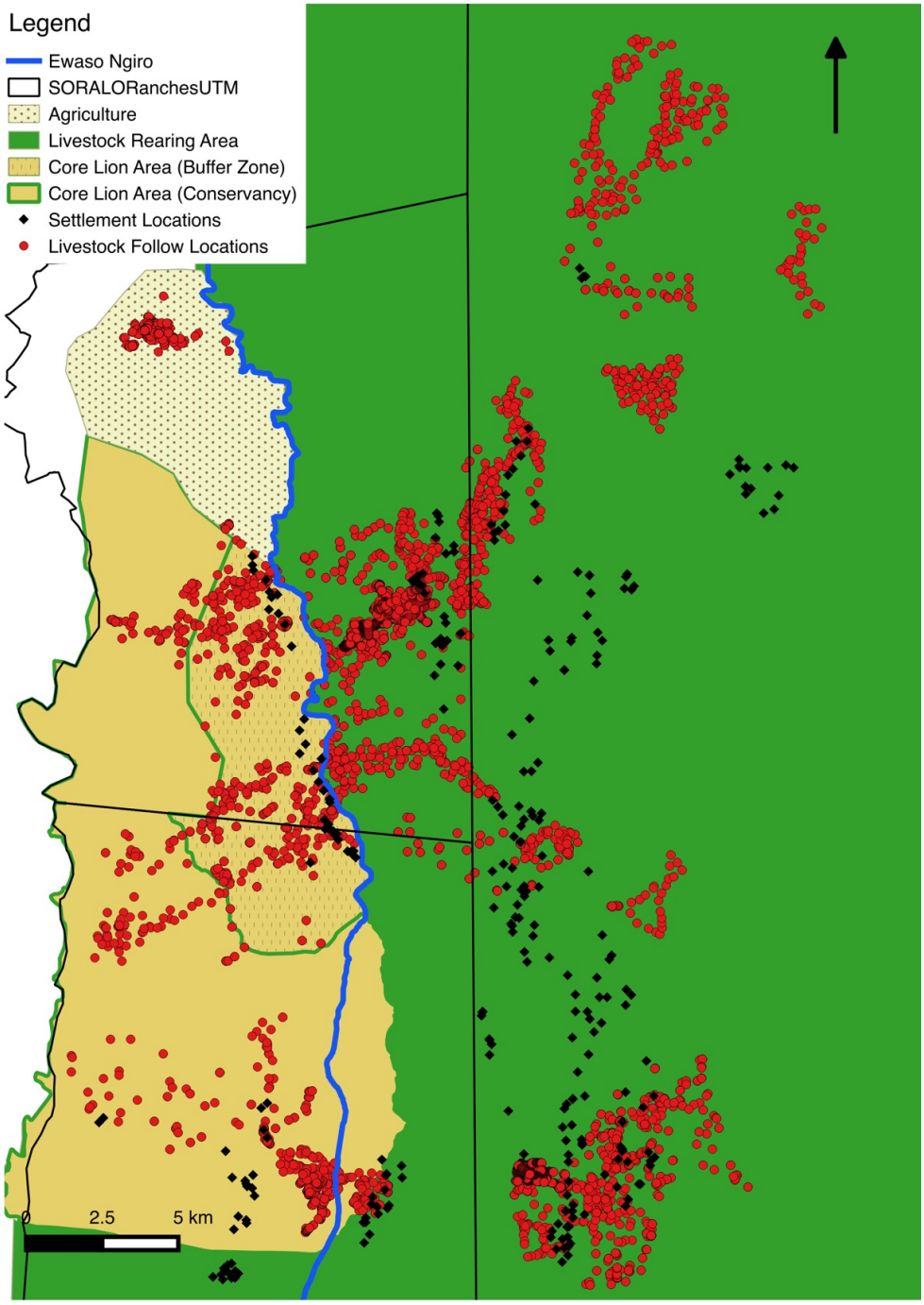


Figure S1: Map illustrating temporary and permanent settlement locations (black), land-use zones, core lion areas (beige), and select livestock locations (red) from the 24 study herds.

Appendix 2

Triangulation of Communal Decision Making

Communal Management and Leadership

Olkiramatian Constitution (2018) Article 4, pg. 12

4.0 THE MANAGEMENT COMMITTEE

4.1 MEMBERSHIP OF MANAGEMENT COMMITTEE

There is hereby established a committee of the community land to be known as the Management Committee. The community Representatives shall be the Management Committee of the community land, the Management Committee shall consist of the following:-

1) Chairperson
2) Vice-Chairperson
3) Secretary
4) Treasurer
5) The other eleven (11) community Representatives where two (2) must be women representative and one (1) position for special need representative.

4.1.1 SUB-COMMITTEES

The sub-committees will be semi-autonomous but reporting the management committee. They will be expected to develop annual plans that will be a basis for monthly reporting. Failure to do so for three consecutive months the management committee shall summon them to show cause why, if this does not work the management committee shall call for Community Assembly for further action to be taken.

The management committee shall spearhead the establishment of five (5) sub-committees within the community land (Conservation and culture, Water and Irrigation, demarcation, urban development and grazing committee). The qualification of the executive position for the sub-committee shall be a minimum of two form four graduate and above.

4.1.2 LEADERSHIP FORUM

I. Executive of the management committee
II. Chair-person of the sub-committee
III. Age set leaders
IV. Administrative (chiefs)
V. Member of the County Assembly

4.2 DUTIES OF THE MANAGEMENT COMMITTEE

The overall management and running of the community land shall be through the Management Committee and without prejudice to the generality of the foregoing and in particular, the management committee shall have the following duties:-

1) Be responsible for the general management of the community land.
2) Be responsible for the management of the general incomes and revenues of the community land.
3) Be accountable to the membership of the community land.
4) Guide the members of the community land inits planning process.
5) Perform such other duties and exercise such other powers as may be conferred upon it by the member at the Community assembly.

Role of Management Committee
Shompole Constitution (2012) Article 5.2, pg. 8

5.2. DUTIES OF THE MANAGEMENT COMMITTEE

The overall management and running of the Group Ranch shall be through the Management Committee and without prejudice to the generality of the foregoing and in particular, the management committee shall have the following duties:

1. Be responsible for the general management of the Group Ranch.
2. Be responsible for the management of the general incomes and revenues of the Group Ranch.
3. Be accountable to the membership of the Group Ranch.
4. Guide the members of the Group Ranch in its planning process.
5. Perform such other duties and exercise such other powers as may be conferred upon it by the members at an Annual General Meeting.

Land-Use Planning and Zoning
Shompole Constitution (2012) Article 9,.pg 12

9. MANAGEMENT, LAND USE AND INVESTMENT PLANNING

For the sustainable management of the Group Ranch, the Management Committee shall guide the members in preparation and implementation of the following:

1. A Management Plan, addressing, but not limited to the following issues:
   - (i) Land use
   - (ii) Zoning of the Group Ranch
   - (iii) Pasture banking
   - (iv) Environmental integrity
   - (v) Investment
   - (vi) Soil erosion
   - (vii) Designated conservation area
   - (viii) To create a dedicated open rangeland
   - (ix) Participation of members in management
   - (x) Role of women in the Group Ranch
   - (xi) Research
   - (xii) Capacity building for members in leadership
   - (xiii) Conflict resolution
   - (xiv) Relationship with donors, and other external agencies

Shompole Constitution (2012) Article 17, pg. 21

17. ZONING OF THE GROUP RANCH

1. The Group Ranch shall be zoned into various land use areas to provide for effective management of natural resources, including but not limited to
   a) Grazing
   b) Conservation (for wildlife and nature conservation and eco-tourism related development projects)
   c) Settlement
   d) Pasture banking
2. In undertaking of the zoning process, and designating the respective land use areas, the management committee shall consult with the Group Ranch membership.
3. The Zoning Process shall be a prominent component of the management Plan, and conservation Area management Plan.
4. For the avoidance of doubt, it is hereby clarified that all members shall be bound to act by these zoning provisions without any exception whatsoever.

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K02-Q4 *"We have chosen to close off settlements such as those in Olirishi and Kikuru, as we have learned from the last drought that we should not have the community living in the middle of their drought refuge. Now that people have to walk from distant settlements to access these areas they cannot graze for as long and the pasture will last the community longer."*

Semantic translation from Maa -Interview K02-Q4 (48m:37s-49m:11s)

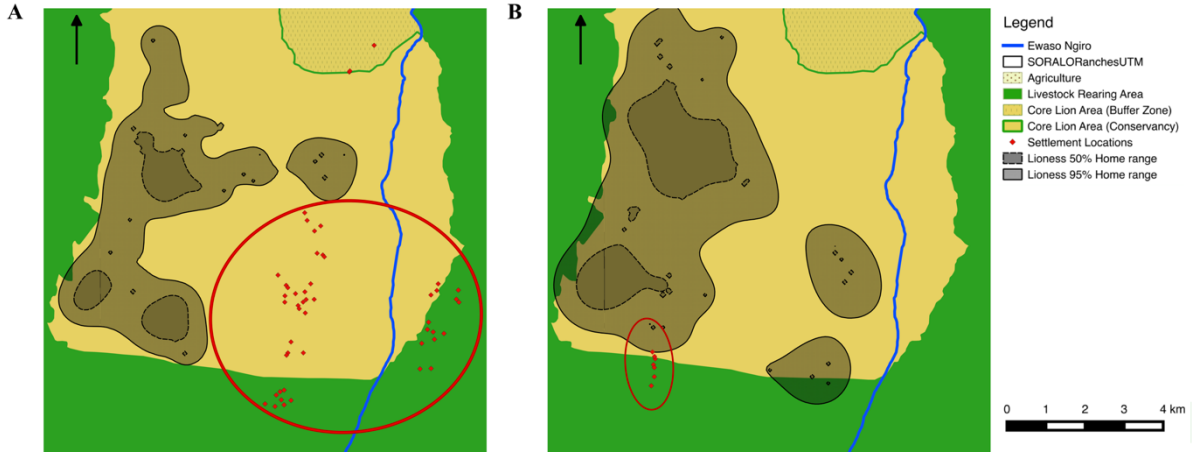


Figure S3: Figure showing changes in dry season settlement and lion distribution (A) before the closure of Olorishi and Kikuru Settlements, and (B) After the closure of Olorishi and Kikuru settlements and the opening up of Olkeriyan settlements.

Olkiramatian Constitution (2018) Article 2,.pg. 5

2.4 ZONATION

The community land shall be classified into two zones herein after referred to as "Phases"

All towns/business centers within Olkiramatian community land are vested fully to Olkejuado County Government and any allocation beyond those towns for public utility shall be regulated by the management committee

1) Current towns in Olkiramatian community land
   i. Olkiramatian
   ii. Naiurrurr
   iii. Oloibortoto
   iv. Entasopia
2) Areas Designated for Development in Olkiramatian community Land

a) Schools
   i. Patterson Secondary School
   ii. Olkiramatian Primary School
   iii. Naiurrurr Nursery school
   iv. Oloibortoto Secondary School
   v. Oloibortoto Primary School
   vi. JENA institute
   vii. Entasopia Polytechnic
   viii. Entasopia primary school

b) Dispensaries/Health Centers

   Entasopia health center

c) Churches
   Catholic Church (oloibortoto)

d) Other Development institutions /facilities
   i. MRTC
   ii. Laleenok
   iii. Agriculture/IWUA
   iv. Agriculture offices(Entasopia)
   v. Olkiramatian cattle dip
   vi. Esajini cattle dip
   vii. Entasopia cattle dip
   viii. Community Land office

Olkiramatian Constitution (2018) Article 2.4.1 .pg. 6

2.4.1 PHASE I

Phase I land area represents the area of land located between the Ewuaso-Ngiro River, the Magadi pipeline road and the Nguruman escarpment to the west of the community land (A map showing the zonation has been appendixed) and Ref 3-Olkiramatian special/Dev map/plan. A consent for subdivision of Phase I land area has been acquired and all the members whose names appear in the Olkiramatian Group ranch register are entitled to equal portions (in acreage). The area is mainly for irrigated agriculture type of land use. (Zonation map to be appendixes)

Although the original consent was for 464 members, but members through an AGM dated 12th May 2002 ratified and opened the register to 1403 members who are entitled as beneficiaries of Phase I

2.4.2 PHASE II

Phase II land area represents the area of land that has been specifically designated for livestock grazing and conservation of natural resources within community land.

