Room to roam and hotspots of conservation conflicts: Lions, livestock and people in the matrix

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Abstract

Globally, large terrestrial carnivores have suffered precipitous declines in population and range. Today, they must persist in increasingly isolated natural habitat patches within a human-dominated landscape matrix. For the African lion (*Panthera leo*), approximately 44% of their remaining range lies outside of protected areas and retaliatory killing in response to the negative impacts of lions on communities is a key driver of lion declines in human-modified landscapes.

In this thesis, I investigate the ecological and social aspects of human-lion interactions in order to understand the viability of the landscape matrix for supporting free-roaming lion populations. My literature review reveals that lion habitat preferences are varied and context-specific. While prey abundance and proximity to water are important drivers, lions adapt their habitat use in response to anthropogenic pressures. I demonstrate the use of two modelling techniques to develop maps of livestock depredation risk in the Ruaha landscape of Tanzania, showing that lion attacks follow predictable patterns in space based on features including distance to protected areas and rivers, and net primary productivity. I then examine the transferability of my approach as a simple, scalable method for predicting livestock depredation across three additional study sites. Finally, I trial the use of a novel experimental game to examine pastoralist decision-making in response to human-lion conflict. My findings suggest that non-lethal deterrents are the preferred mitigation strategy and that while incentive-based instruments can promote pro-conservation behaviour, these may be more effective when targeted at individuals rather than groups.

This work contributes to our understanding of human-lion interactions and the resulting conservation conflicts. I highlight the complexity of the system and the broad range of methods and disciplines needed to understand it. To manage Africa’s changing landscapes effectively for roaming lions, future research should focus on habitat use outside of protected areas and develop collaborative approaches which lead to mutually beneficial results for both people and wildlife.

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Kambona, myself, Elias and Hosenja at the end of a successful field season. Taken by Fenrick Msigwa.

Fieldwork was a truly collaborative effort at every stage and there are many people without whom it wouldn't have been possible. At the planning stages, my gratitude goes to Dr Sarobidy Rakotonarivo, who helped adapt the game and protocols for my study landscape, and Ana Grau and BenJee Cascio for advice on travel and logistics. Thanks to the Tanzanian Wildlife Research Institute and the Tanzania Commission for Science and Technology for granting me permission to carry out my research, and to the IAPETUS DTP and National Geographic for providing me with funding. My time in the field would not have gone so smoothly without the support of all the staff at the Ruaha Carnivore Project who made me welcome. Particular thanks go to Ana and BenJee, to Rashid and Salum for keeping my pikipikis running, to Mama Dani, Mama Bora and Esther for keeping me well fed, and of course most importantly to my field assistants Elias Charles, Hosenja Kilange and Kambona Kanayaah. Their knowledge and experience were invaluable and enabled us to conduct many more games than I had initially thought possible. Thank you to them for their hard work and patience with what was an unusual survey method and for being such a pleasure to work with. Finally, my deepest thanks go to the communities who welcomed us and to all the individuals who gave up their time and knowledge to participate in our game sessions.

And to Mum and Dad, you're the best.

Hosenja and I pose with our new fieldwork vehicle, made possible thanks to a National Geographic Early Career Research Grant. Photo taken by Elias Charles.

Declaration

I declare that this thesis is my own work. I implemented all aspects of the project, analysed the data and wrote all of the material included herein. My supervisor Dr Marion Pfeifer commented on and made contributions to each chapter's development and all additional contributions are stated below. This work was funded by the NERC IAPETUS Doctoral Training Partnership and fieldwork was supported by a National Geographic Early Career Research Grant. All photos included in the thesis were taken by myself unless otherwise stated, and photos of people were taken with consent.

Chapter 2. Room to roam for African lions *Panthera leo*: a review of the key drivers of lion habitat use and implications for conservation.

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Chapter 3. Using landscape characteristics to predict livestock depredation risk by African lions (*Panthera leo*) in the Ruaha landscape of Tanzania.

Data used in this chapter were collected by a variety of Ruaha Carnivore Project staff between 2010 – 2017. The data and shapefiles were shared with me by current project managers BenJee Cascio and Ana Grau. Professor Stephen Rushton gave guidance on data analysis and commented on the chapter.

Chapter 4. Examining the utility of a Linear Discriminant Analysis approach to identify common drivers of livestock depredation across contexts.

Data used in this chapter were collected by several projects (Ewaso Lions, the Laikipia Predator Project, Hwange Lion Project) and all authors are appropriately acknowledged. Professor Stephen Rushton gave guidance on data analysis and commented on the chapter.

Chapter 5. Trialling the use of an experimental game to examine pastoralist decision-making and preferences for coexistence strategies in response to human-lion conflict.

The game used in this chapter was based on those developed by Dr Sarobidy Rakotonarivo and Professor Andrew Reid Bell. AB created the game interface. SR assisted with conception and planning of the game and fieldwork protocol and commented on the chapter. Ana Grau and BenJee Cascio assisted with fieldwork planning and logistics and commented on the chapter. Data collection was conducted by myself alongside field assistants Hosenja Kilange, Kambona Kanayaah and Elias Charles. Professor Stephen Rushton gave guidance on data analysis and provided comments on the chapter. Professor Nils Bunnefeld and Dr Amy Dickman also commented on the chapter. This chapter is in prep for submission to the journal People & Nature.

View over Ruaha National Park, Tanzania.

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Chapter 1. General Introduction

A female lion takes a stroll along the Ewaso Ng'iro river, Samburu National Reserve, Kenya.

1.1 Human-dominated landscapes

Over the past century, human activities have transformed the world's ecosystems more dramatically than during any other period of history (Rodríguez *et al.*, 2011; Steffen *et al.*, 2015; Kennedy *et al.*, 2019). There is no longer any ecosystem on Earth that is free of human influence (Vitousek *et al.*, 1997) and the most recent human footprint data indicates that 75% of the planet's land surface is experiencing measurable human pressure (Venter *et al.*, 2016b). As a result of human impacts, large terrestrial mammals have been extirpated from significant proportions of their natural range and the number of species threatened with extinction has reached unprecedented levels (Faurby and Svenning, 2015; Díaz *et al.*, 2019).

Biodiversity loss has profound consequences for ecosystem functioning which in turn impacts human well-being through disruption of ecosystems services such as pollination, water and air quality regulation, disease control, and provision of natural resources (Millennium Ecosystem Assessment, 2005; Liu *et al.*, 2018; Sintayehu, 2018). In response to the continued degradation of ecosystems, several international initiatives such as the Convention on Biological Diversity's Aichi Targets and the UN Sustainable Development Goals have attempted to coordinate actions to halt the extinction of species and safeguard ecosystems (CBD, 2010; UN, 2015). While there have been some successes, for example in preventing the extinction of several threatened species (Bolam *et al.*, 2021), the majority of these targets have not been met. Suggested reasons for this failure include a lack of funding and political will, a deficiency of regional and national level data on species status, the absence of quantifiable targets and indicators, and trade-offs across goals (Butchart *et al.*, 2016; Johnson *et al.*, 2017; Mair *et al.*, 2021). Indeed, many of the targets are inextricably linked, resulting in complex synergies and trade-offs. For example, pursuing social goals such as reducing poverty and hunger may conflict with environmental goals such as protecting habitats and reducing carbon footprints (Pradhan *et al.*, 2017; Scherer *et al.*, 2018). Furthermore, interactions and feedbacks among threats and goals can vary across species and geographic regions (Brook *et al.*, 2008; Newbold *et al.*, 2019), with diverse and uneven relationships between human activities and biodiversity responses.

A primary driver of biodiversity loss and turnover is globally pervasive land use change (Newbold *et al.*, 2015; Newbold *et al.*, 2016; Song *et al.*, 2018). Activities such as the clearing of forests, expanding urban centres and intensifying agriculture, result in the loss, modification, and fragmentation of natural habitats (Foley *et al.*, 2005; Haddad *et al.*, 2015; IPBES, 2019). Thus, increasingly isolated natural habitat patches exist within a human-dominated landscape matrix encompassing land uses such as plantations, pasture, cropland, and built-up areas (Haddad *et al.*, 2015). Biodiversity responses to these changes in land cover are complex and varied, making them difficult to predict and manage (Chapron *et al.*, 2014; Oliver and Morecroft, 2014; Newbold *et al.*, 2015).

Species differ in their ability to occupy and disperse through habitat matrices. This may be driven by attributes characterising the newly created landscapes such as matrix composition and size (Prugh *et al.*, 2008; Watling *et al.*, 2011). Biological characteristics also play a role in shaping species' responses to land use change, with evidence from the literature indicating that life history traits such as large body size, long lifespans, low population density, slow reproductive rates, and ecological specialisation, make some species more vulnerable to habitat fragmentation (McKinney, 1997; Newbold *et al.*, 2013; Keinath *et al.*, 2017; Newbold *et al.*, 2020).

Large species, such as elephants and large carnivores, have substantial resource requirements and need large functional habitats to meet their demands (Lindstedt *et al.*, 1986; Kelt and Van Vuren, 2001). Movement of these species through landscapes renders them likely to encounter humans and, as such, there is a high risk of negative interactions such as damage to crops (Gross *et al.*, 2018; Tiller *et al.*, 2021), predation on livestock (Widman and Elofsson, 2018; Kissui *et al.*, 2019), attacks on humans (Bombieri *et al.*, 2018; Packer *et al.*, 2019), and retaliatory killing of the species involved (Merson *et al.*, 2019; Ontiri *et al.*, 2019). These issues are of particular concern in the Afrotropical region, which juxtaposes remarkable biodiversity and a large proportion of the planet's remaining megafauna (Du Toit and Cumming, 1999; Malhi *et al.*, 2016), with widespread concern over habitat loss and the pressing development needs of an increasing human population (Laurance *et al.*, 2014; Milder *et al.*, 2014).

1.1.2 Lions in human-dominated landscapes

The lion (*Panthera leo*), Africa's largest cat and one of its most important flagship species, exemplifies the challenges of conserving large, wide-ranging carnivores. While historically lions ranged throughout Europe, the Middle East and Asia they now exist only in East, West, Central and Southern Africa and a small, isolated population in the Gir National Park, India; a mere 8% of their former range (Fig. 1; Riggio *et al.*, 2013; Bauer *et al.*, 2016). Human population growth and agricultural expansion has led to widespread habitat loss and depletion of prey species (Craigie *et al.*, 2010; Loveridge *et al.*, 2010; Ogutu *et al.*, 2011) and lion numbers have declined by approximately 43% over the past 30 years (Riggio *et al.*, 2013).

Current lion population size is believed to be between 20,000-35,000, although for many areas there is considerable uncertainty in population estimates (Henschel *et al.*, 2014; Bauer *et al.*, 2015; Bauer *et al.*, 2016). Lions are listed as Vulnerable by the IUCN Red List, indicating a high risk of extinction in the wild (Bauer *et al.*, 2016).

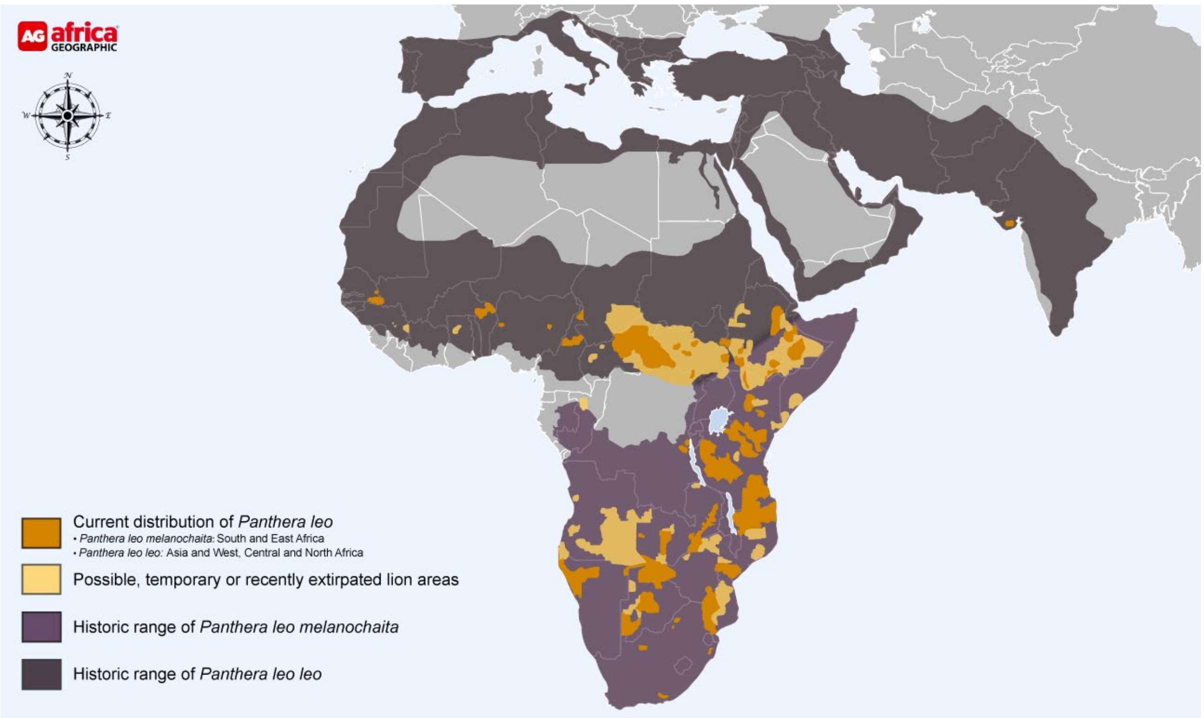

Figure 1.1 Historic and present distribution of the lion (*Panthera leo*) obtained from https://africageographic.com/stories/the-african-lion/. Map created using data from Bauer *et al.* (2016) and Trinkel & Angelici (2016). Recent genetic studies suggest that the lion can be split into two subspecies: *P. leo melanochaita,* distributed across East and Southern Africa, and *P. leo*, found across the remaining range (Bertola *et al.*, 2016; Kitchener *et al.*, 2017).

Lions, like other apex predators, play an important role in regulating ecosystems (Estes *et al.*, 2011). Through a number of top-down mechanisms including direct predation and landscapes of fear (Palmer *et al.*, 2017), mesopredator release (Taylor *et al.*, 2016) and intraguild competition (Searle *et al.*, 2021b), they can affect the behaviour, abundance and habitat use of many other species. Thus, their decline may have cascading effects which impact ecosystem structure and function (Ripple *et al.*, 2014). In many areas, lions are also economically important, being a primary draw for both photographic and trophy hunting tourism (Lindsey *et al.*, 2007; Grünewald *et al.*, 2016), and hold significant cultural value, used as symbols of strength and power across the globe (Good *et al.*, 2017) and considered sacred in many indigenous communities (Stolton and Dudley, 2019). As a result of these social and ecological values, there is considerable political will to protect the species, and lions feature prominently on the agenda of many international conservation treaties and policies (Trouwborst *et al.*, 2017; Hodgetts *et al.*, 2018).

The general causes of lion declines are well-known and include, primarily, direct persecution as a result of threats to livestock and human life, depletion of their natural prey base, and habitat loss, all of which are interlinked (Bauer *et al.*, 2016; Bauer *et al.*, 2020). While protected areas are likely to play an important role in the long-term survival of lions in rapidly changing African landscapes (Bauer *et al.*, 2015; Lindsey *et al.*, 2017b), approximately 44% of their remaining range lies outside of these areas (Riggio *et al.*, 2013). Hence, lions require conservation across a wide mosaic of different land use and habitat types, with particular focus on their ability to utilise human-dominated landscapes and their interactions with people and livestock. In Chapter 2, I assess current understanding of lion habitat use and examine the lack of consensus on what constitutes good lion habitat.

1.2 Human-carnivore conflict

Habitat loss and fragmentation driven by land use transformation and human population expansion brings wildlife and people into close proximity, resulting in increased encounters and both positive and negative interactions (Nyhus, 2016; Acharya *et al.*, 2017). Managing the negative interactions between people and wildlife, often termed human-wildlife conflicts (HWC), is a pressing conservation issue. HWC occurs globally in a wide range of situations, involving a diverse array of species, and can have extremely damaging consequences for both wildlife populations and human communities (Woodroffe *et al.*, 2005; Barua *et al.*, 2013; Nyhus, 2016). These conflicts emerge when the presence or behaviour of wildlife poses actual or perceived, direct, and recurring threat to human interests or needs, leading to negative impacts on people and wildlife (IUCN, 2020). Large carnivores such as lions tend to cause intense conflict issues as they pose a severe threat to peoples' livestock, as well as to human life, thus provoking retaliatory killing (Packer *et al.*, 2005a; Kissui, 2008; Hazzah *et al.*, 2017). As such, HWC has been identified as a key driver of global declines in large carnivores (Dickman and Hazzah, 2016; Ripple *et al.*, 2016), and one of the main threats facing lion populations in Africa (Bauer *et al.*, 2016; Bauer *et al.*, 2020).

The complexity of reconciling international concerns for saving threatened species with local concerns for security and development has led to much debate over the framing of HWC issues (Treves *et al.*, 2006; Peterson *et al.*, 2010). In particular, the use of the term 'human-wildlife conflict' may be considered misleading as it frames animals as 'conscious antagonists' and humans and nature as oppositional, which may perpetuate negative attitudes by labelling nature as threatening (Peterson *et al.*, 2010; Redpath *et al.*, 2015). It is thus increasingly recognised that HWCs are, in reality, human-human conflicts occurring between stakeholders with differing goals and values rooted in economic, socio-political, and cultural history (Redpath *et al.*, 2013). Often the conflict occurs between those supporting conservation and those who prioritise other human activities and land uses, with one party perceived as exerting its interests at the expense of the other (Young *et al.*, 2010; Redpath *et al.*, 2013). Underlining this human dimension could help to broaden the focus from technological solutions to ones that promote better negotiations and dialogue between stakeholders with competing interests (Redpath *et al.*, 2015).

A number of alternative terms have thus arisen in the HWC literature to capture the additional components of the issue. For example: 1) human-wildlife impacts or interactions, describing the direct interactions of humans and wildlife in competition or imposing costs upon each other (Young *et al.*, 2010; Redpath *et al.*, 2015); 2) human-human conflicts or conservation conflicts, centring on interactions between human groups with opposing interests and management priorities (Peterson *et al.*, 2010; Redpath *et al.*, 2013); and 3) human-wildlife coexistence, a more constructive way of framing the issue highlighting the potential for humans and nature to share landscapes (Frank *et al.*, 2019; Pooley *et al.*, 2021).

Throughout the majority of this thesis, I use the term human-wildlife and human-carnivore conflict in line with much of the literature and with the IUCN Human-Wildlife Conflict Task Force (Nyhus, 2016; IUCN, 2020). However, I highlight that the focus falls within the human-wildlife impacts scope of the definition, as I examine the interactions between lions and the communities living alongside them. While international and national audiences place high value on the existence and conservation of large carnivores, these values are not always shared by local communities whose interactions with these species are often negative and result in high social and economic costs (Treves and Karanth, 2003; Dickman *et al.*, 2011; Barua *et al.*, 2013). Thus, the costs of coexisting with dangerous wildlife are disproportionately borne by individuals in rural communities, often in developing nations, while the benefits accrue to society as a whole (Lindsey *et al.*, 2017a; Jordan *et al.*, 2020).

1.2.1 Predation on livestock

Attacks on livestock are one of the main reported reasons for conflict with carnivores and are the root of a deep-seated hostility toward carnivores by pastoralists and ranchers across the world (Sillero-Zubiri and Laurenson, 2001). Every domestic species, from chickens to cattle to camels, is affected and this form of conflict is incredibly well documented in the literature (Inskip and Zimmermann, 2009). Livestock may be an easy target for predators as they exhibit little anti-predator behaviour (Sillero-Zubiri and Laurenson, 2001). In addition, changes in density and/or distribution of wild prey species due to human activities can change patterns of predation by large carnivores (Kissui, 2008; Oriol-Cotterill *et al.*, 2015a). Species involved include lynx, brown bears, and wolves in Norway (Widman and Elofsson, 2018), spotted hyena, leopard, and lion in Tanzania (Abade *et al.*, 2014a), jaguars in Mexico (Peña-Mondragón *et al.*, 2017), red foxes in Australia (Fleming *et al.* 2016) and tigers and leopards in India (Miller *et al.*, 2016a), to name but a few.

In some cases, depredation levels can be severe. For instance, studies in Tanzania (Holmern *et al.*, 2007) and Bhutan (Wang and Macdonald, 2006) found that households lost more than two-thirds of their annual income due to depredation of livestock. Stock lost to lions in three rural villages in Zimbabwe translated to financial losses of between $9,911-$22,472 per year (Loveridge *et al.*, 2017a). However, even where depredation accounts for a relatively small proportion of total stock loss, communities still report highly negative attitudes towards wildlife (Kissui, 2008; Dickman *et al.*, 2014). In poorer households, even low levels of stock loss can impose severe costs (Ikeda, 2004; Barua *et al.*, 2013) and the potential risk of a "surplus killing" (where a carnivore kills multiple animals in one attack) is enough to drive negative perceptions (Muhly and Musiani, 2009). Often, those living alongside carnivores and suffering the severest impacts live in impoverished, rural communities with few economic opportunities outside of livestock keeping, making them particularly vulnerable to the unpredictable, economic shocks caused by depredation events (Dickman *et al.*, 2011).

Furthermore, beyond their direct economic value, livestock can hold cultural significance. For example, the social, religious, and cultural identity of the Maasai of East Africa is closely tied to their relationship with livestock (Galaty, 1982). Cattle in particular are symbols of wealth and status, selling cattle is typically undesirable and they serve as insurance and investment for communities with little access to formal credit and banking (Sperling and Galaty, 1990; Quinlan *et al.*, 2016). Thus, the loss of culturally and economically valuable cattle, often targeted by lions (Loveridge *et al.*, 2017a; Muriuki *et al.*, 2017), elicits a much stronger reaction than the loss of smallstock (Kissui, 2008) and often results in retaliatory killing (Hazzah *et al.*, 2009).

1.2.2 Attacks on humans

Although attacks on humans are significantly less common than those on livestock, they fall at the extreme end of the direct conflict spectrum and generate intense hostility and levels of fear towards wildlife (Quigley and Herrero, 2005; Dickman, 2010). Available and accessible information on attacks is often limited and poorly collated however, in some areas, attacks on humans can pose a significant threat of injury or death (Löe and Röskaft, 2004). The Sundarbans in eastern India suffer from consistent reports of tiger attacks (Quigley and Herrero, 2005) and records suggest that ~20-30 people per year are killed by tigers in this area, with at least 3 tigers a year killed as a result (Inskip *et al.*, 2013).

Lion attacks on humans also appear to be particularly numerous and result in more human fatalities in comparison to other large carnivore species (Löe and Röskaft, 2004; Packer *et al.*, 2019; Mbise, 2021). Near the Gir forest in India, an average of 15 lion attacks occurred annually between 1978 to 1991 (Saberwal *et al.*, 1994), and in Tanzania over 1000 attacks occurred between 1990 and 2007, 65% of which were fatal (Packer *et al.*, 2005a; Kushnir *et al.*, 2010). Most attacks are unprovoked and occur when people are engaged in everyday, domestic activities (Löe and Röskaft, 2004; Kushnir *et al.*, 2010; Mbise, 2021), illustrating the high level of risk imposed upon vulnerable communities on a day-to-day basis.

1.2.3 Hidden impacts on human well-being

Besides the direct impacts of events such as livestock depredation and human injury and death, there exists additional, difficult to quantify, unseen consequences for communities that live alongside large carnivores. Most attempts to address human-wildlife conflict focus on mitigating visible impacts such as stock loss, with scant attention directed towards the hidden impacts on physical and mental well-being (Barua *et al.*, 2013). Hidden impacts of HWC may be defined as those that are uncompensated, temporally delayed and are psychological or social in nature (Ogra, 2009).

The need to guard livestock for fear of predator attacks may pose opportunity costs such as sleep loss, inability to participate in other wage-earning activities and, for children, disrupted school attendance and performance (Hill, 2000; Haule *et al.*, 2002; Ogra, 2009). HWC can also disrupt movement and lead to restrictions in travel and access to resources in areas where predators may be encountered (Kushnir *et al.*, 2010; Mayberry *et al.*, 2017). For example, villagers in the Gir Forest of India reported that they were unable to irrigate their fields at night due to the presence of lions (Saberwal *et al.*, 1994).

Death or injury to one member of a family will mean their responsibilities, be they wage earning or running the household, shift to other family members which may cause disruption in relationships, education, and increased family debt (Jadhav and Barua, 2012; Khumalo and Yung, 2015; Chowdhurym *et al.*, 2016). Furthermore, there are likely to be severe mental health impacts for both victims of attacks and other community members. Chronic fear, anxiety and reduced feelings of safety can lead to restriction of movement for social purposes, as well as loss of sleep (Mayberry *et al.*, 2017). Some studies found that death of family members as a result of HWC led to post-traumatic stress, depression and childhood emotional disorder in spouses and children (Chowdhury *et al.*, 2008; Jadhav and Barua, 2012; Chowdhurym *et al.*, 2016). Hence, beyond the evident visible costs of HWC it is important to consider the wider societal and psychological impacts on human well-being, the effects of which may penetrate deeper than immediate threats from wildlife (Barua *et al.*, 2013).

1.2.4 Retaliation against carnivores

Human persecution in response to the costs imposed by large carnivores has led to the reduction, extirpation, and range contraction of many carnivore species around the world (Inskip and Zimmermann, 2009; Loveridge *et al.*, 2010; Ripple *et al.*, 2016). While historically, widespread eradication of large carnivores was a state-sponsored activity (Breitenmoser, 1998; Treves and Karanth, 2003; Riley *et al.*, 2004), contemporary government policies often render lethal control illegal except in specific cases (Athreya *et al.*, 2013; Trouwborst, 2015; Rauset *et al.*, 2016). However, in areas where livestock depredation is widespread, frequent lethal control still occurs (Woodroffe and Frank, 2005; Kissui, 2008).

Although obtaining accurate data on illegal activity is difficult (St John *et al.*, 2012), retaliatory or preventative killing in response to real and perceived threats is considered a primary driver of carnivore declines outside of protected areas (Inskip *et al.*, 2014; Pohja-Mykrä and Kurki, 2014; Loveridge *et al.*, 2017b; Bauer *et al.*, 2020). For African lions using pastoral areas, levels of conflict-related mortality are high. For example, on community ranches in Amboseli, Kenya, ~88 lions were killed between 2003-2011 in retaliation for lost livestock (Hazzah *et al.*, 2014), while in Laikipia, Kenya between 1998-2002 89% of recorded lion mortality was caused by people (Woodroffe and Frank, 2005). Identifying solutions to resolve these conflicts over the management of large carnivores is therefore vital for both the well-being of human communities and for ensuring the persistence of carnivore populations.

1.3 Key determinants of human-lion conflict

In order to develop effective and well-targeted strategies to alleviate human-lion conflict it is necessary to understand the patterns and trends which drive this conflict. A developing, but still underused, approach known as ‘spatial risk modelling’ is a useful tool for examining the patterns associated with conflict events and identifying priority hotspots where carnivore attacks are more likely (Miller, 2015). Risk models quantify landscape attributes associated with sites where attacks have occurred and, in doing so, reveal the landscape features associated with kill sites (Miller, 2015; Kuiper *et al.*, 2021).

Using spatial mapping of attack locations alongside remotely sensed data can highlight contributing factors for multiple drivers of conflict such as: environmental (habitat types, precipitation; Treves *et al.* (2011); Abade *et al.* (2014a); Miller *et al.* (2016a)), human (land use and governance type, distance to infrastructure; Kissling *et al.* (2009); Soh *et al.* (2014); Miller *et al.* (2016a)) and prey-based influences (biomass, density; Treves *et al.* (2004); Karanth *et al.* (2013)). Understanding what factors are associated with conflict hotspots could significantly improve our ability to manage human-lion conflict with effective, spatially targeted interventions. In Chapters 3 and 4, I demonstrate the use two modelling approaches to examine spatial patterns in conflict risk and identify key drivers of livestock depredation across landscapes.

A wide range of studies have attempted to uncover the underlying drivers of human-carnivore conflict, most focusing on specific local case studies and showing high levels of variation and complexity (Dickman *et al.*, 2014; Miller, 2015; Montgomery *et al.*, 2018a). Human-carnivore conflict, and more specifically human-lion conflict, is an inherently interdisciplinary problem and has several facets beyond just the human and the lion (Beck *et al.*, 2019). Montgomery *et al.* (2018a), present a framework which positions human-lion conflict as having five dimensions: the lion, the wild prey, the livestock, the human and the environment. Each of these dimensions can drive conflict, both individually and in combination, and result in variation in the intensity and spatio-temporal patterns of human-lion conflict.

1.3.1 The lion dimension

This dimension relates conflict levels to the distribution, behaviour, and ecology of lions. In principle, lions are remarkably well adapted to the challenges of changing landscapes and habitats. They have a broad habitat tolerance, absent only from tropical rainforest and the interior of the Sahara Desert, and have been documented at a range of elevations (Nowell and Jackson, 1996; Bauer *et al.*, 2016). They can survive in arid environments and can hunt almost any animal from rodents to rhino, in addition to being frequent scavengers (Bauer *et al.*, 2016). Opportunistic hunting by lions can result in prey species such as warthog and elephant making up a large proportion of their diet in areas where these species are abundant (Davidson *et al.*, 2013; Barnardo *et al.*, 2020). However, the bulk of lion prey falls within the 190 - 550 kg weight range, with preferred prey species including buffalo, wildebeest, and zebra (Hayward and Kerley, 2005; Davidson *et al.*, 2013). Given that lions preferentially hunt medium- to large-bodied ungulates, this makes livestock, particularly cattle, an ideal target (Kolowski and Holekamp, 2006; Loveridge *et al.*, 2017a).

At finer spatial scales, lion behaviour is shaped by interactions between habitat, prey, and people (Patterson *et al.*, 2004). Inside protected areas, understanding of lion habitat selection centres on two main hypotheses: the prey abundance hypothesis, which states that lions use habitats which contain the highest numbers of prey (Spong, 2002; Miller *et al.*, 2018); and the prey catchability hypothesis, which suggests that habitats are selected based on features which improve hunting efficiency, such as increased vegetation cover (Hopcraft *et al.*, 2005; Davidson *et al.*, 2012). It is likely that, when free of other constraints, lion habitat selection is driven by some combination of the two.

Outside of protected areas, anthropogenic pressures may modify behaviour and habitat use due to their effects on feeding behaviour and mortality risk (Mogensen *et al.*, 2011; Loveridge *et al.*, 2017b), confounding expectations that come from the prey-based hypotheses and forcing carnivores into lower quality habitats (Valeix *et al.*, 2012a; Knopff *et al.*, 2014). These behavioural adjustments and their impacts on lion fitness in human-dominated landscapes are less well understood (Mosser *et al.*, 2009; Schuette *et al.*, 2013; Oriol-Cotterill *et al.*, 2015a).

There may also be considerable variation between individual animals in their ranging behaviour and conflict frequency due to factors such as sex and life stage. Lions are social cats, with related females and their dependent offspring living together in prides which can range between 2 - 30 individuals (Wright, 1960; Packer *et al.*, 2005b). Males, often working in coalitions, compete for control of prides and will kill or evict unrelated cubs. Females may leave their natal pride to form new prides in order to avoid infanticide during a male takeover, or if they reach sexual maturity while their fathers' coalition is still resident (VanderWaal *et al.*, 2009). However, they do not typically disperse far beyond their natal range (Packer and Pusey, 1987). In contrast, almost all males leave their natal pride by four years of age. Between leaving their pride and taking over a new pride many males become nomadic and can disperse over large distances, in some cases up to 200 km (Packer and Pusey, 1987; Dolreny *et al.*, 2020).

Perhaps as a result of dispersal of subadult males, some studies attribute more livestock attacks to lone males (Stander, 1990; Patterson *et al.*, 2004). Research indicates that dispersing males are less risk-averse and therefore more prone to conflict (Elliot *et al.*, 2014a;

Elliot *et al.*, 2014b). Furthermore, male and female lions may differ in their hunting strategies. Male lions are thought to hunt less cooperatively than females and have been found to kill a higher proportion of buffalo and to hunt in areas of denser vegetation (Funston *et al.*, 1998; Loarie *et al.*, 2013). Studies of human-lion conflict must therefore consider aspects of lion ecology such as habitat use, demography and hunting behaviour in order to determine which areas are likely to be able to support lion populations and which are likely to be conflict hotspots.

1.3.2 The wild prey dimension

As highlighted above, and as I discuss in Chapter 2, lion habitat use is largely driven by the availability and accessibility of prey species. The distribution, abundance and behaviour of wild prey will therefore affect lion behaviour and the likelihood of attacks on domestic animals. Lion population density is known to correlate with the biomass of their principal prey species; medium-large herbivores (190-550kg; Hayward and Kerley (2005); Hayward *et al.* (2007)). Wild prey populations are increasingly under threat from habitat loss, competition with livestock, unsustainable bush meat trade and poaching (Ripple *et al.*, 2016), leading to collapses in herbivore numbers across large parts of savanna Africa (Lindsey *et al.*, 2013). Regional lion population trends closely mirror data on main prey species monitored between 1970 and 2005 across Africa, with herbivore populations declining by 52% in East Africa and 85% in West Africa (Craigie *et al.*, 2010).

Surveys in Tanzania revealed that districts that suffered from more lion attacks on people reported lower abundances of natural prey (Packer *et al.*, 2005a; Kushnir *et al.*, 2014). Lions are also known to follow concentrations of migratory prey (Schaller, 1972). Hence, migrations of prey onto communal land during the wet season may cause lions to come into more frequent contact with livestock (Kissui, 2008; Koziarski *et al.*, 2016; Mkonyi *et al.*, 2017c). As well as these seasonal variations in distribution, wild herbivore dynamics are also influenced by land use changes and competition and displacement by livestock (Serneels and Lambin, 2001; Bhola *et al.*, 2012; Valls-Fox *et al.*, 2018; Kirathe *et al.*, 2021). Interestingly, given that wild prey depletion is often suggested to be a causal factor for lions targeting livestock and fuelling conflict (Bauer *et al.*, 2020), this dimension is relatively understudied in the conflict literature (Montgomery *et al.*, 2018a).