Part 1: Wet season ranges between Magadi concession area to the East, Shompole group ranch to the South, Ewuaso-Ngiro River to west and Oldonyonyokie Group Ranch to the North

Part 2: Dry season ranges between Ewuaso-Ngiro River to the East, Shompole G/R to the south, Nguruman escarpment (Loita hills) to the West and the Magadi-Nguruman main road to North

K14-Q3 *"When grass is running low, the community leaders allow us to move across the river to access pasture in the conservation areas; when there is plenty of grass we move back to the other side (east side) of the river".*

Olkiramatian Constitution (2018) Article 16,.pg. 22

16.0 ZONING OF THE COMMUNITY LAND

1) The Community land shall be zoned into various land use areas to provide for effective management of the natural resources including but not limited to:-
   a) Grazing
   b) Conservation (for wildlife and nature conservation and eco-tourism related development projects)
   c) Settlement
   d) Pasture banking
2) In undertaking of the zoning process, and designating the respective land use areas, the management committee shall consult with the Community land membership.
3) The Zoning Process shall be a prominent component of the management plan, and conservation area management plan.
4) For the avoidance of doubt, it is hereby clarified that all members shall be bound to act by these zoning provisions without any exception whatsoever.

Appendix 3

Triangulation of individual decision making and Maasai-lion interactions

Maps

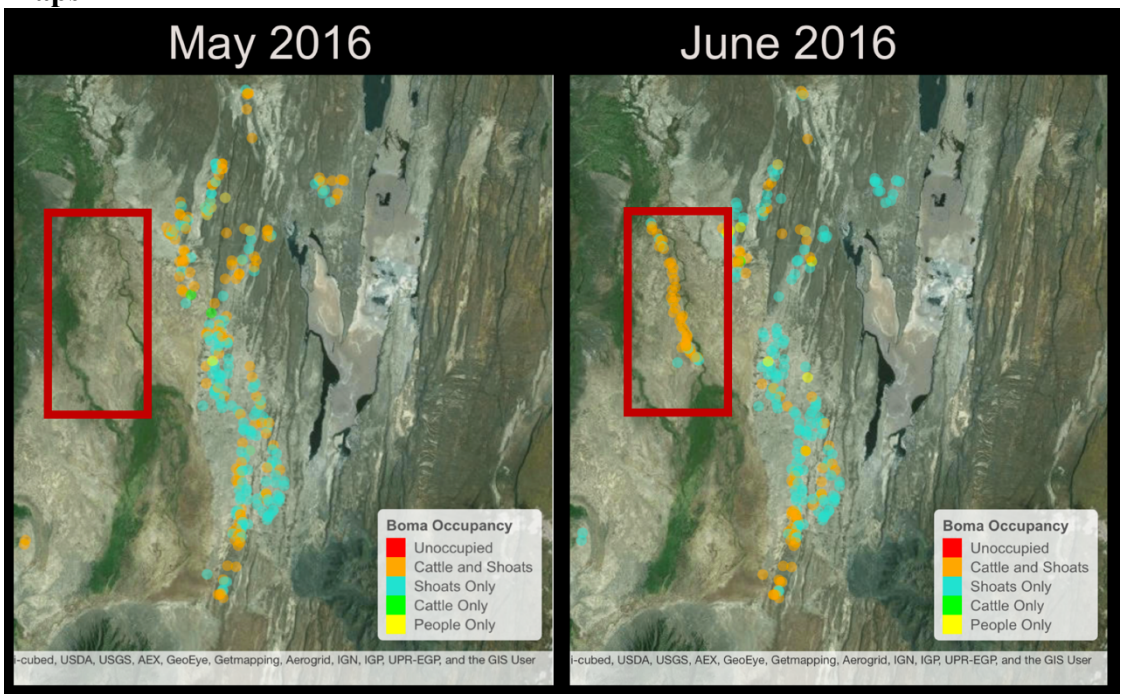


Figure S2: Changes in settlement occupancy between May 2016 (prior to opening of seasonal settlement in the buffer zone) and June 2016 (seasonal settlement in the buffer zone allowed).

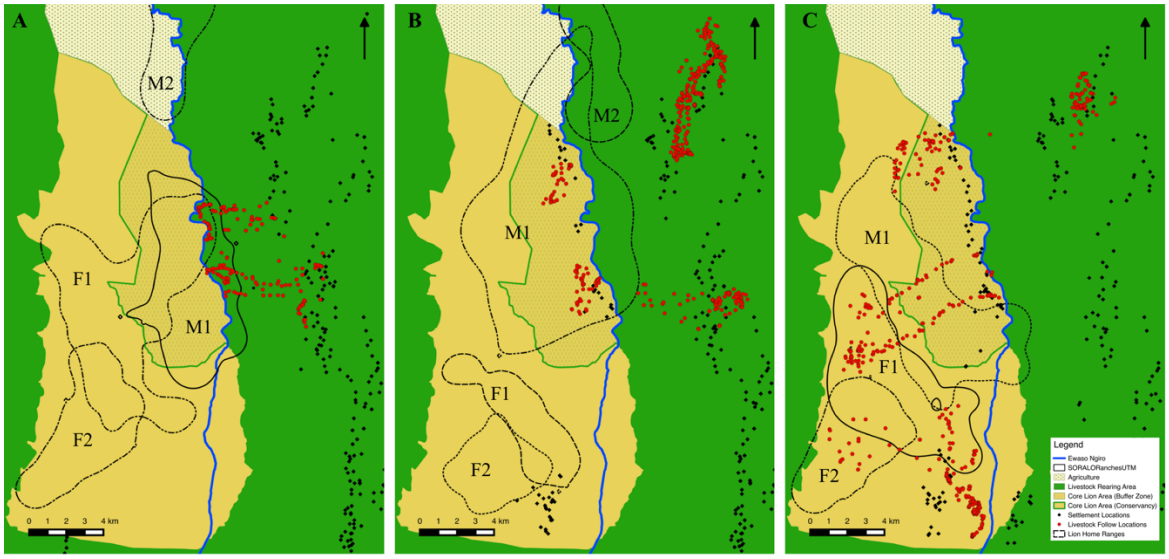


Figure S3: Changes in lion home range (Brownian bridge universal) and livestock ranging patterns during (A) Wet Season (B) Early Dry Season (C) Late Dry Season.

Field Notes corresponding with Figure S2

Field Notes, June 2, 2013 (Wet Season) - Observation GW "Eramatare (F3) and Oldepe (M1) found mating in an abandoned boma in ledama this morning."

Field Notes, Jan 24, 2012 (early dry season) - Observation GW "Oldepe (M3) found in lengungu with gate 1 females the livestock have also been using this corner of lengungu as result of recent floods and that have brought a green flush It also close to the bomas so you can easily access"

Field Notes November 2, 2013 (late dry Season)- Observation GW- "Nasha (F1) was close to ol donyo lalero, cattle from Nkaset are also using this area as it's the only area that pasture is left."

Selection of quotes relating to Maasai-lion interactions

K4-QU13 *"I would rather lose a few cows to lions then my whole herd to drought"*

K3-Q13 *"Early wet season conflict is not as bad the wildlife is following the same pattern so lions are able to hunt them before the cattle arrive"*

K15-QU13- *"During the dry season skilled herder are need therefore herders are paid. But during the rains the paid herders are given time off or allowed to return home and herding is given to the children as they are home from school. Herders are then grazing in one off two ways… how they like and herders just follow or told to graze far from home so they don't return early.*

K9-QU13 *"When the rains come there is not much good grass. So we graze in Oldepe (a known lion area) where are very few poisonous grasses and good grazing on entiamonyua. As compared to kikuru (open plain) which grass doesn't shoot that fast. (grass)*

K11-QU13 *"We are grazing in kikuru swamp as there was not enough grazing to support cattle therefore they drawn to the swamp. The swamp also greens up further when it the rains come"*

K19-QU13 *"The Maasai know how to live with lions; we do not need to separate people and wildlife for we have learned how to move around one another."*

Pictures



Picture 1: Maasai and livestock grazing together in Kikuru (core conservation area) during early wet season (October 31st, 2014) as described in K3-Q13 *"Early wet season conflict is not as bad the wildlife is following the same pattern so lions are able to hunt them before the cattle arrive"*



Picture 2: Eramatare (F3) and Oldepe (M1) mating inside a unoccupied boma (Buffer Zone- Wet Season- June 2nd 2013)



Picture 3: Measuring lions tracks outside a occupied boma (Buffer Zone- Early Rainy Season- March 23rd 2011). Relates to quote K19-QU13 *"The Maasai know how to live with lions; we do not need to separate people and wildlife for we have learned how to move around one another."*



Picture 4: Wildlife grazing outside and abandoned boma in Impaleki (Buffer Zone- Wet Season- June 7th 2013).

Appendix 4

Table S1: List of key informant interviews, indicating leadership category, interview language, translation method, and recording method

Interview Number	Category	Language	Translation	Recording
K01	Group Ranch Leadership	Maa	Semantic	Recording
K02	Group Ranch Leadership	Maa	Semantic	Recording
K03	Group Ranch Leadership	Maa	Semantic	Recording
K04	Group Ranch Leadership	English	none	Notes
K05	Group Ranch Leadership	Maa	Semantic	Recording
K06	Traditional Chief	Maa	Semantic	Recording
K07	Traditional Chief	Maa	Semantic	Recording
K08	Traditional Chief	Maa	Semantic	Notes
K09	Traditional Chief	Maa	Semantic	Notes
K10	Traditional Chief	Maa	Semantic	Recording
K11	Community Elder	Maa	Semantic	Recording
K12	Community Elder	Maa	Semantic	Recording
K13	Community Elder	Swahili	Literal	Notes
K14	Community Elder	Maa	Semantic	Notes
K15	Community Elder	Maa	Semantic	Recording
K16	Administrative Chief	Maa	Semantic	Recording
K17	Administrative Chief	Maa	Semantic	Recording
K18	Administrative Chief	Maa	Semantic	Notes
K19	Administrative Chief	Swahili	Literal	Notes
K20	Administrative Chief	Maa	Semantic	Recording

Table S2: Interview Guide for semi-structured key informant interviews.

Communal Settlement and Grazing Management Decisions	
1)	As a community, how do you manage your grazing and settlement?
2)	Who decides where the community can settle and graze?
3)	As a community, how was your grazing and settlement managed before the the creation of group ranches?
4)	As a community, has your grazing and settlement management changed over the last 5 years, why have these changes been made?
5)	What has been the effect of changes in grazing and settlement areas?

Individual Settlement and Grazing Management Decisions	
6)	How is it that Maasai are able to live alongside wildlife?
7)	Are there areas that you are scared to live in or graze in?
8)	Why are you are scared to live in or graze in these areas?
9)	What practices did you use in the past to keep your livestock safe?
10)	What practices did your father and grandfather's use in the past to keep your livestock safe?
11)	How did you learn to keep you livestock safe?
12)	Why do you live in areas where you know there are lions?
13)	Why do you graze in areas where you know there are lions?

Appendix 5

Table S3: Summary statistics for models predicting the number of settlements (bomas) within core lion areas of Shompole and Olkiramatian group ranch.

Model	K	logLik	AICc	delta	weight	R^2
S ~ P	3	-73.96	155.77	0	0.68	0.51
S ~ Pred + P	4	-73.73	158.79	3.017	0.15	0.53
S ~ P + R	4	-73.95	159.24	3.466	0.12	0.51
S ~ Pred + P + R	5	-73.7	162.86	7.089	0.02	0.53
S ~ P + R + P*R	5	-73.89	163.24	7.462	0.016	0.52
S ~ R	3	-79.37	166.58	10.808	0.003	0.08
S ~ Pred + P + R + P*R	6	-73.67	167.73	11.96	0.002	0.53
S ~ Pred	3	-80.06	167.96	12.188	0.002	0.00
S ~ Pred + R	4	-79.35	170.04	14.261	0.001	0.08

S=Number of occupied settlements within core lion areas
P=Mean Monthly Pasture abundance (g/m^2)
R=Monthly Rainfall (mm)
Pred= Number of lion attack in livestock in the previous month

Table S4: Free listing results showing the ranking by group, frequency of occurrence, average rank, and Smiths Salience Index of factors considered by individuals when deciding where to graze and settle. A full taxonomy of each factor (including sub-factors considered) can be found in Figure 3.

Factor	Rank			Frequency	Average Rank	Salience
	Group 1	Group 2	Group 3			
Pasture	1	2	1	1.00	10.44	0.94
Water	2	3	2	1.00	10.39	0.72
Security	3	1	3	1.00	7.72	0.67
Disease /Pests	4	0	0	0.33	4.00	0.17
Terrain	5	0	0	0.33	5.00	0.11
Market Access	0	5	0	0.33	5.00	0.11
Grazing Management	6	0	0	0.33	6.00	0.06
Resources	0	6	0	0.33	6.00	0.06
Settlement	0	4	0	0.33	4.00	0.00

Chapter 5

Death in the long grass: Understanding the dynamics of lion attacks on people and livestock in southern Kenya.

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Author contributions

Experimental design: GW, Data collection: GW, Data analysis: GW, Writing of 1st draft of manuscript: GW, Improvements to manuscript: GW, DWM, AJL, & AJD

In preparation for: Biological Conservation

Abstract

Human-lion conflict resulting from livestock predation is a major factor contributing to the precipitous decline in lion populations across Africa. Many Maasai communities in Kenya, who traditionally killed lions as a means of mitigating lion depredation on livestock, are actively choosing to conserve them through community-based conservation initiatives. Livestock husbandry thus becomes an essential tool in helping them reduce the risk of lion attacks. The data comes from a two-year investigation of lion depredation within two communally owned Maasai group ranches in Southern Kenya. We explore the factors that increase the prevalence and severity of lion depredation on pastoralists and their livestock and assess the ability of livestock guarding to reduce the damage of lion attacks. Finally, we examine how and when lion depredation triggers acts of relation by people. Over the course of 26 months, lions attacked livestock 29 incidents of livestock depredation occured, which resulted in the mortality of 41 head of livestock and injury of 19. This amounts to a yearly rate of livestock damage of 0.07%. Two attacks on humans also happened in which 3 people were injured. Two lions were killed in retaliation, one in response to a lion attack on a herder and one following repeated livestock depredations by a translocated lioness. Despite the greater number of sheep and goat in the area compared to cattle, lions had a clear prey preference for cattle. Lion attacks on livestock were most prevalent during the dry season and were unaffected by changes in prey abundance or variation in pastoral settlement that brought livestock into closer proximity with lions. Livestock was guarded during 48.2% of lion attacks. Active guarding of livestock at pasture was able to disrupt the majority of lion attacks resulting in lower mortality rates while passive guarding in corrals at night also disrupted attacks but in this instance did not lead to lower livestock mortality.

Introduction

Large free-ranging carnivores are particularly vulnerable to anthropogenic disturbances as they require large areas, high prey densities, and frequently come into conflict with people (Macdonald et al., 2015; Lindsey et al., 2017). The rapid collapse of African lion (*Panthera leo*) populations and range, mainly due to anthropogenic pressure, serves to illustrate the challenges of large carnivore conservation. Historically lions were one of the most widespread terrestrial mammals, ranging from northern Europe to southern Africa. Today lions are confined to less than 8% of their former range (Bauer et al., 2015). Over the last two decades lion populations are estimated to have decreased by 43% to a current population of between 23,000 and 35,000 (Riggio et al., 2013; Bauer et al., 2015). Lions need areas large enough to allow male dispersal and support meta-populations of 50-100 lion prides to maintain genetic viability (Björklund, 2003; Cushman et al., 2016). Lion populations found outside of protected areas still comprise a substantial part of the lions' current range which means that Africa's protected area network alone may be insufficient to secure meta-populations of lions across their existing range (Creel et al., 2013; Dolrenry et al., 2014).

Human-lion conflict stemming from livestock predation is often cited as a major driver of the decline in lion populations (Loveridge et al., 2017). Across Eastern Africa's livestock- and human-dominated landscapes, carnivore attacks on livestock occur frequently and can catalyse retaliatory and preventative lion killing. In Kenya, Patterson et al. (2004) estimated that predators were responsible for 2.4% of livestock losses in the Tsavo region, with lions being responsible for 86% of attacks. Similar predation rates of 2.31% were

reported on Mbirikani Group Ranch near Amboseli National Park, although lions were responsible for only 7% of livestock attacks (Maclennan et al., 2009). Reprisals by local communities, as a result of depredation events on Mbirikani, meant that 78 lions were killed between 2003 and 2006 (Frank et al., 2006). In the Maasai Steppe region of Tanzania, Kissui (2008) documented 395 incidents of livestock predation, as a result of which 85 lions and 71 hyaenas were killed in reprisal during a 19-month period. In southern Tanzania adjacent to Ruaha National Park, over 30 lions were killed around just 3 villages in less than 18 months, mainly in retaliation for attacks upon stock (Dickman, 2015). The prevalence of retaliatory lion killings has led to the development of conservation efforts aimed at reducing depredation to create coexistence between people and carnivores on private and communal lands (Creel et al., 2013; Hazzah et al., 2014).

A recent meta-analysis by Miller et al. (2016) classified mitigation measures aimed at reducing carnivore depredation into four broad categories: improved husbandry, predator deterrents, removal of carnivores, and improved environment management. In Miller and colleagues' analysis, livestock husbandry measures such as guarding of livestock at pasture and corralling livestock at night reduced carnivore depredation by between 42% and 100%. The effectiveness of deterrents such as taste aversion conditioning ranged widely with some being infective and others being 100% effective, while predator removal by lethal and non-lethal methods was between 63% and 83% effective at reducing carnivore depredations. None of the studies evaluated quantified the effectiveness of improved environmental management such as land-use planning, creation of buffer zones, and protection of lions' wild prey base.

In Eastern Africa's rangelands, Maasai pastoralists have traditionally relied on lethal removal of carnivores and livestock husbandry to reduce livestock depredation (Spencer, 1988). Today, many Maasai communities in Kenya, such as those in this study area of Olkiramatian and Shompole, are actively engaged in community-based conservation initiatives and are choosing to refrain from lethal control of carnivores, leaving husbandry as the only tool available to reduce carnivore depredation (Schuette, 2012). Corralling livestock at night and the use of herders to accompany livestock at pasture during the day are the main husbandry practices these communities use (Bauer et al., 2017). Previous studies have shown corralling livestock at night reduces depredation across a range of carnivores including lions, pumas (*Puma concolor*), and spotted hyaena (*Crocuta crocuta*) but their effectiveness appears to be highly context specific and dependent on the type of corral used (Eklund et al., 2017). Empirical evidence of the effectiveness of herding is contradictory. Iliopoulos et al. (2009) indicated the presence of herders reduced the severity of wolf (*Canis lupus)* attacks on sheep in Greece, however around Golestan National Park in Iran 92.5% of livestock losses to leopards occurred when a herder was present (Khorozyan et al., 2017). Questionnaire surveys conducted by Mkonyi et al. (2017a) demonstrated that Maasai communities in the Maasai Steppe region of Tanzania believed the use of adult herders and human presence at livestock corrals reduced the severity and prevalence of lion attacks on livestock.

Kenya's Maasailand is estimated to contain almost half (approx. 825) of the country's remaining lion population (approx. 2000 individuals) (KsNLCT, 2008). Evaluating the ability of existing husbandry practices within Maasailand to reduce lion depredation is

therefore essential to helping conserve lion populations within these landscapes. However, as noted by Eklund et al. (2017), very few studies have been able to evaluate the effectiveness of different husbandry methods. To understand lion attacks on livestock and people within a Maasai pastoral landscape our study focused on two communally owned Maasai group ranches in Kenya (Olkiramatian and Shompole). Here lions and other large carnivores still persist independent of the protection afforded by national parks and reserves (Schuette et al., 2013a). Our study draws on a two-year investigation of lion depredation and retaliatory killing of lions within Olkiramatian and Shompole group ranches and focuses on four main questions:

1. What are the anthropogenic and ecological factors that influence the frequency of lion attacks on livestock?
2. What factors affect the severity of lion attacks on livestock and people?
3. How effective was livestock guarding in disrupting lion attacks and reducing livestock mortality?
4. When do lion attacks trigger acts of retaliation by people?

Methods

Study Area

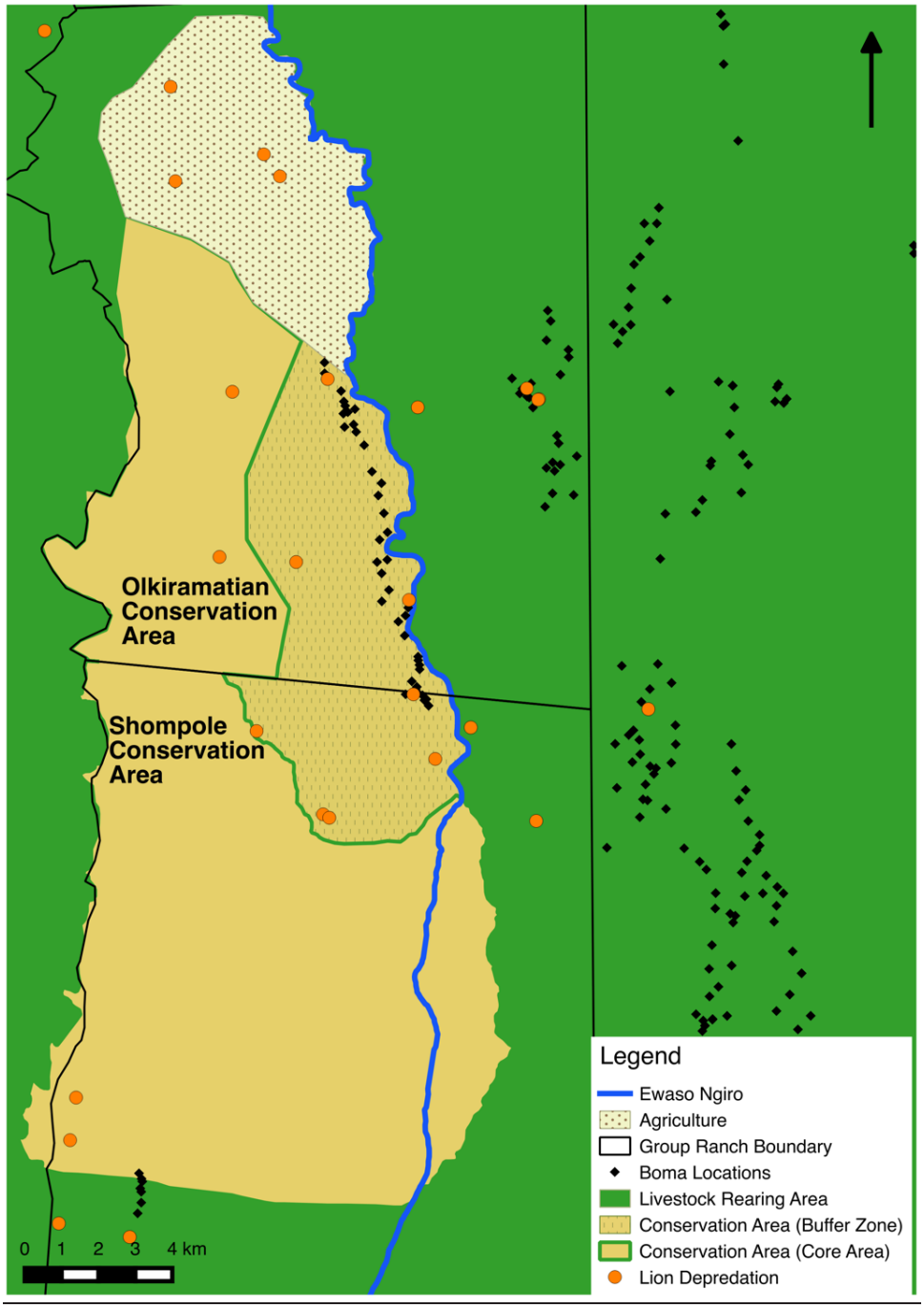


Figure 1: Study area showing locations of lion attacks on livestock (lion depredation), Group Ranch boundaries, Conservation Areas (core and buffer), and settlement locations.

Research was conducted on Olkiramatian and Shompole group ranches, which are two communally owned and managed ranches located in the South Rift region of Kenya. Transhumance Maasai pastoralists occupy the area; they migrate seasonally in search of water and pasture. The region is semi-arid receiving between 200 mm and 600 mm of rainfall annually (Schuette, 2012). The Ewaso Nyiro river runs through the two group ranches providing permanent water within that semi-arid environment. The river is a target for livestock and wildlife in the ecosystem. The two group ranches collectively cover an area of 890 km^2 spanning a multitude of habitats including dense *Acacia tortillis* woodland, *Salvador persica* bushland, and open grassland (Figure 1).