1.3.3 The livestock dimension

The distribution and accessibility of livestock is also a key component to consider when examining the causes of human-lion conflict, yet few studies directly study the livestock dimension (Montgomery *et al.*, 2018a; Kuiper *et al.*, 2021). In some areas, lions have been shown to shift their movement patterns in response to seasonally shifting human settlements and grazing areas (Schuette *et al.*, 2013; Oriol-Cotterill *et al.*, 2015a). The location of livestock and pasture sites in relation to human settlements and lion habitat can strongly affect depredation rates as it influences the likelihood of encounters and the risk for predators attacking livestock (Loveridge *et al.*, 2017b). Thus, distance to protected areas, representing core carnivore habitat, is a common variable associated with conflict frequency, with livestock depredation more likely to occur when herds are grazing near the boundaries of National Parks (Kushnir *et al.*, 2014; Kuiper *et al.*, 2015; Broekhuis *et al.*, 2017; Mkonyi *et al.*, 2017c). Seasonal herding practises have been found to correlate with numbers of lion attacks, as cattle graze further from villages during the growing season (as herders direct them away from crops) meaning they may be in closer proximity to lion habitat (Kuiper *et al.*, 2015).

Husbandry and herding practises are the most common aspect of the livestock dimension that are evaluated, with a particular focus on mitigation methods such as livestock enclosure fortification (Ogada *et al.*, 2003; Woodroffe *et al.*, 2007; Abade *et al.*, 2014a; Sutton *et al.*, 2017). Lions frequently attack livestock that is grazing in the bush, however, attacks on corralled livestock during the night are also common (Ogada *et al.*, 2003; Kolowski and Holekamp, 2006; Kissui, 2008). The general pattern appears to be that attacks on both humans and livestock happen more frequently at night (Kushnir *et al.*, 2010; Oriol-Cotterill *et al.*, 2015a). This is to be expected as lions are typically crepuscular or nocturnal, although can display a high level of flexibility and opportunism, particularly in human-dominated landscapes (Packer *et al.*, 2011; Cozzi *et al.*, 2012; Valeix *et al.*, 2012a). It has also been shown that livestock that are wearing bells are preferentially selected by lions and hyenas, perhaps due to a learned association between the sound of bells and the presence of livestock (Loveridge *et al.*, 2017a).

Age and type of livestock can also affect the overall risk of an attack and the time and location where attacks occur. Lions have typically been found to target adult cattle over smallstock and calves, in particular when stock is grazing away from the homestead (Patterson *et al.*, 2004; Kissui, 2008; Loveridge *et al.*, 2017a; Western *et al.*, 2021). However, when livestock is confined in enclosures lions may be more likely to attack calves, sheep, and goats (Ogada *et al.*, 2003; Weise *et al.*, 2020).

1.3.4 The human dimension

Given that human-wildlife conflicts are often, in reality, human-human conflicts between conservationists and other stakeholders regarding how wildlife should be managed, it is unsurprising that it is the human dimension that has been most commonly addressed in the literature (Inskip and Zimmermann, 2009; Redpath *et al.*, 2015; Montgomery *et al.*, 2018a). This may also be the most extensive dimension to consider, focusing on human perceptions, attitudes, and practises and how these affect interactions and responses to wildlife (Dickman, 2010). It can perhaps be expressed as two key components: the first concerning social factors which drive attitudes and behaviours, and the second relating to direct human impacts on landscapes via land use, infrastructure, and population densities.

Among the myriad factors to consider when attempting to understand attitudes towards carnivores are personal experiences and perceived power imbalances. In Kenya, 75% of Maasai who said they would kill lions had suffered high levels of depredation themselves (Hazzah *et al.*, 2009). However, personal experiences alone are not always a strong predictor of attitudes and actions, with high levels of antagonism towards carnivores based on potential risk or on prior values and beliefs (Dickman *et al.*, 2014; Kansky and Knight, 2014). Religious beliefs can be a strong predictor of people's values and cultural norms and, in Tanzania, adherence to a formal religion has been linked to higher reported problems with carnivores (Dickman *et al.*, 2014). Inequality of power can also play an important role, particularly for rural communities who feel that wildlife conservation is being imposed upon them by powerful external elites (Dickman, 2010). A lack of participation in decision-making regarding wildlife and resource management is an important factor shaping conservation attitudes (Gillingham and Lee, 1999; Redpath *et al.*, 2017; Rakotonarivo *et al.*, 2021a). These kinds of problems intensify distrust and antagonism between stakeholders, making it more difficult to develop cooperative solutions (Redpath *et al.*, 2013). A contentious issue is the exclusion of local communities from protected areas for the protection of wildlife and habitats (Lele *et al.*, 2010; Brockington and Wilkie, 2015). In Kenya, allowing pastoralists to access protected areas during times of drought resulted in more positive attitudes towards lions and a lower propensity to kill them (Hazzah *et al.*, 2013).

Unsurprisingly, given its link to vulnerability, wealth has also been shown to influence human-carnivore conflict. Wealthier households are more able to invest in protection strategies such as better enclosures, livestock guarding dogs and employing herders (Saberwal *et al.*, 1994; Treves *et al.*, 2006). In addition, if damage still occurs it is less likely to be catastrophic for wealthier households, while poorer households have lowered ability to cope with these impacts (Dickman *et al.*, 2013). Human-lion conflict is therefore influenced by a diverse range of underlying social factors and developing a broad understanding of these drivers will help to advance understanding of the patterns and processes involved.

In addition to these social factors, direct human impacts on landscapes also affect conflict occurrence via their influence on lion, livestock, and prey distributions. For example, attack risk for both people and livestock may be related to distances to infrastructure such as roads and settlements (Kuiper et al. 2020, Miller et al. 2015), human population densities (Mpakairi *et al.*, 2018), and proportions of pasture and cropland (Treves *et al.*, 2011; Kushnir *et al.*, 2014).

1.3.5 The environment dimension

The environmental dimension of human-lion conflict relates to information on variables such as climate, vegetation, and land cover. This links back to all four of the above-detailed dimensions as environmental variables directly influence the behaviour and movement of carnivores, prey and livestock and affect human land use.

Precipitation levels and water availability are likely to be key factors contributing towards conflict risk. The distribution of herbivores in semi-arid landscapes is largely influenced by the availability of surface water (Valeix *et al.*, 2010; Abade *et al.*, 2014b) and the preferred prey species of lions are water-dependent grazers (Hayward and Kerley, 2005; Davidson *et al.*, 2013). A large number of studies have recorded higher levels of livestock depredation during the wet season, when precipitation levels are highest (Kolowski and Holekamp, 2006; Kissui, 2008; Loveridge *et al.*, 2017a; Mkonyi *et al.*, 2017c). During the dry season wild prey are more predictably distributed around water sources and have poorer body condition, making them more easily accessible for predators (Kuiper *et al.*, 2015). Thus, in the wet season, when wild prey is unevenly scatted and in better condition, lions may to switch to livestock as an alternative food source (Valeix *et al.*, 2012a; Kuiper *et al.*, 2015).

Other environmental variables that are commonly examined include proximity measures to various features of interest such as protected area boundaries, water sources and habitat edges. Vegetation type is also an important factor to consider. As highlighted above, lion habitat use is partly driven by prey catchability and, as ambush hunters, lions are likely to hunt in areas with higher vegetation which provide access to grazing prey and cover for stalking (Hopcraft *et al.*, 2005; Davidson *et al.*, 2012). Studies have shown increased conflict frequency in areas of intermediate to dense vegetation (Woodroffe *et al.*, 2007; Broekhuis *et al.*, 2017), as well as in areas with a high proportion of open woodland/bushland (Kushnir *et al.*, 2014).

1.4 Mitigation of human-lion conflict

Understanding these five dimensions and the spatiotemporal factors associated with conflict could produce valuable results for management and mitigation at a wide scale (Treves *et al.*, 2011; Abade *et al.*, 2014a). The development of mitigation strategies to encourage human-carnivore coexistence is challenging and can be expensive to implement (Dickman *et al.*, 2011; Mkonyi *et al.*, 2017a; van Eeden *et al.*, 2018a). For example, construction of predator-proof fencing at protected area boundaries can cost between \$6,000 - \$12,000/km, with further budget needed for inspection and maintenance (Lindsey *et al.*, 2012; Pekor *et al.*, 2019). Costs for fortification of livestock enclosures can vary from \$80 -\$1,500 (Sutton *et al.*, 2017; Kissui *et al.*, 2019), and programmes which offer compensation for livestock lost to carnivores can require budgets of up to \$250,000/year (Hazzah *et al.*, 2014).

Given these costs, it is vital to ensure that interventions are targeted towards high-priority areas and that they are effective in reducing human-carnivore conflict. Typically, effectiveness is measured as success in reducing livestock depredation and there is a lack of consensus and wide variation in what methods work (Eklund *et al.*, 2017; van Eeden *et al.*, 2018b). However, alongside technical effectiveness, other aspects which must be considered when developing interventions include perceived effectiveness, affordability, and cultural appropriateness, which may also contribute to the uptake and success of strategies (Khorozyan and Waltert, 2019; Rakotonarivo *et al.*, 2021b; Volski *et al.*, 2021). For example, while fortified livestock enclosures were perceived to be highly effective at reducing livestock depredation in Manyara, Tanzania, the majority of individuals did not use them because of their construction expense (Mkonyi *et al.*, 2017a). Similarly, in the Ruaha landscape of Tanzania, uptake of reinforced enclosures has been limited as they do not offer the flexibility and mobility required by local pastoralists (B. Cascio 2019, pers. comm.). Hence, studies must also consider the local feasibility and acceptability of mitigation approaches and engage local stakeholders to develop collaborative solutions.

1.4.1 Collaborative or coercive approaches

Historically, top-down, command-and-control approaches have played a crucial role in carnivore conservation. Strict protection and its enforcement via legislation has been responsible for rebounds in carnivore populations across Europe and the US (Chapron *et al.*, 2014; Treves *et al.*, 2017). International and national cooperation through legal instruments and policies provide a supportive framework through which countries can address conservation issues (Redpath *et al.*, 2017). This is of particular importance for large carnivores whose ranges overlap various national jurisdictions (Trouwborst, 2015).

However, given that these expansive home ranges result in the cooccurrence of humans and carnivores in shared landscapes outside of protected areas (Di Minin *et al.*, 2016), it is increasingly recognised that bottom-up, collaborative approaches are needed to negotiate the challenges of living with carnivores (Redpath *et al.*, 2017; Pooley, 2021). Particularly in developing countries with the pressures of poverty, limited resources, poor governance, and other social concerns (Abrams *et al.*, 2009; Redpath *et al.*, 2017), coercive approaches that do not resonate locally may lead to breakdowns in trust, disempowerment, and exacerbation of HWCs (Brockington and Igoe, 2006; Redpath *et al.*, 2013; Davis and Goldman, 2019).

Collaborative approaches which engage local communities as key stakeholders, emphasise local ownership of wildlife, and incorporate traditional, indigenous knowledge and management practices, can improve conservation outcomes and address some of the problems associated with restrictions imposed by governments (Measham and Lumbasi, 2013; Hazzah *et al.*, 2014; Ogutu *et al.*, 2017; Reed *et al.*, 2021). However, the success of such initiatives depends on fair stakeholder representation and participation, effective knowledge sharing and mechanisms for conflict resolution (Redpath *et al.*, 2013; Sjölander-Lindqvist *et al.*, 2015).

Top-down and bottom-up approaches represent two opposite extremes and ultimately elements of both approaches, from national and international legal instruments to local stakeholder-driven methods, are likely to be needed and will be dependent on the conservation context (Reed and Ceno, 2015; Trouwborst *et al.*, 2017). However, a lack of communication between stakeholder groups can be a key factor contributing to failures in effective conservation implementation (Biggs *et al.*, 2011; Gray *et al.*, 2020). Participatory, transparent, and deliberative processes are therefore needed to help all parties engage and co-develop techniques that can mitigate conflicts. This can be challenging and requires the integration of social science approaches to gather data on diverse knowledge systems, perspectives, and values (Bennett *et al.*, 2017). In Chapter 5, I trial the use of a novel, experimental game framed around livestock protection, as a tool to examine stakeholder decision-making and individual preferences for different mitigation methods and incentive structures.

1.4.2 Livestock husbandry interventions

The most common approach for reducing human-carnivore conflict is attempting to reduce livestock loss via various livestock management and husbandry techniques (van Eeden *et al.*, 2018b). These typically include methods such as visual and auditory deterrents (Lesilau *et al.*, 2018; Radford *et al.*, 2020), improved guarding by both dogs and people (Ogada *et al.*, 2003; Tumenta *et al.*, 2013) and fortifying livestock enclosures (Lichtenfeld *et al.*, 2014; Mkonyi *et al.*, 2017a; Sutton *et al.*, 2017). Other strategies such as changing herd size and composition and developing adaptive grazing plans have rarely been examined in the literature (Kuiper *et al.*, 2015; Eklund *et al.*, 2017; Weise *et al.*, 2019).

Where technical interventions are implemented, there is a lack of consensus on what is effective (Eklund *et al.*, 2017; Lute *et al.*, 2018) and direct evaluation of the efficacy of different mitigation techniques is noticeably lacking in the literature (Miller *et al.*, 2016b; van Eeden *et al.*, 2018b). Reviews of interventions to reduce livestock depredation have found considerable biases, including a tendency towards only publishing positive outcomes and a lack of replication across species and geographic regions (Møller and Jennions, 2001; Miller *et al.*, 2016b). Various husbandry techniques such as guard dogs, electric fences and night-time enclosures have mixed effects and show high variability in reported levels of depredation reduction (Miller *et al.*, 2016b; van Eeden *et al.*, 2018a). Several interventions have only been properly evaluated in a single study (Eklund *et al.*, 2017).

1.4.3 Financial incentives

Various schemes have also been developed to provide financial incentives in areas where there is a lack of economic benefits to encourage human-wildlife coexistence (Dickman *et al.*, 2011). These come in several forms, one of which is compensation schemes which pay individuals to offset the cost of livestock lost to carnivores, often stressing the requirement that compensation will only be paid if the carnivore responsible is not killed (Bauer *et al.*, 2017; Braczkowski *et al.*, 2020). An alternative approach is the use of conservation performance payments which provide financial incentives conditional on specific conservation outcomes (Zabel and Engel, 2010; Dickman *et al.*, 2011). These may include payments based on the number of carnivore reproductions that occur on village land (Zabel and Holm-Müller, 2008), or incentives to protect habitats, leave areas free of human use and support prey populations (Mishra *et al.*, 2003; Nelson *et al.*, 2010).

The effectiveness of these approaches varies widely and is context-dependent but, particularly for performance payments, there are limited operational examples from which to assess effectiveness and acceptability (Nelson, 2009; Zabel and Engel, 2010). Compensation payments have been found to reduce predator killing and improve tolerance towards wildlife in some contexts (Mishra *et al.*, 2003; Bauer *et al.*, 2017), but not all (Naughton-Treves *et al.*, 2003; Gusset *et al.*, 2009). Criticisms of the approach includes its financial sustainability, failure to diminish the frequency of depredation and address the full costs associated with it, inequality of access and delays in processing of claims (Madhusudan, 2003; Dickman *et al.*, 2011; Anyango-Van Zwieten *et al.*, 2015; Braczkowski *et al.*, 2020).

An alternative method is the creation of revenue-sharing initiatives, where benefits generated by wildlife through tourism, trophy hunting or other activities are channelled back to local communities (Archabald and Naughton-Treves, 2001; Dickman *et al.*, 2011). In many countries this approach has led to the creation of community conservancies and wildlife management areas. These conservancies are ostensibly community-run institutions, where villages come together to manage a portion of their land for wildlife conservation purposes (Kiwango *et al.*, 2015; Bersaglio and Cleaver, 2018). The aim of these initiatives is to transfer management of natural resources to local communities and promote conservation by generating revenues through wildlife-based enterprises, improving land management, diversifying livelihoods, and enhancing security (Taylor, 2009; Fox, 2018; Homewood *et al.*, 2020; Keane *et al.*, 2020). Again, there are multiple criticisms of this approach such as 'elite capture' of benefits, lack of infrastructure for tourism in many areas, and opportunity costs associated with restrictions on land use (Frost and Bond, 2008; Dickman *et al.*, 2011; Bersaglio and Cleaver, 2018). It is likely, therefore, that a combination of approaches, both technical and financial, will be needed to best promote human-carnivore coexistence.

1.5 Knowledge gaps

As discussed above, the African lion epitomises the challenges associated with balancing conservation and human well-being goals in human-dominated landscapes. Continuing declines in lion populations (Henschel *et al.*, 2014; Bauer *et al.*, 2015) suggest that current data and understanding has been insufficient to properly evaluate how the species is using these landscapes and to develop strategies which lead to successful conservation action. Management to facilitate lion survival in these matrix landscapes requires evaluation of key drivers of species occupancy and habitat use and detailed understanding of interactions with people and livestock, in order to develop collaborative approaches to coexistence.

While the literature on human-lion conflict has increased dramatically in recent years, a current review found that only 29% of papers evaluated more than two dimensions with most focusing only on the human and the lion (Montgomery *et al.*, 2018a). No paper examined all 5 dimensions concurrently to develop a broad understanding of the underlying patterns and examine how human-lion conflict risk can be predicted (Dickman, 2010; Montgomery *et al.*, 2018a). Furthermore, in addition to the 5 dimensions being examined in isolation, studies are primarily site-specific with limited comparability of research between study areas (Montgomery *et al.*, 2018a). While local context is important (e.g., in determining value differences caused by culture/religion etc; Lute *et al.* (2018)), using comparable research techniques and facilitating comparisons across studies would lead to conservation actions that are applicable at broader scales. In this thesis I attempt to address these knowledge gaps by considering several dimensions of human-lion conflict. First, I evaluate existing knowledge to identify consistent drivers of lion habitat use across the species' range. Second, I implement two modelling techniques to reveal key spatial drivers of livestock depredation at a Tanzanian study site. I then apply one of these models across several additional study landscapes to assess the transferability of the approach for identifying areas at high risk of human-lion conflict.

Despite the growth in research papers focussing on human-lion conflict in the last decade (Montgomery *et al.*, 2018a), lion numbers have continued to decline (Bauer *et al.*, 2015). This raises the question as to whether research truly leads to effective conservation solutions (Mascia *et al.*, 2003) and whether mitigation interventions are based on sound science (Lute *et al.*, 2018; van Eeden *et al.*, 2018b). Conservation professionals exhibit a diverse range of opinions on which mitigation strategies are most effective depending on factors such as their nationality, local context, and employment sector (Lute *et al.*, 2018). Lack of reliable information and the use of inappropriate interventions may result in mistrust of conservationists by local communities and increased frustration and hostility towards carnivores (Eklund *et al.*, 2017). Management to support conservation in human-dominated landscapes therefore requires knowledge of what solutions are appropriate and acceptable to local stakeholders. In my final data chapter, I trial the use of an experimental game as a method to explore stakeholder preferences for different mitigation types and to understand the factors that drive decision-making.

1.6 The Ruaha landscape of Tanzania

Much of this thesis utilises data collected in the Ruaha landscape located in the Ruaha-Rungwa ecosystem of south-central Tanzania. The landscape is centred on the ~ 23,000 km^2 Ruaha National Park (RNP) and contains a mixture of land use types, including game reserves and the Pawaga-Idodi Wildlife Management Area (WMA), a community conservation area managed by local villages as part of a national scheme to generate revenue from wildlife (Fig. 1.2). Data were collected in unprotected village lands adjacent to the WMA, part of the Iringa Rural District (Fig. 1.2).

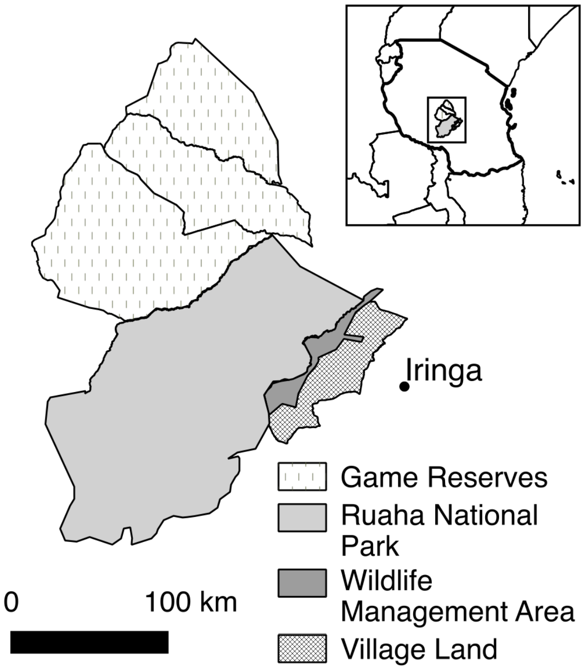

Figure 1.2 Map of the Ruaha-Rungwa landscape *from* Dorward (2018). Inset shows the location of the landscape within Tanzania. The study area for this thesis is located in the village land to the east of Ruaha National Park.

The climate in the region is semi-arid to arid, with an average annual rainfall of 600mm which falls during a single wet season from December to April (Searle *et al.*, 2021a). Vegetation cover is a mosaic of miombo woodland, semi-arid savanna and *Acacia-Commiphora* bushland and thickets (Hardouin *et al.*, 2021), with village lands containing cropland (primarily rice and maize fields) and livestock grazing areas (Abade *et al.*, 2019).

The RNP and the WMA are unfenced, meaning that wildlife can move freely across the area. The Ruaha-Rungwa landscape is considered to be a high priority region for carnivore conservation. It is believed to contain one of only four cheetah populations in East Africa numbering at least 200 individuals and to support the third largest population of African wild dogs in the world (IUCN, 2007; Strampelli *et al.*, 2021). The landscape is also considered to be one of only four lion 'strongholds' in East Africa (defined as areas containing > 500 individuals with stable or increasing numbers based on 2006 IUCN assessments (Riggio *et al.*, 2013)), estimated to be home to ~ 3779 lions (Mesochina *et al.*, 2010). However, despite the identification of Ruaha as a high value area for carnivore conservation, no recent lion population estimates are available (Strampelli *et al.*, 2022). Data on prey species populations in the region are similarly lacking. However, aerial surveys provide some evidence of declining abundance and range contractions for several herbivore species, including buffalo, giraffe, and zebra (Mtui *et al.*, 2016).

Furthermore, very little research exists on lion ecology and behaviour in this ecosystem. One recent study inside Ruaha National Park observed that lions had higher than average pride sizes of ~ 6 individuals and that giraffe were the most hunted species, followed by buffalo, elephant, and zebra (Muneza *et al.*, 2022), suggesting that lions in this landscape may be selecting for larger than average prey. Similarly, there is a lack of data on occurrence and space use of lions and prey in village lands. A previous camera trapping study detected no lions on village land, despite their known presence there as evidenced by depredation events (Abade *et al.*, 2019). Notably, there were also no detections of several preferred prey species including giraffe, buffalo, and zebra on village land (Abade *et al.*, 2019), although there were observations of other potential prey such as greater kudu. This suggests that wildlife densities on village lands are low. A more recent camera trapping survey, which did not sample on village land, did capture both male and female lions inside the WMA at densities of 4.06 per 100 km^2 (Strampelli *et al.*, 2022), relatively high for the species (Bauer *et al.*, 2016).

The village land is inhabited by over 60,000 people from at least 30 different ethnic groups, with livelihoods predominated by agriculture and pastoralism (Abade *et al.*, 2019). Lion, cheetah, leopard, and spotted hyena have all been cited as problem animals by communities in this landscape, due to attacks on both people and livestock (Dickman *et al.*, 2014). Although depredation accounts for a relatively small percentage of total stock loss, experience of depredation is widespread and generates intense hostility (Dickman *et al.*, 2014). Consequently, lions in this landscape have experienced high-levels of human-induced mortality due to retaliatory and preventative killing, with at least 136 lions killed between 2006 - 2018 (Dickman *et al.*, 2014; Coals *et al.*, 2020) and 27 lion hunts taking place in 2019 (A. Grau 2020, pers. comms.).

The Ruaha Carnivore Project (RCP), a research organisation established in 2009 (ruahacarnivoreproject.com), works in and around Ruaha National Park with the aim of improving understanding of carnivore ecology and reducing levels of human-carnivore conflict. The project first conducted interviews in the region in 2008 and found that communities reported highly negative attitudes towards wildlife (Dickman, 2008; Dickman *et al.*, 2014). RCP now works across 16 villages in the area adjacent to the WMA. They run a range of conservation-based initiatives including education and outreach (DVD nights, safaris, school scholarships), livestock protection (predator-proofing bomas, hiring local conflict officers), scientific research (lion collaring, national park sightings programme), and provision of community benefits (RCP 2019). Community benefits are provided via an innovative 'community camera trapping' initiative to ensure that benefits are perceived as being directly linked to wildlife. Camera traps are placed on village land and each village receives points for any wildlife photos captured, with high scores awarded for potentially dangerous species such as lions. At the end of each quarter these points are translated into benefits requested by the community such as medical supplies, school supplies and veterinary medicines, with the highest scoring village receiving the most gifts. In 2019, RCP estimates to have provided nearly $90,000 worth of benefits reaching approximately 40,000 people, as well as predator-proofing 35 bomas and taking 495 people on safaris into the National Park (RCP 2019). Communities in this area have therefore had significant exposure to a conservation organisation.

The importance of Ruaha's carnivore populations, the lack of data on wildlife abundance and distributions, and the level of human-carnivore conflict in the area highlight the need for continued research into human-carnivore interactions in the Ruaha landscape.

1.7 Thesis aims and outline

This thesis was developed to investigate the complexities of human-lion interactions and expand understanding of the ecological and social variables that contribute towards human-lion conflict. The thesis aims to determine the viability of the human-dominated landscape matrix for supporting free-roaming lion populations via focusing on three objectives: 1) to synthesise current understanding of lion habitat use and suitability; 2) to identify the ecological and anthropogenic variables associated with livestock depredation events across contexts; and 3) to investigate stakeholder preferences for mitigation interventions.

This thesis comprises four data chapters followed by a general discussion and conclusions:

Chapter 2. *Room to roam for African lions (Panthera leo): a review of the key drivers of lion habitat use and implications for conservation.*

Effective conservation aimed at supporting lions in human-dominated landscapes first requires detailed understanding of the species' habitat requirements. In this chapter I aim to identify common drivers of lion habitat use across contexts. I present the results of a literature review, extracting information from 154 relevant articles, to: 1) quantify the ecological and anthropogenic attributes of habitats associated with lions; 2) develop a conceptual framework identifying key drivers of lion habitat use; and 3) critically reflect on biases and gaps in the literature that hinder our ability to predict habitat suitability for lions in human-dominated landscapes.

Chapter 3. *Using landscape characteristics to predict livestock depredation risk by African lions in the Ruaha landscape of Tanzania.*
Managing the impacts of human-lion conflict effectively and promoting coexistence requires robust understanding of where and why livestock depredation happen. Here, I study the spatial patterns of livestock depredation by lions in the Ruaha landscape of Tanzania, a high priority region for carnivore conservation. I demonstrate the use of two modelling techniques, Linear Discriminant Analysis and Integrated Nested Laplace Approximation, for quantifying the landscape features associated with lion attacks on corralled and grazing livestock. I use the derived models to develop risk maps identifying conflict hotspots in the Ruaha landscape and discuss the applicability of the approaches and possible management actions.

Chapter 4. *Examining the utility of a Linear Discriminant Analysis approach to identify common drivers of livestock depredation across contexts.*
Using comparable research techniques can facilitate comparisons across studies and could identify variables which are consistently important in predicting conflict risk. In this chapter, I aim to examine the transferability of the Linear Discriminant Analysis approach by assessing the extent to which models can accurately predict livestock depredation across three additional study sites. Using data from two Kenyan and one Zimbabwean study areas, I first test the transferability of the model derived in the Ruaha landscape and second, implement the same approach with landscape-specific variables to develop risk maps for each study site. I interpret my findings to discuss whether a simple, scalable approach for modelling human-lion conflict is feasible and can identify common drivers across geographic contexts.

Chapter 5. *Trialling the use of an experimental game to examine pastoralist decision-making and preferences for coexistence strategies in response to human-lion conflict.*
Having developed predictive maps to identify potential conflict hotspots, these can be used to target mitigation interventions towards high-risk areas. To implement effective strategies to alleviate human-lion conflict, it is necessary to understand the acceptability of different options to local stakeholders and their impacts on behaviour and decision-making. In this chapter I use a novel experimental game framed around lions and livestock protection, played across 8 villages in Tanzania, to examine pastoralist behaviour in response to different mitigation methods and incentive structures. Using data from 172 participants, I aim to explore individual preferences for coexistence strategies and the relationship between in-game behaviour and personal characteristics which may affect support for conservation.

Chapter 6. *General discussion.* In this chapter, I synthesise key findings, discuss the implications of my results and outline further areas of research that will contribute to our understanding of human-lion conflict.

Chapter 2. Room to roam for African lions (*Panthera leo*): a review of the key drivers of lion habitat use and implications for conservation

A male lion observes researchers conducting vegetation surveys in the grasslands of Lewa Wildlife Conservancy, Kenya.

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2.1 Abstract

1. Globally, large terrestrial carnivores (Carnivora) have suffered precipitous declines in population and range. Today, they must persist in increasingly isolated natural habitat patches within a human-dominated matrix. Effective conservation aimed at supporting carnivores in such landscapes requires species-specific understanding of habitat requirements.
2. We present results from a review of the published literature to assess the current state of knowledge regarding habitat preferences of the African lion *Panthera leo*, with the aim of identifying common drivers of habitat use across contexts.
3. Using the Web of Science, we identified 154 usable articles and extracted information relating to study topic, location, habitats described, land-use type and any documented habitat preferences.
4. Only 31 studies documented evidence of habitat use, and collectively they suggested that preferences for specific habitat types were varied and context-specific. The importance of prey abundance and proximity to water was highlighted in multiple studies. Anthropogenic factors interfered with expected patterns of habitat use. There was evident bias in study locations: 83% of the habitat-use studies were based in only three countries, and 70% were focussed on protected or managed areas.
5. Our synthesis suggests that lions demonstrate behavioural plasticity in habitat use in response to anthropogenic pressures. To understand the limits of this plasticity and to manage Africa's changing landscapes effectively for roaming lions, future research should be focussed on analysis of habitat use outside protected areas, taking into account gradients of distance to water, prey abundance and anthropogenic risk.

2.2 Introduction

Over the past century, humans have altered the world's ecosystems more severely than during any other period of history, and there is overwhelming evidence that human impacts are accelerating (Steffen *et al.*, 2015). Globally pervasive land-cover change has caused declines in biodiversity through the loss, modification, and fragmentation of natural habitat (Foley *et al.*, 2005; IPBES, 2019). Consequently, the number of species currently threatened with extinction has reached unprecedented levels (Díaz *et al.*, 2019).

Biological characteristics, such as large body size, slow reproductive rate, and low population density, make large terrestrial carnivores (Carnivora) particularly vulnerable to habitat fragmentation (McKinney, 1997; Keinath *et al.*, 2017). Large carnivores play vital ecological roles as apex predators (Estes *et al.*, 2011; Ripple *et al.*, 2014), thus their extirpation may have cascading effects on ecosystem structure and functioning. Due to their considerable human-wildlife conflict potential and significant spatial requirements, large carnivores feature prominently in many global conservation projects and policies, and the general causes of their declines are well recognised (Ripple *et al.*, 2014; Trouwborst *et al.*, 2017). However, this understanding has not always translated into adequate conservation action (Ripple *et al.*, 2014).

The African lion *Panthera leo* exemplifies the challenges of conserving top predators. Lions have suffered precipitous population declines in the last century and now occupy only 8% of their historic range (Bauer *et al.*, 2016). Protected areas (PAs), whether large tracts of wilderness or small fenced reserves, are crucial to the long-term survival of lions (Packer *et al.*, 2013; Lindsey *et al.*, 2017b). However, approximately 44% of their remaining range lies outside of PAs (IUCN, 2018a). Hence, lion conservation strategies must be adaptive to a range of contexts, across a wide mosaic of different land-use and habitat types. To determine the extent to which lions can adapt to habitat modification, and which conservation actions can facilitate this process, it is necessary to understand how lions use existing habitats throughout their remaining range.

Habitat describes the physical nature (biotic and abiotic) of a location of interest (Kearney, 2006), referring, for example, to vegetation, climate, and food resources (Gaillard *et al.*, 2010). Habitat use and selection by a species may vary within a range of suitable habitats, based on the quality of resources such as forage, water and shelter (Hall *et al.*, 1997). Habitat selection is a hierarchical process and inherently scale-dependent (Mayor *et al.*, 2009). At each scale, determinants of habitat selection may differ (Gaillard *et al.*, 2010). Home range selection decisions may be driven by interspecific and intraspecific competition (Rich *et al.*, 2012; Vanak *et al.*, 2013). At a finer scale, habitat selection may be centred on the availability and abundance of resources (Hopcraft *et al.*, 2005; Mueller *et al.*, 2008).

Lions occupy a broad range of biomes and can be found throughout East, West, Central and Southern Africa (Bauer *et al.*, 2016), suggesting high tolerance to habitat variation and quality. However, lion ecology and behaviour is shaped at finer spatial scales by interactions between lions and habitat, prey, and people (Patterson, 2007). Current understanding of lion habitat selection inside PAs centres on two main hypotheses: the prey abundance hypothesis and the prey catchability hypothesis (Davidson *et al.*, 2012). The prey abundance hypothesis states that habitats are selected to include the highest numbers of prey, and that home range size is inversely correlated with prey density (Spong, 2002; Davidson *et al.*, 2012). The prey catchability hypothesis proposes that lions select habitats based on attributes that increase hunting efficiency (Hopcraft *et al.*, 2005), e.g., vegetation cover and topography (Hebblewhite *et al.*, 2005). The two hypotheses are not mutually exclusive, and habitat selection by lions is likely to be driven by a combination of prey density and hunting efficiency.

Outside of PAs, anthropogenic pressures can modify habitat use, forcing carnivores into lower quality habitats (Knopff *et al.*, 2014) and confounding patterns expected from the prey-based hypotheses (Valeix *et al.*, 2012a). With the rapid expansion of human activities into remaining natural habitats throughout the African continent (Oakleaf *et al.*, 2015), quantifying the consequences for lion habitat use is crucial for developing effective, spatially-targeted lion conservation strategies.

We present the results of a literature review to identify common drivers of lion habitat use across contexts. In particular, we aimed to: 1) extract information relating to ecological and anthropogenic attributes of habitats associated with lions and standardise these factors to quantify their relative importance; 2) use these attributes to develop a conceptual framework for assessing habitat suitability for lions; and 3) critically reflect on biases, gaps and uncertainties in the data that hinder our ability to predict habitat suitability for lions in increasingly human-dominated landscapes.