In 2000 and 2004, Shompole and Olkiramatian communities set aside conservation areas which collectively cover an area of 450 km^2 situated on the western banks of the Ewaso Nyiro river. The conservation areas comprise of a core conservancy (total=400 km^2) and buffer zones (total=50 km^2). No settlement is allowed in the core areas but seasonal grazing is permitted. Within the buffer zones, seasonal grazing and settlement are permitted. Locally elected group ranch and conservation committees govern grazing and settlement within the conservation areas. Access to the conservation areas is only granted during the dry season (generally September to March). Temporary settlement is permitted within the buffer zones during the dry season to allow for grazing within the conservation areas. During the wet season (April to August) no settlement or grazing is permitted within the buffer zones or core conservation areas. Community leaders enforce heavy penalties on any member found breaking established grazing and settlement regulations.

The Olkiramatian and Shompole group ranches have 21 different species of carnivores (Schuette et al., 2013b). There are also high densities of livestock and wild ungulates in the two group ranches (sheep/goats: 59.1 individuals/km^2, cattle: 15.8 individuals/km^2, wild ungulates: 28.2 individuals /km^2) as well as many lions (lion densities: 13.6 adult lions/100 km^2). Lion density (13.6 adult lions/100 km^2) is similar to many of East Africa's protected areas, such as the Maasai Mara (17-35 adult lions/100 km^2) and Serengeti National Park (11-18 adult lions/100 km^2) (Schuette et al., 2013a; Schuette et al., 2016). High densities of livestock and lions with comparatively low human densities (~10 people/km^2) in the same ecosystem make Shompole and Olkiramatian ideal sites to investigate the ecological and anthropogenic factors that influence lion depredation on livestock and people in this landscape.

Collection of Conflict Data

GW trained a team of five local Maasai research assistants to document and verify incidents of lion depredation. Depredation was defined as verified cases of lion attacks on people or livestock. Damage was defined and measured as the total number of livestock or people killed and injured during a depredation incident. Between September 2014 and November 2016, lion depredations were also reported to one of three entities: Kenya Wildlife Service (KWS), our research team, or the South Rift Association of Land Owners (SORALO) community rangers, after which at least one member of our research team investigated and verified depredation cases. Kenya's Wildlife Act of 2013, under which compensation for all wildlife related damages was re-introduced to offset the cost of living with wildlife incentivized reporting lion depredation. Additionally, our research team and

SORALO community rangers conducted extensive community awareness campaigns to encourage local livestock owners to report lion depredation incidents to KWS, SORALO, or our research team.

Research assistants used Garmin Etrex 10 handheld GPS units, digital cameras, and sign and spoor identification to document and verify lion depredation incidents. Location, time of incident, and the number of livestock or people killed and injured were recorded. Additionally, sex and number of lions involved, and individual identification of the lions were also collected where possible. Concurrently, contextual information on how and where the incident occurred, and who was present during the attack was collected via direct observation of sign and spoor, eye-witness accounts, and interviews with the livestock owners, where relevant. Verification of lion attacks relied on visual inspections of injuries and carcasses, as well as the use of sign and spoor to reconstruct the attack. Only verified incidents and damage were recorded and used in this analysis.

Contextual information helped to classify lion attacks on livestock. They were grouped into four locations: *within the boma* (community homesteads), *adjacent to the boma* (within 200m of the *boma* but not enclosed within it), out grazing *at pasture* (at pasture), and on *lost livestock* (lost livestock*)* i.e. those which had become separated and did not return to the homestead with the main herd. In addition, we recorded if humans were present when the attack occurred. The type of livestock of guarding was also recorded and classified as (i) *passive guarding*, (ii) *active guarding*, and (iii) *no guarding*. Passive guarding was the corralling of livestock at night, while active guarding occurred when livestock were outside

of the homestead and accompanied by a herder. When there was no evidence of active or passive guarding, the incident was labelled as no guarding. Lion attacks were distinguished further as *disrupted* or *undisrupted*. Disrupted lion attacks happened when humans disturbed the attack and as a result, they were not fatal to the livestock. Disrupted attacks also included when lions were unable to consume their prey because of people. Undisrupted lion attacks on livestock were when lions killed and ate livestock.

Human and Environmental Variables

Rainfall, season, pride home range size, pasture availability, prey density, livestock density, changes in human settlement, and cattle ranging distance were explored as variables that could affect the frequency of lion attacks on livestock.

Rainfall was measured using a HOBO UB30 automated weather station located centrally within the study from which monthly totals were generated. *Season* was based on median monthly rainfall (26.80 mm), with months receiving less than 28.60 mm of precipitation categorized as dry, and those receiving more considered wet. Quantitative estimates of *pride home range* were unavailable for this period due to GPS collar failures hence rainfall was taken to be representative of pride home range size based on the findings of Chapter 3.

Pasture, prey, and livestock abundances were studied by Tyrrell et al. (2017) who conducted randomized point counts and vegetation plots during 22 of the 26 month study period. Livestock and prey densities were calculated from Tyrrell and colleague's raw data using the Jolly 2 methodology (Jolly, 1969) to provide an index of abundance

(individuals/km^2) for each sampling period. Subsequently, Loess interpolation in the statistical package R was used to calculate monthly metrics of prey, livestock, and pasture availability. Lions in the study ecosystem exhibited a preference for zebra and wildebeest over other wildlife species (Schuette, 2012; Creel et al., 2014). Consequently, monthly zebra and wildebeest abundances were combined to provide a monthly measure of lion wild prey availability. Similarly, we used the combined monthly density of cattle, sheep, goats, and donkeys as the index of livestock prey availability.

Human Settlements were mapped monthly as an indication of the amount and distribution of livestock and humans across the ecosystem. The location of a *bomas*, whether they were temporary or permanent, occupied or unoccupied, the type of livestock present, and the names of the families occupying the *boma* comprised the data. Seasonal presence of settlement in buffer zone was a proxy for human presence within the conservation areas (Figure 1). The number of occupied settlements within the study system was calculated from monthly mapping.

Livestock Ranging Distance was demonstrated in Chapter 4 to be closely related to mean monthly Normalized Distance Vegetation Index (NDVI). GPS tracking of all livestock herds (sheep, goat and cattle) within the study system would have been logistically impossible so to provide a reliable index of likely livestock ranging distance across the entire study area mean monthly NDVI was used. Monthly estimates were created using *MODIS* tools in R which extracted 16 day composites from 20 randomly selected sites across the ecosystem at 250 m resolution.

Data Analysis

The Statistical Package for R (version 3.3.0) tested trends in the data. The frequency of lion attacks on people and livestock were summarized using the total number of incidents (n). Severity of lion damage employed the mean damage (not killed and injured) by location, and mean number of fatalities per incident (mean mortality). Chi-square and Kruskal-Wallis tests were used investigate the severity of livestock conflict by comparing mean livestock mortality and livestock damage when herders were present compared to absent, when lion attacks were disrupted compared to undisrupted, and livestock mortality when lion attacks occurred in different contexts.

Jacobs Selection Index (Jacobs, 1974) was used to test lion preference for sheep and goat (shoats), donkeys, and cattle using the equation $D=(r-p)/(r+p-2p)$ in which r was the proportion of lion attacks involving different livestock. The proportional availability of livestock (p) was determined using the mean monthly livestock density. Variation in the frequency of lion depredation on livestock by season, settlement, and context were assessed using Kruskal-Wallis, Chi-square, and Mann–Whitney U test (Wilcoxon rank-sum test).

Generalized linear model (glm) with a Poisson distribution identified which of the five variables (rainfall, prey density, livestock density, pasture availability, and human settlement) best predicted the frequency of lion attacks on livestock. Variance inflation factors (VIF) were calculated for all six predicator variables to access multicollinearity and variables with VIF >3 excluded from the model formulation (Zuur et al., 2010).

Additionally, Pearson's correlation investigated pairwise relationships between predictor variables.

The package *Mass* in R (Ripley, 2015) was used to produce comparative qqplot and access whether the response variable (count data) best conformed to a Poisson distribution or to a negative binomial distribution. Subsequently the model fit was assessed through a chi-square goodness of fit test using the residuals' deviance and degrees of freedom. The package *MuMin* in R (Barton 2016) was used to create and compare a full set of candidate models based on Akaike's Information Criterion (AICc) (Burnham & Anderson, 2004; Symonds & Moussalli, 2011).

Results

Lion Attacks on People and Livestock

Over the 26-month study period a total of 31 lion depredation incidents, including 29 on livestock and 2 on humans, were reported throughout the 890 km^2 study area of which all were verified. During the 2 lion attacks on people, 3 people were injured but none died. The total livestock damaged was 60 (41 killed, 19 injured), including 30 cattle (17 killed, 13 injured), 7 donkeys (4 killed, 3 injured), and 23 sheep and goat (20 killed, 3 injured). Mean livestock damage was 2.07 livestock per incident (range=1-8), while mean mortality was 1.41 (range=1-7). Maximum livestock populations within the study were estimated by Tyrrell et al. (2017) to be 42,350 (± 13480) livestock hence the average annual livestock damage caused by lions was 0.07%.

Both lion attacks on people happened when herders went in search of their lost livestock. In the process of searching they followed livestock tracks and blood trails and arrived at a patch of dense vegetation where the lions had killed and stashed the livestock. Victim and eye-witness statements indicated that in both cases the search party either did not expect lions to still be in the vicinity or expected them to flee from the search party. During the first incident, a lioness with cubs attacked a member of the search party, seriously injuring him; other members of the community were alerted and a retaliatory hunt ensued in which another member of the hunt was injured and the lioness fatally speared. The second lion attack happen in a similar manner; however the livestock owner was on his own when he came across the carcasses of his sheep and goats that had been killed. He was then attacked by a lioness when he tried to approach these livestock carcasses.

Table 1: Overview of lion depredation on livestock by location and variation in the (i) number of depredation incidents, (ii) total number of livestock killed and injured (livestock damage), and (iii) total number of livestock killed (livestock mortality).

	Incidents	Total Damage	Mean Damage	Mortality	Mean Mortality
Season					
Dry	23	53	2.30 .	37	1.68
Wet	6	7	1.17	4	0.67
Settlement Presence					
Absent	9	21	2.33	12	1.50
Present	20	39	1.95	29	1.45
Location of Attack					
At Pasture	9	13	1.44	5	0.56
In Boma	8	26	3.25 *	18	2.25 **
Lost	7	14	2.00	14	2.00
Outside Boma	5	7	1.40	4	0.80
Human Presence					
Yes	14	34	2.43 **	21	1.50
No	15	26	1.73	20	1.33
Type of Guarding					
Active Guarding	6	8	1.33	3	0.50
Passive Guarding	8	26	3.25 *	18	2.25 **
No Guarding	15	26	1.73	20	1.33
Attack Disrupted					
Disrupted	13	26	2.00	13	1.00
Undisrupted	16	34	2.13	28	1.75

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1

Lion attacks on livestock were not more prevalent in any particular location (X^2=1.20, *df*=3, P =0.751), whether it was *in boma* (n=8), *at pasture* (n=9), *lost livestock* (n=7), or *adjacent to boma* (n=5). However, total livestock mortality did differ by location (X^2=13.42, *df*=3, P =0.003; Table 2), with the highest mortality occurring *in boma* and lowest *adjacent to the boma*. Mean livestock mortality per incident was also significantly different across locations, with lowest mean livestock mortality in attacks *at pasture* (0.56 livestock per incident) and highest *in boma* (Kruskal Wallis = 12.72, p = 0.005) (Table 2). Jacobs' index analysis of lion attacks on livestock showed that lions had a clear preference for large stock (donkeys and cattle) over small stock (sheep and goat) (Figure 2). Lions attacked cattle at pasture most frequently (Fishers exact test, P < 0.001) representing 27% (n=8) of the cases and 50% (n= 8) of lion attacks on cattle. Small stock was most commonly attacked *in boma* (Table S1). A single lioness who had been translocated from the southern end of the study area to the north after being caught in a leopard trap was responsible for 5 of the 8 lion attacks *in boma*.

Livestock Guarding and Disrupted Attacks

Overall, livestock owners or herders claimed to be present in 17 (58.6%) of the 29 attacks although verification of human presence was only possible in 14 (48.3%) of the attacks. Active guarding, where herders were present, occurred in 7 instances (20.7% of all cases), which represented 66.7% of the 9 attacks on stock *at pasture*. Passive guarding, where livestock were corralled, occurred during all 8 attacks on *bomas*, representing 28.6% of all verified attacks.

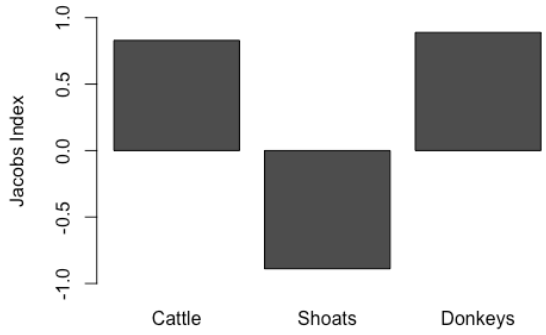


Figure 2: Jacobs index (+1 to -1) showing lion preference for livestock, positive scores indicate preferential selection.

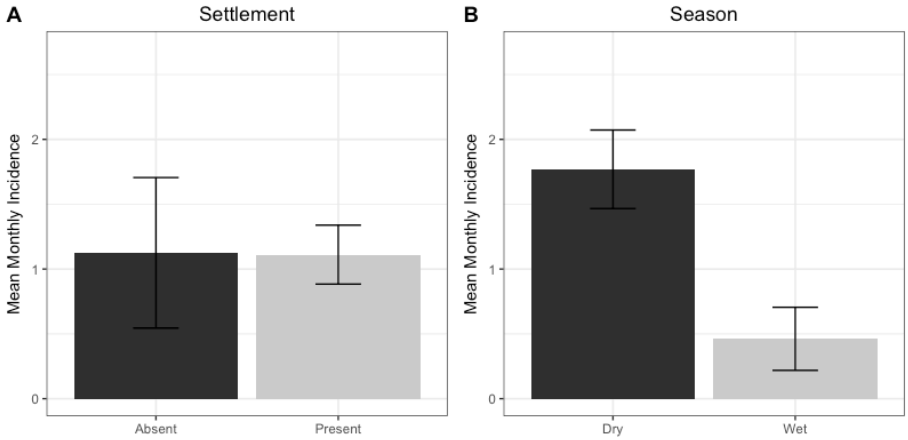


Figure 3: Varation in mean monthly frequency of lion depredation (A) when settlement was present or absent in the conservation areas (Settlement), and (B) during different seasons (Season).

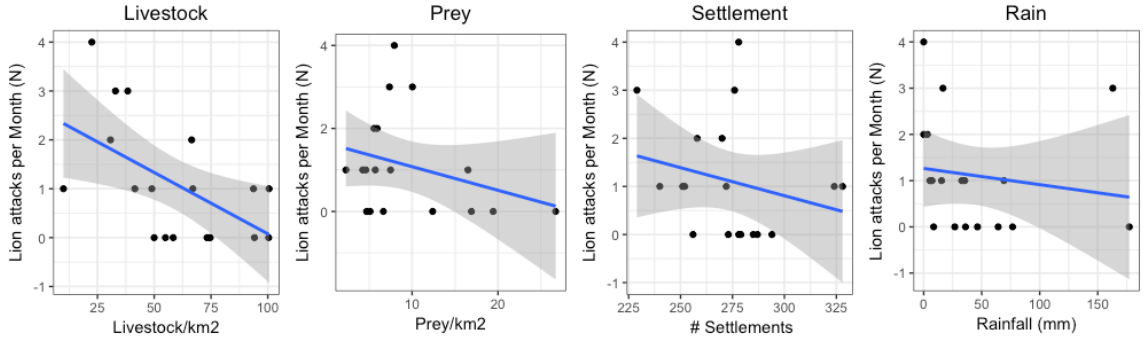


Figure 4: Line graphs depicting linear relationships (blue) with 95% confidence intervals (grey) between the four explanitory variables (Livestock Abundance, Prey Abundance, Settlement, and Rainfall) and prevelance of lion attacks (black points) included in model formulation.

Lion attacks were disrupted during 44.8% (n=13) of 29 incidents of lion depredation. These disruptions happened in 88.3% (n=5) of 6 instances where there was active guarding and disrupted in 62.5% (n=5) of the cases with passive guarding. During the other three disrupted lion attacks, two occurred when lions were chased off by herders who were grazing their livestock nearby, while the third occurred when herders harassed lions who had attacked a donkey outside their *boma*. The single undisrupted attack during active guarding happened when the herder (a 9-year-old boy) fled during the attack leaving the herd behind. Undisrupted incidents of lion depredation (n=3) all involved lions chasing livestock out of the corrals at night (passive guarding). The lions subsequently killed them adjacent to the homestead. Disrupted attacks did not significantly reduce the severity of livestock damage per incident or livestock mortality (Table 1).

When humans were present, livestock damage per incident was significantly higher than when humans were not present but mean livestock mortality per incident was no different. This was because the type of human presence played an important role in determining the severity of lion depredations. Mean damage and mortality was highest when livestock was passively guarded in corrals and lowest when livestock was actively guarded at pasture (Table 1).

The Role of Human Settlements in Rate of Lion Attacks

Humans and livestock were present in the conservation areas for 20 months and absent for 6 months during the study period. Lion depredation was not more prevalent when settlement was present compared to absent with lion attacks occurring in 55.0% (n=11) of

months in which there was human settlements and livestock grazing, and in 50.0% (n=3) of months in which humans and livestock were absent (X^2=0.47, *df*=1, p=0.491). Furthermore, the mean frequency of lion depredation incidents per month was not significantly different in months when settlement was present compared to absent (Wilcox test, W=75, p=0.89) (Figure 3). The presence of settlement had little effect on the severity of livestock depredation, neither mean livestock mortality per incident nor livestock damage per incident differed significantly because of presence or absence of settlement (Table 1).

Months were classified as wet and dry based on median rainfall producing 13 wet months and 13 dry months. Lion attacks on livestock happened more in dry months (76.9%; n=11) than in wet months (30.8%; n=4) (X^2=3.869, *df*=1, p = 0.049), a pattern also found in the mean frequency of lion attacks (Wilcox Test, W=41.5, p=0.02) (Figure 3). But rainfall had little effect on the severity of any attack, nor was mean livestock mortality per incident significantly different between dry and wet months. Livestock damage per incident was only marginally higher during dry months (Table 1).

Predicting Livestock Depredation

Collinearity was present (VIF > 3) in several of the predictor variables, so further investigation was needed to determine which variables to include in our models. Pearson pairwise comparisons revealed a statistically significant correlation between pasture abundance and livestock ranging distance (r_p=0.81, p < 0.01) as well as between livestock ranging distance and prey abundance (r_p=0.71, p < 0.01). Therefore, pasture abundance and

quality was excluded from the model and prey abundance assumed to be a representative index of pasture abundance and livestock ranging distance. The total number of occupied settlements within the ecosystem was used to quantify the extent of human and livestock presence within the study area. Rainfall and livestock density were also included as explanatory variables. To account for possible presence of interaction effects between livestock densities, prey availability and rainfall, interaction terms were included in the model formulation.

Livestock abundance was the best predictor of lion depredation. Model selection (Table S2) revealed the livestock model (L) was a substantially (ΔAICc = 2.68) better predictor of frequency of predation than the expanded model containing livestock density (L) and prey availability (P). Models which included only livestock (L), settlement (S) or rainfall (R) were worse predictors of depredation than the null model which included only the intercept. Depredation was inversely correlated to livestock abundance density (Figure 4) and explained 34% of variance in frequency of predation on livestock.

Retaliatory Lion Hunts

Two retaliatory lion hunts happened because of lion attacks. The first incident was in response to 5 attacks on small stock by a single lioness in a 10-day period. Prior to the hunt, community members had requested KWS to deal with the lion but no action was taken. The second incident occurred when a member of the community was mauled by a lioness while in search of lost livestock. In both hunts, men carried spears; more than 20 participants were involved. Both hunts killed the lioness responsible for the attacks.

Discussion

Livestock Attacks and Guarding

Despite measures being taken by livestock owners to protect their livestock, almost half (48.3%) of lion attacks on livestock took place while livestock were being actively or passively guarded. Previous studies by Ogada et al. (2003) and Woodroffe et al. (2007) showed that good pastoral care both *at pasture* and *in boma* was able to deter lion attacks. Our results show livestock guarding was also able to disrupt the majority (55.2%) of lion attacks on livestock. Surprisingly, the severity of attacks was not significantly lower when livestock attacks were disrupted than when they weren't, suggesting that guarding may deter and disrupt attacks but may not necessarily reduce livestock mortality or damage. During this 2-year study, lion attacks on livestock caused mortality and injury rates to an average of 0.07% of total livestock present per year. Comparatively, on Kuku group ranch in southern Kenya Maasai herders lost 0.49% of total livestock per year to lions, while in pastoralist areas around Ruaha herders lost 1.2% livestock per month (Dickman et al., 2014; Bauer et al., 2017).

In Olkiramatian and Shompole lions predominantly attacked cattle at pasture while sheep and goats were attacked *in bomas*, and donkeys *adjacent to bomas* (Table S1). Similar patterns were observed surrounding Tarangire National Park in Tanzania, and surrounding Kenya's Maasai Mara Reserve (Ogada et al., 2003; Kissui, 2008). Jacobs index scores reveal that lions preferentially attacked cows and donkeys (large stock) over sheep and goat (small stock) despite small stock being four times more abundant than large stock (Russell et al., submitted). Elsewhere, lions have been shown to preferentially hunt large wild

ungulates ranging between 190-550 kg (Hayward & Kerley, 2005). In Hwange district in Zimbabwe, lion prey size preferences was also applicable to domestic stock (Loveridge et al., 2017). Lions' preference for cattle over small stock as prey has the potential to exaggerate the impact of attacks since cattle are the corner stone of Maasai identity and livelihoods yet in Olkiramatian and Shompole, no retaliatory hunts occurred as a direct result of cattle predation.

Livestock mortality was lowest when livestock were actively guarded (0.50 livestock per incident), a rate that is lower than in comparable studies conducted in Maasai communities in the Maasai Mara (1.0 livestock/incident) and Laikipia (1.3 livestock/incident) (Ogada et al., 2003; Woodroffe et al., 2007). Although almost a third (31.0%) of all lion attacks took place at pasture these attacks only accounted for a mere 12.1% of all livestock mortality demonstrating active guarding was effective at reducing livestock mortality.

Passive guarding of livestock in bomas resulted in disruption of lion attacks but not did little to reduce the severity of the attack. Passive guarding played a role in disrupting 75% of lion attacks on livestock *in bomas*, however attacks where most severe these contexts. Livestock attacks *in boma* were predominantly on small stock (62.5%, n=5) which may account for the high livestock mortality *in boma*. This may be partially due to livestock being confined in a small area within *bomas*, lions are thus able to inflict substantial damage on stock before being disrupted. The translocation of a "trapped" lioness may have also compounded impact of lion attacks since she was responsible for all 5 of the small

stock attacks *in bomas*. Excluding her attacks makes lion attacks on livestock *in bomas* the least frequent type of lion depredation.

Good livestock husbandry practices such as active guarding at pasture and passive guarding of livestock in corals observed in Olkiramatian and Shompole are also prevalent more widely within Maasailand. Herders are employed in the Mara and Tarangire ecosystems to deter lion attacks on livestock at pasture, and fortifying traditional Maasai *bomas* has been shown to further reduce livestock predation (Kolowski & Holekamp, 2006; Lichtenfeld et al., 2015; Mkonyi et al., 2017a). Elsewhere in Africa, lack of guarding left livestock vulnerable to lion predation in Botswana's Makgadikgadi ecosystem (Valeix et al., 2012a) and in Zimbabwe (Loveridge et al., 2017) surrounding Hwange Park in Zimbabwe. Both studies showed that the majority of lion attacks happened when livestock was left unguarded at pasture. In our study 51.7% (n=15) of attacks by lions were on unguarded livestock. Unlike in Hwange where livestock where intentionally left out to graze over night (Kuiper et al., 2015), the only animals that were left out at night were donkeys and lost livestock.