2.3 Methods

2.3.1 Literature search

We conducted our literature search using the Web of Science, which returns articles based on a search of the title, abstract and key words. We performed our search on 14 October 2019, using the terms *Panthera leo* OR African lion AND habitat OR landscape OR land use, with no specified timespan. We first screened articles for relevance based on titles and abstracts, and then read in full all articles still considered relevant for our study aims (Appendix A1; Moher *et al.* (2009)). We only included articles that referred to the African lion *Panthera leo*, included a primary empirical observation of lion presence (i.e., not from other literature or modelling), and in which estimates of lion presence could be linked to metrics of habitat in a spatially explicit manner.

For articles presenting continent-wide assessments, we examined the source of the data. If the data were collected by the authors themselves, the article was included as a primary observation (e.g., Packer *et al.* (2013) provided lion densities for a variety of PAs based on authors' contributions). Articles were included if their focus was on another species, but they documented lion presence with data or observations (e.g., Balme *et al.* (2017)). Articles were also included where there was unequivocal qualitative evidence of lion presence (*n* = 6); for example, Chizzola *et al.* (2018) compared differences in prey behaviour and stress levels on reserves with and without lions. Articles were excluded where the land-use type of the study area was unclear and could not be determined, and where geographic coordinates for the study area were not provided and the location could not be found on Google Earth.

2.3.2 Data extraction and analyses

From the final set of articles, we extracted data on study site locations, habitat types present and any documented habitat preferences. We extracted contextual information, including details of main study topic, methods used to document lion presence, land use in the study area, and which environmental factors were included in models (e.g., distance to water, vegetation cover, prey biomass). We extracted the geographic coordinates provided in the article, where possible. If this was not possible, we used Google Earth to identify locations based on the names of the study areas.

For the purpose of this review, we defined habitat type as any named land-cover or vegetation type extracted for each study site. Habitat type was typically stated in the 'Study Area' section of the article, which described the landscape in a wider sense rather than fine-scale information on where lions were located. We grouped habitat descriptors into broad habitat types using the International Geosphere-Biosphere Programme classification system mapped by the Moderate Resolution Imaging Spectroradiometer land-cover product MCD12Q1 (MODIS MCD12Q1: IGBP; Friedl and Sulla-Menashe (2019); Appendix A2). For example, an article describing the study area as short grass plains and open deciduous woodland was coded as 'Grassland' and 'Woodland'. To identify the most commonly occurring habitat types, articles were grouped by location (e.g., Hwange National Park, Zimbabwe) and the number of distinct habitats described for each location was recorded. As some articles included more than one study site, and some articles pertained to the same study site, the sample size for the habitat analysis was not equal to the number of articles included in the review.

To fill data gaps for articles that did not describe the habitat types present at their study site (*n* = 29), we extracted land-cover type for each study from MODIS MCD12Q: IGBP, including all habitats mapped within a buffer around the study site coordinates. Three buffers were tested based on minimum lion home range size, and an 8 km buffer was considered broadly sufficient for capturing habitat type in each study area (Appendix A3). To assess differences between reported and extracted habitat, data from those articles which had stated habitat type were compared with habitat data for the same locations extracted from the MODIS layer (Appendix A3).

To examine the anthropogenic pressures being exerted on lion habitats, we used the Human Footprint Index, which quantifies the cumulative impact of built environments, intensive agriculture, pasture lands, human population density, night-time lights, roads, railways, and navigable waterways (Venter *et al.*, 2016a; Venter *et al.*, 2016b). Results are provided on a 0-50 scale, with zero representing no measurable anthropogenic pressure. We overlaid the most recent lion range map provided by the International Union for Conservation of Nature (IUCN; Bauer *et al.* (2016)) with the Human Footprint Index map to determine the number of pixels within the African lion's range that are subject to various levels of anthropogenic pressure.

For articles that specifically covered habitat use or selection, we used a vote-counting procedure to determine which habitat factors were consistent correlates of lion habitat use. This procedure involved counting the number of studies with significant positive results, significant negative results, and non-significant results. We acknowledge the constraints of this method in failing to account for effect size and sample size (Bushman and Wang, 2009), and, therefore, we simply aimed to provide a descriptive summation and narrative for patterns and conflicts and to highlight the relative importance of variables contributing to lion habitat selection. Based on the most commonly observed patterns, we created a conceptual framework showing the expected interactions between drivers of habitat use and the key habitat preferences of lions. We also used this framework to highlight several factors which are likely to be important but for which data are currently lacking.

To assess biases in the literature, we explored spatial representativeness using plots of occurrence in the literature of countries within the lion geographic range and the land-use types covered by the study areas. All data exploration and analysis was implemented in R statistical software version 3.6.3 (R Core Team, 2020).

2.4 Results

2.4.1 Literature search

The search in the Web of Science returned 337 articles. After filtering by title and abstract, 206 articles were retained and read in full. These were assessed against the inclusion criteria and data were extracted from 154 articles covering 128 independent study sites (Appendix

A1; A4). Articles identified as relevant were published between 1997 and 2019, and 49% of these were published in the last five years. We identified nine broad study themes based on aims and key words (Appendix A5). The dominant topic was focussed on species other than the lion, but documented lion presence (29% of the 154 articles), followed by studies on human-wildlife conflict (21%) and habitat use (15%). Study foci for the habitat use category included habitat use, selection, quality, and occupancy (Appendix A5).

2.4.2 Habitat use and selection

Grassland was the dominant habitat type across study sites, occurring at 88% of locations (112 of the 128 study locations represented in the 154 articles) followed by woodland (62%), shrubland (60%) and savanna (52%; Fig. 2.1). Habitats created by humans (cropland, mosaic and urban) were present at 37 study sites (29%). However, the majoritiy of incidences of these human-modified habitats occurred where data had been extracted from the MODIS land-cover product (89% of human-created habitat locations) rather than from study area descriptions.

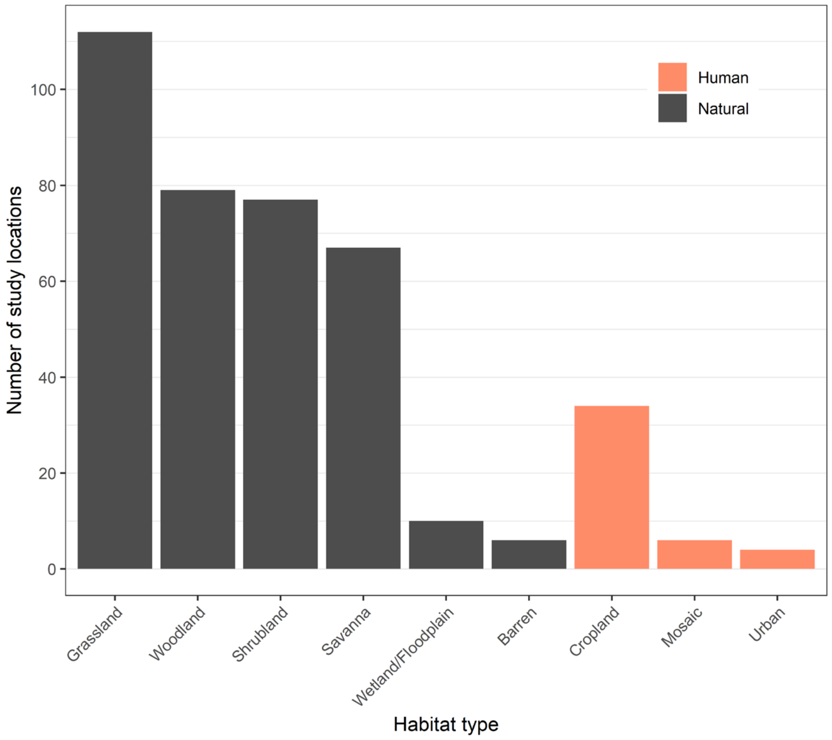


Figure 2.1 Habitat types occurring at 128 study locations represented in the 154 articles included in this review of African lion habitat use. Colours indicate whether the habitat type is naturally occurring or human-created. Study locations including several habitat types are represented multiple times in the graph: in total, the 128 study locations included 395 habitat type data points.

Based on the Human Footprint Index, 31% of the land within the geographic range of the African lion is under high or very high anthropogenic pressure (Human Footprint Index ≥6;

Venter *et al.* (2016b)), while 28% remains under no or low anthropogenic pressure (Human Footprint Index 0-2).

Landscapes in which lions occurred were most often composed of three or four habitat types (59% of the study locations), compared to 14% locations with only one habitat type (50% of which were grassland). When considering only the four most common habitat types, the most frequently observed habitat composition (*n* = 24) encompassed grassland, savanna, woodland and shrubland (Fig. 2.2). This summary does not account for spatial scale; studies conducted in larger National Parks or at broader spatial extents may encompass a wider range of habitats. However, it may also be the case that studies at broader spatial extents describe habitats in a broader sense, while smaller site descriptions contain more specific detail on local habitat types.

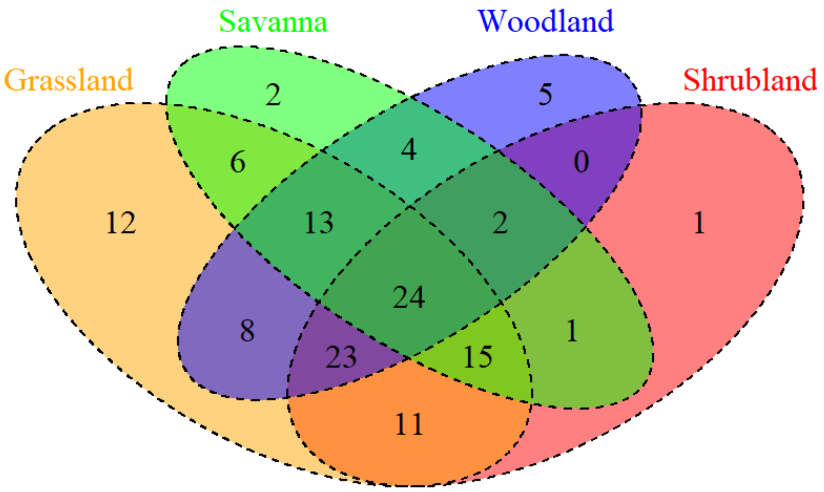


Figure 2.2 Diagram representing the co-occurrence of the four most common habitat types at study sites used for African lion *Panthera leo* research. Numbers indicate the number of study locations containing that habitat composition.

We present our findings with a note of caution. The majority of articles described habitat at the scale of the study area in general terms, with only few spatially explicit details on lion observations within their study area. With the current state of evidence, it was not possible to determine whether lions used all documented habitats.

More detailed evidence regarding lion habitat use was extracted from the 23 articles that were focussed on habitat use and selection, and from a further eight articles, in which the main focus was not habitat use but which documented evidence of lion habitat preference (Appendix A6; Table 2.1). Studies were split into those that were conducted solely inside PAs and those that considered multiple land-use types (Table 2.1). Mixed land-use studies typically contained a combination of protected and unprotected areas, but only two of these made a direct comparison of habitat use inside vs outside the PA (Appendix A6). There was evidence for habitat use being highly variable and context dependent. Of studies that considered habitat types inside PAs, 45% found that lions selected for open habitat such as grassland, while 18% found a preference for woodland. Some studies found that habitat use varied seasonally or based on behaviour (e.g., selecting grassland at the home range scale but hunting in dense thickets). Lions typically selected habitats with high prey abundance, both inside PAs and in the wider landscape (Table 2.1). In PAs, lions were often found to use habitats in close proximity to water (Table 2.1). However, in studies which considered distance to water across a mixed-use landscape, only 33% found an association with lion presence (Table 2.1). In response to anthropogenic variables, lions appeared to adapt their behaviour and habitat use. This occurred at both a land-use scale, with lions avoiding pastoral areas, increasing their use of closed habitats, and avoiding water when outside of PAs; and at a temporal scale, as lions exhibited increased avoidance of anthropogenic habitats during the day, when human activity was high (Appendix A6).

Table 2.1 Summary of environmental and anthropogenic variables related to habitat use of lions, *Panthera leo*, split by articles which were focused only on protected areas and those which considered multiple land-use types. Only variables measured in >2 articles are included in the table. Measures of habitat use included occupancy, density, and selection. See Appendix A6 for details of each article. *n* = the number of articles in which the variable was examined; *n* positive/negative = the number of articles that found a significant positive or negative association between the variable and lion habitat use; % = Percent of articles in which the variable was related to habitat use in some way, including positive/negative associations and more complex interactions; n/a = not applicable because the variable is categorical.

Variable	**Protected areas only (*n*=16)**				**Mixed land use (*n*=15)**			
	n	*n* positive	*n* negative	%	*n*	*n* positive	*n* negative	%
Environmental								
Habitat type	11	n/a	n/a	100%	6	n/a	n/a	67%
Distance to water	8	0	7	88%	9	1	3	33%
Prey abundance (density/biomass)	6	4	0	67%	3	2	0	67%
Elevation	3	0	2	67%	3	0	1	33%
Precipitation	2	1	0	50%	3	2	0	100%
Vegetation cover	4	1*	*	50%*	7	*	1*	29%*
Slope	3	0	1	33%	3	0	0	0%
Anthropogenic								
Land use	n/a	n/a	n/a	n/a	9	n/a	n/a	100%
Distance to settlements/buildings	3	*	*	33%*	11	3*	2*	64%*
Human density	1	0	0	0%	4	0	1	25%

*Often varied based on other factors

There was considerable variation in sample size between studies: some presented data for only four individual lions, while other long-term projects had data for as many as 84 lions (Appendix A6). However, these differences in sample size did not appear to be driving observed patterns.

We used the literature to construct a conceptual framework, presenting likely lion habitat preferences and links between the key components underpinning lion habitat use (Fig. 2.3). The most consistently observed habitat preferences were for areas of high prey abundance close to water. Land-use type was also important, with lions typically avoiding unprotected community lands used for agro-pastoralism and human settlement (Appendix A6). However, of other anthropogenic variables, only distance to settlements/buildings was examined frequently in the literature (Table 2.1), and there was considerable variation depending on season, time of day and lion behaviour. We identified data gaps for several other anthropogenic drivers which are likely to modify lion habitat use, but which were measured in only one or two studies (Fig. 2.3).

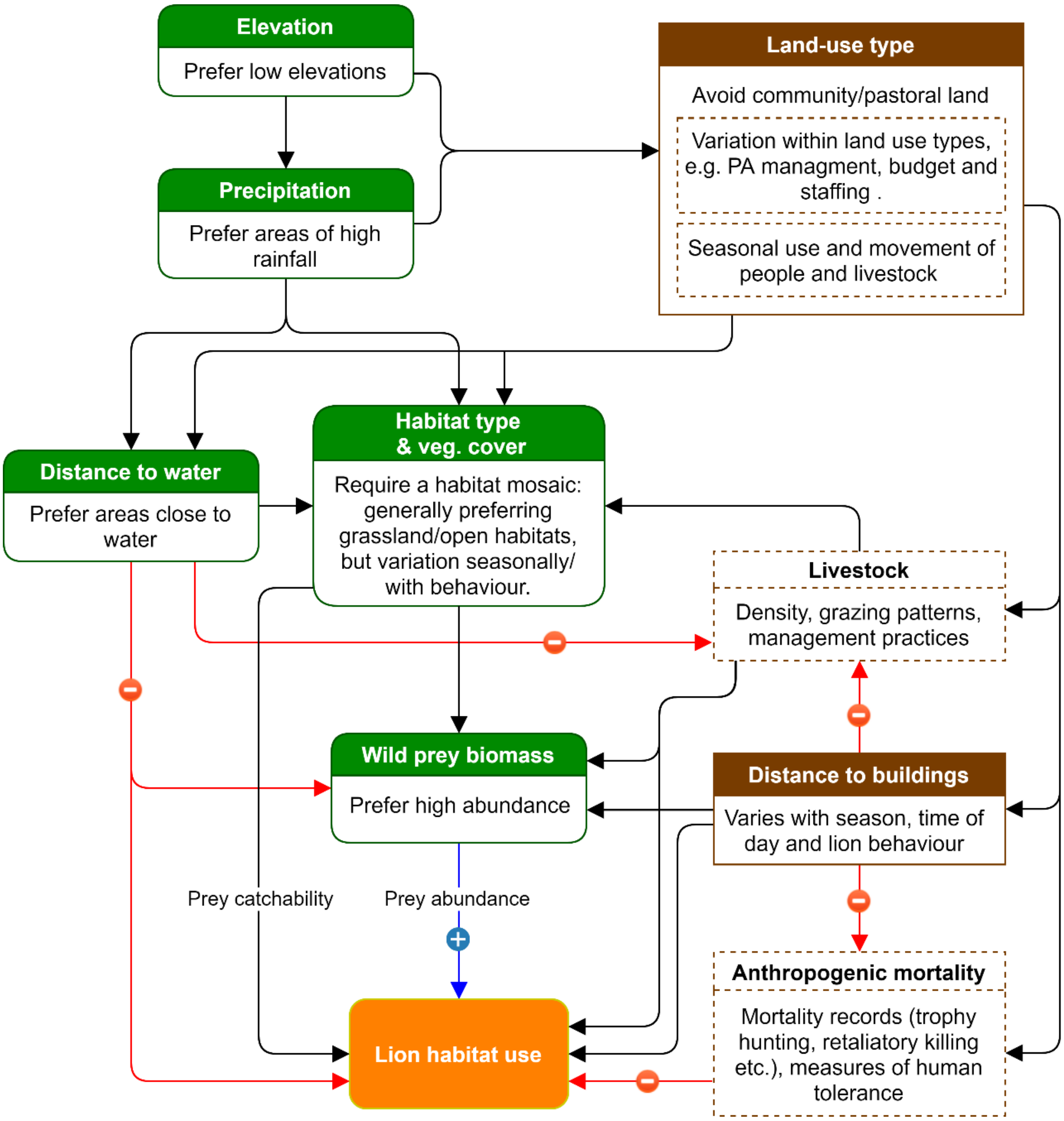


Figure 2.3 Conceptual framework of the direct and indirect pathways via which environmental and anthropogenic variables affect African lion habitat use. Boxes with rounded corners represent key environmental drivers and expected habitat preferences of lions when free of anthropogenic pressures. Boxes with straight edges show anthropogenic factors and pathways via which they may interact with environmental drivers and alter lion habitat use. Boxes with dashed outlines indicate factors which we expect to have an impact on habitat use but which were studied in ≤2 papers, highlighting knowledge gaps which should be the focus of future research. Arrows indicate directions of main effects, e.g., distance to water influences wild prey biomass. For key quantitative drivers where dominant effect directions could be hypothesised, arrows with a “-” symbol represent a negative association and arrows with a “+” represent a positive association. However, we highlight that these relationships may vary with context and that there is a hierarchy of drivers that are too complex to be captured fully in this framework. For example, some of these interactions may vary temporally or with lion behaviour.

2.4.3 Land use

Land use was grouped into three broad types: PAs, other managed areas, and unprotected areas (Fig. 2.4). Most study sites contained PAs (*n* = 120 articles), which included National Parks, National Reserves, and private game reserves; 38 articles had study sites that encompassed some form of wildlife-managed area (hunting zones, community land management areas, wildlife-friendly ranches, buffer zones adjacent to National Parks); and 32 articles (21%) included completely unprotected areas (community and village land, commercial ranches). Of the 154 articles, 29 included more than one land-use type. Of the 31 articles that documented evidence of habitat use, 29% (9 articles) had study sites that contained unprotected areas (Fig. 2.4; Appendix A6).

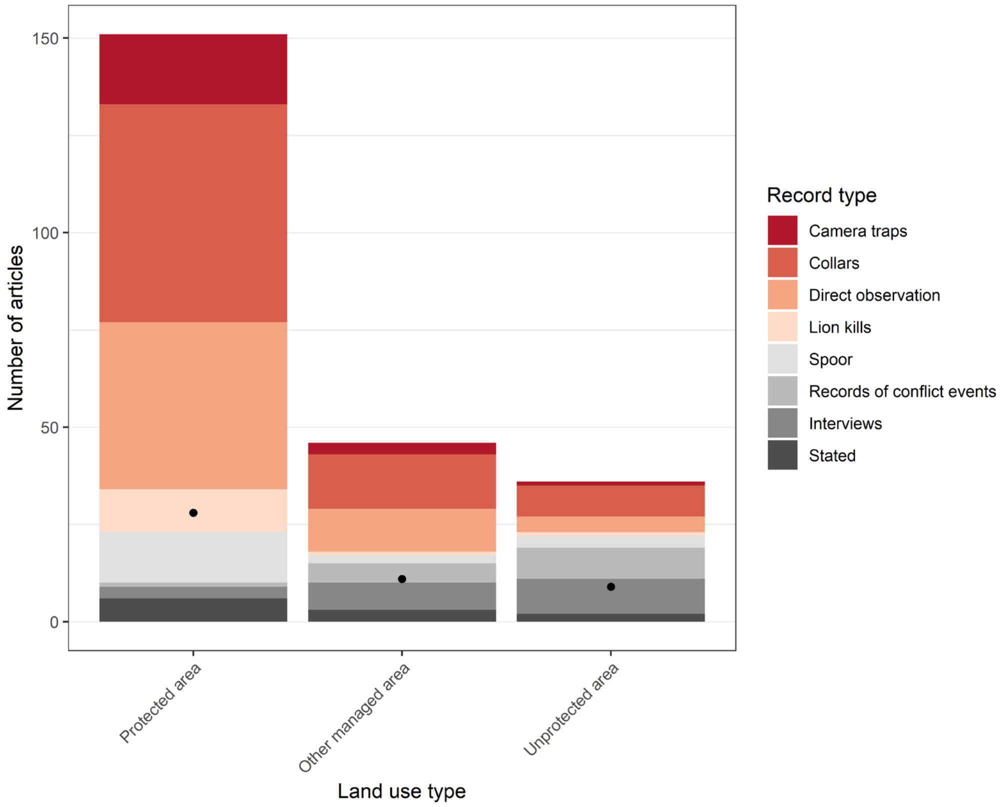


Figure 2.4 Number of articles studying African lions inside and outside protected areas, and the methods used to document lion presence. Articles are represented more than once if they included more than one land use or record type: in total, there are 233 data points. Black dots represent the number of articles that documented evidence of lion habitat use per land-use type (48 data points from 31 articles).

Studies inside PAs primarily used unambiguous detection methods to document lion presence, such as Global Positioning System collars, camera traps or direct observation of lions (Fig. 2.4). In contrast, outside PAs it was more common for researchers to use methods such as interviews (28% of articles that included unprotected areas) and records of conflict events, such as livestock depredations or attacks on humans (25% of articles that included unprotected areas; Fig. 2.4).

2.4.4 Spatial representativeness

Lions are believed to be resident in 25 African countries (Bauer et al. 2016). Around two thirds (*n* = 15) of these countries were represented in the relevant literature for this review. We also found three articles documenting lion presence in countries where lions are considered extinct or possibly extinct (Ghana and Gabon; Fig. 2.5). The majority of articles presented data from just four countries (Tanzania, Kenya, South Africa, and Zimbabwe; Fig. 2.5), which are also among the nine countries that are likely to still contain >1000 lions; the remaining being Botswana, Mozambique, Zambia, Central African Republic and possibly Angola (Riggio et al. 2013). Only 4.5% of articles included study sites representing the West and Central African region (Fig. 2.5). Of the 31 articles that provided data on habitat use, eight had study sites in Tanzania, eight in South Africa and seven in Zimbabwe (Fig. 2.5; Appendix A6).

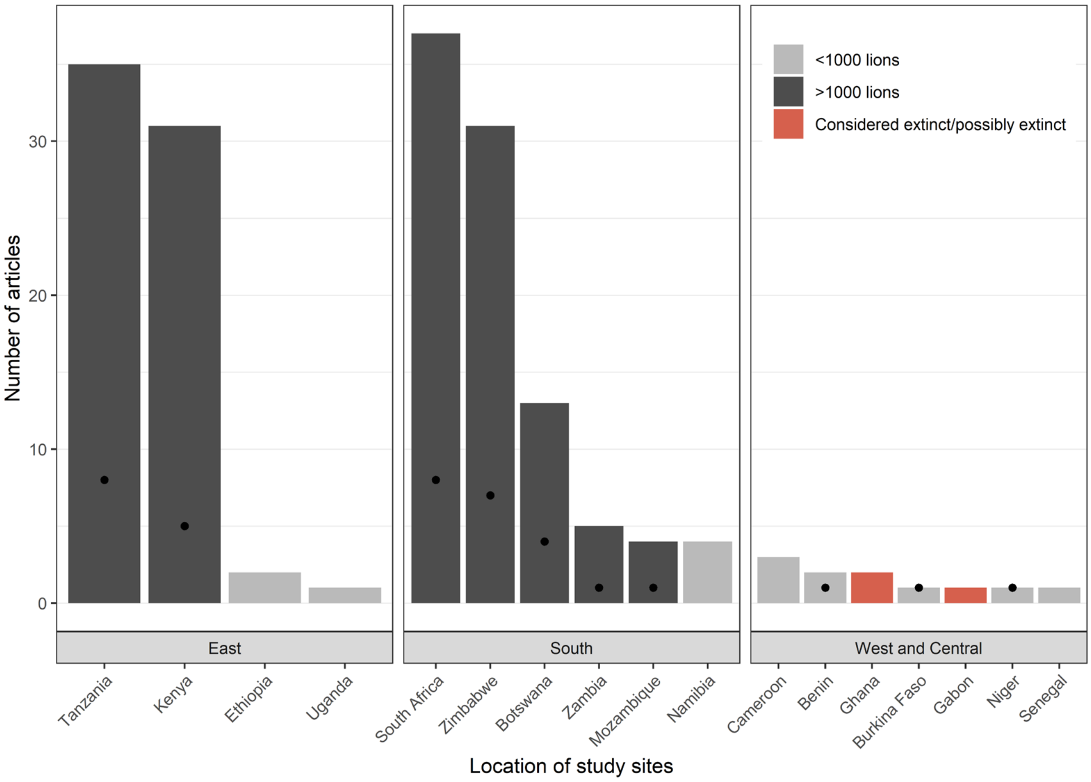


Figure 2.5 Locations of study sites in the 154 articles in the review, grouped by country and region of Africa. Colours indicate the estimated size of each country's African lion population. Articles with study sites spanning more than one country are represented more than once in the graph: in total, the 154 articles included 174 country data points. Black dots represent the number of articles documenting lion habitat use per country (37 data points from 31 articles).

With reference to specific study sites within countries, of the 128 study locations named in the 154 articles, the majority (n = 104) were represented just one or two times in the literature. Hwange National Park and surroundings, in Zimbabwe, and Serengeti National Park, in Tanzania, were notable exceptions, contributing 22 and 18 articles, respectively.

2.5 Discussion

2.5.1 Habitat use and drivers

Our findings, drawing from the 31 studies that documented evidence of habitat use, indicate that space use and habitat preferences of African lions are highly context and scale dependent, with prey abundance and proximity to water being consistent, prominent drivers. African lions, when free from anthropogenic pressures, appear to select open areas, such as grassland and open shrubland (Cristescu *et al.*, 2013; Courbin *et al.*, 2016), probably because these habitats support a higher abundance of their preferred prey species (Spong, 2002; Miller *et al.*, 2018). However, when engaged in certain behaviours, such as hunting or dispersal, lions may utilise habitats with increased vegetation cover (Hopcraft *et al.*, 2005; Davidson *et al.*, 2012; Elliot *et al.*, 2014b). The importance of varying levels of vegetation cover is supported by our finding that grassland was the most common habitat type present at study sites, but that the majority of locations contained some combination of open and closed habitats (Fig. 2.2).

Within PAs, proximity to water is a key driver of lion habitat selection (Valeix *et al.*, 2010; Davidson *et al.*, 2012; Abade *et al.*, 2014b). In arid and semi-arid landscapes, the distribution of herbivores is largely influenced by the availability of patchily distributed surface water. Lions, therefore, have a greater chance of encountering prey in areas around water sources (Valeix *et al.*, 2010). However, a negative relationship between lion habitat use and distance to water was less often observed in those studies which considered landscapes outside of PAs.

Anthropogenic pressures alter expected patterns of habitat use, probably due to their effect on feeding behaviour and mortality risk (Mogensen *et al.*, 2011; Loveridge *et al.*, 2017b). Compared to lions in areas of low anthropogenic pressure, lions on pastoral lands have been found to occur more frequently in closed habitats, consume prey inside bushes, abandon kills more often and avoid areas close to water (Mogensen *et al.*, 2011; Schuette *et al.*, 2013; Mkonyi *et al.*, 2018). Where natural prey is depleted due to hunting by humans, displacement by livestock or seasonal variation in prey abundance, lions may increase their proximity to humans in order to access livestock as secondary prey (Patterson *et al.*, 2004; Valeix *et al.*, 2012a). However, when doing so, they are likely to make temporal adjustments to their behaviour to avoid overlap with periods of high human activity (Valeix *et al.*, 2012a; Oriol-Cotterill *et al.*, 2015a).

The results of the studies based outside of PAs suggest that hypotheses for habitat use of lions in human-dominated landscapes could be framed around diurnal and seasonal shifts in behaviour to facilitate avoidance of people. To develop these hypotheses, future research should be focussed on temporal variation in habitat use, and researchers should consider a wider range of possible anthropogenic pressures to fill current knowledge and data gaps (Fig. 2.3).

The behavioural flexibility exhibited by lions may suggest that they have the potential to tolerate increasingly human-dominated environments. However, the use of refuge habitats when in proximity to humans is likely to result in a trade-off between nutritional intake and mortality risk (Oriol-Cotterill *et al.*, 2015b). The fitness consequences of using these sub-optimal habitats, abandoning kills, and being displaced from water sources are not yet understood. Indeed, only one study attempted to examine fitness-based measures of habitat quality, finding that lion reproductive success, productivity, and density were often positively correlated with proximity to river confluences and dry-season rainfall (Mosser and Packer, 2009).

2.5.2 Data gaps and sampling bias

Our work reveals a surprising lack of robust evidence on the species' use of habitats for large parts of its geographic range, and specifically for landscapes dominated by human activities. The majority of studies were located in only four countries and, furthermore, some locations within countries, such as Hwange National Park and Serengeti National Park, were distinctly overrepresented. In West and Central African counties, which have seen rapid human-driven changes in land use in the past decades (Mallon *et al.*, 2015), the lion is not only genetically distinct but also classified as Critically Endangered (Bertola *et al.*, 2011; Henschel *et al.*, 2014). However, only 4.5% of articles had study sites based in West and Central Africa, a knowledge gap previously highlighted by Henschel *et al.* (2014).

Thus, our understanding of lion ecology and habitat preferences is based on a few well-known case studies representing a fraction of the species' range. Using this evidence-base to develop conservation strategies should be approached with caution, as the literature unequivocally highlights the spatial and temporal complexity of lion-human-environment interactions. Collecting evidence from countries that represent the range of variation in this system should be prioritised in the coming years, in order to develop effective conservation interventions.

Studies were also predominantly conducted inside PAs. Although our Human Footprint Index analysis revealed that some areas of the lion range have yet to suffer severe human impacts, projections suggest a doubling of the human population in East, West, Central and Southern Africa by 2050 (UN, 2019) and a tripling of the extent of land converted to human use in Africa in the coming decades (Oakleaf *et al.*, 2015). This makes understanding the use of human-dominated landscapes by lions vital for effective conservation. It was therefore promising to see that, of the studies specifically focussed on habitat use, almost one third contained study sites which encompassed unprotected areas, at least as part of their methodological design.

The observed bias towards PAs may be driven in part by practical constraints on monitoring wildlife outside of PAs. Several articles note that lions in community land can be shy and difficult to locate (Mogensen *et al.*, 2011; Schuette *et al.*, 2013), and some researchers failed to detect any lions outside PAs despite their known presence there, as confirmed by conflict reports (Abade *et al.*, 2019). With the increasing use and development of Global Positioning System collars and camera traps, it may be that we see an increase in studies focussed outside of PAs. Indeed, of the nine habitat-use studies that considered land outside of protected or managed areas, five were published in 2018 or 2019.

However, even within the studies which considered multiple land-use types, the scope of the anthropogenic variables considered was often limited. Most studies were focussed on distance to human structures, using this to infer levels of risk rather than records of actual lion mortality (Loveridge *et al.*, 2017b). Furthermore, while most studies consider static land-use types (e.g. PA, community land), lions may respond at finer scales to differences in land management, such as changing numbers of patrol staff (Henschel *et al.*, 2016) and seasonal movement of people and livestock (Schuette *et al.*, 2013). Measures of livestock abundance and distribution were rarely considered, representing a significant data gap in the literature on lion habitat use. One study that did measure livestock presence found a negative association between lion occupancy and the presence of cattle (Everatt *et al.*, 2019).

2.5.3 The challenge of defining habitats

Terms used to describe habitat types are used inconsistently in the literature, complicating our attempt to standardise habitats across studies and scale up to the wider lion range. Savanna, for example, is described in one study as an area “dominated by bushlands” (Courbin *et al.*, 2016) and in another as “dominated by perennial grasses” (O'Brien *et al.*, 2018). While savanna is considered a distinct habitat type characterised by continuous grass cover and widely spaced trees and shrubs (IUCN, 2018b), it can encompass a broad spectrum of woody cover transitional between grassland and forest (Sankaran *et al.*, 2004; Parr *et al.*, 2014), making it inherently difficult to define.

Some studies describe habitat using maps created from ground surveys of vegetation composition, soil type, geology, and topography (Davidson *et al.*, 2012; Millspaugh *et al.*, 2015). Others use maps derived from Earth observation products (Elliot *et al.*, 2014b; Mkonyi *et al.*, 2018), with land-cover categories and map accuracy differing between products. This can introduce considerable confusion and result in a mismatch between the definitions of habitat classes depending on the product used (Giri *et al.*, 2005).

2.5.4 Future directions of research

We recommend that future studies of lion habitat use aim to address existing biases by directing research towards less well-studied countries, focussing on landscapes outside of PAs and measuring a wider range of anthropogenic pressures. Our conceptual framework illustrates the key factors that should be considered when assessing habitat suitability for lions. Montgomery *et al.* (2018a) posit that there are five dimensions which determine patterns of human-lion conflict: the lion, the wild prey, the environment, the human and the livestock. We suggest that these dimensions should also be considered when examining lion habitat use in human-dominated landscapes. At present, there is a significant gap in the literature with regard to the livestock dimension, as well as only limited consideration of human variables, the main focus being on distance to buildings. Our framework can be used as a starting point to guide future research towards filling these data gaps and disentangling the complex interplay of variables affecting lion habitat use (Fig. 2.3).