Predicting Lion Attacks on Livestock

Livestock densities were negatively correlated with the frequency of lion attacks in the study area. Seasonal patterns of prey and livestock movements may explain this counter-intuitive result. During periods of low pasture quality and quantity, pastoralists moved their herds out of the study areas in search of grazing (Tyrrell et al., 2017). At the same time, the herds of livestock and of wild ungulates that remain behind concentrate on the remaining

patches of good-quality pasture. Consequently, low livestock densities are indicative of an environmental context in which livestock and prey are concentrated in a few remaining drought refugia. If lions are structuring their home ranges around these resource rich patches (Chapter 2) then the likelihood and prevalence of lion attacks on livestock would increase.

Within Olkiramatian and Shompole, the frequency of lion predation was also higher during the dry season further supporting the suggestion that water and pasture scarcity forces both cattle and wild prey to converge on drought refugia, thereby precipitating an increase in the frequency of livestock predation. Our findings contrast with previous studies where higher livestock predation rates occur in the wet season when wild prey was less abundant (Patterson et al., 2004; Kissui, 2008; Loveridge et al., 2017). The shift from predation on wildlife to predation on cattle has been linked to prey abundance so that predation on cattle increases when wild prey biomass falls below a minimum threshold of 812.41 kg per km^2 (Khorozyan et al., 2015). Based on Tyrrell et al. (2017) we calculated that zebra and wildebeest biomass within Shompole and Olkiramatian ecosystem did not drop below a minimum 1287 kg per km^2 even during severe droughts, suggesting that lions had more than ample prey, explaining why prey density was a poor predictor of lion attacks.

Increases in pride home range size, the presence of settlement within buffer zones of the conservation area, and livestock ranging distance did not increase the prevalence of lion incidents. A possible explanation for this is that lions and wild ungulates within Olkiramatian and Shompole were shifted away from the buffer zone when human

settlement was present increasing utilization of the core conservation areas by both lions and their prey (Schuette et al., 2013a; Schuette et al., 2016). Given this displacement away from human settlements, increases in settlement, pride home range size, and livestock ranging distance may not equate to an increase in human-lion encounters.

Lion Attacks on People and Retaliatory Killing

Communities within Olkiramatian and Shompole proved remarkably tolerant of lion attacks since there were only two retaliatory killing during the study period. By contrast, in the Maasai Steppe region of Tanzania, Kissui (2008) suggested that livestock depredation resulted in the retaliatory killing of 85 lions in a 19-month period and that the prevalence of retaliatory killing of lions was correlated to the number of lion attacks on livestock. Our sample size is not large enough to speak definitively about what triggers the retaliatory killing of lions, but it appears that serial livestock attacks and attacks on people are both probable catalysts. The first incident of retaliatory killing of livestock was catalysed by the translocation of a lioness within the study area who then killed 11 livestock in a 10-day period. As a community elder who partook in the retaliatory hunt of the lioness explained: *"Do not see us as lion killers; we still want to protect lions; however this lion was different, it was causing a major problem so it was killed"*. The injury of a human motivated the second retaliatory killing.

Lion attacks on humans were rare but in both cases happened when community members looked for lost livestock. This highlights the potential risk of searching for lost livestock and illustrates how lion attacks on livestock can lead to lion attacks on people and then

retaliatory killing of lions. Lion attacks on humans within our study appeared to result from lions defending themselves, their cubs, and/or their kill, and not incidents of man-eating as documented in Tanzania where lions have been recorded to hunt and eat their human victims (Packer et al., 2007).

Conclusions

Lion depredation on livestock in Olkiramatian and Shompole happened much less than reported for other localities across Maasailand. Lion attacks were most prevalent during the dry season when livestock and wild prey target the few remaining patches of high quality forage. This concentration of prey, pasture, and predators may result in more human-lion interactions, leading to an increase in lion attacks on livestock. Prey abundance seemed to have little or no effect on the frequency of lion attacks on livestock, indicating that lion predation on livestock was not driven by a lack of wild prey. Seasonal migration of people and livestock into the conservation areas also did not increase the frequency of lion attacks on livestock.

Active guarding helped to disrupt and potentially deter lion attacks on cattle at pasture. This may further explain the low prevalence of lion depredation within our study. However, lion attacks on livestock still occurred in the presence of active and passive guarding indicating that guarding alone is not always sufficient to prevent lion attacks. Community members within the Olkiramatian and Shompole group ranches refrained from retaliatory action against lions in most cases of lion predation on livestock. However, serial killing of livestock and lion attacks on humans motivated retaliatory killing of lions.

Guarding of livestock and searching for lost livestock are necessary to reduce the risk of depredation but also have important inherent risks since herders may be attacked in the process.

This study provides a better understanding of the dynamics of lion depredation in a pastoralist rangeland that has a conservancy area, offering lessons for better management strategies to ensure continued coexistence between humans and lions. Our findings suggest that use of herders who are able and willing to deter and disrupt lion attacks on livestock can reduce the severity of these attacks by lowering livestock mortality. However, the safety of herders and search parties looking for livestock should be considered to ensure that lion attacks on livestock do not result in human fatalities and retaliatory lion hunts as well. Establishment of rapid response teams to assist in the recovery of lost livestock and attend to cases of livestock predation could be one way of achieving this. Creation of wildlife damange databases and protocols that facilitate the reporting of lost livestock and lion depredations is another way of providing conservation managers and stakeholders with accurate and timely information. This then would be the basis of informed decisions and actions to prevent isolated incidents of livestock depredation do not escalate into serial lion depredation.

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Appendix

Table S1: Overview of lion depredation on livestock by location and variation in the (i) number of depredation incidents, (ii) total number of livestock killed and injured (livestock damage), and (iii) total number of livestock killed (livestock mortality).

	Location of Lion Attacks				
	At Pasture	In Boma	Lost	Adjacent Boma	Total
Number of depredation incidents					
Cattle	8	3	5	0	16
Shoat	1	5	2	0	8
Donkey	0	0	0	5	5
Total Number of Incidents	9	8	7	5	29
Total Livestock Damage					
Cattle	11	13	6	0	30
Shoat	2	13	8	0	23
Donkey	0	0	0	7	7
Total	13	26	14	7	60
Mean Damage per Incident	1.44	3.25	2.00	1.40	2.07
Total Livestock Mortality					
Cattle	4	7	6	0	17
Shoat	1	11	8	0	20
Donkey	0	0	0	4	4
Total	5	18	14	4	41
Mean Mortality per Incident	0.56	2.25	2.00	0.80	1.41

Table S2: Model comparison showing predictive models of factors affecting the frequency of monthly livestock depredations by lions.

Model	K	logLik	AICc	ΔAICc	weight
D ~ L	2	-22.32	49.44	0.00	0.40
D ~ L + P	3	-22.20	52.12	2.68	0.11
D ~ L + R	3	-22.26	52.23	2.79	0.10
D ~ L + S	3	-22.32	52.35	2.91	0.09
Null Model	1	-26.04	54.33	4.89	0.04
D ~ L + P + L:P	4	-21.65	54.38	4.94	0.03
D ~ P	2	-24.79	54.39	4.95	0.03
D ~ L + R + L:R	4	-21.71	54.50	5.06	0.03
D ~ L + P + R	4	-22.17	55.42	5.98	0.02
D ~ L + P + S	4	-22.19	55.46	6.02	0.02
D ~ S	2	-25.34	55.48	6.04	0.02
D ~ L + R + S	4	-22.23	55.53	6.09	0.02
D ~ P + S	3	-24.14	56.00	6.56	0.02
D ~ R	2	-25.76	56.32	6.88	0.01
D ~ R + S	3	-24.73	57.17	7.72	0.01
D ~ P + R	3	-24.76	57.24	7.80	0.01
D ~ P + R + P:R	4	-23.45	57.98	8.54	0.01
D ~ L + P + S + L:P	5	-21.59	58.17	8.73	0.01
D ~ L + P + R + P:R	5	-21.60	58.20	8.76	0.01
D ~ L + P + R + L:P	5	-21.62	58.24	8.80	0.01
D ~ L + R + S + L:R	5	-21.71	58.41	8.97	0.01
D ~ L + P + R + L:R	5	-21.71	58.42	8.98	0.01
D ~ P + R + S	4	-23.93	58.94	9.50	0.00
D ~ L + P + R + S	5	-22.13	59.26	9.82	0.00
D ~ P + R + S + P:R	5	-23.17	61.34	11.90	0.00
D ~ L + P + R + L:P + P:R	6	-21.30	62.24	12.80	0.00
D ~ L + P + R + L:P + L:R	6	-21.32	62.27	12.83	0.00
D ~ L + P + R + L:R + P:R	6	-21.43	62.49	13.05	0.00
D ~ L + P + R + S + L:P	6	-21.49	62.61	13.17	0.00
D ~ L + P + R + S + P:R	6	-21.60	62.84	13.39	0.00
D ~ L + P + R + S + L:R	6	-21.70	63.04	13.60	0.00
D ~ L + P + R + L:P + L:R + P:R + L:P:R	8	-17.54	67.08	17.64	0.00
D ~ L + P + R + L:P + L:R + P:R	7	-21.18	67.56	18.12	0.00
D ~ L + P + R + S + L:P + L:R	7	-21.27	67.74	18.30	0.00
D ~ L + P + R + S + L:P + P:R	7	-21.28	67.76	18.32	0.00
D ~ L + P + R + S + L:R + P:R	7	-21.42	68.04	18.60	0.00
D ~ L + P + R + S + L:P + L:R + P:R	8	-21.17	74.34	24.90	0.00
D ~ L + P + R + S + L:P + L:R + P:R + L:P:R	9	-17.05	74.59	25.15	0.00

D=Monthly incidence of lion predation
L= Livestock abundance
S= Settlement (number of occupied settlements within the study area)
P=Prey and pasture abundance
R=Rain

Chapter 6

Final Discussion and Conclusion

General Discussion

Towards a framework for coexistence

A principle aim of this study was to evaluate whether coexistence was possible and mutually beneficial to carnivores and people, especially under conditions of decreasing space and increasing land pressures caused by humans. Here, I integrate and expand on four key findings from previous chapters which gives a novel insight into the socio-economic and environmental factors that influence both the desire and the ability of Maasai communities to coexist with lions. Firstly, Chapter 2 demonstrated that conservation education and perceived benefits from wildlife promoted a desire to see lion population maintained or increased but the ability to do so is influenced by a variety of other socio-economic, and political factors such as governmental policy and perceived ownership of wildlife. Secondly, lion home range analysis in Chapter 3 showed that ecological rather than anthropogenic factors were the key determinants of range size and that lion ranges were contiguous with protected area populations. Thirdly, from the point of view of decisions made by pastoralists, in Chapter 4 lion occupancy and predation risk were shown to be of little importance in determining landscape utilization and livestock ranging patterns. Instead these are predominantly driven by pasture abundance and quality. Finally, the analysis of livestock depredation in Chapter 5 revealed that dry periods in which pasture declined, also increased the frequency of livestock depredation. However, active guarding of livestock at pasture played an important role in disrupting lion attacks on livestock and reduced livestock mortality during high risk periods.

To integrate these findings, I draw on factors highlighted in the social science literature. These include social ecological systems, social capital, and traditional ecological knowledge. Previous studies of coexistence are examined using this perspective. The results clarify the dynamics of human-lion coexistence within Maasailand.

Defining Social Ecological Systems (SES)

Social ecological systems (SES) frameworks incorporate interactions between people and the environment, making humans agents of change within the natural world (nature) rather than merely an external force to it (Berkes & Folke, 1998). The concepts of *vulnerability*, *resilience*, and *adaptation* are often found in the conservation biology and development literature (Gallopín, 2006). Both these disciplines reference resilience and vulnerability but conservation biology tends to focus on ecosystems and non-human species while the development literature is centered around human communities and individuals. Social-ecological systems incorporate the two spheres into one framework.

Vulnerability is defined by Adger (2006) as "the susceptibility to harm from exposure associated with environmental and social change, and the absence of capacity to adapt" (page 268). *Resilience* within SES systems has been defined as "the ability of people, communities, societies, and cultures to live and develop with an ever-changing environment" (Folke et al., 2016). Borrowing from Brooks (Brooks, 2003) I define *adaption* to be "adjustments that enable overcoming negative environmental and social stresses".