It is also important to consider habitat definitions and improve clarity on how these are categorised and mapped. The Land Cover Classification System developed by the Food and Agriculture Organization and the IUCN Habitat Classification Scheme aim to address this problem by providing a standardised system that can be used globally and would allow for comparable research and sampling designs (Di Gregorio and Jansen, 2000; IUCN, 2018b). However, authors of landscape ecology studies have also called for a move away from categorical land-cover descriptors, towards metrics that represent continuous environmental gradients in resource quality and availability (Manning *et al.*, 2004; Fischer and Lindenmayer, 2006). We lend further support to this move, highlighting that Earth observation increasingly allows us to study relevant habitat metrics, such as vegetation structure and productivity, at fine spatial resolutions (Coops and Wulder, 2019; Oeser *et al.*, 2020).

Our results highlight that many environmental factors drive lion habitat use via their relationship with prey abundance. We suggest directing research towards understanding the habitat preferences of primary prey species across a gradient of anthropogenic pressure. Given that lions are frequently found in habitat mosaics that include grassland, and that the preferred prey species of lion are water-dependent grazers (Hayward and Kerley, 2005), managing pressures on grassland habitats is likely to be fundamental for protecting prey populations.

We also encourage a more targeted approach to monitoring lions in relation to water sources. Displacement of wildlife at water sources and competition with livestock for water and forage affects wild herbivore abundance and distribution (Ogutu *et al.*, 2014). Managing water points outside of PAs to provide safe access for both people and wildlife may be a way of increasing landscape suitability for wild prey species and, therefore, lions. Water availability will become an increasingly important issue for both wildlife conservation and human well-being as climate and land-use change affect rainfall, surface water supply and vegetation productivity throughout Africa (de Wit and Stankiewicz, 2006; Ogutu *et al.*, 2008).

2.5.5 Conclusions

The IUCN Guidelines for the Conservation of Lions state that a key objective is “to conserve current lion habitat and prey base” (IUCN, 2018a). However, without clearly defined targets for the habitat features required by lions, there is little guidance for how to manage landscapes and develop effective intervention measures. Our review reveals a relatively infrequent focus on habitat use amid the extensive catalogue of lion research. The studies that are focussed on habitat use show that under optimal conditions of low anthropogenic pressure and high prey abundance, lions select for open grassland habitats and areas near water. However, lions demonstrate a high degree of flexibility, and can adapt their habitat use to improve their security and prey catchability. To target conservation interventions effectively and predict how lions will adapt to changing landscapes, future research should strive for detailed analysis of factors such as distance to water, prey abundance and anthropogenic risk, in order to determine what makes good lion habitat.

Chapter 3. Using landscape characteristics to predict livestock depredation risk by African lions (*Panthera leo*) in the Ruaha landscape of Tanzania

Goats inside a traditional thornbush boma near Kitisi village, Ruaha, Tanzania.

3.1 Abstract

1. Carnivore depredation of livestock is a global conservation concern, having significant negative impacts on human well-being and contributing to carnivore declines. To manage these impacts effectively and promote coexistence requires robust understanding of where and why depredations happen.
2. Here, we study spatial patterns of livestock depredation by the African lion (*Panthera leo*) in the Ruaha landscape of Tanzania, a high priority region for carnivore conservation. We use Linear Discriminant Analysis and Integrated Nested Laplace Approximation to quantify the ecological and anthropogenic landscape features associated with recorded lion attacks on corralled and grazing livestock.
3. Risk of depredation on grazing livestock was high close to the protected area, near rivers and in areas of higher net primary productivity (NPP) and lower tree cover. For enclosed livestock, while depredation risk was also influenced by high NPP and low tree cover, anthropogenic drivers were important, with high risk in areas further from villages with a low human population count.
4. We used our results to predictively map depredation risk across our study area. The final models mapped between 26 - 39% of the landscape as being high risk for grazing livestock, and 61 - 69% as being high risk for enclosed livestock.
5. *Synthesis and applications.* We provide evidence that lion attacks on livestock may follow predictable patterns in space. Predictive maps offer an easily interpretable method to visualise risk distribution and can be used to target mitigation strategies in areas where attacks have a high likelihood of occurrence. Understanding spatial variation in depredation risk could improve stakeholders' ability to develop management interventions which foster human-carnivore coexistence.

3.2 Introduction

Throughout the world, anthropogenic impacts on ecosystems are accelerating (Steffen *et al.*, 2015), resulting in the loss, modification and fragmentation of natural habitats and increased exposure of wildlife to edge effects (Foley *et al.*, 2005; Haddad *et al.*, 2015). Consequently, people and wildlife are coming into increasing contact, often provoking widespread human-wildlife conflict (Woodroffe *et al.*, 2005; Nyhus, 2016). Large species have substantial resource requirements which can only be met by roaming across large areas (Lindstedt *et al.*, 1986; Kelt and Van Vuren, 2001), rendering them likely to encounter humans. Where interactions occur, these species, including apex predators such as the African lion (*Panthera* *leo*), can pose a severe threat to human life and livelihoods (Packer *et al.*, 2005a; Kissui, 2008). Depredation of livestock by large carnivores can impose considerable economic costs on households (Mkonyi *et al.*, 2017c; Khadija *et al.*, 2021). Other impacts such as mental health issues and opportunity costs due to movement restriction or the need for increased guarding, often undertaken by children and leading to poor school attendance, are less well understood (Barua *et al.*, 2013; Dickman and Hazzah, 2016).

The African lion exemplifies the challenge of conserving a top predator and managing negative impacts to protect both people and wildlife. Lions are a conservation flagship species with important ecological, cultural, and economic value (Goldman *et al.*, 2010; Di Minin *et al.*, 2013; Ripple *et al.*, 2014; Stolton and Dudley, 2019). However, approximately 44% of their remaining range lies outside of protected areas (Lindsey *et al.*, 2017b), bringing them into frequent contact with human communities (Di Minin *et al.*, 2021). Livestock depredation is widespread, with lions typically targeting culturally and economically valuable cattle (Broekhuis *et al.*, 2017; Muriuki *et al.*, 2017). Thus, while the benefits of lion conservation are perceived across multiple stakeholder groups, the costs are experienced only by those communities who live alongside them (Redpath *et al.*, 2017).

Livestock depredation reduces local tolerance for carnivore presence and can lead to pre-emptive and retaliatory killing of wildlife (Dickman *et al.*, 2014). Several non-lethal mitigation options have been developed to attempt to alleviate human-carnivore conflict. These include financial incentives to promote coexistence (Zabel and Engel, 2010; Dickman *et al.*, 2011), technical interventions to protect livestock, such as physical barriers and visual and auditory scaring devices (Lichtenfeld *et al.*, 2014; Lesilau *et al.*, 2018), and other livestock management strategies such as the use of guarding animals and changes to herd and pasture sizes (Miller *et al.*, 2016b). Finding effective mitigation techniques and developing collaborative approaches to encourage coexistence is vital, as retaliatory killing in response to realised or perceived negative impacts of lions on communities is a key driver of lion declines in human-modified landscapes (Dickman *et al.*, 2014; Bauer *et al.*, 2016). However, shifting to alternative mitigation strategies is challenging and can be expensive to implement (Dickman *et al.*, 2011; Mkonyi *et al.*, 2017a; van Eeden *et al.*, 2018a).

Understanding drivers of spatial variation in depredation risk across landscapes could significantly improve our ability to manage human-carnivore conflict effectively, using targeted interventions, thus potentially reducing costs for local conservation efforts. Spatial risk modelling is one approach that can be used to identify habitat attributes that are associated with carnivore attack sites and to delineate ‘conflict hotspots’, priority areas at high risk of a depredation event (Miller, 2015). The resulting risk maps can then be used to guide conflict mitigation by targeting assistance towards households in priority areas, allowing stakeholders to recognise distributions of risk in their landscape, and monitoring the efficacy of mitigation strategies (Abade *et al.*, 2014a; Miller, 2015).

Broadly, there are five dimensions which contribute to spatio-temporal patterns and intensity of human-lion conflict (Montgomery *et al.*, 2018a): the lion, the wild prey, the environment, the livestock, and the human. These dimensions are all interlinked, for example: human land use affects habitat types and livestock densities which influence the behaviour and distribution of wild prey, thereby affecting lion habitat use (Sargent *et al.*, 2022). While it is often difficult to obtain data on all five dimensions of the system, ecogeographical variables may be used as a proxy for prey presence and have been used in several studies to map the probability of livestock depredation (Abade *et al.*, 2014b; Broekhuis *et al.*, 2017; Mpakairi *et al.*, 2018). The way these proxy variables affect depredation risk may differ based on whether livestock are grazing in the bush or corralled inside an enclosure (Abade *et al.*, 2014a; Loveridge *et al.*, 2017a).

To identify areas of risk, landscapes can be divided into points where lion attacks occur and those where they do not. If we find distinguishing characteristics of the two classes of point, then we can discriminate between them. Linear Discriminant Analysis (LDA) is a method of classifying objects into sets of mutually exclusive categories based on a set of independent variables (Morrison, 1969; Williams, 1983). However, LDA assumes that each event and the associated covariates are independent of each other. Since lions exhibit behaviourally grounded hunting strategies (Hopcraft *et al.*, 2005; Valeix *et al.*, 2011), and people and livestock may demonstrate predictable patterns in space use (Valeix *et al.*, 2012a; Schuette *et al.*, 2013), then there is likely to be spatial dependence between points. An alternative approach, Integrated Nested Laplace Approximation (INLA), provides a simple method for computing hierarchical models that include a component that reflects spatial correlation between events (Rue *et al.*, 2009).

Here, we focus on the African lion and use Linear Discriminant Analysis (LDA) under the assumption of independence of events, test for spatial dependence and use the Stochastic Partial Differential Equation approach (INLA-SPDE), to investigate key drivers of livestock depredation risk in the Ruaha landscape of Tanzania. Previous work in this landscape utilised species distribution modelling to develop a depredation risk map and identified proximity to rivers, elevation, and tree cover as key factors affecting livestock depredation risk (Abade *et al.*, 2014). However, the modelling methods used did not include a spatial correlation component. Furthermore, this study conducted a collective analysis of depredation events without identification of the predator species responsible (Abade *et al.*, 2014). Targeting management and mitigation based on this approach may not be appropriate as key carnivore species present in this landscape (e.g., leopard, lion, and hyena) differ profoundly in their habitat use and hunting strategies (Balme *et al.*, 2007; Cozzi *et al.*, 2013; Searle *et al.*, 2021b).

In this study, we first identify the ecological and anthropogenic landscape features associated with lion attacks on livestock and how these differ for grazing vs corralled livestock. Second, we use the derived models to develop risk maps identifying lion conflict hotspots in the Ruaha landscape and compare the results generated by the two statistical approaches. Finally, we discuss possible management actions for these high-risk areas and the applicability of this approach for guiding mitigation strategies in landscapes where human-carnivore conflict poses a significant threat to lion populations and human well-being.

3.3 Methods

3.3.1 Study area

The study area is located in the Ruaha-Rungwa region of south-central Tanzania. The landscape includes the Ruaha National Park (RNP), spanning over 20,000 km^2, and the Pawaga-Idodi Wildlife Management Area (WMA), an area of land set aside by local villages as part of a national scheme aimed at generating revenue via both consumptive and non-consumptive use of wildlife (Keane et al. 2020; Fig. 3.1). The study was focussed on the adjoining village land, part of the Iringa District, located to the south-east of the WMA and RNP (Fig. 3.1).

The climate in the region is semi-arid to arid, with an average annual rainfall of ~ 600mm which falls almost exclusively during a single wet season from December to April (Mtahiko *et al.*, 2006; Searle *et al.*, 2021a). Vegetation cover is a mosaic of miombo woodland, semi-arid savanna and *Acacia-Commiphora* bushland and thickets (Hardouin *et al.*, 2021), with village lands containing cropland (primarily rice and maize fields) and livestock grazing areas (Abade *et al.*, 2019). The RNP and the WMA are unfenced, meaning that wildlife can move freely across the area (Fig. 3.1). The Ruaha-Rungwa landscape is considered to be a high priority region for carnivore conservation, containing significant populations of cheetah, wild dog, and leopard (IUCN, 2007; Searle *et al.*, 2021a; Strampelli *et al.*, 2021), and home to an estimated 3779 lions, representing one of four lion strongholds in East Africa (Riggio *et al.*, 2013).

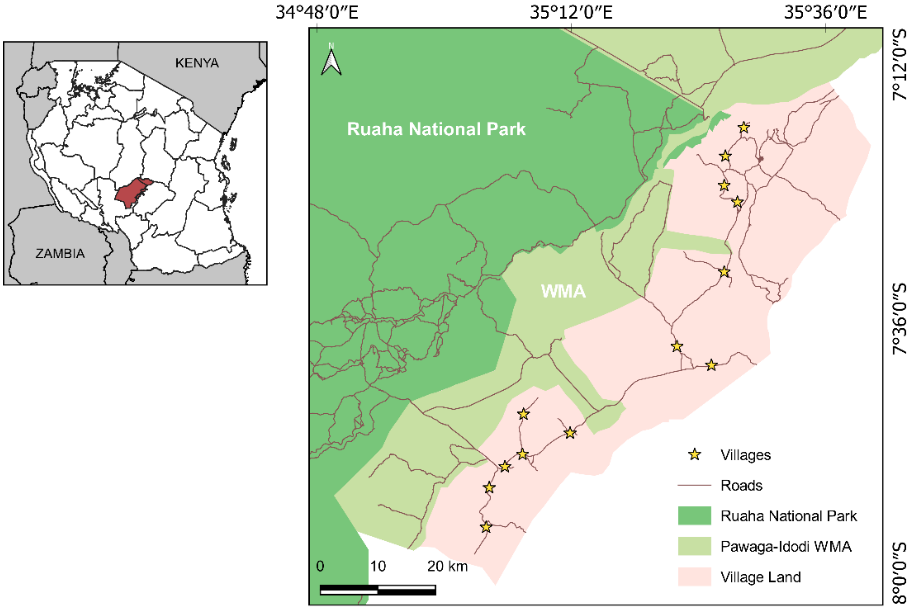


Figure 3.1 Maps highlighting the location of Ruaha National Park in Tanzania (left) and the study area located within the village land adjacent to the protected areas (right).

The village land is inhabited by over 60,000 people from at least 30 different ethnic groups, with livelihoods predominated by agriculture and pastoralism (Abade *et al.*, 2019). During the day, livestock herds, comprised of small-stock and cattle, graze across the village land reportedly under the surveillance of herders and untrained guarding dogs (Abade *et al.*, 2014a). At night, herds are typically contained in enclosures called bomas, made predominantly from thorn bushes. The use of alternative methods of livestock protection such as lights, horns or fire is rare in this area (Abade *et al.*, 2014a). Although depredation accounts for a relatively small percentage of total stock loss, experience of depredation is widespread and generates intense hostility (Dickman *et al.*, 2014). Consequently, lions in this landscape have experienced high-levels of human-induced mortality due to retaliatory and preventative killing (Dickman *et al.*, 2014; Abade *et al.*, 2019), with 27 lion hunts taking place in 2019, in response to attacks on people and livestock (A. Grau 2020, pers. comms.).

3.3.2 Depredation data

Georeferenced depredation locations were collected between 2010 and 2017 by the Ruaha Carnivore Project (RCP), a research organisation established in the region in 2009. RCP conflict officers regularly monitor bomas across the landscape, with monthly visits to collect information on livestock losses, as well as responding directly to depredation events when they occur. When RCP staff visit a depredation site various information is collected including:

the GPS location, number of animals killed/injured, the carnivore species responsible and whether the attack occurred on enclosed livestock (‘boma events’) or on grazing livestock (‘bush events’). From this database, we extracted those attacks which livestock owners and/or conflict officers attributed to lions, including events where livestock were killed and/or merely injured. While we accept that there may be some incidences where attacks were wrongly attributed and another predator species was responsible, in the majority of cases (78%) the livestock owners claimed to have witnessed the attack. Of those that did not, 60% of incidents were verified by conflict officers based on signs such as spoor, and bite and claw marks on carcasses. We removed 23 data points where livestock owners believed the attack to have been caused by a lion but did not directly witness it, and it could not be verified by conflict officers. This resulted in a final dataset including 119 boma depredation points and 103 bush depredation points.

In 2017, RCP completed a boma mapping exercise which collected GPS locations of monitored bomas (N = 521) across the landscape. Each of these bomas is visited by RCP staff on a monthly basis and details of all livestock losses, whether due to depredation, disease, theft, or other reasons, are recorded. Based on this boma map, the database of depredation events, and the monthly monitoring data we were able to extract the locations of bomas which had never reported any losses due to depredation. We included bomas which had never reported an attack by any carnivore, regardless of species. We hope to have, therefore, avoided any ‘false absences’ where attacks may have been caused by lions but were attributed to another species, or where conflict officers were uncertain which predator species was responsible. We identified 108 households which had never experienced a carnivore attack during the study period and these bomas were used as absence points for our conflict modelling exercise.

To generate pseudo-absence points for bush attacks we used a shapefile provided by RCP which covers the Pawaga-Idodi village land monitored by the project. We generated a slope layer using the ‘Slope’ function in QGIS v3.16.5, based on elevation data from the Shuttle Radar Topographic Mission (SRTM 2013). Based on the methods used to delineate suitable areas for livestock by the Gridded Livestock of the World database (Robinson *et al.*, 2014), we excluded sections of the landscape which had slopes of > 40%, assuming that livestock was unlikely to be grazed on steep slopes. We further excluded crop fields and village centres, as identified via Google Earth satellite imagery. In the remaining area we used the ‘Random Points Inside Polygons’ tool to drop 100 random points which could be used as absences for bush depredation events, with the condition that they did not fall within 500m of any depredation sites. Although we do not have data on livestock distributions, observations on the ground reveal that stock is grazed across the majority of the village land. We therefore believe that the generated pseudo-absences should be largely drawn from truly grazed areas.

In summary, the data comprised 119 presence and 108 absence points for boma depredations, and 103 presence and 100 absence points for bush depredations. Bush attacks and boma attacks were analysed independently of each other at each stage of the analysis due to the likelihood that key drivers will differ depending on whether livestock are grazing or corralled (Abade *et al.*, 2014a; Loveridge *et al.*, 2017a).

3.3.3 Predictor variables

We collated a suite of putative explanatory variables that we hypothesised may affect the distribution of depredation events. Explanatory variables were selected based on their potential influence on lion habitat use and human-lion conflict (Montgomery *et al.*, 2018a; Sargent *et al.*, 2022) and included both environmental and anthropogenic factors (Table 3.1). Prey availability has previously been shown to be a key driver of lion habitat use (Abade *et al.*, 2019; Sargent *et al.*, 2022), however data on wild prey and livestock distributions and densities were unavailable at resolutions relevant to our study landscape. Several studies have demonstrated robust scaling laws for consumer-producer relationships based on energy availability and primary productivity (Coe *et al.*, 1976; Pettorelli *et al.*, 2009; Hatton *et al.*, 2015; Fløjgaard *et al.*, 2021). In particular in African ecosystems, large herbivore biomass has been found to correlate with ecosystem productivity (Fløjgaard *et al.*, 2021). We therefore used the MODIS (MOD17A) Net Primary Productivity (NPP) product as a proxy for prey abundance.

Where products provided data on an annual basis (Table 3.1: NPP, Tree cover, Human population count), values were extracted for the year of the depredation event. For absence points, data was extracted for the year 2017. Examination of the change in NPP, tree cover and human population count between 2010 - 2017 for a random sample of absence points, revealed that there was little variation across years and no consistent trends over time. We therefore do not believe that using the 2017 products for these points will introduce any substantial bias to the results.

To obtain ‘distance to’ various landscape features, shapefiles of rivers, villages, roads, and protected areas (data sources listed in Table 3.1) were converted to 10 x 10 m rasters using QGIS and the ‘Proximity’ tool was used to create a raster indicating the distance to each feature. All spatial data preparation and extraction on to the depredation points was conducted in QGIS v3.16.1. Elevation was excluded from our analysis as Pearson's correlations indicated that it was strongly correlated with both rainfall ($r = 0.87$) and NPP ($r = 0.7$). No other predictors had $r \geq 0.7$ in pair-wise comparisons.

Table 3.1 Variables included in INLA-SPDE and LDA models to identify landscape attributes associated with depredation events

Explanatory variable	Source	Resolution
Mean annual precipitation (mm)	Worldclim v2. (www.worldclim.org/data)	30 arc seconds (~1km)
Annual net primary productivity (kgC/m^2/year)	MODIS: MOD17A3HGF Net Primary Productivity (https://lpdaac.usgs.gov/products/mod17a3hgfv006/)	500m
Tree cover (%)	MODIS: MOD44B Vegetation Continuous Fields (https://lpdaac.usgs.gov/products/mod44bv006/)	250m
Human population count	WorldPop UN-adjusted population counts (worldpop.org)	100m
Distance to protected area (m)	World Database on Protected Areas (https://www.protectedplanet.net)	10m
Distance to rivers (m)	Open Street Map, plus further digitising using Google Earth (https://www.openstreetmap.org)	10m
Distance to roads (m)	Open Street Map, plus further digitising using Google Earth (https://www.openstreetmap.org)	10m
Distance to villages (m)	Digitised villages using Google Earth	10m

3.3.4 Data analysis

3.3.4.1 Predicting depredation without spatial autocorrelation

First, forward stepwise selection was used to reduce our variable set using the *greedy.wilks* function of the *klaR* package (Weihs *et al.*, 2005). Beginning with a preliminary model that best separates the groups, this approach then uses the Wilk's lambda criterion (Mardia *et al.*, 1979) to select which new variables should be included in a simplified model. Wilk's lambda (Λ) is a direct measure of the proportion of variance in the dependent variable that is unaccounted for by the independent variable. The scale ranges from 0 to 1, where 1 indicates that no variance is accounted for. If a large proportion of the variance is accounted for by the independent variable, then it suggests that there is an effect and that the groups (in this case the attack and non-attack locations) have different mean values. The *greedy.wilks* function starts with the predictor variable which has the smallest Λ value and adds further variables in order of increasing Λ (Weihs *et al.* 2005). The significance of the change in Λ is measured with an F-test. When a variable is added to the model and the p-value remains statistically significant then the variable is retained. The process is complete when addition of new variables does not improve the model, or when model accuracy reaches 100% (Mardia *et al.*, 1979). Variables retained in the model were significant in separating attack and non-attack events.

Second, we implemented Linear Discriminant Analysis (LDA) on the retained set of predictor variables using the *lda* function in the *MASS* package (Venables and Ripley, 2002). LDA finds linear combinations of features that best separate groups by seeking to maximise the ratio of inter-group to intra-group variance (Williams, 1983). The model generates a set of parameters which can be used to transform the measured variables into a discriminant function which can classify new data into lion attack versus non-attack events, given measures of the relevant predictor variables. The analysis provides a classification function that determines which group an event or location belongs to, based on the values of *n* predictor variables:

$$D_i = c_1 X_{1i} + c_2 X_{2i} + \cdots + c_n X_{ni}$$

where X_{ji} is the i^{th} value of predictor variable j, c_j is the discriminant coefficient for the variable j, and D_i is the overall discriminant score which predicts membership of attack or non-attack groups.

We used a bootstrapping procedure to ensure results were robust and to prevent overfitting. For this we randomly selected 90% of the data and ran the LDA with this subset. We used the resulting discriminant function to reclassify the data into attack and non-attack events using the *predict* function and calculated the error rate of the model (the proportion of cases incorrectly assigned to attack and non-attack groups). Model performance was evaluated by calculating the area under the curve (AUC) of a receiver operating characteristic. AUC values range from 0 to 1 where at 0 no events are correctly classified and at 1 all events are correctly classified. In general, a value of 0.7-0.8 is considered to be acceptable and >0.8 is considered excellent (Hosmer Jr *et al.*, 2013). We repeated this process 500 times, randomly sampling 90% of the data each time, and then calculated the mean error rate, AUC, and coefficients of linear discriminants. LDA assumes multivariate normality in the variables, so analyses were repeated with square root transformed data, since several of the predictor variables had skewed distributions.

To create a map of areas at high risk of a depredation event, raster layers of the retained predictor variables were resampled, using the *raster* package (Hijmans, 2020), to a 250 m resolution. Where variables were mapped on an annual basis (Table 3.1: NPP, Tree cover, Human population count), we built our predictions using the 2020 data. Values were extracted from the rasters and were used alongside the mean coefficients of linear discriminants in the *predict* function to calculate the probability of a lion attack occurring in each cell of the landscape. The predicted posterior probability of an attack occurring ranges between 0-1, with higher values indicating that the cell is more at risk. To delineate conflict hotspots, we split the predictive map into 3 categories: low risk (< 0.33), medium risk (0.33 - 0.66), and high risk (> 0.66). All analyses were conducted in R version 4.1.0 (R Core Team, 2021).

3.3.4.2 Testing for spatial dependence in depredation events

The analysis of spatial data is complicated by the potential for spatial autocorrelation. This occurs when values of a variable sampled close to each are more similar than those further apart, causing non-independence of the dependent variable (Dormann *et al.*, 2007). If patterns in depredation of livestock are spatially autocorrelated the number of lion attacks will exhibit clustering at close distances (Hoffmann *et al.*, 2019). The presence of such non-independence can bias parameter estimates and lead to an increase in type 1 errors due to a reduction in degrees of freedom (Dormann *et al.*, 2007; Legendre and Legendre, 2012). If clustering patterns are revealed, further analysis is required to control for spatial autocorrelation (Miller, 2015).

K function analysis is a method to assess spatial clustering by estimating the proximity of events to each other and comparing observed counts of attacks to those that would occur by chance (Ripley, 1976). We used a modified $\hat{k}$ function routine in the *splancs* package to calculate a measure of the expected number of attack events within a given distance of an arbitrary event (Rowlingson and Diggle, 2021). Typically, *K* function analysis compares the clustering of events to those that might occur with complete spatial randomness. However, given that livestock bomas are not randomly distributed, we used the known distribution of all monitored bomas and bush events/absences to draw random samples that represented possible locations where no attacks occurred.

We compared the estimated *K* function of boma and bush depredation events over a range of distances (1 - 40 km) with that obtained from 100 random draws of an equivalent sample size from all the known bush and boma locations. We then assessed the significance of clustering by observing whether the observed *K* values lay outside the 95% confidence intervals derived for the simulated maximum and minimum *K* values obtained from the random sample of locations.

3.3.4.3 Predicting depredation with spatial autocorrelation

Next, we employed a Bayesian modelling approach using Integrated Nested Laplace Approximation (INLA) to compute hierarchical models that included a spatial component. This method assumes that the risk of an event is a smoothly varying surface over which we have occasional measures of real events at specific points. The use of stochastic partial differential equations (SPDE) allows fast computation of the Matérn correlation across a Gaussian Random Field through the creation of a Delauney triangulation mesh (Lindgren *et al.*, 2011; see Appendix B1 for further details).

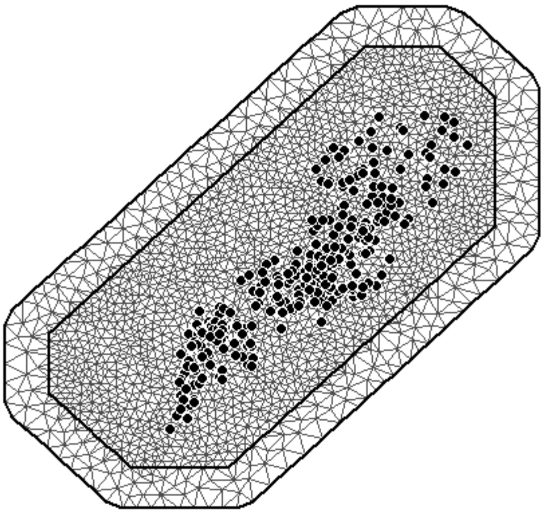


Figure 3.2 Delauney triangulation mesh of the study area on which the values of the spatial model were defined. Points indicate all attack and non-attack data points. The mesh is extended beyond the sampling area in order to avoid edge effects, an inflation of variance at the boundaries of the space (Lindgren *et al.* 2011).

The Delauney triangulation mesh is a method of dividing the study extent into triangles such that the vertices of the triangles pass through the sampling points (Fig. 3.2). The mesh creates a subset of regions on which to calculate the values of the model and allows for discretization of space to identify which points have neighbours. This enables a calculation of spatial autocorrelation, represented as a residual error which can be attributed to location and may reflect an unmeasured predictor which varies through space (Myer *et al.*, 2020). More detailed technical explanations of INLA-SPDE and its application in ecological modelling can be found elsewhere (Carson and Mills Flemming, 2014; Lindgren and Rue, 2015; Bakka *et al.*, 2018; Bersacola *et al.*, 2021). Models were run using the R package, *R-INLA* (Rue *et al.*, 2009).

Following creation of the mesh, the response variable, presence (1) or absence (0) of a lion attack, was modelled using a binomial logistic model with a continuous-space random-field:

$$logit(y_s) = \beta_1 X_1 + \cdots + \beta_n X_n + u_s$$

where y_s represents the odds of an attack event at location s, β_1 ... β_n are the n regression coefficients, X_1 ... X_n are the n predictor variables, and u_s is the value of the spatial random effect at location *s*. *Logit* is the logarithm of the odds in favour of an event, also referred to as log odds.

As we had no prior information regarding the expected distribution and magnitude of the effects and spatial correlation, non-informative default priors were used throughout. Model selection was implemented using backward-stepwise removal of non-significant variables to identify the model with the lowest deviance information criteria (DIC). When similar DIC values were observed (a difference of < 2), the simpler model was selected. The predictive power of the covariates was determined based on the 95% credible interval of the marginal posterior probability distribution not overlapping zero.

Following the example of Blangiardo *et al.* (2013), performance of the final model was assessed via holdout cross validation, with the data split into two parts: 75% of the data was randomly selected for training and the remaining 25% was held back for testing. The model was then created using the training dataset and validated using the test data. We extracted the mean posterior predictions for the testing dataset and predictive power was examined by calculating the Area Under Curve (AUC). Holdout validation was repeated 100 times using the final model to obtain a mean AUC and 95% confidence intervals. We used the final models to predict the mean posterior probability of bush and boma attacks across the whole spatial domain using continuous rasterised maps of the relevant environmental predictors.

3.4 Results

3.4.1 Predicting depredation without spatial autocorrelation (LDA)

3.4.1.1 Bush attacks

Six predictor variables were retained in the final model used in the LDA (Table 3.2). Attack and non-attack events were best distinguished by distance to protected area (PA), followed by distance to rivers and human population count (Table 3.2).

Table 3.2 Wilk's lambda and discriminating ability of variables at each stage of forward stepwise variable selection for bush attacks. Variables retained show significance in separating attack and non-attack events.

Variable	Wilk's lambda	F	p-value	F difference	p difference
Distance to PA	0.904	21.427	p<0.001	21.427	p<0.001
Distance to Rivers	0.858	16.489	p<0.001	10.535	p<0.01
Population Count	0.814	15.152	p<0.001	10.852	p<0.01
Tree Cover	0.784	13.642	p<0.001	7.603	p<0.01
NPP	0.746	13.434	p<0.001	10.100	p<0.01
Distance to Village	0.730	12.093	p<0.001	4.242	p<0.05

The bootstrapped LDA, based on 500 repeat random samples of 90% of the data indicated that attack events occurred in areas closer to the PA, closer to rivers and with lower human population counts (Table 3.3; Appendix B2). On average, 74.8% (95% CI [72.1, 77.5]) of the data were correctly classified. The percentage of false negatives, i.e., where the model predicted no attack when an attack had occurred, was 8.9% (95% CI [7.0, 10.9]). The bootstrapped LDA had an average area under the curve score (AUC) of 0.82 (95% CI [0.79, 0.84]), indicating that it performed well in differentiating between attack and non-attack events. Results of the analyses using square root transformed data were very similar and are not discussed further (Appendix B3).

Table 3.3 Mean coefficients and confidence intervals of linear discriminants obtained from bootstrapped LDA of bush attack locations, based on 500 repeat random samples of 90% of the data.

Variable	Mean LD	95% CI
Distance to PA	-1.02E-04	-1.34E-04, -8.60E-05
Distance to Rivers	-2.53E-04	-3.09E-04, -1.97E-04
Population Count	-6.55	-7.57, -5.53
Tree Cover	-0.16	-0.18, -0.13
NPP	3.51	2.79, 4.24
Distance to Village	9.57E-05	6.59E-05, 1.25E-04

We created a risk map of the area using the mean linear discriminants from the bootstrapped analysis and measures of the significant predictor variables at all points in the landscape at a resolution of 250 x 250 m (Fig. 3.3a). When excluding protected areas, 26% of the landscape (550 km^2 of the 2000 km^2 mapped area) had a predicted probability of attack > 0.66 (high risk).

3.4.1.2 Boma attacks

Five predictor variables were retained in the final model used in the LDA (Table 3.4). Attack and non-attack events were best distinguished by distance to village, followed by human population count and net primary productivity (NPP; Table 3.4).

Table 3.4 Wilk's lambda and discriminating ability of variables at each stage of forward stepwise variable selection for boma attacks. Variables retained show significance in separating attack and non-attack events.

Variable	Wilk's lambda	F	p-value	F difference	p difference
Distance to Village	0.735	80.981	<0.001	80.981	<0.001
Population Count	0.687	51.099	<0.001	15.867	<0.001
NPP	0.675	35.806	<0.001	3.897	<0.05
Tree Cover	0.647	30.327	<0.001	9.700	<0.01
Annual Rainfall	0.632	25.779	<0.001	5.260	<0.05

The bootstrapped LDA, based on 500 repeat random samples of 90% of the data indicated that boma attack events occurred in areas further from villages, with lower human population and higher NPP (Table 3.5; Appendix B4). Using the LDA model to reclassify the data into attack and non-attack events led to, on average, 76.4% (95% CI [74.2, 78.6]) of the data being correctly classified. The mean error was highest for false negatives (14.8%, 95% CI [13.2, 16.5]), i.e., the model predicted no-attack for an attack site. The bootstrapped LDA had an average AUC of 0.88 (95% CI [0.87, 0.90]), indicating that it performed very well in differentiating between attack and non-attack events.