Defining Social Capital

Definitions of *social capital* vary widely. It is most often thought to be relationships which enable a community to work collaboratively to achieve a common goal (Putnam, 1993; Bowles & Gintis, 2002). Social capital is comprised principally of *generalized trust, reciprocity*, and *social networks* which exist between and within communities (Coffé & Geys, 2007). Fukuyama (1995) considers *generalized trust* to exist when "a community shares a set of moral values in such a way as to create regular expectations of regular and honest behavior" (p.153). *Reciprocity* has been proposed as an evolutionary adaption within human society that contributes to resilience to catastrophic environmental shocks. It is the willingness of an individual to cooperate with other members of society even when it isn't economically rational or motivated by self-interest (Gintis, 2000). *Social networks* are the result of linkages or ties to other individuals in society. Galvin (2008) distinguishes between bonding ties and bridging ties. Bonding ties exist within families, extended kinship networks and between friends, while bridging ties link outside an individual's immediate network and give access to resources.

Defining Traditional Ecological Knowledge (TEK)

Ecological Knowledge, indigenous knowledge and traditional ecological knowledge (TEK) are often used interchangeably and do not adhere to a singular strict definition. Based on Berkes (1999), I consider TEK to be knowledge acquired through experience, adaptive learning, and intergenerational transmission about the natural history of an ecosystem and its inhabitants. TEK has been proposed as a mechanism in the context of carnivore

conservation and ecosystem management that facilities adaptive management and allows communities to respond to environmental variability. Similarly, the existence of resource and habitat taboos (RHT) as part of TEK can serve to mitigate and manage human-wildlife interactions (Berkes et al., 2000; Colding & Folke, 2001).

Creating a Desire for Coexistence with Lions

Site specific case studies (Chapter 2) revealed there was no common factor that influenced the desire to see lions increase. Personal benefits from conservation increased the desire to see more lions in Ruaha and Maasailand but not in Hwange suggesting that conservation agendas were confounded by environmental histories and human-human conflicts. Differences in socio-political and economic context are factors that contributed to differing levels of vulnerability, resilience, and adaption of communities in the three locations explaining differences in willingness to see changes in lion numbers. In Hwange and Ruaha, disempowerment, subjugation of resource stewardship, and inequality of conservation benefits were central narratives contributing to increased vulnerability and negative perceptions of lion conservation. In the contrary in Maasailand, personal conservation and communal ownership were linked to positive perceptions.

Conservation benefits in Maasailand accrued at the individual and community levels and illustrated how Community-Based Conservation (CBC) and Community-Based Natural Resource Management (CBNRM) can complement existing traditional ecological knowledge and social capital. CBC initiatives in Kenya were not constrained by

government regulation making them inherently flexible. They were able to adapt to local cultural contexts which sets these initiatives apart from the type of rigid solutions advocated for by development organizations and increasingly in the conservation community (Roe, 1993; Western et al., 1994). Successful CBC in Maasailand was facilitated by governments and NGOs devolving control of natural resources to the community level, transparently and through local participation, thus reinforcing existing social capital and providing an economic incentive to maintain traditional management practices.

The inability of CBC/CBNRN in Ruaha and Hwange to produce tangible benefits from conservation was likely inhibited by lack of social capital in the environmental and political narratives for the two sites. Collapse of Zimbabwe's economy appears to have crippled the CAMPFIRE program undermining the financial incentives for coexistence (Sibanda, 2014). The country's economic instability had an impact on the decline of generalized trust and reciprocity among heterogeneous communities surrounding Hwange. This may have also increased individual vulnerability to livestock predation leading to the desire to see lion numbers decrease. In Ruaha, appropriation of environmental stewardship by the Tanzanian government disenfranchised communities and eroded *institutional trust* and *generalized trust* also feeding into negative perceptions of conservation and wildlife. Trust has been shown to influence perceptions of carnivores and conservation. Elsewhere in the world Sponarski et al. (2014) argued that perceptions of wolves in Canada were strongly influenced by societal trust in conservation management agencies. Individuals who felt state agencies were unable to manage human-wolf conflicts were more negative

towards wolves. Stern (2008) maintained that in the United States of America and Ecuador distrust of park managers, and not economic benefit, was the most consistent determinant of negative perception toward protected areas.

The failure of many CBC/CBNRM projects to prevent land conversion demonstrates that financial incentives from conservation and wildlife cannot always generate substantial revenue or offset the benefits of natural resource exploitation (Calfucura, 2018). There is now an increasing awareness that CBC/CBRM initiatives should supplement pre-existing tangible and non-tangible benefits, rather than replacing them. In Shompole and Olkiramatian, community conservation areas were based around existing TEK and land-use practices and managed by pre-existing governance committees. TEK and the cultural belief that tigers contributed to a healthy ecosystem shaped positive perceptions of tigers in Chitwan, Nepal (Carter & Allendorf, 2016). Analogously, cultural acceptance of coexistence with wildlife in Maasailand was influenced by a similar belief as explained by a Maasai elder who stated: "*If I see somewhere without wildlife, I ask myself what is wrong with this place that no wild animals live here"*. Connecting community-based conservation with local institutions and cultural beliefs greatly increases the effectiveness of conservation. For instance, Ghana's Wechiau Community Hippo Sanctuary aligns conservation with TEK with measurable conservation and development success (Sheppard et al., 2010). Similarity in India's Western Ghats, Ormsby and Bhagwat (2010) found that sacred forests proved an effective model for CBNRM and local resource protection. Together these examples highlight local variation in cultures and with it, thus highlighting the need for a case-by-case approach that is sensitive to varying traditions.

The Ecology of Coexistence

Coexistence between Maasai pastoralists and lions in Olkiramatian and Shompole is dependent on adaption to changing environmental and socio-political conditions. Transhumance pastoralism facilitates this coexistence by maintaining access to seasonal pasture and water resources within an open and resource abundant (pasture and water), heterogeneous landscape (BurnSilver et al., 2008; Butt, 2010). Spatial heterogeneity of pasture in the Olkiramatian and Shompole ecosystem allowed herders to avoid areas of high lion occupancy for a large portion of the year, creating temporal and spatial separation between lions and livestock within the ecosystem (Tyrrell et al., 2017). As shown in Chapter 4, lion presence was seldom a consideration in decisions about land-use planning or even in grazing regulations, however both types of management further enabled coexistence. Zoning of settlement in permanent areas and temporary areas gave seasonal access to pasture but also decreased the amount of time livestock spent in areas of high lion presence. Seasonal closure of the conservancies to grazing ensured abundant year-round forage and also maintained zebra abundance in areas of high lion presence (Russell et al., 2018).

Important resources like prey, water, and cover were abundant and distributed across the Shompole and Olkiramatian ecosystem (Schuette et al., 2016), allowing lions to occupy smaller home ranges than in other human-dominated landscapes. Small ranges enabled coexistence by allowing lions to shift away from areas of temporary settlement, such as the buffer zone, when livestock and people were present. Prey densities in lion areas did not change because of human settlement (Schuette et al., 2013), indicating that lions were able

to maintain year-round access to prey and did not have to resort to targeting livestock because wildlife prey were scarce, as is a common pattern in Botswana (Valiex et al., 2012). Prey abundance was a poor predictor of lion attacks on livestock adding support to the claim that lions in Olkiramatian and Shompole had ample prey year-round.

The ability of lions in Olkiramatian and Shompole to access prey may have been facilitated by the presence of livestock and people. The Maasai have long believed that landscape heterogeneity is created by coexistence between livestock and wildlife as epitomized by a Maasai saying *"elephants make grassland; cattle make woodlands*". Wildlife-livestock interactions are mutually beneficial; areas with cattle grazing have more bush and eventually trees while those utilized by elephants have more grass because the elephants destroy the bushes and trees (Odadi et al., 2011; Kimuyu et al., 2017). These grazing dynamics combined with land-use and grazing management in the Olkiramatian and Shompole ecosystem concentrated zebra and wildebeest in conservation areas during periods of highest human presence (Tyrrell et al., 2017). This may have partially counteracted the effect of increased human and livestock presence within the conservation areas so that there were lower than expected levels of lion predation on livestock. Consequently, the frequency of livestock depredation did not increase when settlement and livestock were present within the conservation areas compared to absent.

The Sociology of Coexistence

Adaption to ecological variability within pastoral societies is facilitated by formal and informal institutions that govern communal property rights and access to pooled resources

(Fratkin et al., 2004). Traditional ecological knowledge and social capital further reduce vulnerability and increase resilience to environmental, economic and socio-political perturbations (Berkes & Folke, 1998). These same mechanisms enabled coexistence and adaption to the variable presence of lions in Olkiramatian and Shompole. Reciprocity and cooperation emerge along with ecological knowledge as central themes that allowed for coexistence.

Reciprocity and Cooperation

Social capital forms the back bone of Maasai society and is reinforced through *reciprocity,* enabling individuals and communities to reduce vulnerability to environmental change and livestock predation. Reciprocity serves as a societal safety net and acts as an informal insurance scheme (Spear & Waller, 1993; Galvin, 2008). Three types of reciprocity exist within Maasai society; (i) balanced reciprocity, (ii) delayed reciprocity, (iii) generalized reciprocity (Potkanski, 1994).

Balanced reciprocity usually takes the form of direct exchange of livestock and operates in similar ways to traditional "barter systems". Both parties benefit from a mutually agreed exchange of goods or services (Spear & Waller, 1993). High grade Sahiwal bulls were frequently exchanged for several lower quality Zebu animals by livestock owners in Olkiramatian and Shompole allowing one beneficiary to grow his herd and the other increase the genetic potential of his breeding herd.

Delayed reciprocity is still common in Maasailand and is exemplified by bridging ties known as the "stock friendships" or "associates". In these, age-mates gift livestock to each other in order to reinforce friendships (Spencer, 1988; Galvin, 2008). Stock friendships dissipate the effects of livestock losses by drought, disease, and predation, and provide a mechanism by which herd owners can replenish their herds following livestock losses (Rutten, 1992). Bonding ties and delayed reciprocity in Maasai society expand the communities' ability to adapt thus reduce a household's vulnerability to livestock predation and increases community's resilience to drought. During the droughts of 2012, 2013, 2014, and 2017, community members from Olkiramatian and Shompole moved to Oldonyo Lengai in Northern Tanzania in search of pasture. Their ability to do so depended on existing bridging ties and reciprocal arrangements with Northern Tanzanian Maasai communities. Migration helped cattle herds to survive the drought and reduced the likelihood of human-lion conflict during times of resource scarcity when lion attacks on livestock are likely to be greatest.

Generalized reciprocity allowed poor individuals within Maasai society to be financially supported by members of their extended family or clan (Potkanski, 1994). Donations of livestock or money from the wider community were commonly collected through *Harambee's* (formal gatherings to solicit donations) and were used by members of the Shompole and Olkiramatian to pay for school fees, medical bills, or to replenish herds following substantial losses.

Maasai are not alone in using delayed and generalized reciprocity. These are important components of many traditional societies shown to reduce the vulnerability of communities living adjacent to protected areas (Naughton-Treves et al., 2003; Dickman et al., 2011). Cooperation is also important in traditional societies and is enabled by social capital. Surrounding Corbet Tiger Reserve in India, villages with higher social capital were more likely to work collaboratively to deal with the human-tiger conflict (Rastogi et al., 2014). Nomadic pastoralism, like many traditional livelihoods, requires strong community cohesion and cooperation (Bekure, 1991; Niamir-Fuller & Turner, 1999). Grazing and settlement management within Maasailand are rooted in inter- and intra-community collaboration among livestock owners who are willing to collaborate in communal management. This gives them greater access to resources and the ability to adapt to changing environmental conditions including carnivore presence (Galaty, 1980; Butt et al., 2009). The willingness of Shompole and Olkiramatian communities to adhere to group ranch management and planning at the ecosystem-scale maintained mobility and open space within pastoral rangelands which facilitated coexistence (Russell et al., 2018). Parallel examples of communal management through collaborative processes are present in rancher-led initiatives in the United States of America, such as the Malpai Group in Arizona which reconstituted individual land parcels into communally managed rangeland (Keough & Blahna, 2006; Curtin & Western, 2008).

Conversely, individualism is promoted by land subdivision with the subsequent loss of social capital. Maasai group ranches in Central Kajiado have moved ahead on land

subdivision leading to limited access, landscape heterogeneity and concurrent drop in livestock production (Rutten, 1992; BurnSilver et al., 2004).

Ecological Knowledge

Members of Olkiramatian and Shompole communities possessed a breadth and depth of traditional ecological knowledge that helped them select areas of highest resource abundance while simultaneously reducing predation risk through resource tracking and active guarding. The process of *Ele'enore* enabled herders to track changes in pasture, water, and carnivore presence and adapt to changing environmental, social, and political contexts. Herders claimed they were able to identify where large carnivores were likely to be on a given day and understood seasonal changes in occupancy. Ecological knowledge was acquired from experiential learning while collective knowledge came from other community members. Similarly, pastoralists in India used traditional ecological knowledge to track the movement of tigers and wolfs surrounding Panna Tiger reserves (Kolipaka et al., 2015).

The accuracy of traditional ecological knowledge to predict wildlife movements has been questioned by some and yet TEK often closely conforms to scientific studies (Service et al., 2014; Frans & Augé, 2016). This study could not evaluate the ability of *Ele'enore* to identify areas of high lion occupancy but information provided by local herders frequently assisted the research team to locate lions. Goldman (2007) advocated integrating Maasai ecological knowledge into conservation science and rangeland management. For example,

settlement and grazing management in the Olkiramatian and Shompole conservation areas demonstrates how collective resources tracking and utilization can lead to ecologically sensible rangeland management and year-round access to pasture (Russell et al., 2018). In turn, ecologically sensible land-use and rangeland management allowed lions access to areas of high prey abundance even during times of increased human activity thereby promoting coexistence (Schuette et al., 2013).

Maasai appear to have developed and continue to adopt cultural practices that allow for coexistence with large carnivores (Kissui, 2008; Goldman et al., 2010). Cattle are highly valued in Maasai society; accordingly, herders traditionally emphasized protection of livestock, active guarding and persecution of problem carnivores (Hollis, 1905; Spencer, 1988). Corralling of livestock in *bomas* reduces predation at night while active herding deters daytime attacks (Kolowski & Holekamp, 2006; Woodroffe et al., 2007; Lichtenfeld et al., 2015). Lion hunts may have helped maintain coexistence by making lions afraid of people while at the same time making people respect lions (Goldman et al., 2010). Savvy herders in this study were capable of disrupting lion attacks and reduced the incidence of livestock mortality at pasture. Maasai in Northern Tanzania also perceive adult herders to substantially reduce predation at pasture (Mkonyi et al., 2017). Conversely, evidence shows that poor livestock husbandry increases the likelihood of depredation (Kuiper et al., 2015; Loveridge et al., 2017).

Within Olkiramatian and Shompole wealthier families choose to send their children to school and employed herders for the pastoral care to their livestock. Like others in the

Maasai steppe (Mkonyi et al., 2017), cattle owners in Shompole and Olkiramatian who couldn't pay for herders often combined their herd with stock associates or extended family who employed herders. Those isolated from community and family reciprocity were less able to provide active protection and consequently more likely to be vulnerable to livestock predation. It is not surprising that elders within Olkiramatian expressed concern over the erosion of cultural husbandry practices exaggerated by sending children to school which they felt was leading to loss of pastoral and ecological knowledge and increases the prevalence of livestock depredation, as explained by a herder in Maasailand:

"Before the people in my area used to herd their cows well and guard them so they did not get killed. Carnivores rarely came to attack our livestock because they knew they would be chased and killed. Now people do not herd their cows well and animals are no longer scared of people"

Semantic translation from Maa July 2012 – Maasailand Interviews number PM-RC-1

Elsewhere in the world, traditional husbandry practices and habitat taboos influence livestock predation. For example, in Panna Tiger reserve, India, traditional taboos simultaneously prevented and facilitated livestock predation. On one hand, they prevented conflict by dictating that livestock should not be left out to pasture at night and religious beliefs also prohibited the killing of carnivores. On the other hand however, the practice of disposing of dead cattle on the village periphery attracted predators to settlements thereby leading to greater conflict and livestock predation (Kolipaka et al., 2015). In Romania, traditional methods of livestock management, namely nightly corralling of livestock and active guarding of livestock with shepherds and dogs, reduced sheep depredation by bears (Dorresteijn et al., 2014).

Final Conclusions

Interdisciplinary research in practice

The revelation that conservation is primarily about people and not wildlife has promoted repeated calls for interdisciplinary research (Campbell, 2005; Balmford & Cowling, 2006; Knight et al., 2008). As described by Pooley et al. (2014), "Interdisciplinary projects involve unrelated academic disciplines in a way that requires them to cross disciplinary boundaries to create new knowledge and theory in pursuit of a common research goal"(pg. 23). Pooley et al. (2014) further identified five broad obstacles to interdisciplinary research namely methodological challenges, value judgments, theories of knowledge, disciplinary prejudices, and interdisciplinary communication. The writing of this thesis provided firsthand insight into both the importance and challenge of interdisciplinary research in human-wildlife relationships.

One of the major strengths of this thesis was its interdisciplinary nature and broad focus on human-lion relationships and coexistence as advocated by Pooley et al. (2017), rather than a narrow focus of human-lion conflict, lion killing, or lion ecology. A recent meta-analysis by Montgomery et al. (2018) investigated interdisciplinarity in human-lion conflict research and proposed that human-lion conflict is comprised of five dimensions: interactions between people, carnivores, livestock, prey, and the environment. Their analysis highlighted the importance of interdisciplinarity to investigate all five dimensions concurrently but revealed that no published studies have done so. Previous studies of human-lion relationships have focused on either one of two dimensions: pastoral

relationships with lions (human dimensions) (Lichtenfeld, 2005; Hazzah et al., 2009; Goldman et al., 2010) or lion behavioural adaptions (carnivore dimensions) to living alongside pastoralists (Schuette et al., 2013; Oriol-Cotterill et al., 2015).

My research adopts a multi-perspective approach to investigating human-lion relationships and coexistence. Through the integration of ecology, anthropology, conservation biology and livestock science I aimed to understand how lions adapt to living alongside pastoralists and similarly how pastoralists adapt to living with lions. My research is among the first to incorporate all five dimensions of human-lion interactions concurrently. Understanding and integrating the vast bodies of literature and methods needed to conduct this type of research is a major obstacle facing interdisciplinary research (Campbell, 2005) and one I experienced during the preparation of this thesis. Consequently, the thesis does not provide a detailed background of all the theoretical underpinnings on which the research is based but rather provides an overview of the key concepts (Chapter 1, pg. 14).

Interdisciplinary conservation research requires the integration of natural and social sciences. However, conservation science remains predominantly rooted in ecology and natural science methods placing emphasis on quantitative data and testable hypotheses (Bennett et al., 2017). My research uses qualitative and quantitative data to complement each other in discerning both the patterns (Chapters 3) and processes of coexistence (Chapters 4), thus combining the strengths of natural and social science methods and data. Collecting sufficient qualitative and quantitative data is a major challenge faced by many interdisciplinary researchers as the two types of data collection often have differing time

scales and conform to differing burdens of proof (Strang, 2009). Overcoming this challenge necessitated the collection of data over a five-year period (2011- 2016), far longer than most doctorate research. Furthermore, the process of articulating information across disciplines is itself a challenge. For example, as demonstrated by Cumming et al. (2006), a concept as simple as *scale* has two fundamentally different meanings and interpretations in ecology and sociology.

A final challenge of interdisciplinary research is that while it can provide novel insights, it is often hard to replicate because it is context specific (Rust et al., 2017). This thesis epitomizes the tension between providing replicable research and novel insights and understanding. I set out to understand human-lion coexistence in a particular place and time, the the study is only snapshot of coexistence at a specific study site (Olkiramatian and Shompole). Furthermore, the cultural acceptance of wildlife within Maa culture (Roque de Pinho, 2009; Goldman et al., 2010) is the context of the research findings and may limit its generality. Finally, focusing on human-lion relationships also ignores and simplifies the ecological and social complexity that underlies human –wildlife coexistence more generally (Montgomery et al., 2018). Despite the challenges of context specificity, today conservation challenges everywhere are complex. That means looking at that complexity in as holistic a manner as possible requires multiple disciplinary tools.

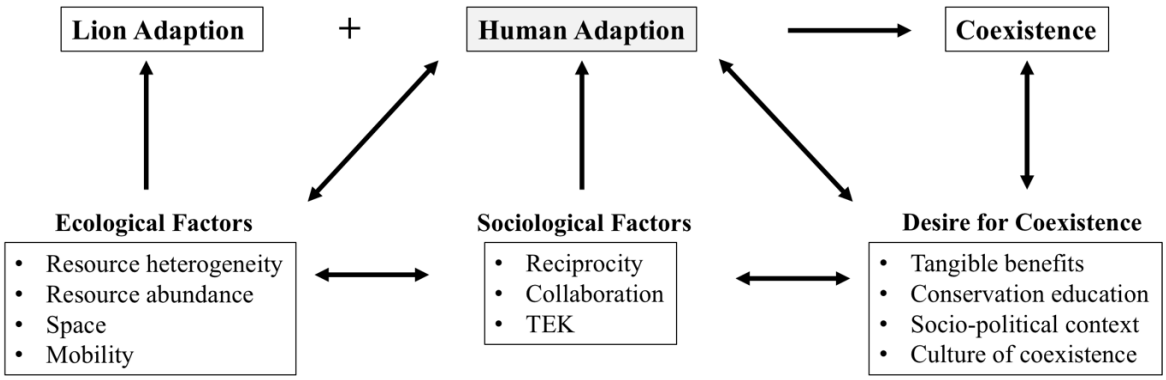


Figure 1: Framework of human-lion coexistence as a template for carnivore coexistence within human-dominated landscapes.

A Framework for Coexistence in Maasailand

This study's findings and insights can be consolidated into a single framework that helps explain human-lion coexistence in Maasailand. Adaptation sits at the core of the coexistence framework and is influenced by ecological and sociological factors and contributes to the desire for coexistence and the ability of lions and Maasai to adapt to each other's presence. Social capital and collaboration work together in traditional societies to reduce vulnerability to environmental and socio-political variability (Galvin, 2008). Reciprocity, collaboration, and traditional ecological knowledge are fundamental components that allow households in Olkiramatian and Shompole to adapt. They also decreased vulnerability through the communal redistribution of risks and costs associated with coexistence. Together they reduced vulnerability to drought and disease and created

economic support mechanisms based on social capital that lessened the impact of predation on Maasai livestock. Collaboration between households and within the broader community also helped minimize the risk of livestock depredation through communal guarding and herding. Ecological knowledge-belief-practices (Berkes 2012), especially those surrounding resource tracking and livestock husbandry, formed the basis of decision-making about coexistence with lions.

Resource heterogeneity, resource abundance, space and mobility create the ecological foundations that allow lions and pastoralists to access communal resources while minimizing interactions. Space and mobility let lions in Olkiramatian and Shompole shift their home ranges in response to human perturbation but unlike in other human-dominated systems, an increase in human presence did not lead to more lion predation (Valeix et al., 2012; Schuette et al., 2013; Kuiper et al., 2015). Group ranch committees and other cultural institutions maintained mobility and landscape heterogeneity so that Maasai households could access high quality and quantity pasture throughout most of the year. Mobility as well as ecological heterogeneity allowed lion home range sizes to remain constant despite shifts in human and livestock distribution. Predation on livestock increased when resources were scarce pointing to resource abundance as a critical ecological foundation of coexistence. But it is the management plans and social institutions that contributed to the prevalence of both pasture and prey at Olkiramatian and Shompole.

Coexistence is predicated on individual and communal willingness to share space with wildlife rather than eliminate wildlife-related risks and vulnerabilities. Socio-political and economic context and a culture of coexistence underpinned the desire to coexist (Chapter 2). Comparisons between Hwange, Ruaha, and Maasailand show how differing socio-political contexts and environmental narratives shape individual and communal willingness to coexist with lions. Hwange did not exhibit a culture of coexistence that was present in Maasailand. Connecting conservation benefits with conservation education similarly proved a better predictor of an individual's willingness to see lions increase than did benefits alone. Therefore, the desire for coexistence could be improved by concurrently increasing the instrumental and intrinsic value of carnivores.

This study supports earlier findings of Schuette et al. (2013), Dorresteijn et al. (2014), Kolipaka et al. (2015), which demonstrate that under the right conditions coexistence between large carnivores and people is possible without significant ecological or economic costs to either party. Previous studies of coexistence have focused on either sociological or ecological factors. By contrast, my framework for coexistence incorporates socio-economic, cultural, political and ecological factors into a single model. Although this model focuses on the coexistence of Maasai and lions, it is also more general to carnivore coexistence within human-dominated landscapes. However, as this thesis has demonstrated, coexistence is highly context specific. Therefore, we need more holistic investigations to test the wider validity of the model both in other sites within Maasailand and applied to other carnivores.

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