Table 3.5 Mean coefficients and confidence intervals of linear discriminants obtained from bootstrapped LDA of boma attack locations, based on 500 repeat random samples of 90% of the data.

Variable	**Mean LD**	**95% CI**
Distance to Village	3.14E-04	2.84E-04, 3.43E-04
Population Count	-3.54	-4.24, -2.84
NPP	5.41	4.63, 6.20
Tree Cover	-0.16	-0.19, -0.13
Annual Rainfall	-0.008	-0.01, -0.006

The risk map constructed from the mean LDA coefficients (Fig. 3.3b), indicated that, 61% of the landscape outside of PAs had a predicted probability of attack > 0.66 (high risk). This is approximately 1275 km^2 of the 2000 km^2 mapped area, and more than double the area found to be at high risk of bush attacks.

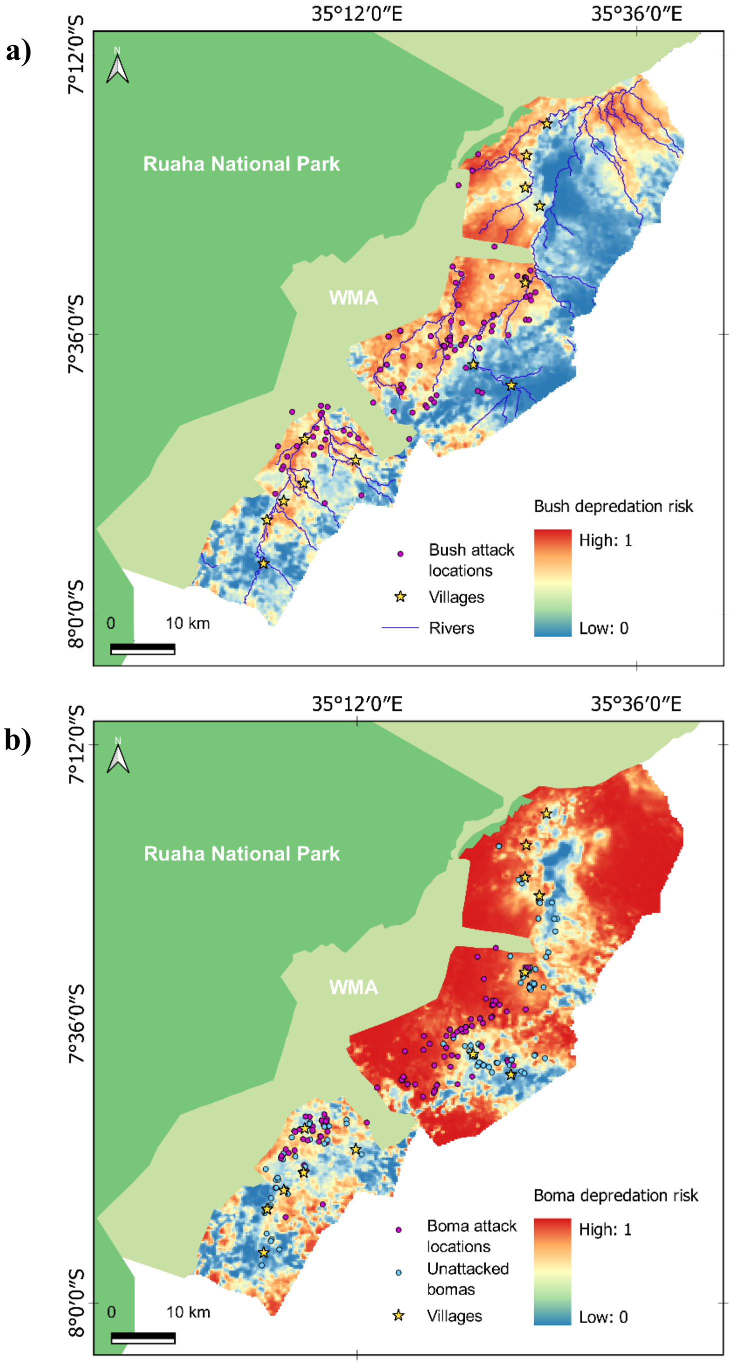


Figure 3.3 Predictive maps of depredation risk for grazing livestock (a) and livestock inside bomas (b) on village land in the Ruaha landscape of Tanzania, generated through linear discriminant analysis. Models of bush depredation risk (a), based on 103 attack points and 100 absences, included the variables: distance to PAs, rivers and villages, tree cover, net primary productivity, and human population count. Models of boma depredation risk (b), based on 119 attack points and 108 absences, included the variables: distance to villages, tree cover, net primary productivity, human population count, and annual rainfall. High risk (in red) represents areas where attacks are more likely to occur.

3.4.2 Predicting depredation with spatial autocorrelation (INLA-SPDE)

K function analysis revealed that values of $\hat{k}$, which represent attack to attack proximity, were higher than expected by chance up to a distance of 35 km for bush events (Appendix B5). For boma attacks, values of $\hat{k}$ were higher than expected at short distances (1 - 10 km) and at distances of > 30km (Appendix B5). This indicates that patterns of livestock depredation are significantly clustered in space. We therefore proceeded with INLA-SPDE analysis, which explicitly models spatial dependency between points.

3.4.2.1 Bush attacks

The model with the lowest DIC (129.3) included four fixed effect predictors and a spatial component (Table 3.6). Risk of livestock depredation in the bush was driven by NPP and tree cover, with attacks happening in areas of higher NPP and lower tree cover (Table 3.6). Distance to the protected area also exhibited a negative association with risk of a lion attack. Although the 95% credible interval overlapped zero, distance to roads was included in the final model as its removal increased the DIC by > 2 (132.9). However, unlike in the LDA model, distance to rivers and villages, along with human population count, did not improve the model.

Table 3.6 Posterior estimates (mean, sd and quantiles) for fixed and random effects in final INLA-SPDE model for bush attacks. The mean posterior coefficients for the fixed effects are presented in log-odds and represent the estimated response to a one standard deviation change in the predictor variable when all other variables are held constant.

	Mean	**SD**	**0.025**	**0.5**	**0.975**
Fixed effects					
Intercept	-30.99	14.40	-62.62	-29.29	-8.55
NPP	38.54	16.48	13.93	36.38	76.40
Tree Cover	-0.48	0.26	-1.11	-0.42	-0.13
Distance to PA	-1.73	1.15	-4.69	-1.46	-0.32
Distance to Roads	-0.84	0.91	-2.95	-0.72	0.68
Spatial random effect					
Variance	148.50	139.75	24.22	105.72	529.02
Correlation range	16.82	5.86	8.70	15.65	31.42

The inclusion of the spatial correlation component provided a better model fit (DIC increased to 248.4 if removed). The nominal variance of the spatial effect had a wide posterior distribution (Table 3.6; 95% CI [24.2, 529.02]) suggesting that the variability in attack occurrence attributable to location is high. The posterior mean of the spatial correlation range, which indicates the distance at which spatial correlation declines to ~0.1, was 16.82 km. This indicates the approximate distance within which the odds of a lion attack can be considered to be correlated.

The mean AUC, based on holdout validation of 100 random samples, was 0.89 (95% CI [0.79, 0.99]), indicating an excellent degree of discrimination between attack and non-attack locations. According to our mapped predictions (Fig. 3.4a), 39% of the landscape outside of PAs was at high risk of a lion attack (predicted probability > 0.66).

3.4.2.2 Boma attacks

For boma attacks, the model with the lowest DIC (177.4) included only two fixed effect predictors along with a spatial component (Table 3.7). Risk of livestock depredation at bomas was driven by NPP and distance to village, with attacks happening in areas of higher NPP and further from villages (Table 3.7). Unlike in the LDA model, human population count, tree cover and rainfall, were not significant and did not improve the model.

Similar to the INLA-SPDE model for bush attacks, removal of the spatial component increased the DIC (232.9), and the nominal variance of the spatial effect had a wide posterior distribution (Table 3.7; 95% CI [2.82, 316.66]). The posterior mean of the spatial correlation range, indicating the distance at which spatial correlation declines to ~0.1, was 75.42 km. Effectively there was spatial dependency across the whole region. This might reflect large ranges of foraging or multiple prides of lions across the landscape.

The mean AUC, based on validation of 100 random samples, was 0.90 (95% CI [0.83, 0.97]). According to our mapped predictions (Fig. 3.4b), 69% of the landscape outside of PAs was at high risk of a lion attack (predicted probability > 0.66).

Table 3.7 Posterior estimates (mean, sd and quantiles) for fixed and random effects in final INLA-SPDE model for boma attacks. The mean posterior coefficients for the fixed effects are presented in log-odds and represent the estimated response to a one standard deviation change in the predictor variable when all other variables are held constant.

	Mean	**SD**	**0.025**	**0.5**	**0.975**
Fixed effects					
Intercept	-12.93	13.15	-37.46	-13.65	21.34
NPP	12.40	3.45	6.05	12.25	19.60
Distance to Village	0.60	0.21	0.24	0.58	1.07
Spatial random effect					
Variance	61.35	99.17	2.82	29.84	316.66
Correlation range	75.42	66.91	12.92	55.41	257.27

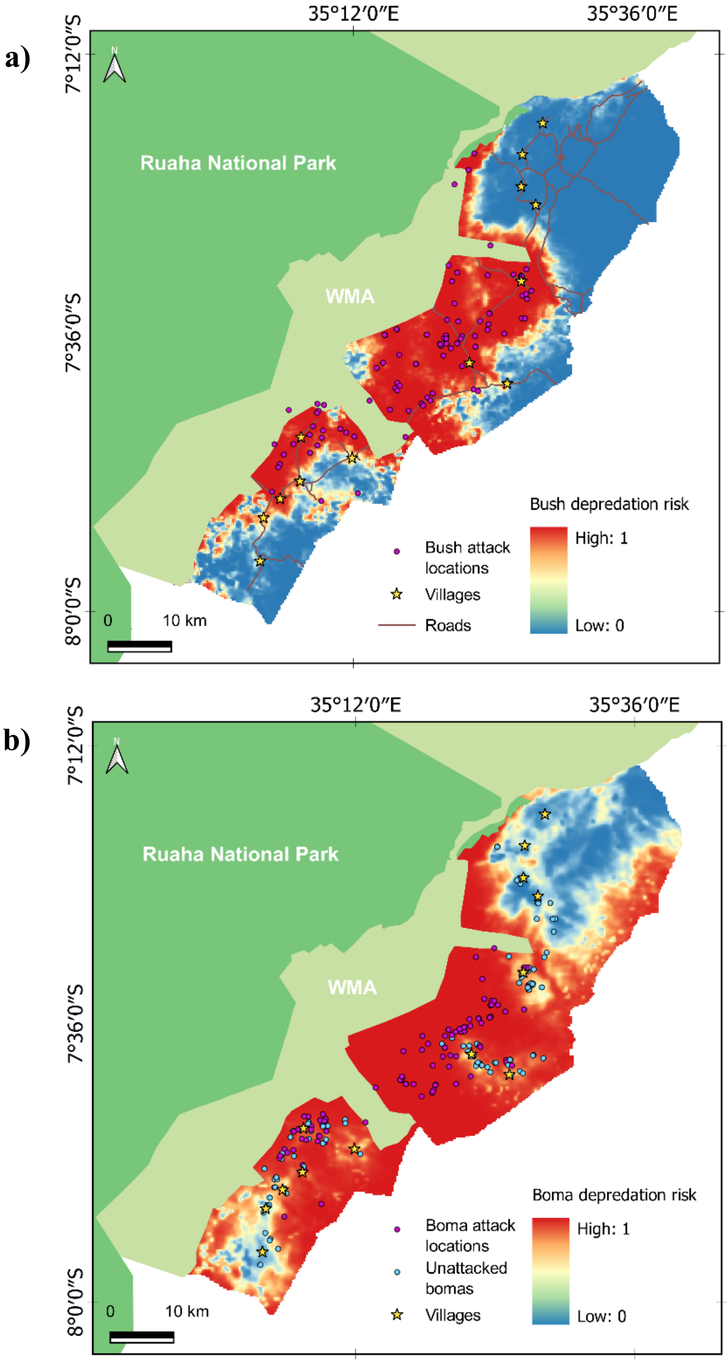


Figure 3.4 Predictive map of depredation risk for grazing livestock (a) and livestock inside bomas (b) on village land in the Ruaha landscape of Tanzania, generated through INLA-SPDE analysis. High risk (in red) represents areas where attacks are more likely to occur. Models of bush depredation risk (a), based on 103 attack points and 100 absences, included the variables: distance to PAs and roads, tree cover, and net primary productivity. Models of boma depredation risk (b), based on 119 attack points and 108 absences, included the variables: distance to villages, and net primary productivity.

3.4.3 Comparison of modelling approaches

Both the INLA-SPDE and the LDA approaches, had a high success rate in discriminating between attack and non-attack events (AUC > 0.8). The INLA-SPDE models had higher AUC values and included fewer explanatory variables than the LDA models (Table 3.8). However, the confidence intervals (CIs) of the AUC values overlapped, indicating that the accuracy of the modelling approaches did not differ significantly for either bush or boma depredation events (Table 3.8). Across all models NPP was a key factor affecting likelihood of an attack. For bush attacks, tree cover and distance to the protected area were also present in both models, while for boma attacks, distance to village was an important driver.

Table 3.8 Summary of outputs from INLA-SPDE and LDA models. Order of variables included in the final LDA models indicates order of significance in discriminating ability between attack and non-attack events. Variables highlighted in bold show common predictors in final models for each type of depredation event. Levels of depredation risk were categorised as: low (< 0.33), medium (0.33 - 0.66), and high (> 0.66).

Attack location	**Method**	**AUC**	**Variables included in final model**	**% Study area in each risk category**
Bush	INLA-SPDE	0.89 (95% CI [0.79, 0.99])	**Distance to PA; Tree cover; NPP;** Distance to Roads (not sig.)	Low: 53% Medium: 8% High: 39%
	LDA	0.82 (95% CI [0.79, 0.84])	**Distance to PA**; Distance to rivers; Population count**; Tree cover**; **NPP**; Distance to village	Low: 43% Medium: 31% High: 26%
Boma	INLA-SPDE	0.90 (95% CI [0.83, 0.97])	**Distance to village; NPP**	Low: 19% Medium: 12% High: 69%
	LDA	0.88 (95% CI [0.87, 0.90])	**Distance to village**; Population count; **NPP**; Tree cover; Annual rainfall	Low: 17% Medium: 22% High: 61%

A higher percentage of the landscape was at high risk of boma attacks than bush attacks (Table 3.8; Fig. 3.5). Combined, the INLA-SPDE and LDA models map 48% of the study area as high risk for bush attacks, and 88% as high risk of boma attacks. However, if we consider only the areas where there is agreement between the INLA-SPDE and LDA model, 18% of the landscape is at high risk for bush attacks and 42% for boma attacks (Fig. 3.5). Overall, the maps suggest that the central portion of the landscape, which is largely surrounded by the wildlife management area (WMA), is a conflict hotspot for both bush and boma attacks (Fig. 3.5). For bush attacks the probability of attack decreases in the northeast and southwest sections of the study area. However, for boma attacks, the INLA-SPDE model maps parts of the southwest section as being high risk while the LDA model considers some areas to the northeast to be high risk.

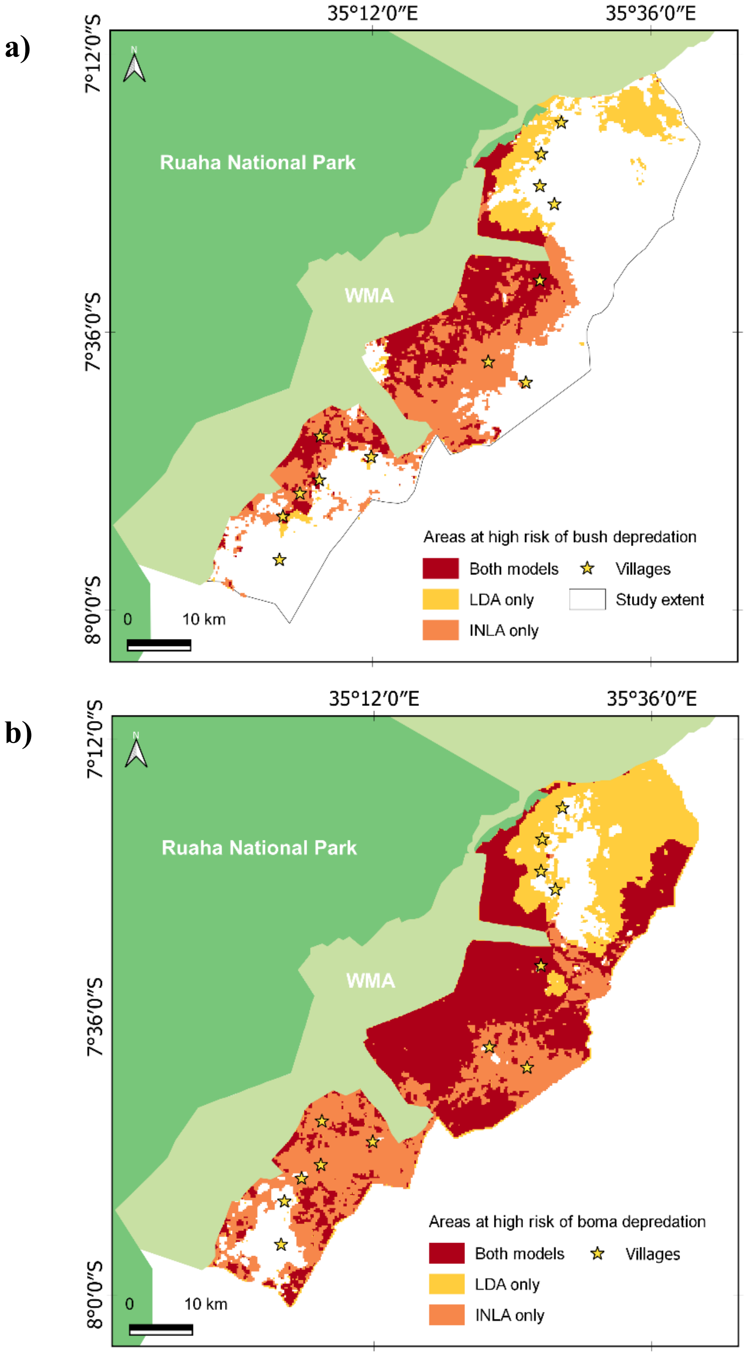


Figure 3.5 Comparison of risk maps generated by INLA-SPDE vs LDA models, showing where the high-risk categories (areas with predicted probability of lion attack > 0.66) overlap for bush attacks (a) and boma attacks (b).

3.5 Discussion

African lion populations have declined by almost half in the past 20 years and lions now occupy only 8% of their historic range (Riggio *et al.*, 2013; Bauer *et al.*, 2016). A key driver of these declines, alongside prey base depletion, is retaliatory or pre-emptive killing to protect human life and livestock (Dickman *et al.*, 2014; Bauer *et al.*, 2016). The future persistence of lions in Africa thus depends, in part, on the ability of stakeholders to adapt to and mitigate human-lion conflict. Our findings provide some evidence that lion attacks on livestock follow predictable patterns in space, driven by a combination of ecological and anthropogenic factors. However, spatial predictions of conflict hotspots vary to some extent depending on the type of modelling approach used in analyses. Predictive modelling mapped between 26-39% of the landscape as being high risk for grazing livestock and a higher proportion, 61-69%, was deemed to be at high risk for livestock depredation from bomas. Understanding and predicting spatial variation in depredation risk may provide a first step to aid conservationists and pastoralists in managing and minimising risks, either through mitigation interventions or through avoidance of risk-prone areas.

For grazing livestock, both modelling approaches found that attack risk was higher in locations close to the protected area, with high net primary productivity and low tree cover. The LDA approach also suggested that distance to rivers and villages and human population count were important predictors of depredation risk for livestock in the bush. For livestock in the boma, both modelling approaches found that attacks were more likely in areas of high vegetation productivity, further from villages. Again, the LDA model found several additional variables, including population count, tree cover and annual rainfall, affected boma attack risk.

3.5.1 Landscape features predicting lion-livestock conflicts

The prey abundance hypothesis posits that carnivore habitat selection is driven by prey availability, and that habitats are selected to include the highest numbers of prey (Davidson *et al.*, 2012). Indeed, multiple studies have found that prey abundance is key driver of lion habitat use (Spong, 2002; Abade *et al.*, 2019; Sargent *et al.*, 2022). Protected areas carrying higher prey densities and areas with higher net primary productivity, and thus large herbivore biomass (Coe *et al.*, 1976; Pettorelli *et al.*, 2009; Fløjgaard *et al.*, 2021), are therefore likely to be more attractive to lions resulting in a higher risk of depredation for livestock in those areas. Protected areas represent core carnivore habitat and contain resident wildlife populations (Abade *et al.*, 2019; Kuiper *et al.*, 2021). Hence, while livestock is not permitted inside the protected area, grazing closer to the boundaries increases the likelihood of encountering lions (Røskaft *et al.*, 2013; Mkonyi *et al.*, 2018).

Being ambush predators, it might be expected that lions would favour habitats which improve prey catchability, such as those with increased vegetation cover (Hopcraft *et al.*, 2005). Yet, we also find increased depredation risk in areas of low tree cover, which supports earlier studies that showed an association between low tree cover and higher risk of depredation by carnivores (Abade *et al.*, 2014a), albeit indiscriminate of predator species identity. Lion habitat use is highly context- and scale-dependent and lions have been found to select grassland and open habitats over areas with a high percentage of woody cover in several studies (Cristescu *et al.*, 2013; Elliot *et al.*, 2014b; Miller *et al.*, 2018).

Proximity to water is another known driver of habitat selection in lions (Valeix *et al.*, 2010; Kittle *et al.*, 2016; Sargent *et al.*, 2022), and we did find it to be important for predicting bush depredation events using the LDA approach. The distribution of herbivores in arid/semi-arid landscapes is largely influenced by the availability of water and thus lions frequently hunt in areas close to water sources where prey congregate (Valeix *et al.*, 2012b; Davidson *et al.*, 2013). These results suggest that lion habitat suitability could be used as a predictive parameter for mapping areas that are high risk for grazing livestock.

Livestock depredation from bomas was driven by anthropogenic factors as well as vegetation productivity and tree cover. Attacks were more likely in areas further away from villages and with lower human population counts. This differs from bush attacks, which appear to be predominantly driven by ecological variables and is supported by our understanding of lion behaviour in human-dominated landscapes. Anthropogenic pressures affect mortality risk for lions, with conflict-related mortality increasing as distance to households decreases and household density increases (Loveridge *et al.*, 2017b). Lions may therefore adjust their behaviour to avoid areas of high human density (Valeix *et al.*, 2012a; Schuette *et al.*, 2013), meaning that bomas located further from villages in areas with low human activity are more likely to experience a depredation.

3.5.2 Comparing modelling approaches and conflict hotspots

Spatial risk modelling in order to identify priority areas at high risk of human-carnivore conflict is rapidly emerging as an important tool for carnivore conservation (Miller, 2015). The use of predictive maps may be used to target mitigation strategies in areas where attacks are more likely to occur and develop adaptive management and grazing plans (Treves *et al.*, 2011; Miller, 2015). A wide variety of modelling techniques have been used such as generalised linear models, ecological niche factor analysis, Getis-Ord G clustering and MaxEnt, all of which have different benefits and constraints (Abade *et al.*, 2014a; Amirkhiz *et al.*, 2018; Mpakairi *et al.*, 2018; Hoffmann *et al.*, 2019). A common approach is to use multiple methods to identify overlapping areas of consistent prediction (Zarco-González *et al.*, 2013; Carvalho *et al.*, 2015).

Indicators for both modelling approaches used here, LDA and INLA-SPDE, suggested that they had high predictive ability with excellent discrimination between attack and non-attack events (AUC >0.8; Mandrekar (2010)). However, the predictive maps produced differed considerably and retained diverse combinations of explanatory variables. Some of the observed differences may be explained by the model structure, as the INLA-SPDE method included a spatial autocorrelation component, necessary for systems in which events are clustered in space (Hoffmann *et al.*, 2019). Spatial autocorrelation was particularly strong for boma attacks, with the odds of a lion attack being correlated up to a distance of ~ 75 km. However, it should be noted that bomas themselves are clustered in space (up to 20 km; Appendix B6), suggesting that the observed spatial autocorrelation may be partially explained by patterns in boma placement as well as lion behaviour. In protected areas, lion foraging behaviour is typically driven by resource dispersion and prey catchability (Hopcraft *et al.*, 2005; Valeix *et al.*, 2011; Valeix *et al.*, 2012b). However, substantially less is known about how lions respond when encountering domestic prey (Hoffmann *et al.*, 2019).

Both modelling methods reveal a key conflict hotspot located in the centre of the study area and indicate a broader extent of risk for boma attacks than bush attacks. However, there was more variability in the results of the LDA models, which mapped a larger percentage of the landscape as being at ‘medium’ risk of depredation (i.e., reflecting some uncertainty in probability of conflict), while the INLA-SPDE model maps more of the landscape as high risk. We would suggest that overestimating risk is preferable to underestimating if the maps are to be used to target mitigation measures. Inaccurate guidance on the location of high-risk areas and mistakes in conflict management may have serious consequences for local livelihoods and lead to a breakdown in trust between stakeholder groups (Miller, 2015; Eklund *et al.*, 2017).

While the outcomes of the modelling approaches are broadly similar, INLA-SPDE allows for finer scale differentiation. Our results suggest that lion attack locations can be predicted, and that the use of two different modelling approaches is useful for allowing us to examine disagreements and uncertainties and for preventing the underestimation of potential risk areas.

It is likely that no model will perform best in all cases (Zarco-González *et al.*, 2013), and examining consensual areas between predictions should enable reliable estimations. In areas where the models disagree it would be useful to conduct further validation exercises when more data becomes available. Future work could also consider the inclusion of a temporal component, i.e., date and time of attack, which would enable identification of attacks which are clustered in both space and time. This would indicate whether boma attacks are clustered as a result of lions repeatedly returning to the same area following a successful depredation. Similarly, seasonality is likely to be important as increased water availability in the wet season may cause wild prey to be more widely dispersed and in better condition (Patterson *et al.*, 2004; Valeix *et al.*, 2012a). Livestock may therefore offer an alternative source of prey when wild herbivores become scarce, and indeed multiple studies have observed increased livestock depredation during the rainy season (Mponzi *et al.*, 2014; Kuiper *et al.*, 2015; Kissui *et al.*, 2019).

One constraint of our models is the use of pseudo-absence data for bush attack events. While we were able to obtain true absences for boma locations, the generation of pseudo-absence points for grazing livestock may have biased model coefficients and variable selection (Hirzel *et al.*, 2002; Gibson *et al.*, 2007). Detailed understanding of livestock distributions would allow for the collection of accurate absence data, i.e., sites in the landscape where livestock is present, but no attacks have occurred. However, use of pseudo-absences is a common approach in ecology (Mpakairi *et al.*, 2018; Struebig *et al.*, 2018; Liu *et al.*, 2019), where species absences cannot be inferred with certainty, and studies suggest that robust models can be generated using randomly selected pseudo-absences (Wisz and Guisan, 2009; Barbet-Massin *et al.*, 2012).

3.5.3 Management implications

Our modelling suggests that bomas located in areas with high net primary productivity and further from villages are most at risk. We highlight that we were unable to consider the influence of boma quality in determining boma attack risk and individual features such as wall height and material, visibility of stock and the presence of dogs may make some bomas more vulnerable to attacks by carnivores (Ogada *et al.*, 2003; Broekhuis *et al.*, 2017). However, in our landscape, husbandry practices are of a low average standard, with bomas typically weakly constructed and with few additional guarding strategies in place (Abade *et al.*, 2014a). Of participants interviewed for Chapter 5 of this thesis, only 3.7% had wire bomas, with the remaining using thorn bushes. Furthermore, previous research in Tanzania found no relationship between overall boma quality and levels of depredation (Ikanda and Packer, 2008) and, in our landscape in particular, tree cover and rainfall were more strongly associated with boma depredations than were husbandry practices (Abade *et al.*, 2014a).

If it is not possible for livestock owners to relocate or avoid high risk areas, then these bomas should be prioritised for the development of improved husbandry strategies. Uptake of reinforced, wire bomas has been limited in this landscape as they do not offer the flexibility and mobility required by herders. Therefore, it is vital to collaborate with stakeholders to identify mitigation options which are feasible and locally acceptable. Approaches such as mobile canvas bomas, 'lion lights' (Lesilau *et al.*, 2018), and specialised livestock guarding dogs (Van Der Weyde *et al.*, 2020) may be appropriate alternatives.

For livestock in the bush, we identified areas of high vegetation productivity, low tree cover, near to protected areas and rivers as being at high risk of a lion attack. Unfortunately, features such as proximity to water and low tree cover also characterise suitable pasture areas for livestock, meaning there is a trade-off between accessing resources and avoiding habitats where encounters with lions are more likely (Abade *et al.*, 2014a). If using these areas, increased surveillance by herders and alternative guarding strategies may reduce the risk of a lion attack. Developing novel livestock watering strategies, such as creation of mobile water supplies or limited-access water points that are only accessible to livestock, may also reduce the likelihood of depredation near rivers (Valls-Fox *et al.*, 2018; Beattie *et al.*, 2020). Sharing risk maps directly with stakeholders may enable them to incorporate the results into their decision-making and livestock management strategies. For example, reflecting on locations of key resources required by people and livestock alongside distributions of risk could inform adaptive grazing plans, the designation of pastures and improved supervision of livestock in these areas (Zarco-González *et al.*, 2013; Miller, 2015).

Given that we were unable to account for livestock distribution and density, it is likely to that, to some extent, our predictions of risk reflect where lions and livestock are most likely to encounter each other, rather than because these areas are inherently risky (Kuiper *et al.*, 2021). These maps are useful as they can effectively predict future attacks and identify areas that are good targets for mitigation measures, where absolute levels of livestock loss are high and may lead to retaliatory killing of lions (Kissui, 2008; Miller, 2015). However, models that capture the probability of depredation risk *given* livestock presence may enable herders to identify areas that are relatively safer for grazing livestock (Kuiper *et al.*, 2021). Therefore, collecting accurate data on livestock movement and abundance over time and across seasons should be a priority for future studies. Methods such as GPS collars and camera traps enable researchers to gather such data at fine spatial scales (Abade *et al.*, 2019; Beattie *et al.*, 2020; Kuiper *et al.*, 2021).

One study that accounted for cattle space use found that, consistent with our models, risk of depredation increased closer to the protected area and further from homesteads, in areas of low human density (Kuiper *et al.*, 2021). Of other risk mapping studies focussed on African carnivores, several suggest that carnivores attack livestock at sites near to rivers and with high vegetation productivity (Abade *et al.*, 2014b; Mpakairi *et al.*, 2018; Beattie *et al.*, 2020). These corroborate our results and indicate that some key drivers of livestock depredation risk may be transferable across regions and species. The modelling approaches used here may also be easily applicable across contexts for which depredation data and remotely sensed landscape attributes are available.

3.5.4 Conclusions

We demonstrate that the combined use of LDA and INLA-SPDE analysis can provide detailed understanding of risk factors associated with depredation and enable the identification of high-risk areas. Our results suggest that measures of vegetation productivity, tree cover and distance to rivers are key environmental drivers of lion attack risk, while distance to villages and human population count represent important anthropogenic influences. However, we echo previous studies in highlighting the need to collect data on a wider range of anthropogenic variables and their seasonal and annual variation, in particular livestock abundance and distribution (Kuiper *et al.*, 2021; Sargent *et al.*, 2022). Risk maps, such as the ones developed here, offer an easily interpretable method to allow stakeholders to visualise distribution of risk, stimulate discussions and guide decision-making (Miller, 2015). In landscapes where livestock depredation imposes significant costs on human and carnivore communities, understanding the factors which underlie carnivore-livestock interactions will be vital for developing effective mitigation interventions that may ultimately make human-carnivore coexistence possible.

Chapter 4. Examining the utility of a Linear Discriminant Analysis approach to identify common drivers of livestock depredation across contexts.

A calf peeks out from a fortified, wire livestock enclosure near Kitisi village, Ruaha, Tanzania.

4.1 Abstract

1. Livestock depredation by carnivores is one of the most widespread forms of human-wildlife conflict. Finding a simple, generalisable approach for modelling depredation risk could allow for the identification of consistent risk factors and the upscaling of risk maps across landscapes, thus leading to more effective, targeted mitigation measures.
2. We test the transferability of a Linear Discriminant Analysis (LDA) approach, as used in Chapter 3, to examine the extent to which we can predict risk of livestock depredation by lions (*Panthera leo*) across three additional study sites, using both the original model and landscape-specific derivations.
3. Landscape-specific models derived using the same predictor variables as the original, Ruaha model were successful in identifying conflict locations in two Kenyan study sites. However, no variation of the modelling approach led to acceptable discriminating ability in the Zimbabwean study site.
4. The use of this approach revealed that some key predictor variables, including distance to water and precipitation, are important across landscapes. However, other unmeasured variables and context-specific factors such as differences in land use and livestock distributions are likely to affect model accuracy when transferring to new study sites.
5. The LDA method displays some potential as a scalable technique for modelling depredation risk. However, local context must be considered and obtaining accurate data on site-specific variables is critical. Using analogous approaches across study sites is essential for enabling robust comparisons and identifying common conflict drivers to facilitate actions which reduce livestock losses and promote human-carnivore coexistence.

4.2 Introduction

Carnivore attacks on livestock are one of the most widespread forms of human-wildlife conflict (Kissui, 2008; van Eeden *et al.*, 2018a), representing a major challenge for pastoralists and conservation practitioners. Globally, large terrestrial carnivores have suffered precipitous declines in population (Ripple *et al.*, 2014), in large part due to retaliatory killing in response to the negative costs they impose on the communities that live alongside them (Hazzah *et al.*, 2009; Inskip and Zimmermann, 2009; Nyhus, 2016). Carnivore attacks on domestic animals can have significant social and financial impacts on households (Barua *et* *al.*, 2013; Dickman and Hazzah, 2016; Mkonyi *et al.*, 2017c; Khadija *et al.*, 2021) and thus, developing effective mitigation techniques to reduce livestock depredation is vital. This in turn may increase community tolerance towards living with large carnivores. Interventions previously used to manage carnivore-livestock contact include physical barriers, improved guarding strategies and non-lethal deterrents (Miller *et al.*, 2016b; Lesilau *et al.*, 2018; van Eeden *et al.*, 2018b). Yet, evidence for their effectiveness varies widely and implementing or adapting mitigation strategies is challenging and can be expensive (Dickman *et al.*, 2011; Mkonyi *et al.*, 2017a; van Eeden *et al.*, 2018a). For example, building a fully fortified livestock enclosure in Kenya can cost ~$890 (Sutton *et al.*, 2017) and in South Africa, the total cost to obtain and care for a specialised livestock guardian dog during the first year of its life are ~$2780/dog (Rust *et al.*, 2013).

Understanding what factors are associated with conflict ‘hotspots’ could significantly improve our ability to manage human-carnivore conflict with pre-emptive, spatially-targeted interventions, reducing costs. Spatial risk modelling can be used to identify the landscape attributes associated with sites where carnivores have attacked livestock and to quantify predation risk and its variation in space (Miller, 2015). Maps derived from these models can be used to target conflict mitigation measures towards high-risk areas and allow stakeholders to visualise distribution of risk in their landscape. Landscape attributes that can be used to calibrate spatial risk models should include ecological and anthropogenic variables known to affect carnivore habitat use, such as: wild and domestic prey abundance and distribution, environmental factors such as climate and vegetation type, and human impacts such as infrastructure and land management (Miller, 2015; Sargent *et al.*, 2022). These attributes are also likely to contribute towards spatio-temporal patterns in human-carnivore conflict (Montgomery *et al.*, 2018a).

In the Afrotropics, a high priority region for large carnivore conservation with widespread human-wildlife conflict (Di Minin *et al.*, 2016; Seoraj-Pillai and Pillay, 2017), several studies have mapped livestock depredation risk using a variety of different modelling approaches (Table 4.1). Some variables appear to be consistently important in predicting conflict risk across contexts. For example, proximity to protected areas (PAs), which represent core carnivore habitat (Kuiper *et al.*, 2021), and areas close to water sources, where both wild prey and livestock concentrate in semi-arid environments (Valeix *et al.*, 2010; Davidson *et al.*, 2013), represent increased risk for grazing stock across several landscapes (Table 4.1). Other important drivers include vegetation cover and productivity, although the effect of these factors appears more varied (Table 4.1).

Table 4.1 Summary of risk mapping studies that examine livestock depredation in Africa

Study	Location	Species responsible	Modelling approach	Variables associated with increased risk
Abade *et al.* (2014a)	Ruaha, Tanzania	Lion, leopard, spotted hyena	Ecological Niche Factor Analysis; Support Vector Machines; Maxent	Bush attacks: close to rivers, low slope and elevation, low tree cover. Boma attacks: low tree cover, high annual precipitation.
Beattie *et al.* (2020)	Manyara, Tanzania	Lion	Logistic regression	Dry season: close to water, high NDVI. Wet season: close to water and bomas.
Broekhuis *et al.* (2017)	Maasai Mara, Kenya	All carnivores	GLM	Boma attacks: high proportion of closed habitat, close to PA.
Kuiper *et al.* (2021)	Hwange, Zimbabwe	All carnivores	Resource selection functions; GLMM	Accounting for livestock distribution: close to PA, further from households, low human density, high tree cover.
Mpakairi *et al.* (2018)	Matetsi, Zimbabwe	All carnivores	Gradient boosting; Random Forest models	Low NDVI, close to PA and rivers.
Wilkinson *et al.* (2021)	Nakuru, Kenya	All carnivores	GLM	Low NDVI, high road density, close to PA, low slope.

The majority of studies map livestock attacks without identification of the predator species responsible. However, large African carnivores such as leopard, lion and hyena differ in their habitat use and hunting strategies (Balme *et al.*, 2007; Cozzi *et al.*, 2013; Searle *et al.*, 2021b). Specific risk factors for depredation are, therefore, likely to vary by species and particular mitigation interventions may be appropriate for some species but not others (Kolowski and Holekamp, 2006; Miller, 2015; Chaka *et al.*, 2021). Creating species-specific models would enable identification of predation risk factors which are consistent across contexts, potentially allowing for the development of risk models which are applicable across landscapes.

In Chapter 3 of this thesis, we developed a conflict risk map for livestock depredation by African lions (*Panthera leo*) in the Ruaha landscape of Tanzania. Across Africa, lion populations have declined by >43% over the last two decades (Bauer *et al.*, 2016) and approximately 44% of their remaining range lies outside of protected areas (Lindsey *et al.*, 2017b). Frequent interactions with human communities result in widespread livestock depredation (Muriuki *et al.*, 2017; Di Minin *et al.*, 2021) and subsequent retaliatory killing (Dickman *et al.*, 2014; Bauer *et al.*, 2016). We identified several landscape features which affected the likelihood of a lion attack, some of which concurred with work by Beattie *et al.* (2020), who mapped depredation by lions in Manyara, Tanzania (Table 4.1). These included proximity to water and increased vegetation productivity and suggest that some common features underlie lion-livestock interactions across landscapes. However, lion habitat use is varied and context-dependent and lions can exhibit behavioural flexibility in response to human pressures (Oriol-Cotterill *et al.*, 2015a; Sargent *et al.*, 2022). For example, specific landscape features such as human densities, land use and grazing patterns can alter lion habitat use (Mogensen *et al.*, 2011; Schuette *et al.*, 2013; Elliot *et al.*, 2014b). Therefore, key drivers of livestock depredation risk may differ depending on the environmental and anthropogenic characteristics of the study area (Hoffmann *et al.*, 2019).

To examine the transferability of our risk model, we assess the extent to which we can predict risk of conflict across three other study sites. First, we use newly collected data from the Ruaha landscape to further validate our model from Chapter 3. Second, we test whether our model calibrated to the Ruaha landscape, developed using Linear Discriminant Analysis (LDA), can be used to accurately predict and map conflict hotspots across contexts. We here discard the Integrated Nested Laplace Approximation (INLA) approach used in Chapter 3, as this method includes a Ruaha-specific spatial autocorrelation component and as such would not be directly transferable to other locations. Third, we investigate the utility of the LDA approach, using (1) the set of environmental variables used in the Ruaha landscape, and (2) a new set of landscape-specific explanatory variables, for developing risk maps for each of the three new sites. We hypothesise that, while the Ruaha-specific model may not be directly transferable, the LDA approach could offer a generalisable method for mapping conflict which can be easily adapted to new landscapes. We interpret our findings to discuss whether a simple, scalable approach for modelling human-lion conflict is feasible and whether we can identify common drivers across geographic contexts.

4.3 Methods

4.3.1 Original maps and study landscape

The study landscape in the Ruaha region of Tanzania is a semi-arid mosaic of woodland, savanna, bushland, and cropland, containing the Ruaha National Park and the Pawaga-Idodi Wildlife Management Area. Livestock depredation locations were collected on the adjoining village land, part of the Iringa District, located to the south-east of the WMA and RNP (Fig. 4.1D). The landscape is a high-priority region for carnivore conservation, supporting the third largest population of the endangered African wild dog, a cheetah population of at least 200 adults (IUCN, 2007; Strampelli *et al.*, 2021) and one of the largest lion populations in Africa, estimated at around 3779 individuals (Riggio *et al.*, 2013). Experience of livestock depredation is widespread among communities in this area resulting in negative attitudes towards wildlife, with lions experiencing high levels of conflict-induced mortality (Dickman *et al.*, 2014).

In Chapter 3 of this thesis, we developed conflict risk maps for the Ruaha landscape, using georeferenced depredation locations collected between 2010 and 2017. We used two modelling approaches to develop risk maps, one which accounted for spatial autocorrelation within the data (Integrated Nested Laplace Approximation) and one which did not (Linear Discriminant Analysis (LDA)). Both approaches had high discriminatory ability and enabled us to identify several landscape attributes that were associated with lion attacks on livestock grazing in the bush and livestock corralled in enclosures (known locally as bomas) in this environment. Grazing livestock was at higher risk of predation near to protected areas (PAs), in proximity to rivers, in areas of higher net primary productivity (NPP) and lower tree cover (see Chapter 3). For livestock in bomas, tree cover and NPP were also important drivers of conflict risk, but livestock were further at risk of predation in areas of low human population count, further from villages.

Since completing this modelling exercise further data from the Ruaha landscape has become available. Livestock depredation data from the past year (2020 - 2021) provided an additional 22 bush and 42 boma attack locations. We use these data to further validate our models by overlaying the new locations onto the existing risk maps to determine whether they fell in the predicted high-risk areas.

4.3.2 New study landscapes and depredation data

4.3.2.1 Laikipia, Kenya

In Laikipia County, northern Kenya (Fig. 4.1A), georeferenced depredation locations were collected by the Laikipia Predator Project. This semi-arid region, comprised of shrubland and *Acacia* savanna interspersed with open grasslands, supports a diverse and abundant wildlife population (Kinnaird and O'brien, 2012; Suraci *et al.*, 2019). The study landscape contains a mosaic of communally owned, pastoral land and group ranches and large, privately-owned commercial ranches. Across these land use types people, livestock, and wildlife share space (Oriol-Cotterill *et al.*, 2015a). Most of Laikipia's ranches rely primarily on income from livestock production, however ecotourism has become increasingly important in recent decades with both private and group ranches setting aside land for wildlife conservancies (Yurco, 2017).

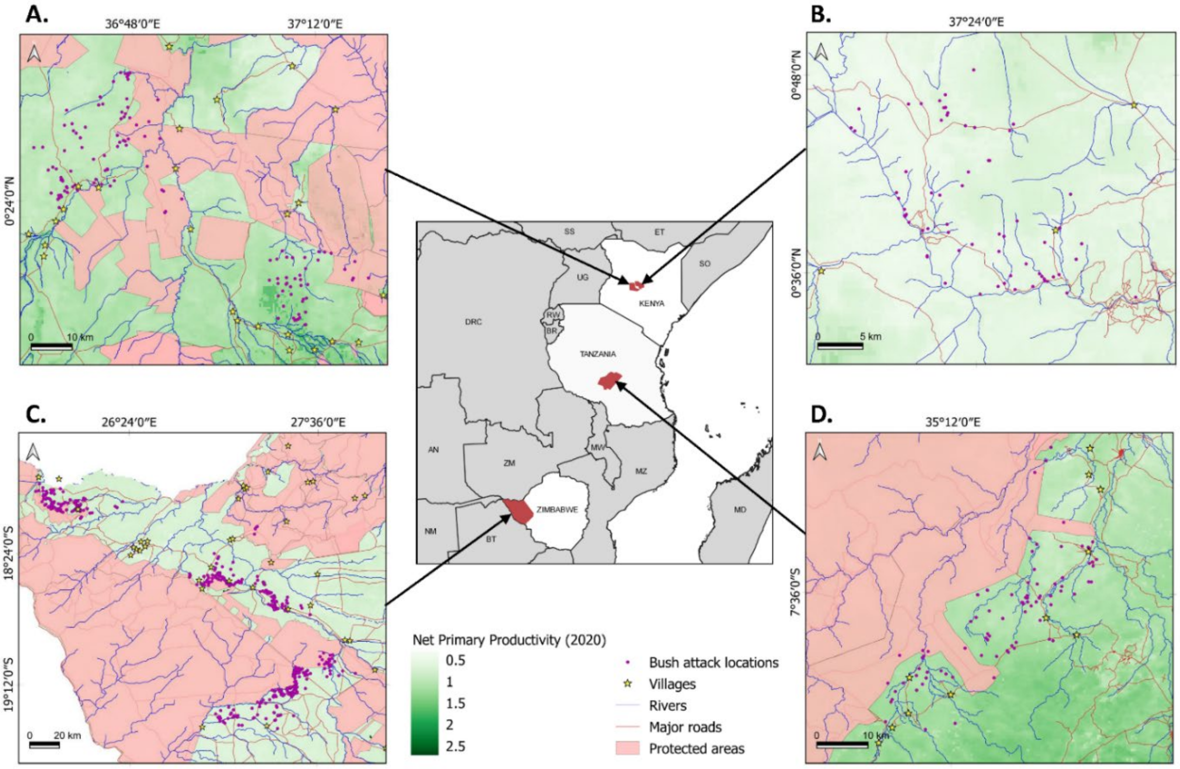


Figure 4.1 Maps displaying key geographic features of the four study landscapes and indicating their locations within Africa: **A.** Laikipia, Kenya; **B.** Samburu, Kenya; **C**. Hwange, Zimbabwe; **D.** Ruaha, Tanzania. The Samburu study site (B) was located within protected areas (both national reserves and community conservancies); hence protected areas are not shown on the map.

Data collected between 2007 and 2011 included 205 boma depredation events and 132 bush depredation events. While it was not possible to obtain data on bomas which had not suffered a lion attack, pseudo-absences were generated for bush attacks. To obtain pseudo-absences we used the same method as in Chapter 3 of this thesis (section 3.3.2). Using QGIS v3.16.5, we created a shapefile based on the study area monitored by the Laikipia Predator Project, covering a 1000 km^2 area in northern Laikipia and a 450 km^2 section in eastern Laikipia (Frank *et al.*, 2008). In this shapefile we excluded any areas with a slope of > 40% and used the ‘Random Points Inside Polygons’ tool to drop 100 random points which could be used as absences for bush depredation events.

4.3.2.2 Samburu, Kenya

In the Samburu and Isiolo Counties of northern Kenya (Fig. 4.1B), georeferenced depredation locations were collected by Ewaso Lions, an NGO founded in 2007. The region is a typical arid savanna landscape with frequent droughts and a mix of *Vachellia* grassland and shrubland vegetation (Kirathe *et al.*, 2021). The study landscape falls entirely within PAs, including the Samburu, Buffalo Springs and Shaba National Reserves and multiple community conservancies. The main economic activity in the area is livestock production, however over the past decade livelihoods have diversified to include ecotourism (Low *et al.*, 2009). The development of community-owned conservancies which aim to improve biodiversity conservation, land management and livelihoods has been primarily coordinated by the Northern Rangelands Trust, an NGO established in 2004 (Bersaglio and Cleaver, 2018). The landscape is unfenced and thus wildlife can move freely between the reserves and conservancies.

Between 2007 and 2018, 19 lion attacks on bomas and 69 attacks on livestock in the bush were recorded. Pseudo-absences for bush attacks were generated as above, by creating a shapefile of the roughly 4500 km^2 area monitored by the Ewaso Lions team (Ewaso Lions, 2019), excluding steep slopes, and dropping 100 random points.

4.3.2.3 Hwange, Zimbabwe

In north-western Zimbabwe (Fig. 4.1C), georeferenced depredation locations were collected by the Hwange Lion Project. This semi-arid region with low-fertility soils consists of woodland and bushland savanna interspersed with patches of grassland (Loveridge *et al.*, 2017b). The study site falls within the larger Kavango-Zambezi Transfrontier Conservation Area and contains one of Africa’s 10 remaining lion ‘strongholds’ (PAs containing >500 individuals with a stable or increasing population; Riggio *et al.* (2013)). The unfenced landscape is made up of multiple land use types including Hwange, Zambezi and Victoria Falls National Parks, trophy hunting areas, forest reserves and private and communally owned wildlife areas (Elliot *et al.*, 2014b). Livestock depredation data were collected in community lands set aside for agro-pastoralism (Loveridge *et al.*, 2017a).

Data collected between 2009 and 2013 included 132 boma depredation events and 597 bush depredation events. We created a shapefile of the Tsholotsho, Mabale and Mvuthu-Shana community lands (Loveridge *et al.*, 2017a), covering an area of approximately 14,000 km^2. Within these areas we excluded slopes > 40% and dropped 500 random points to be used as pseudo-absences for bush depredation events.

A summary of several key attributes of the four study landscapes can be found in Table 4.2.

Table 4.2 Overview of the key characteristics of the study regions

	Ruaha	**Laikipia**	**Samburu**	**Hwange**
Annual rainfall	Unimodal 500-600 mm	Bimodal 400-750 mm	Bimodal 300-400 mm	Unimodal 530-630 mm
Elevation[1]	703-1702 m	1278-2260 m	775-1637 m	461-1211 m
Vegetation types	Woodland and savanna	Grassland and shrubland	Grassland and shrubland	Woodland and bushland savanna
Average human density[2] (people/km^2)	16.13	16.03	18.03	12.58
Average cattle density[3] (cattle/10km^2)	973	1299	1120	642
Protected land uses	National Park; Wildlife management area	Wildlife-friendly, private and community ranches/reserves	National Reserves; Community conservancies	National Parks; Forest reserves; Trophy hunting areas; Private and community wildlife areas
Unprotected land	Communal land	Communal land	None	Communal land
Fencing	unfenced	fencing on some private reserves	unfenced	unfenced
References	Kiwango *et al.* (2018); Searle *et al.* (2021a)	Evans and Adams (2016); Kirathe *et al.* (2021)	Bhalla (2017); Kirathe *et al.* (2021)	Chamaillé-Jammes *et al.* (2007b); Loveridge *et al.* (2017a)

Data sources: [1]SRTM (2013); [2]WorldPop (2020); [3]Gilbert *et al.* (2018)

4.3.3 Predictor variables

The same set of explanatory variables that were collated for Chapter 3 (section 3.3.3), were also extracted here for each of the three study landscapes (Table 4.3). These variables were selected based on their potential influence on lion habitat use and human-lion conflict (Montgomery *et al.*, 2018a; Sargent *et al.*, 2022) and were found to be important predictors of conflict in the Ruaha landscape (Chapter 3). Where products provided data on an annual basis (Table 4.3: NPP, Tree cover, Human population count), values were extracted for the year 2020. Average annual precipitation was obtained from Worldclim, a dataset which aggregates weather station data from 1970-2000 to calculate mean annual rainfall (Fick & Hijmans 2017). When calculating distance to PA, we included all protected areas captured by the UNEP-WCMC World Database on Protected Areas (Table 4.3). This database defines a protected area as "a *geographically defined area, which is designated or regulated and managed to achieve specific conservation objectives"* (UNEP-WCMC, 2017). We, therefore, did not differentiate between governance categories such as strictly protected national parks, privately-owned conservancies, or community managed areas. All spatial data preparation and extraction on to the depredation points was conducted in QGIS v3.16.1.

Table 4.3 Variables included in the models

Explanatory variable	Source	Resolution
Mean annual precipitation (mm)	Worldclim v2. (www.worldclim.org/data)	30 arc seconds (~1km)
Annual net primary productivity (kgC/m^2/year)	MODIS: MOD17A3HGF Net Primary Productivity (https://lpdaac.usgs.gov/products/mod17a3hgfv006/)	500m
Tree cover (%)	MODIS: MOD44B Vegetation Continuous Fields (https://lpdaac.usgs.gov/products/mod44bv006/)	250m
Human population count	WorldPop UN-adjusted population counts (worldpop.org)	100m
Distance to protected area (m)	World Database on Protected Areas (https://www.protectedplanet.net)	10m
Distance to rivers (m)	Open Street Map, plus further digitising using Google Earth (https://www.openstreetmap.org)	10m
Distance to roads (m)	Open Street Map (https://www.openstreetmap.org)	10m
Distance to villages (m)	Digitised villages using Google Earth	10m

4.3.4 Data analysis

4.3.4.1 Transferability of original risk model and original parameters

To transfer the Ruaha-specific model to new landscapes, we used the final LDA models developed for bush and boma attacks in Chapter 3. Raster layers of the retained predictor variables (Bush model: distance to PA, distance to rivers, population count, tree cover, NPP, distance to village; Boma model: distance to village, population count, NPP, tree cover, annual rainfall) were resampled to a 250m resolution for each of the three new study landscapes. Using the mean coefficients of the linear discriminants for bush attacks (Chapter 3: Table 3.3) and boma attacks (Chapter 3: Table 3.5), the probability of a lion attack occurring in each raster cell was calculated using the *predict* function of the MASS package (Venables and Ripley, 2002) in R version 4.1.0 (R Core Team, 2021).

The predicted posterior probability of an attack occurring ranges between 0-1, with higher values indicating that the cell is more at risk. We split the predictive map into 3 categories: low risk (< 0.33), medium risk (0.33 - 0.66), high risk (> 0.66). To determine how successfully the models predicted conflict events in the new landscapes we examined the number of attacks that fell within high-risk areas of the map. For bush attacks, the generation of pseudo-absences allowed us to calculate the area under the curve (AUC) of a receiver operating characteristic (ROC). ROC curves map the sensitivity (probability of correctly predicting an attack location) and specificity (probability of correctly predicting an absence) for all possible values of the cut-off point between attacks and absences (Habibzadeh *et al.*, 2016; Unal, 2017). The AUC can be used as an index of the discriminating ability of the model, with a range from 0 to 1 where at 0 no events are correctly classified and at 1 all events are correctly classified. A value of 0.7 - 0.8 is considered to be acceptable and > 0.8 is considered excellent (Hosmer Jr *et al.*, 2013).

4.3.4.2 Transferability of modelling approach and predictor variables for bush attacks

As the bush attack data included both presences and absences, we were able to run new LDA models to make further comparisons between the variables affecting attack risk in each landscape. First, we ran LDAs using the same explanatory variables that were included in the Ruaha models (see 4.3.4.1). This allowed us to examine if the same drivers could be used to develop risk maps in each landscape using the LDA approach, even while the exact discriminant functions may change. As in Chapter 3 (section 3.3.4.1), we used a bootstrapping procedure where 90% of the data was randomly selected and the LDA was run with this subset. We used the resulting discriminant function to reclassify the data into attack and non-attack events using the *predict* function and calculated the accuracy of the model (the percentage of cases correctly assigned to attack and non-attack groups) and the AUC. We repeated this process 500 times and then calculated the mean and the confidence intervals of the classification accuracy and the AUC. We performed this procedure separately for the Laikipia, Samburu and Hwange landscapes.

Second, we ran LDAs including new explanatory variables based on forward stepwise selection using the *greedy.wilks* function of the *klaR* package (Weihs *et al.*, 2005). This approach uses the Wilk's lambda criterion (Mardia *et al.*, 1979) to select which new variables should be included in a simplified model (see 3.3.4.1). Variables retained in the model were significant in separating attack and non-attack events. Following reduction of the variable set, we then followed the same bootstrapping procedure as above to implement LDAs on the retained set of predictor variables and extract mean accuracies and AUCs with confidence intervals.

4.4 Results

4.4.1 Validity of original maps for identifying future conflict risk in Ruaha

In the Ruaha landscape, of the 22 bush attacks that have occurred since May 2020, 73% fell within high-risk areas (>0.66) of the map developed using the LDA approach, and 77% fell within high conflict areas of the INLA map. For boma attacks, 70% of the 42 new attacks occurred within high-risk areas as identified by the LDA, and 84% within risk areas identified by the INLA map. Of the recent depredations, only 1 occurred at a boma that had also been attacked in the first modelling exercise (Chapter 3). The remaining 41 attacks occurred at new locations. This suggests that the maps are relatively robust in identifying likely locations of conflict events in the Ruaha landscape. The attack locations that fell outside of the high-risk areas differed between the INLA and LDA maps, showing the utility of including both approaches to avoid under-estimation of risk. When combining both maps, only 5% of bush attacks and 9% of boma attacks fell outside high-risk areas. However, it is worth noting that the combined maps identified the majority of the village land (88%) as being high risk for bomas (section 3.4.3).

4.4.2 Transferability of Ruaha-derived risk model for conflict prediction in other landscapes

We find that predictively mapped high-risk areas in the new landscapes do not show high overlap with attack locations. This is particularly true for the Samburu and Hwange landscapes where < 50% of the conflict events fell within apparently high-risk areas (Table 4.4). For bush attacks, AUCs were ~ 0.5 for all three landscapes, meaning that the map of predicted conflicts was not able to discriminate between attack and non-attack events (Table 4.4).

Table 4.4 Summary of results examining the accuracy of the original, Ruaha-derived LDA model when transferred to new landscapes. High-risk areas are those with a predicted probability of conflict > 0.66.

Landscape	Attack location	% attacks falling in high-risk areas	AUC
Laikipia, Kenya	Bush *(n=132)*	54.5%	0.56
	Boma *(n=205)*	66.8%	
Samburu, Kenya	Bush *(n=69)*	30.4%	0.53
	Boma *(n=19)*	26.3%	
Hwange, Zimbabwe	Bush *(n=597)*	41.7%	0.58
	Boma *(n=132)*	30.3%	

4.4.3 Transferability of modelling approach to predict bush attacks in other landscapes with locally specific predictors

The locally calibrated models, using the same predictor variables but generating new coefficients for the linear discriminants, were more accurate at predicting conflict locations in the new landscapes than the direct transfer of the original model (Fig. 4.2). AUCs of > 0.7 for the Laikipia and Samburu landscapes indicate that the models had acceptable discriminating ability (Table 4.5; Fig. 4.2). However, for the Hwange landscape the new LDA still had a weak discriminating ability with an AUC of 0.65 and only 57% of the data correctly classified (Table 4.5; Fig. 4.2). For the Laikipia landscape, the mean error rate was highest for false positives (18%, 95% CI [16, 21]), i.e., the model was predicting an attack where none had occurred (overpredicting). For the Ewaso landscape, the opposite was true and the mean error rate was highest for false negatives (16%, 95% CI [13, 19]).

Table 4.5 Mean coefficients of the linear discriminants, AUC values and classification accuracy obtained from a bootstrapped LDA of bush attack locations using the same predictor variables as the final Ruaha model. 95% confidence intervals are shown in square brackets.

Variable	**Ruaha**	**Laikipia**	**Samburu**	**Hwange**
Distance to PA	-1.02e-04	4.33e-05	n/a**	-1.61e-04
Distance to Rivers	-2.53e-04	-3.88e-04	-6.75e-04	-8.44e-05
Population Count	-6.55	-3.77	0.36*	-0.62*
Tree Cover	-0.16	0.03	-0.04*	-0.07
NPP	3.51	5.00	-4.16	4.36
Distance to Village	9.57e-05	-1.08e-05*	-9.91e-06*	1.13e-05
AUC	0.82 [0.79, 0.84]	0.79 [0.77, 0.81]	0.74 [0.70, 0.77]	0.65 [0.64, 0.66]
Classification accuracy	75% [72, 78]	69% [67, 72]	73% [69, 76]	57% [54, 60]

*95% confidence intervals overlapped zero

**Distance to PA was removed from the Samburu model as all points fell within PAs

Depredation risk was higher closer to rivers in all four landscapes (Table 4.5). However, for the remaining predictor variables the direction of the relationship differed between landscapes. For example, in Samburu, in contrast to the other study sites, net primary productivity exhibited a negative relationship with depredation risk (Table 4.5), while in Laikipia depredation risk was higher further from PAs (Table 4.5).

The *greedy-wilks* function revealed that the discriminatory power of the selected predictor variables differed between the four landscapes. Importantly, different variables were included in each of the final models (Table 4.6). Each landscape was distinct, for example, proximity to rivers was important in both Laikipia and Samburu but not Hwange (Table 4.6). Distance to roads was identified as a driver of risk in Samburu and Hwange, with attacks more likely closer to roads, but was not included in the Laikipia or original Ruaha models. Annual rainfall was important across all three of the new landscapes, although it was not a significant predictor in Ruaha (Table 4.6). Where the same variables were included across landscapes, the directions of the relationships with depredation risk were consistent except in the case of rainfall, which was negatively associated with depredation in Laikipia and Samburu, but positively associated in Hwange (Table 4.6).

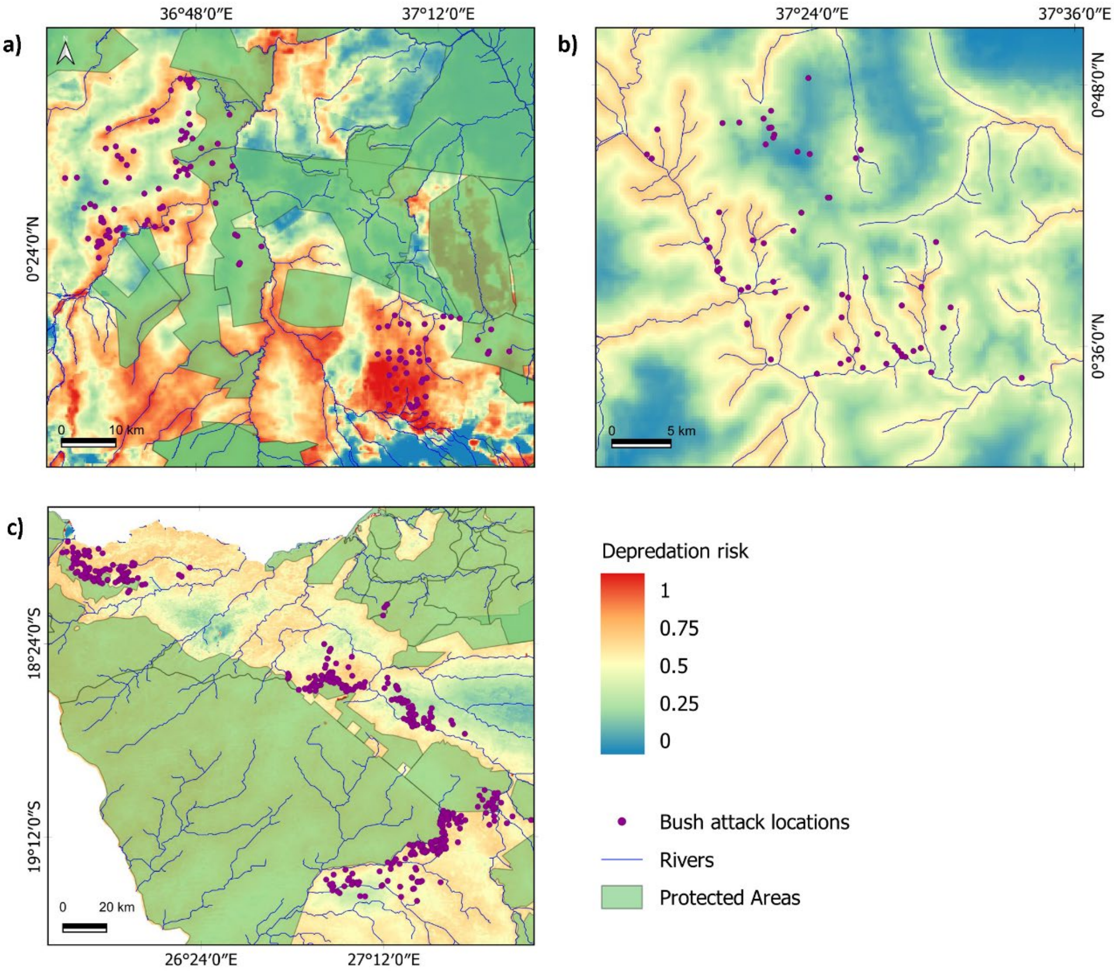


Figure 4.2 Predictive maps of depredation risk for grazing livestock in a) Laikipia, Kenya, b) Samburu, Kenya, and c) Hwange, Zimbabwe. High risk (in red) represents areas where attacks are more likely to occur. Maps were generated through linear discriminant analysis using the same predictor variables that were significant in the Ruaha landscape. These included: distance to PAs, rivers and villages, net primary productivity, tree cover and human population count. The Samburu study site (b) fell entirely within protected areas; hence protected areas are not shown on the map. Number of attack points for each landscape: a) Laikipia = 132; b) Samburu = 69; c) Hwange = 597.

Running LDAs with the new predictor variables did not improve the discriminatory power of the models for the Laikipia and Hwange landscapes, as the confidence intervals for both the AUC and the classification accuracy (Table 4.6) overlapped those returned when the model was run with the variables used in Ruaha (Table 4.5). For the Samburu landscape there was an improvement in the AUC when new variables were included, although the classification accuracy of the model remained the same (Table 4.6).

Table 4.6 Mean coefficients of the linear discriminants, AUC values and classification accuracy obtained from a bootstrapped LDA using new predictor variables, determined via stepwise selection with *greedy.wilks*. 95% confidence intervals are shown in square brackets. - indicates that variable was not included in the final model

Variable	**Ruaha**	**Laikipia**	**Samburu**	**Hwange**
Distance to PA	-1.02e-04	-	-	-1.01e-04
Distance to Rivers	-2.53e-04	-4.28e-04	-4.36e-04	-
Population Count	-6.55	-2.95	-	-
Tree Cover	-0.16	-	-	-
NPP	3.51	6.23	-	-
Distance to Village	9.57e-05	-	6.45e-05	-
Distance to Roads	-	-	-2.77e-04	-5.83e-04
Annual Rainfall	-	-4.64e-03	-0.006	7.46e-03
AUC	0.82	0.79	0.81	0.66
	[0.79, 0.84]	[0.77, 0.81]	[0.79, 0.83]	[0.65, 0.67]
Classification accuracy	75%	69%	73%	62%
	[72, 78]	[67, 72]	[70, 76]	[60, 63]

4.5 Discussion

The use of spatial risk modelling to map human-wildlife conflict across landscapes is a valuable method for identifying key drivers and patterns in conflict risk. Maps created to characterise hotspots of lion-livestock conflict in the Ruaha landscape of Tanzania, successfully captured more recent depredation events and could provide a useful tool for guiding mitigation strategies. While the exact final models used in Ruaha were not successful in predicting conflict locations in new landscapes, updating the Linear Discriminant Analysis (LDA) using the same predictor variables but with locally derived coefficients of discrimination, led to acceptable discriminating ability for two Kenyan study sites. Furthermore, addition of new predictor variables identified as potentially important in these landscapes did not significantly improve the models' accuracy in predicting depredation locations. This suggests that some variables are important across contexts and using the LDA approach with these common drivers could be successful for identifying conflict hotspots in multiple landscapes. However, this was not the case for the Hwange landscape in Zimbabwe, where models created with neither the original nor the landscape-specific variables were successful in predicting attack locations. This indicates that some additional, unmeasured variable(s) had an influence on depredation in this landscape and points towards the need for context-specificity in analysing drivers of human-wildlife conflict and predicting hotspots of conflict for subsequent management.

The process of transferring ecological models in time and space could support conservation and resource management in the face of limited funding, data deficiencies and accelerating climate and land use change (Mouquet *et al.*, 2015; Yates *et al.*, 2018). However, there are several fundamental challenges which impact on model accuracy and precision in novel contexts. These include issues such as: whether models are trait or taxon specific, data quality and sampling biases, environmental dissimilarity, nonstationary species-environment interactions, and model complexity (Wenger and Olden, 2012; Zurell *et al.*, 2012; Yates *et al.*, 2018; Regos *et al.*, 2019). Given that our model was grounded in mechanisms expected to drive depredation, was taxon-specific, and the range of values of the predictor variables was similar across landscapes, this suggests that some other factors may be at play in limiting transferability.

4.5.1 Environmental dissimilarity

Novel conditions, either just beyond those observed in the original model or those that are extremely dissimilar, may result in poor model transferability. It is therefore necessary to understand similarities and differences in both the environmental and anthropogenic contexts of each landscape and how these might influence human-lion conflict. One factor which appears to be important across locations is water availability, either via distance to rivers or rainfall. Proximity to water has been shown to be a key driver of lion habitat use (Davidson *et al.*, 2012; Abade *et al.*, 2014b; Sargent *et al.*, 2022), likely as the distribution of herbivores in semi-arid landscapes is largely influenced by the availability of surface water (Valeix *et al.*, 2009; de Boer *et al.*, 2010). All four of the landscapes examined here are semi-arid to arid, with similar levels of rainfall (average annual rainfall ~500-700mm; Fick and Hijmans (2017)), although Samburu is the driest (Kirathe *et al.*, 2021) and all can experience high inter-annual variation and drought (Valeix, 2011; Ndiritu, 2021).

However, the availability and distribution of surface water differs between the landscapes. In the Kenyan and Tanzanian study sites, large permanent rivers and their associated tributaries are the main sources of water for wildlife in the area (Pas, 2018; Western *et al.*, 2019) and other perennial sources of water exist in the form of springs and waterholes (Epaphras *et al.*, 2007; Bhalla, 2017). This is in contrast to the Zimbabwean study site, where a key feature of Hwange National Park is the absence of any perennial rivers and the near absence of any perennial water sources (Valls Fox, 2015). Instead, boreholes have been installed across the landscape and are used to pump groundwater into both natural and artificial waterholes during the dry season (Chamaillé-Jammes *et al.*, 2007a; Valls-Fox *et al.*, 2018). This represents a key difference in surface water access between study sites, and while some of these waterholes may be captured by our digitised river layer, many are not. Thus, the lack of georeferenced data on artificial surface water points in this landscape could be contributing to the poor performance of our models for predicting conflict in the Hwange landscape.

Differences in habitat types and vegetation cover present in each landscape could also be driving differences in conflict events. Lions exhibit considerable flexibility in their use of different habitat types, with some studies suggesting that lions select for more open habitat such as grassland (Spong, 2002; Cristescu *et al.*, 2013), while others indicate that, particularly when engaged in hunting behaviour, lions prefer areas with increased vegetation cover (Hopcraft *et al.*, 2005; Davidson *et al.*, 2012). Examination of the 2019 Copernicus Global Land Cover Dataset, a dynamic land cover product provided at 100m resolution (Buchhorn *et al.*, 2020), revealed that the Samburu and Laikipia landscapes comprised almost solely shrubland and grassland (Appendix C1). By contrast, the Ruaha landscape was covered by shrubland and woodland with some areas of cropland. The Hwange landscape was dominated by open woodland, also with some areas of shrubland and cropland (Appendix C1). While we included a measure of tree cover in our model, this variable may have failed to capture finer scale differences in vegetation composition and structure which affect lion habitat use and livestock distributions.

The extent of cropland across the study sites reflects the differences in livelihood strategies employed in these areas. In Hwange, agro-pastoral subsistence farming is the dominant economic activity, meaning that while livestock production is important, cropland is also widespread (Guerbois *et al.*, 2013; Nhemachena *et al.*, 2014). Similarly, Ruaha contains a mixture of ethnic groups, including both farmers and traditional pastoralists (Dickman, 2008; Dickman *et al.*, 2014). In contrast, in Samburu and Laikipia pastoralism has dominated as a livelihood strategy for hundreds of years and >80% of the population rely on livestock production as their primary source of income (Butynski and Jong, 2014; Lenaiyasa *et al.*, 2020). These differences between landscapes result in contrasts in livestock distributions and land management strategies which are likely to impact the way humans and wildlife interact.

For example, while all of the study sites have similarly low average population density (WorldPop, 2020) and human footprint index (a cumulative measure of human pressures including infrastructure, population densities, crop and pasture lands; Venter *et al.* (2016b)), the land use types found within the study areas differ considerably. In the Samburu landscape the entire study site fell within PAs, according to the World Database on Protected Areas (UNEP-WCMC and IUCN, 2021), due to the presence of multiple community conservancies. These conservancies are ostensibly community-run institutions in which members transform sections of land into conservation areas and promote tourism enterprises (Bersaglio and Cleaver, 2018; Fox, 2018). Community conservancies also form a part of the Laikipia landscape, alongside both community-owned and private livestock ranches many of which are managed as 'pro-wildlife' ranches with involvement in tourism and conservation (Sundaresan and Riginos, 2010; Yurco, 2017). Thus, the Samburu and Laikipia landscapes provide a large network of contiguous space which supports sizeable wildlife populations (Butynski and Jong, 2014; Bersaglio and Cleaver, 2018) and the lack of separation between people and wildlife may result in differences in carnivore habitat use which affect drivers of conflict (Mogensen *et al.*, 2011; Oriol-Cotterill *et al.*, 2015a).

This integrated approach, where human settlements and livestock form part of the landscape for wildlife (Georgiadis *et al.*, 2007; Kinga *et al.*, 2018), differs somewhat to the land use of Ruaha, Tanzania. This landscape contains a Wildlife Management Area (WMA), Tanzania's model for community-based conservation which involves villages setting aside a portion of their communal land for wildlife conservation purposes (Kiwango *et al.*, 2015). However, this comes with restrictions and typically forbids access for activities such as livestock grazing and collection of natural products (Homewood *et al.*, 2020; Keane *et al.*, 2020). This means that wildlife and livestock are notionally separate, interacting only when wildlife leaves the WMA and other protected areas.

The landscape in Hwange, Zimbabwe contains a mosaic of different land use types including National Parks, forest reserves, trophy hunting concessions, and private and community land managed for wildlife tourism (Loveridge *et al.*, 2017b). Thus, while the system in this area is complex, it resembles the Ruaha landscape in that wildlife and livestock inhabit different areas and large carnivores remain largely inside the PAs, with little wildlife permanently resident in communal lands (Loveridge *et al.*, 2017a; Western *et al.*, 2019). This may explain why proximity to PAs, and thereby resident wildlife populations, was identified as a key driver of conflict risk in our models for Ruaha and Hwange but not Samburu and Laikipia.

4.5.2 Non-static relationships between species and environment

Transfer of ecological models also assumes that the underlying species-environment relationships are stationary, both at the original site and beyond it (Yates *et al.*, 2018). However, species' responses to environmental conditions are rarely static and it is important to consider the underlying mechanisms that affect the response variable. Here, we selected environmental and anthropogenic predictors that are known to affect lion habitat use and, therefore, human-lion conflict (Montgomery *et al.*, 2018a; Sargent *et al.*, 2022). However, the relationship between these variables and lion habitat use can vary non-linearly with resource availability, life stage and human activity (McLoughlin *et al.*, 2010; Elliot *et al.*, 2014a; Yates *et al.*, 2018). For example, while lions may be considered habitat-generalists, occupying a broad-range of biomes across East, West, Central and Southern Africa (Bauer *et al.*, 2016), they exhibit highly adaptable behaviour and resource use in response to changes in prey abundance and anthropogenic risk in a given landscape. In human-dominated landscapes, lions have been found to use areas of increased vegetation cover, further from water and to abandon kills more frequently (Mogensen *et al.*, 2011; Schuette *et al.*, 2013). Lions also adjust their behaviour to avoid temporal overlap with human activity and to access livestock as secondary prey (Valeix *et al.*, 2012a; Oriol-Cotterill *et al.*, 2015a).

Several studies have documented increased livestock depredation in the wet season (Mponzi *et al.*, 2014; Kuiper *et al.*, 2015; Kissui *et al.*, 2019). Increased water availability means that wild prey are more widely dispersed and in better condition and livestock may therefore offer an alternative source of prey when wild herbivores become scarce, or carnivores may come into more frequent contact with livestock when following migratory prey (Patterson *et al.*, 2004; Valeix *et al.*, 2012a; Mkonyi *et al.*, 2017c). Furthermore, in Hwange, cattle herding practices exhibit spatio-temporal fluctuations, with cattle driven further away from homesteads, closer to PA boundaries, in the wetter, crop-growing months in order prevent damage to crop fields (Kuiper *et al.*, 2015). Thus, resulting in higher rates of depredation in the wet season (Kuiper *et al.*, 2015). Inclusion of a temporal component would therefore be an important next step in model development to begin to examine some of the non-static patterns in livestock depredation risk. This would enable assessment of possible seasonal and diurnal changes in conflict risk across landscapes.

4.5.3 Data quality and gaps

Additionally, there may be some other unmeasured variable(s) affecting conflict risk which are absent from our modelling. For example, although net primary productivity frequently correlates with herbivore biomass (Pettorelli *et al.*, 2009; Fløjgaard *et al.*, 2021), we do not have explicit data on wild prey abundance and distributions in these landscapes. Given that lion habitat use is largely driven by prey abundance (Sargent *et al.*, 2022) this lack of information on prey availability limits our fine scale understanding. While we can assume that prey congregate near water sources there may be seasonal changes in distribution which affect depredation risk, as highlighted above, and wild prey density is also influenced by land use and competition and displacement by livestock (Valls-Fox *et al.*, 2018; Kirathe *et al.*, 2021).

A further limitation of our model is the lack of information on livestock distributions and densities, the influence of which remains largely unstudied in the literature on lion habitat use (Sargent *et al.*, 2022). The Gridded Livestock of the World (GLW) database maps the global distribution of major livestock species and suggests that mean cattle density is lowest in the Hwange study site, while remaining comparable across the remaining three landscapes (Table 4.2; Gilbert *et al.* (2018)). This tallies with the more mixed livelihood strategies in this region in comparison to the predominance of pastoralism in Kenya. However, the GLW product is mapped at a coarse scale (10 x 10 km) and is a derived variable using some of the predictors that we have already included, such as rainfall, slope, and vegetation productivity (Gilbert *et al.*, 2018). Characterising livestock densities and grazing patterns at finer spatial scales using methods such as participatory mapping of grazing areas (Basupi *et al.*, 2017), livestock GPS collars (Kuiper *et al.*, 2021), spoor surveys (Everatt *et al.*, 2019) and camera traps (Beattie *et al.*, 2020), would enable livestock density to be incorporated into models and allow for more reliable generation of absence data.

The use of pseudo-absences for non-attack events may have affected model accuracy. This is a common difficulty in studies which examine species distributions, where absences cannot be inferred with certainty and false absences can bias results (Hirzel *et al.*, 2002; Gibson *et al.*, 2007). Our pseudo-absence points may be unreliable if they fall in locations where a kill occurred but was not reported, or in areas where no livestock is present. This is a particular issue in the new study sites, where we are less familiar with the distributions of people and wildlife. In particular, in the Kenyan study sites livestock is present inside several of the PAs however no information exists as to which areas are allocated for grazing and which are maintained for conservation purposes. Detailed understanding of livestock distributions within each landscape would allow for the generation of accurate absence points, i.e., locations where livestock is grazed but no lion attacks have occurred.

As noted in Chapter 3, a further complication when analysing spatial data is the potential for spatial autocorrelation (Miller, 2015). This could result in lion attacks exhibiting clustering at close distances which violates the assumptions of normality required by LDA models. Given that lions do not pursue prey randomly and exhibit behaviourally grounded hunting strategies (Hayward and Kerley, 2005; Hopcraft *et al.*, 2005; Valeix *et al.*, 2011) we might expect there to be spatial dependence between points. However, substantially less is known about the hunting behaviour of lions in response to domestic prey, and it is possible that they respond randomly to encounters with livestock (Hoffmann *et al.*, 2019). Although the LDA approach produced accurate maps for the Ruaha landscape despite the presence of spatial clustering (see 3.4 Results), a useful next step would be to examine the presence of clustering at the new study sites and develop models that include a spatial component (see 3.3.4; Rue *et al.* (2009); Lindgren *et al.* (2011)).

4.5.4 Conclusions

The LDA modelling approach used here, while easily applicable across contexts for which depredation data and remotely sensed landscape attributes are available, demonstrated mixed success in accurately predicting conflict locations. The use of this approach revealed that some key predictor variables, such as distance to rivers and precipitation, can be used to identify high-risk areas across landscapes. However, we highlight the necessity of considering context-specific factors and interactions, such as differences in land use and water access which impact on human and carnivore space use. We suggest that freely available global datasets, such as those used here, be integrated with more detailed local information. For example, where researchers have information on livestock distributions and artificial water points in their study landscapes, incorporating this data would likely result in improved model outputs. In particular, we emphasise the importance of collecting data on both wild prey and livestock abundance and distributions, which remain among the least studied dimensions of human-lion conflict (Montgomery *et al.*, 2018a; Kuiper *et al.*, 2021; Sargent *et al.*, 2021).

While the creation of range-wide maps to identify areas most at risk of human-wildlife conflict can be useful for judging where to focus conservation efforts and funding at a broad scale (Di Minin *et al.*, 2021), the results of these assessments may be too coarse to inform meaningful management actions at the landscape or community scale (Montgomery *et al.*, 2018b). Techniques which can be easily applied to produce accurate risk maps at a finer scale could produce valuable results for management and mitigation of conflict at a local level. The LDA approach displays some potential as a simple method which can be transferred across contexts where landscape attributes are similar. However, local context is important and obtaining accurate data on site-specific variables is key. Using comparable research techniques across studies will enable robust comparisons to identify common conflict drivers and advance our understanding of human-wildlife conflict to facilitate actions which reduce livelihood losses and strengthen conservation efforts (Miller, 2015; Montgomery *et al.*, 2018a).

Chapter 5. Trialling the use of an experimental game to examine pastoralist decision-making and preferences for coexistence strategies in response to human-lion conflict.

Maasai pastoralists playing the ‘lion game’ near Tungamalenga village, Ruaha, Tanzania.

5.1 Abstract

1. Reconciling conflicts between wildlife conservation and other human activities is a pervasive, multifaceted issue. Large carnivores, such as the African lion (*Panthera leo*) are often the focus of such conflicts as they have significant ecological and cultural value but impose severe social and financial costs on the communities that live alongside them.
2. To effectively manage human-lion conflict, it is vital to understand stakeholder decision-making and preferences regarding mitigation techniques and coexistence strategies.
3. We used a novel experimental game framed around lions and livestock protection, played across 8 villages in Tanzania, to examine stakeholder behaviour in response to three incentive structures: support for non-lethal scaring and individual- and community-level subsidies for provision of wildlife habitat.
4. We found that non-lethal scaring was the preferred mitigation strategy and that individual subsidies increased the provision of wildlife habitat. Subsidies that were shared and conditional on other community members' decisions were less effective at increasing habitat choices. Player characteristics and attitudes appeared to have little influence on game behaviour. However, there was some evidence that gender, wealth, perceptions of respect, and the behaviour of other players affected decision-making.
5. Achieving success in managing conservation conflicts requires genuine stakeholder participation leading to mutually beneficial results. Our findings suggest that, while incentive-based instruments can promote pro-conservation behaviour, these may be more effective when targeted at individuals rather than groups. We demonstrate how experimental games offer a practical and engaging approach that can be used to explore preferences and encourage discussion of conflict management.

5.2 Introduction

Negative interactions between people and wildlife, often termed human-wildlife conflicts (HWC), emerge when the presence or behaviour of wildlife poses actual or perceived, direct, and recurring threat to human interests or needs, leading to negative impacts on people and wildlife (Nyhus, 2016; IUCN, 2020). Examples include damage to crops and predation on livestock (Pozo *et al.*, 2021), direct attacks on humans (Packer *et al.*, 2019), disease transmission between wildlife and people (Gibb *et al.*, 2020), and retaliatory killing or lethal control of the species causing the conflict (Ontiri *et al.*, 2019). Managing HWC to mitigate negative outcomes for biodiversity and human well-being is becoming increasingly important as anthropogenic pressures on ecosystems have escalated (Madden, 2004), rapidly encroaching into remaining wilderness areas (Watson *et al.*, 2014) and increasing risk of contact between humans and wildlife.

HWCs exemplify the fundamental challenge of reconciling local concerns for security and development, with international concerns for saving threatened species (Treves *et al.*, 2006; Peterson *et al.*, 2010). HWCs can therefore be reframed as human-human conflicts or, more broadly, conservation conflicts (Redpath *et al.*, 2015), i.e., conflicts between stakeholders with differing goals and values rooted in economic, socio-political and cultural history (Redpath *et al.*, 2013). In East, West, Central and Southern Africa, conservation conflicts can be particularly profound, as a large proportion of the planet's remaining megafauna (Du Toit and Cumming, 1999; Malhi *et al.*, 2016) exists alongside a growing human population with associated development needs (Laurance *et al.*, 2014; Milder *et al.*, 2014).

Apex predators such as the African lion (*Panthera leo*) are often the focus of conservation conflicts. Lions are a conservation flagship species, with important ecological, cultural, and economic value (Di Minin et al. 2013; Ripple et al. 2014; Stolton and Dudley 2019). Yet they pose a severe threat to human life (Packer *et al.*, 2005a; Sommers *et al.*, 2010) and can incur considerable social and financial costs on the communities who live alongside them (Packer *et al.*, 2005a; Kissui, 2008). Livestock depredation is widespread, with lions targeting culturally and economically valuable cattle (Muriuki *et al.*, 2017). Attacks on humans, although rare, generate intense hostility and greatly increase levels of fear and perceptions of personal risk (Kushnir and Packer, 2019). Other impacts, including mental health issues and opportunity costs due to movement restriction or the need for guarding are less well understood (Barua *et al.*, 2013; Dickman and Hazzah, 2016). Lion populations have declined by > 43% over the last two decades (Bauer *et al.*, 2016), with local extinctions in several regions of the species' range (Riggio *et al.*, 2013). Realised or perceived negative impacts of lions on communities and subsequent retaliatory killing is a key driver of these declines (Dickman *et al.*, 2014; Bauer *et al.*, 2016).

Identifying solutions for managing human-lion conflict is, therefore, a priority both for people and wildlife. Conservation advocates, perhaps primarily natural scientists, tend to assert their interests through legislation and enforcement (Redpath *et al.*, 2013), which renders lethal retaliation illegal and/or socially unacceptable (Treves *et al.*, 2006). To reduce livestock losses to lions, technical interventions are often implemented and include physical barriers, improved guarding, and non-lethal deterrents such as visual and auditory scaring devices (Lichtenfeld *et al.*, 2014; Miller *et al.*, 2016b; Lesilau *et al.*, 2018). Conservation performance payments, providing financial incentives conditional on a specific conservation outcome, have been suggested as an additional strategy to encourage human-wildlife coexistence (Zabel and Holm-Müller, 2008; Dickman *et al.*, 2011). Examples include payments based on the number of carnivore reproductions that occur on village land (Zabel and Holm-Müller, 2008), or incentives to protect habitats and set aside areas of land to be free of human use (Mishra *et al.*, 2003; Nelson *et al.*, 2010). The effectiveness of all of these management interventions varies widely and is context-dependent (Miller *et al.*, 2016b; Eklund *et al.*, 2017) but particularly for performance payments, there are limited operational examples from which to assess effectiveness and acceptability (Nelson *et al.*, 2010; Zabel and Engel, 2010).

Experimental games are emerging as a low risk, low-cost tool in the exploration of conservation conflicts and acceptable mitigation solutions (Redpath *et al.*, 2018; Rakotonarivo *et al.*, 2021a; Rakotonarivo *et al.*, 2021b). Games allow affected stakeholders to explore the potential of various mitigation methods, including those that are sensitive, such as lethal control, in a safe and relaxed atmosphere (Rakotonarivo *et al.*, 2021a). Experimental games have been used to understand the effects of payments and incentives in a range of situations, including harvesting of fish from protected areas (Travers *et al.*, 2011), pesticide use and cooperative management (Bell *et al.*, 2016) and forest resource use (Andersson *et al.*, 2018). Typically, they model the use of a static, common-pool resource (Travers *et al.*, 2011; Salk *et al.*, 2017; Andersson *et al.*, 2018). More recently, games have begun to incorporate spatial and temporal dynamics, which represent ecological processes more realistically at landscape scales (Bell and Zhang, 2016; Meinzen-Dick *et al.*, 2016; Rakotonarivo *et al.*, 2021a).

In this study, we developed an experimental game framed around lions and livestock protection, for a case study of rural, pastoralist communities in Tanzania. First, we use the game to explore individual preferences for coexistence strategies and to test the effects of three incentive structures on the players' propensity to scare lions using non-lethal deterrents and to provide wildlife habitat. Second, using structured survey data we explore the relationship between within-game behaviour and attitudes/characteristics known to affect stakeholder support for conservation, including wealth, education, experience of stock loss and perceptions of the well-being benefits of lions (Kideghesho *et al.*, 2006; Hazzah *et al.*, 2017).

The three incentive treatments include: 1) Support to compensate the cost of non-lethal scaring; 2) Individual subsidies for provision of wildlife habitat; and 3) Community subsidies for provision of wildlife habitat. We tested two main hypotheses: 1) We expected that under the scenario of 'no incentive', stakeholders would prefer the use of non-lethal scaring over sacrificing land for wildlife habitat; 2) Under the 'provision of habitat subsidies' scenario, we expected that the number of habitat choices would increase, and more so when subsidy levels were higher. However, increase in habitat provision may vary based on whether the subsidy is allocated at an individual or group level (Narloch *et al.*, 2012; Salk *et al.*, 2017; Gatiso *et al.*, 2018). To our knowledge, this is the first time a game approach has been used to explore the management of human-carnivore conflict.

5.3 Methods

5.3.1 Study area and population

We conducted experimental games in village land adjacent to Ruaha National Park (RNP) and Pawaga-Idodi Wildlife Management Area (WMA), in the Iringa Rural District of Tanzania (Fig. 5.1). The Ruaha landscape is considered a high priority region for carnivore conservation and is home to significant numbers of lion, cheetah, leopard, and spotted hyena (Abade *et al.*, 2014a). The village land located on the south-east border of RNP is inhabited by over 60,000 people from at least 30 different ethnic groups, with livelihoods predominated by agriculture and pastoralism (Abade *et al.*, 2019). There are no fences separating RNP and the WMA from the village land and, thus, wildlife can move freely. Local communities previously reported highly negative attitudes towards lions and other carnivores due to their predation on livestock (Dickman *et al.*, 2014). Although depredation accounts for a relatively small percentage (~ 9%) of total monthly stock loss, direct experience of depredation is widespread (Dickman *et al.*, 2014).

During the day, livestock graze across the village land, typically guarded by a herder and untrained guarding dogs. At night, herds are contained in enclosures made predominantly from thorn bushes. The use of non-lethal deterrents such as lights, horns or fire is relatively rare in this area (Abade *et al.*, 2014a). Traditional lion hunts were formerly a rite of passage for some ethnic groups in this landscape. These traditional hunts are now uncommon (though they still occur, with two events in 2019) and have sometimes been forbidden by tribal elders. Levels of retaliatory and preventative killing remain high (27 events in 2019; Grau pers. comm). There can also be mixed motivations, where retaliatory hunts also serve some traditional purpose, with young men receiving community accolades and sometimes gifts for killing problem lions (A. Dickman 2021, pers. comm.).

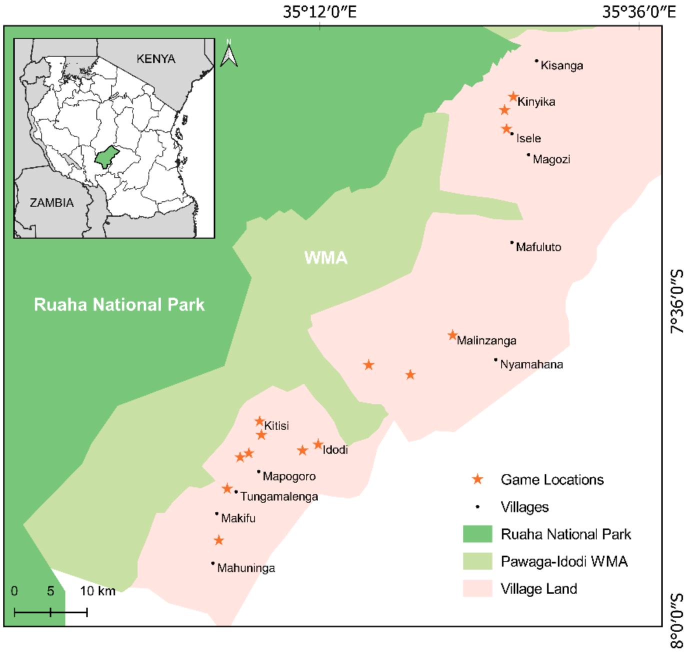
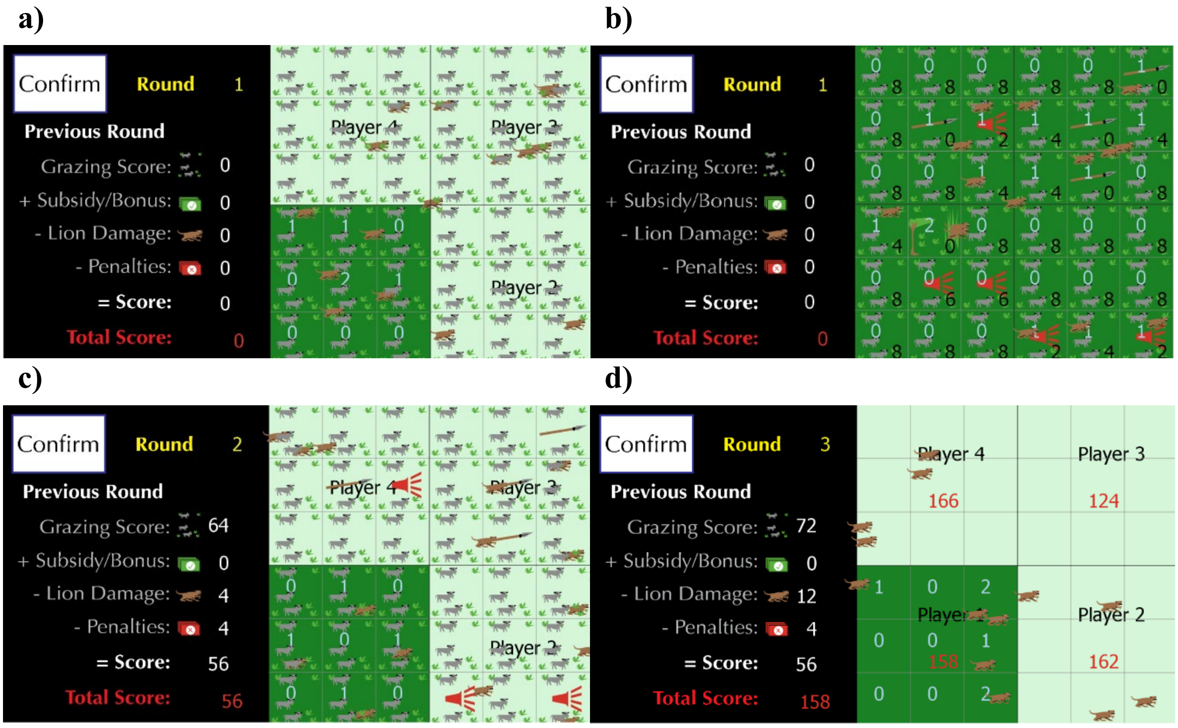


Figure 5.1 Study area in the Iringa Rural District of Tanzania showing the Ruaha National Park, the Pawaga-Idodi Wildlife Management Area and the village land. Inset indicates the location of Ruaha National Park within Tanzania. Experimental games were conducted at 14 locations across 8 villages.

The Ruaha Carnivore Project (RCP), a research organisation established in 2009 (ruahacarnivoreproject.com), provides several benefits to local communities including assistance for building wire bomas, school scholarships and employing local warriors as ‘Lion Defenders’ to assist with livestock protection. A camera-trapping initiative, known as ‘community camera-trapping’ is also used to link community benefits directly with wildlife presence. Camera traps are placed on village lands and each village receives points for any wildlife photos captured. At the end of each quarter, these points are translated into benefits requested by the community such as medical supplies, school supplies and veterinary medicines.

5.3.2 Game design

We developed an experimental game to be played by four participants using tablet computers linked by a mobile hotspot. The game was created using NetLogo (Wilensky, 1999), a multi-agent modelling environment, and adapted from Goosebumps, a coordination game focussed on crop management and goose conservation (Rakotonarivo *et al.*, 2021a). Each of the four players makes management decisions on 9 cells arranged in a 3x3 contiguous section of the game board (Fig. 5.2). In each of these cells a player can either: 1) graze livestock; 2) graze livestock and scare lions off cells using non-lethal methods (horns, lights); 3) graze livestock and attempt to spear lions in the cell (lethal control); 4) leave the cell free from livestock to provide habitat for lions and wild prey (lion habitat). Each option has different costs, benefits, and parameter settings (Table 5.1). The parameter values and game settings were pre-tested by ~ 50 players, made up of community members and RCP staff, prior to data collection.


a)

Confirm Round 1
Previous Round
Grazing Score: 0
+ Subsidy/Bonus: 0
- Lion Damage: 0
- Penalties: 0
= Score: 0
Total Score: 0

b)

Confirm Round 1
Previous Round
Grazing Score: 0
+ Subsidy/Bonus: 0
- Lion Damage: 0
- Penalties: 0
= Score: 0
Total Score: 0

c)

Confirm Round 2
Previous Round
Grazing Score: 64
+ Subsidy/Bonus: 0
- Lion Damage: 4
- Penalties: 4
= Score: 56
Total Score: 56

d)

Confirm Round 3
Previous Round
Grazing Score: 72
+ Subsidy/Bonus: 0
- Lion Damage: 12
- Penalties: 4
= Score: 56
Total Score: 158

Player 4 166
Player 3 124
Player 1 158
Player 2 162

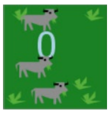
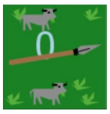
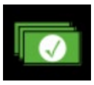
Figure 5.2 Examples of the game screen at various stages of the game. **a)** Bottom left corner of the landscape is the active player at the start of Round 1; the white number in each cell is the number of lions in the cell. **b)** Game screen after all four players have made decisions; management decisions of each player are visible; the black numbers show the score for each cell. **c)** Game screen at the start of Round 2; actions taken by other players in previous turn are visible; the scores of the active player in the previous round are shown in the left-hand panel. **d)** Game screen showing the total score for each player at the end of the practice game.

In each game round, there are a number of lions in the landscape which select cells based on the ‘attractiveness’ of the land use options. Each management choice has a ‘weight’ assigned to it, with bigger weights meaning higher probability of attracting lions (Table 5.1). Wildlife habitat is the most attractive option, given that lions will avoid people and hunt wild prey where possible (Patterson *et al.*, 2004; Valeix *et al.*, 2012a). Lion habitats have a ‘neighbourhood effect’ of adding to the weight of any cell around them (Table 5.1), affecting 8 cells in total. This captures the increased likelihood of livestock depredation near the boundaries of protected areas and natural habitats (Loveridge *et al.*, 2010). Lions on grazed cells generate livestock losses (Table 5.1). The participant’s overall score on their set of $n = 9$

squares is calculated as:

$$Score = \sum_{n=1}^{9} Grazing\ score_n + Subsidy_n - Lion\ damage_n - Costs_n$$

Table 5.1 Costs and benefits of the different management options available in the lion game.

	1. Graze 	**2. Graze and scare** 	**3. Graze and kill** 	**4. Lion habitat** 
Grazing score 	8	8	8	0
Subsidy 	0	0	0	X [4,8,12] *
Damage 	-4 per lion	-4 per lion	-4 per lion	0
Cost 	0	-2**	-4	0
Weight	10	5	2	90
Effectiveness		80%	30%	
Habitat neighbourhood effect	None	None	None	Adds 5 points of weight to all squares in a neighbourhood of 1

* In some treatments, a subsidy of X points is awarded for each square of lion habitat at either the group or individual level, where X is an integer taking one of three values [4, 8, 12].
**In the 'support for scaring' treatment this cost is reduced to zero.

Each game starts with 16 lions 'roaming' the landscape. Lions move independently and stochastically among the landscape cells and decisions of players in the current round can affect payoffs in future rounds. 'Scaring' displaces lions from cells that experience it with a probability of 80% (Table 5.1). In any given round, if a player chooses to scare on any of their cells, lions in those cells will move to another location probabilistically based on cell weights. If a player chooses the lethal option, the lion will be removed from the landscape with a probability of 30% (Table 5.1). The number of lions in subsequent rounds therefore decreases based on the frequency of killing choices. 'Failed' attempts at scaring or spearing result in lions remaining in the cell on which the decision has been made. Once all four players have confirmed their decisions in the current round, the position of lions in the landscape will reorient for the following round.

5.3.3 Experimental design and data collection

Each session started with a short practice game of 3 rounds, to enable players to become familiar with the tablets and the game setup. This was followed by four randomly ordered treatments of six to eight rounds each (Table 5.2). The number of rounds was randomised to prevent participants from anticipating the conclusion of a game. Communication between participants was permitted at the start of each round to mirror real-world decision-making. Players were informed of the changes in parameters before beginning each new treatment (Table 5.2). Following the game, we administered a questionnaire survey with each player (Appendix D1). This enabled us to collect detailed information on participants, including household demographics and socio-economic characteristics, experience with carnivore conflict, and attitudes towards wildlife, trust, and equity.

Table 5.2 Parameters for each of the four treatment conditions used in the lion game.

Treatments	Details	Subsidy for lion habitat	Cost of scaring lions
Baseline	Default parameters used	0	2
Support for scaring	Cost of non-lethal scaring option reduced to zero	0	0
Individual subsidy	Bonus given to each player for every cell of lion habitat they provide	4, 8 or 12*	2
Community subsidy	Bonus given for each cell of habitat across the entire game landscape, and the total shared equally among the 4 players	4, 8 or 12*	2

*Subsidy values were randomly selected at the start of the game and kept constant for the remainder of the session.

The games were facilitated by a three-person team (R.S. and two local field assistants) between May and July 2019. The game settings, instruction protocol and questionnaires were piloted prior to data collection in April 2019. Games were implemented in Swahili, with instruction also provided in two local languages, Maa and Barabaig. The research ethics committee of Newcastle University approved the study, and all field assistants received an ethics briefing before carrying out the fieldwork. Participants were informed that only the aggregated results would be published and would not be linked to individuals or households.

Fieldwork was hosted by the RCP, who provided logistic support, field assistants and local contacts. We ensured that before each session all participants were aware that the lead author was independent of RCP, that only the aggregated results would be shared with RCP and emphasised the neutrality of the research.

In total, we conducted 43 game sessions across 7 villages (Fig. 5.1), with a total of 172 players. Participants were found using word-of-mouth and recruitment at market days and community events. Only one representative per household was permitted to participate in the game, preferably the head of the household or person who was responsible for making livestock management decisions, in most cases men. We also targeted individuals who relied primarily on livestock as a source of income, mainly the Maasai and Barabaig ethnic groups.

At the start of each session, we dedicated sufficient time to the practise game to ensure comprehension, typically ~30 minutes. The use of images and a Swahili game screen allowed accessibility to participants with low literacy, who were also closely assisted by facilitators. The full session (practice, 4 game treatments, individual questionnaires) lasted between 2-3 hours. We offered phone airtime vouchers to compensate participants for their time and provided refreshments during the game session. Although it is common practice in experimental economics to provide variable incentives based on scores (i.e., prizes), there is precedence in the experimental games literature for flexibility in incentive structure depending on local context (Bell *et al.*, 2015; Meinzen-Dick *et al.*, 2016; Rakotonarivo *et al.*, 2021b). Our aim was to ensure that players used the game as a tool to express their preferences and think about how they would behave in reality, rather than fixate on rewards (Hur and Nordgren, 2016) and aim to win.

To gain additional details on participants’ rationale for their decisions and attitudes towards management options, at the end of study period we invited 20 random participants to attend a debriefing. These informal discussions were conducted in groups of 5 and were not audio recorded. During these 30-minute debriefings, notes and direct quotes were taken to further understand participants’ reasoning and motivations.

5.3.4 Data analysis

5.3.4.1 The effect of game variables on player choices

We examined two game outcomes measured at the individual participant level: 1) decisions to provide wildlife habitat and 2) decisions to scare lions. We modelled these outcomes as the number of scare or habitat provisioning decisions using linear mixed effects models (LME) in the *nlme* package (Pinheiro *et al.*, 2021). Both outcomes were measured as counts and were therefore log transformed to normalise the data. Player ID was included as a random effect nested within Game ID, to account for unmeasured individual and inter-group variation. As the data consisted of repeated measures of the same individuals, we also controlled for learning by including round in the game as an explanatory variable, and by including an autocorrelation structure to adjust for serial correlation between rounds.

To examine the lagged effect of one round on the next, we ran additional LMEs excluding the first round. We then considered the amount of lion damage suffered in the previous round, and the sum of habitat and scare decisions of the three other players in the previous round as fixed effects. Model selection involved stepwise selection of fixed effects based on the Akaike Information Criterion (AIC). We used likelihood ratio tests to compare and identify the best model. If models differed significantly, the model with the lowest AIC was selected. For models that did not differ significantly, the model with fewer degrees of freedom was selected, and we subsequently interpreted the results of the most parsimonious model.

5.3.4.2 The effect of participant characteristics on player choices

To relate behaviour in the game to demographic and attitudinal variables, we extracted the random effect coefficients (RE) for each player and each game group in the model which included all rounds of the game. To determine whether individual RE could be explained by any measured player characteristics, we checked for correlations between the RE and the data from the questionnaire survey using the heterogenous correlation function of the *polycor* package (Fox, 2019). Given the large number of player characteristics measured and the mixture of numeric, categorical, and ordinal data, post-hoc analysis of RE was necessary to avoid over-parameterisation of the LME. For each game group we also calculated the mean of several socio-demographic variables and categorised gender and ethnic group as either mixed or uniform. We then compared these variables with the RE effect of game ID to examine group-level variation. We used bootstrapping to resample the observed data and constructed mean correlation coefficients (r) and confidence intervals (CI) for the 100 bootstrapped r-values (Fieberg *et al.*, 2020). We then discussed those correlations where r exceeds the critical value considered to be significant for Pearson's correlations and the 95% CI do not overlap this value (i.e., where we are 95% confident that the true r value exceeds the critical cut-off that would be expected based on the known distribution of Pearson's r). The critical value at $\alpha = 0.05$ is $r = 0.15$ for our sample of players (df=170) and $r = 0.30$ for our sample of groups (df = 41). All analyses were conducted in R version 3.6.3 (R Core Team, 2020). For a full list of the variables included in the analysis see Appendix D2.

5.4 Results

5.4.1 Participant characteristics

On average participants were 32.6 years old and owned 30.4 livestock, typically a mixture of cattle, goats, and sheep (Appendix D1). Over half of the players (57%) had no formal education. Of those that attended school, the average time spent in education was 7.4 years, equivalent to completing primary school. Most participants were men (89%) and of the pastoralist ethnic groups Maasai (44%) and Barabaig (40%). Other ethnic groups included Sukuma, Bena, and Hehe (16%), who were traditionally agriculturalists but now practise more diverse livelihood strategies (Dickman 2008). 77% of players reported no livestock losses to lions in the past year, and 23% reported an average 3 livestock killed over the last 12 months.

More than half of the participants recognised some benefits from the presence of lions, particularly at the village level (Fig. 5.3; P1 - P2). These pertained to tourism and the receipt of benefits from RCP's Community Camera Trapping programme (see Methods 5.3.1). 55% of participants had received benefits from RCP, including wire bomas, attending educational film nights, assistance from Lion Defenders and through the community camera trapping initiative. Most participants reported that it was not acceptable to kill lions for either prestige (83%) or to protect family and livestock (66%; Appendix D1). When asked about the acceptability of various options for fostering coexistence with lions, the majority viewed actions such as lethal control and trophy hunting tourism as unacceptable, with negative responses of 90% and 94% respectively (Appendix D1). In contrast, both non-lethal scaring and provision of wildlife habitat were perceived as being acceptable by 95% of participants. Ecotourism was viewed as a positive action by 99% of players, although only 5% of households received any income from tourism (Appendix D1).

Participants reported highly positive attitudes regarding trust and equity. Measures of community trust exceeded 91% (Fig. 5.3; C1 - C3). NGOs were the most trusted type of organisation, with 81% players viewing them positively, compared to 78% for the Tanzanian government and 74% for the National Parks Authority (Fig. 5.3; I1 - I3). However, a large proportion of participants reported 'Don't know' responses to the 3 questions on institutional trust, and also with regard to the fair distribution of finances for wildlife management (Fig. 5.3; E2), suggesting some uncertainty regarding these issues. Of questions relating to fairness and equity, 24% of participants felt that they did not have the right to use the land around their village according to their wishes (Fig. 5.3; E4).

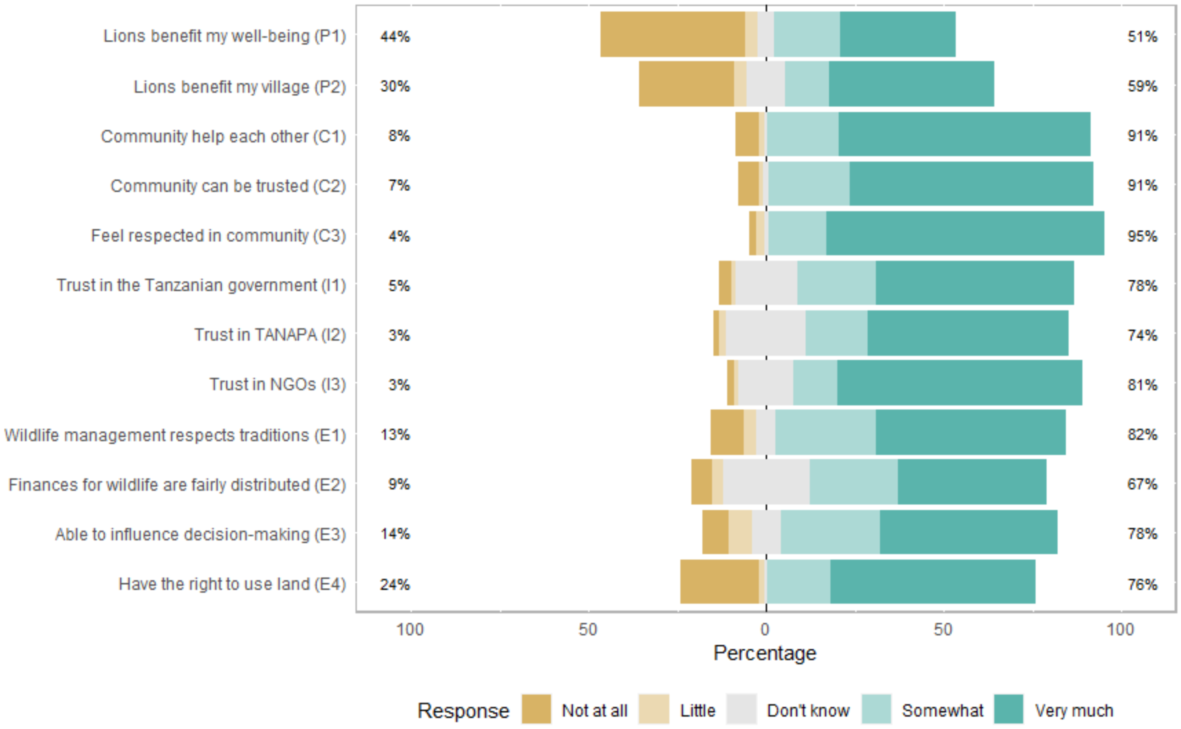


Figure 5.3 Diverging stacked bar chart of responses to questions on perceptions of lions (P1-P2), community trust (C1-C3), institutional trust (I1-I3) and equity (E1-E4). Answers were provided on a likert scale from 'Not at all' to 'Very much'. TANAPA=Tanzania National Parks Authority, NGOs=Non-governmental organisations. Number of respondents = 172.

Individuals were asked to rate their familiarity with each of the other three players on a scale of 1-4 (from 'very limited - I hardly know this person' to 'very familiar - I know them well and frequently meet them'), to obtain a total, overall familiarity with the group ranging between 3 and 12. 87% of players had total scores of ≥ 9 indicating that, unsurprisingly for a small rural community, the majority of players knew each other. When participants were asked what their main goal was when playing the game, 48% said it was to win and 43% said it was to behave as they would in real life (Appendix D1).

5.4.2 The effect of game variables on players' willingness to provide wildlife habitat

In the Baseline (no intervention) treatment, on average, the proportion of cells over which players chose to graze livestock without using any deterrents ranged between 59 - 64% across rounds, with the remaining cells made up mostly of non-lethal scaring (Fig. 5.4). Across all treatments and rounds kill decisions made up < 4% of choices (Fig. 5.4). We thus focussed our analysis on the provision of wildlife habitat and use of non-lethal scaring.

All Individual Subsidies generated an increase in decisions to provide wildlife habitat in comparison to the Baseline, although the effect was strongest for the higher subsidies of 8 and 12 (Table 5.3; Fig. 5.4). Provision of lion friendly habitat decreased in the Support for Scaring treatment. For the Community Subsidies, a subsidy of 4 points had no effect on number of habitat choices, while 8 and 12 points did increase habitat provision in comparison to the Baseline, but to a much lower extent than the Individual Subsidies (Table 5.3; Fig.5.4).

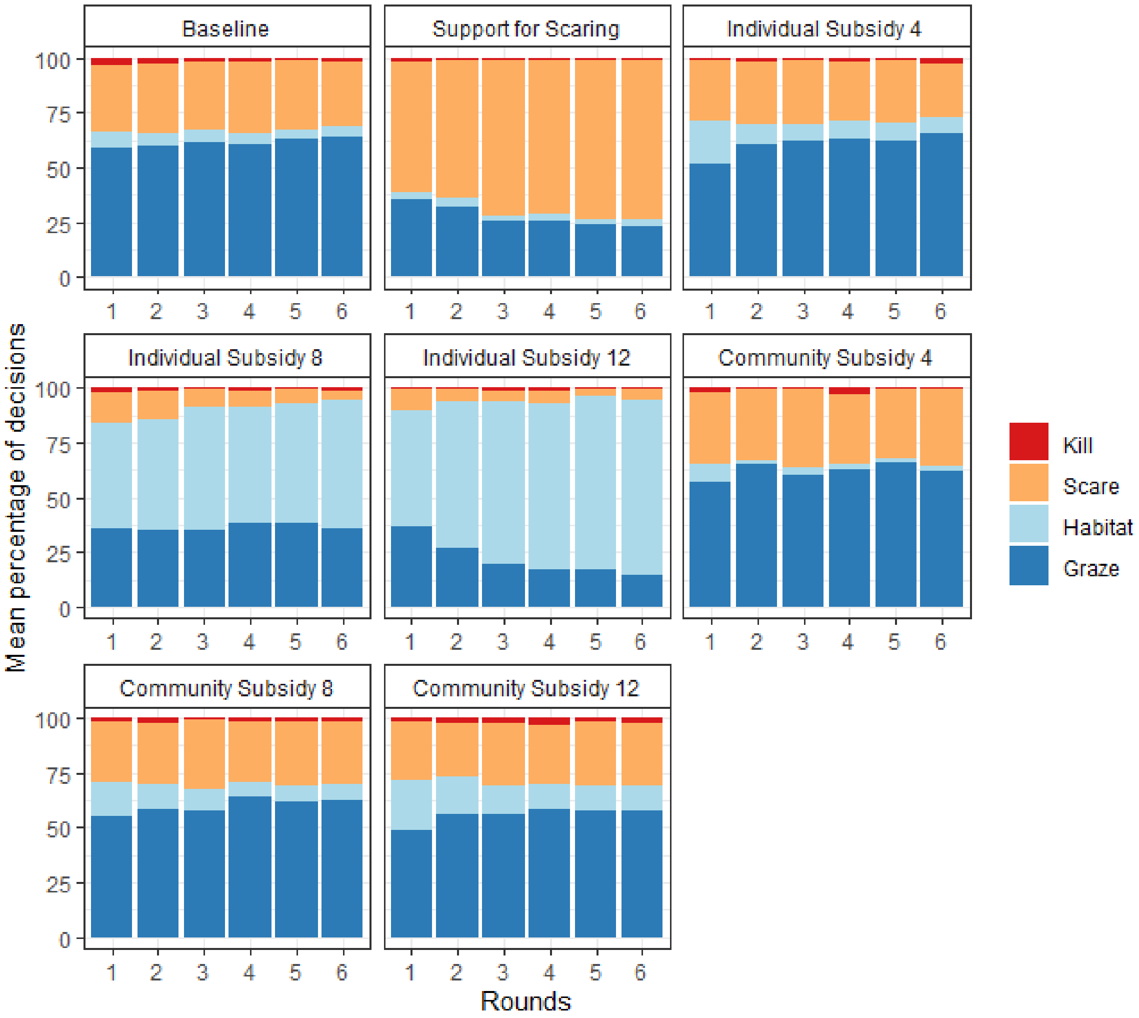


Figure 5.4 Mean percentages of four game decisions (kill, scare, habitat and graze) made by 172 players in Ruaha, Tanzania across treatments and rounds of the 'lion game'.

For the Baseline treatment, round number did not influence the number of habitat choices. However, there were significant interactions between rounds and treatments, indicating that the impact of some treatments varied with repetition. As players progressed through the Community 8 and 12, and the Individual 4 games, the number of habitat decisions decreased. Conversely, with the higher Individual Subsidies habitat choices increased across rounds, suggesting that players were learning from results of previous rounds (Table 5.3).

There was a moderate autocorrelation (ϕ =0.43, 95% CI [0.40, 0.46]), indicating a positive correlation between choices of individuals across rounds. There were also random effects of Player ID and Game ID, indicating variation between subjects and groups. Comparing the standard deviation of the residual vs random effects, indicated that 15% of the residual variation in the model could be explained by Player ID and 24% by Game ID (Table 5.3).

Table 5.3 Output of the linear mixed effects model for number of habitat choices made by 172 players in 43 game sessions. SS = Support for Scaring; IS 4, 8 & 12 = Individual Subsidies of 4, 8 & 12; CS 4, 8 & 12 = Community Subsidies of 4, 8 & 12. No. observations = 4516.

Random effects	Game ID			Player ID: Game ID	Residual
Std. Dev.	0.184			0.115	0.468
Fixed effects	Value	S.E.	D.F.	t-value	p-value*
Main effects					
Intercept	0.306	0.048	4329	6.378	**<0.001**
Rounds	-0.012	0.008	4329	-1.460	0.144
SS	-0.124	0.053	4329	-2.324	**<0.05**
IS 4	0.501	0.078	4329	6.384	**<0.001**
IS 8	1.039	0.076	4329	13.645	**<0.001**
IS 12	1.196	0.074	4329	16.264	**<0.001**
CS 4	0.061	0.077	4329	0.797	0.426
CS 8	0.275	0.075	4329	3.692	**<0.001**
CS 12	0.457	0.071	4329	6.398	**<0.001**
Interactions					
SS x Rounds	0.000	0.012	4329	0.004	0.997
IS 4 x Rounds	-0.062	0.018	4329	-3.548	**<0.001**
IS 8 x Rounds	0.059	0.017	4329	3.513	**<0.001**
IS 12 x Rounds	0.097	0.016	4329	5.737	**<0.001**
CS 4 x Rounds	-0.017	0.017	4329	-0.981	0.326
CS 8 x Rounds	-0.043	0.017	4329	-2.540	**<0.05**
CS 12 x Rounds	-0.056	0.016	4329	-3.394	**<0.001**

*bold values indicate relationships that are statistically significant

When excluding round 1, rounds, with and without an interaction term, and lion damage suffered in the previous round did not improve the model and were removed (see Appendix D3 for full summary of model selection). In the Baseline treatment, the number of habitat squares provided by other players in the previous round had a positive effect on an individual's habitat choices in the current round (Table 5.4), suggesting that participants were taking cues from each other. As indicated by the interaction term, this positive relationship significantly increased in the Individual 4 and Community 8 and 12 treatments (Table 5.4), while remaining comparable to the Baseline in all other treatments. With the exclusion of round 1, the main effects of Community Subsidy 8 and Individual Subsidy 4 were no longer significant (Table 5.4).

Table 5.4 Results of the most parsimonious liner mixed effects model for number of habitat choices when excluding round 1. Habitat others = the total number of habitat squares provided by other players in the previous round; SS = Support for Scaring; IS 4, 8 & 12 = Individual Subsidies of 4, 8 & 12; CS 4, 8 & 12 = Community Subsidies of 4, 8 & 12. No. observations = 3828.

Random effects	Game ID			Player ID: Game ID	Residual
Std. Dev.	0.119			0.141	0.421
Fixed effects	Value	S.E.	D.F.	t-value	p-value*
Main effects					
Intercept	0.224	0.023	3641	7.542	**<0.001**
Habitat others	0.019	0.007	3641	2.744	**<0.01**
SS	-0.096	0.028	3641	-3.383	**<0.001**
IS 4	0.029	0.045	3641	0.634	0.526
IS 8	0.923	0.070	3641	13.234	**<0.001**
IS 12	1.502	0.085	3641	17.577	**<0.001**
CS 4	-0.058	0.044	3641	-1.317	0.188
CS 8	-0.071	0.045	3641	-1.585	0.113
CS 12	0.102	0.045	3641	2.266	**<0.05**
Interactions					
SS x Habitat others	-0.007	0.012	3641	-0.565	0.572
IS 4 x Habitat others	0.035	0.010	3641	3.419	**<0.001**
IS 8 x Habitat others	0.010	0.008	3641	1.188	0.235
IS 12 x Habitat others	-0.009	0.008	3641	-1.077	0.282
CS 4 x Habitat others	-0.010	0.017	3641	-0.608	0.543
CS 8 x Habitat others	0.047	0.009	3641	5.001	**<0.001**
CS 12 x Habitat others	0.022	0.009	3641	2.583	**<0.01**

*bold values indicate relationships that are statistically significant

5.4.3 The effect of game variables on players' willingness to use non-lethal scaring

The Support for Scaring treatment significantly increased the number of scare choices in comparison to the Baseline (Table 5.5; Fig. 5.4). All Individual Subsidies reduced the amount of scaring as players began to switch to habitat provision (Table 5.5; Fig. 5.4), with the higher subsidies of 8 and 12 having the greatest effect. Of the Community treatments, only subsidy level 12 had an effect and resulted in reduced scaring (Table 5.5).

For the Baseline treatment, round number did not influence the number of scare choices. Interactions between treatments and rounds revealed that as participants progressed through the Support for Scaring game, the effect of this treatment on the number of scare decisions increased (Table 5.5). Conversely, with the higher Individual Subsidies the strength of the effect decreased across rounds (Table 5.5). There was a moderate autocorrelation (ϕ =0.36, 95% CI [0.32, 0.38]), and the random effect of Player ID explained 16% of the residual deviation in the model, while Game ID explained 19% (Table 5.5).

Table 5.5 Output of the linear mixed effects model for number of scare choices made by 172 players in 43 game sessions. SS = Support for Scaring; IS 4, 8 & 12 = Individual Subsidies of 4, 8 & 12; CS 4, 8 & 12 = Community Subsidies of 4, 8 & 12. No. observations = 4516.

Random effects	Game ID			Player ID: Game ID	Residual
Std. Dev.	0.150			0.127	0.512
Fixed effects	Value	S.E.	D.F.	t-value	p-value*
Main effects					
Intercept	1.199	0.047	4329	25.255	**<0.001**
Rounds	0.003	0.009	4329	0.296	0.767
SS	0.500	0.057	4329	8.812	**<0.001**
IS 4	-0.186	0.085	4329	-2.195	**<0.05**
IS 8	-0.694	0.082	4329	-8.470	**<0.001**
IS 12	-0.801	0.079	4329	-10.096	**<0.001**
CS 4	0.041	0.083	4329	0.495	0.623
CS 8	-0.087	0.081	4329	-1.073	0.283
CS 12	-0.188	0.077	4329	-2.433	**<0.05**
Interactions					
SS x Rounds	0.034	0.013	4329	2.645	**<0.01**
IS 4 x Rounds	0.016	0.019	4329	0.857	0.392
IS 8 x Rounds	-0.040	0.018	4329	-2.191	**<0.05**
IS 12 x Rounds	-0.041	0.018	4329	-2.210	**<0.05**
CS 4 x Rounds	0.002	0.019	4329	0.114	0.909
CS 8 x Rounds	0.003	0.018	4329	0.164	0.870
CS 12 x Rounds	0.013	0.018	4329	0.736	0.462

*bold values indicate relationships that are statistically significant

Excluding round 1, we again see an effect of other player decisions on individual choices. In the Baseline treatment, the number of scare choices made by other players in the previous round had a positive effect on individual scare choices in the current round (Table 5.6). The interaction between ‘scare others’ and treatment indicates that this positive relationship significantly increased in the Individual 4 and Community 8 treatments (Table 5.6), while remaining comparable to the Baseline in all other treatments. Rounds and lion damage in previous round were again not significant and did not improve the model so were removed (Appendix D3). With the exclusion of round 1, Community Subsidy of 8 significantly decreased the number of scare choices in comparison to the Baseline (Table 5.6).

Table 5.6 Results of the most parsimonious liner mixed effects model for number of scare choices when excluding round 1. Scare others = the total number of scaring squares provided by other players in the previous round; SS = Support for Scaring; IS 4, 8 & 12 = Individual Subsidies of 4, 8 & 12; CS 4, 8 & 12 = Community Subsidies of 4, 8 & 12. No. observations = 3828.

Random effects	Game ID	Player ID: Game ID	Residual
Std. Dev.	0.081	0.158	0.483

Fixed effects	Value	S.E.	D.F.	t-value	p-value*
Main effects					
Intercept	1.064	0.053	3641	20.213	**<0.001**
Scare others	0.019	0.005	3641	3.475	**<0.001**
SS	0.390	0.074	3641	5.300	**<0.001**
IS 4	-0.339	0.090	3641	-3.758	**<0.001**
IS 8	-0.773	0.065	3641	-11.946	**<0.001**
IS 12	-0.876	0.062	3641	-14.163	**<0.001**
CS 4	0.200	0.112	3641	1.779	0.075
CS 8	-0.294	0.093	3641	-3.151	**<0.01**
CS 12	-0.197	0.086	3641	-2.308	**<0.05**
Interactions					
SS x Scare others	0.004	0.006	3641	0.639	0.523
IS 4 x Scare others	0.033	0.010	3641	3.181	**<0.01**
IS 8 x Scare others	-0.003	0.010	3641	-0.283	0.778
IS 12 x Scare others	0.007	0.013	3641	0.556	0.578
CS 4 x Scare others	0.033	0.010	3641	3.181	0.145
CS 8 x Scare others	0.029	0.011	3641	2.781	**<0.01**
CS 12 x Scare others	0.007	0.013	3641	0.556	0.475

*bold values indicate relationships that are statistically significant

5.4.4 Correlation of participant characteristics with random effects

The random effect (RE) of Player ID was explaining ~15% of the residual variation in the models for both habitat choices and scare choices (Table 5.3 & 5.5). Most of the players' demographic and attitudinal characteristics were not correlated with the random effects (see Appendix D4 for full correlation matrix). For habitat decisions there was a weak positive correlation with gender (r = 0.27, 95% CI [0.20, 0.34]), and a weak negative correlation with total livestock owned (r = -0.21, 95% CI [-0.25, -0.16]) suggesting that women and those with more livestock made less habitat choices. For scare decisions there were weak positive correlations with responses to the questions 'Do you feel you are respected in this community?' (r = 0.23, 95% CI [0.16, 0.30]) and 'Do you feel that current wildlife management schemes respect your local traditions and culture?' (r = 0.25, 95% CI [0.18, 0.32]). These responses were measured on a Likert scale from -2 (not at all) to 2 (very much) and the correlation suggests that those who responded more positively to these questions made more scare choices.

Several of the socio-economic and attitudinal characteristics were intercorrelated (Appendix D4). For example, the number of livestock lost to lions was moderately correlated with village (r = 0.44, 95% CI [0.39, 0.48]), with gender (r = 0.41, 95% CI [0.31, 0.52]) and with total number of livestock owned (r = 0.32, 95% CI [0.23, 0.41]). Years of formal education and ethnic group were moderately correlated with each other (r = 0.38, 95% CI [0.34, 0.42]). On average, the Barabaig had only 1.4 years of education, compared to 6.3 years for the Bena and Hehe. In addition, there were strong correlations between several of the trust and equity questions (Appendix D4).

The random effect of Game ID was explaining 24% of the residual variation in the model for habitat choices and 19% for scare choices. Comparing group-level variables to the random effect coefficient for Game ID, revealed a moderate negative correlation between gender and scare decisions (r = -0.48, 95% CI [-0.59, -0.37]), with groups comprised solely of men making more scare choices than mixed gender groups (there were no women-only groups in our sample). No further patterns were detected (Appendix D5).

5.5 Discussion

Large carnivores can have profound impacts on the well-being of communities in rural landscapes. We provide some evidence that experimental games can be used to evaluate the feasibility and acceptability of mitigation interventions to encourage human-carnivore coexistence. Whilst interpretations of game results must be treated with caution, our results support our hypothesis that stakeholders in the Ruaha landscape, Tanzania, prefer the use of non-lethal scaring in the absence of incentives, and this preference increased when the cost associated with this intervention was reduced to zero. Non-lethal deterrents include anything you might use to scare an animal, but most participants interpreted this option as a torch. Also, as hypothesised, monetary payments based on individual habitat choices incentivised players to provide wildlife habitat and this effect strengthened with increasing subsidy levels.

However, when the subsidy was shared based on community-level habitat choices only the mid to high subsidy levels increased habitat provision and to a much lesser extent than the individual-based subsidies, with a decreasing effect across rounds. Finally, gender and wealth (here indicated by size of livestock herd) and the participants' social status appear to affect - if weakly - decision-making on interventions. Women and those with more livestock were less likely to engage in pro-conservation behaviour (habitat choices) and perceived higher respect in the community increased uptake of non-lethal scaring.

Increasing payment levels has been found to improve engagement in pro-conservation behaviour in several studies (Tuanmu *et al.*, 2016; Handberg and Angelsen, 2019; Rakotonarivo *et al.*, 2021a). However, our results suggest that these incentives are more effective when targeted towards individuals rather than being shared by the group, which concurs with other studies (Midler *et al.*, 2015; Gatiso *et al.*, 2018; Ngoma *et al.*, 2020). In Africa, due to the history of community-based resource management and ill-defined land tenure and land use rights (Dickman *et al.*, 2011; Goldman, 2011), incentive schemes have typically targeted groups rather than individuals (Gatiso *et al.*, 2018) despite mixed evidence for the success of such approaches (Hayes *et al.*, 2019). Community-based payments require functional systems of collective action (Dickman *et al.*, 2011) and create a social dilemma with the potential for free-riding, where non-complying individuals can benefit from payments while not bearing the cost (Vollan *et al.*, 2018). Our data support this assertion as habitat provision in the community treatment declined across rounds, suggesting that individuals may have been adapting their strategy in response to other players' cooperativeness (Narloch *et al.*, 2012).

We highlight, however, that games may not necessarily reflect complex real-world social interactions, and we emphasize the importance of capturing narratives around game results, e.g., through debriefings. Informal debriefings provided anecdotal evidence that most participants approached the games 'to win', but in reality, benefits for the community were considered important. For example, one player stated that "*because it's only a game people are looking at points. In real life you cannot live without your community, you have to help each other*". Thus, while people may respond more strongly to individual benefits, the importance of community action and incentives is likely to be more nuanced when relating to real world management strategies. The debriefing discussions also revealed that the preferred mitigation options among participants were torches/lights and improved livestock enclosures.

The evidence for socio-economic variables such as age, gender and education being predictors of attitude and tolerance to wildlife is mixed (Kideghesho *et al.*, 2006; Kansky and Knight, 2014; Kimmig *et al.*, 2020), and thus our findings of limited explanatory power of these variables is perhaps not surprising. While direct experience of conflict may shape peoples' attitudes (Kideghesho *et al.*, 2006; Liu *et al.*, 2011), whether these attitudes affect behaviour is varied and context-specific (St John *et al.*, 2010; Liu *et al.*, 2011; Hazzah *et al.*, 2017). As suggested by our results, women may be less likely to engage in pro-conservation behaviour due to higher levels of fear towards wildlife (Kaltenborn *et al.*, 2006) or due to feeling excluded from decision-making and political participation in conservation initiatives (Ogra, 2009; Homewood *et al.*, 2020). Those with more livestock may be less willing to provide wildlife habitat due to it creating restrictions on grazing (Kideghesho *et al.*, 2006). However, both correlations were weak (r < 0.3), and our sample size of women was small.

We found positive correlations between number of scare decisions and perceptions of being individually respected in the community and feeling that current wildlife management schemes respect local culture. Several studies have found that perceptions of trust and equity affect uptake of management strategies and cooperation (Baynham-Herd *et al.*, 2020; Rakotonarivo *et al.*, 2021a; Rakotonarivo *et al.*, 2021b). This highlights the need for interventions to be developed in an inclusive and collaborative manner, with fair representation of stakeholder interests and genuine participation in decision-making processes (Sjölander-Lindqvist *et al.*, 2015; Redpath *et al.*, 2017; Armitage *et al.*, 2020).

The observed group-level random effect indicates that some unmeasured group characteristics play a role in shaping decisions. Most of the participants in our game indicated that they knew each other very well. This familiarity may have affected preferences and cooperation (Cárdenas and Ostrom, 2004; Goette *et al.*, 2012) and resulted in unmeasured dominance or leadership effects. However, our observations did not indicate support for this assumption as most groups (81%) did not engage in discussions between rounds and there was no evidence of peer pressure or dominance resulting in increased cooperation or habitat provision. There was, however, evidence of player learning throughout the game and decisions of other participants in previous rounds affected behaviour in the current round. This suggests that players were taking cues from each other and were more likely to use a strategy that others had used. This finding lends support to assertions that social norms are an important predictor of environmental decision-making (Thøgersen, 2008; St John *et al.*, 2015) and may suggest potential for real-world behaviour change. Levels of uncertainty, which can affect an individual's propensity to cooperate (Pollard *et al.*, 2019), are reduced in our game, as players are able to see the decisions that others have made. Future studies could focus on the impacts of social norms and uncertainty on pro-conservation behaviour by allowing for different levels of transparency in decision-making between rounds and players.

Finally, both our questionnaire survey and debriefing interviews revealed that participants reported high levels of opposition to killing lions. These attitudes were reflected in the games, where such a low number of kill choices were made that they precluded further analysis. This apparent change in perceptions in an area which previously reported highly negative attitudes towards wildlife (Dickman et al. 2014) may be due to the impact of the Ruaha Carnivore

Project which has operated here since 2009, with just over half of participants stating that they had received benefits from this project. However, given that lion killings do still occur locally, it is likely that these attitudes do not guarantee real-world behaviour in response to conflict events, where the complexity of human-wildlife interactions goes beyond what can be captured in a game scenario. Furthermore, given that killing carnivores without legal cause and permit is illegal, our findings may be a result of participants feeling unable to admit their true behaviours or biasing responses towards what they wanted us to hear. Responses may, therefore, have been affected by some combination of social desirability bias, where participants over-report on behaviours considered to be 'good' and under-report those that are 'bad', and demand characteristics, where participants change their responses based on their knowledge of the research (Nichols and Maner, 2008; Krumpal, 2013).

Future work could consider ways to reduce response bias and possible bystander effects, for example, by developing games which can be played anonymously by single players. However, this may be difficult in situations where low literacy necessitates demonstration and coordination by researchers. When conducting questionnaire surveys, indirect questioning methods such as randomised response (RRT) and unmatched count techniques (UCT) may be used to measure sensitive behaviours (Nuno *et al.*, 2013; Ibbett *et al.*, 2021). These approaches allow interviewees to respond with answers that provide information on a probability basis. For example, in RRT participants are given a randomising device such as a dice and, depending on the number rolled, are told to answer truthfully or to give a prescribed response irrespective of the truth (St John *et al.*, 2012). The interviewer does not see the dice, so no sensitive information is revealed, but it is possible to calculate the proportion of true responses and, therefore, the prevalence of the illegal behaviour. This technique could be used to corroborate the results of games and questionnaires to reveal if lion killing is indeed uncommon in this landscape.

However, similar work on human-elephant conflict in rural Gabon, where lethal control is also illegal, found that players were willing to shoot elephants in a game context to both protect crops and express discontent with current policies (Rakotonarivo *et al.*, 2021b). This suggests that players are prepared to engage in illegal behaviour when playing experimental games (Travers *et al.*, 2011; Redpath *et al.*, 2018). Our study provides some of the first experimental evidence for the role of games in investigating human-carnivore conflict management. Generalisation of these results for the wider human-lion conflict context is challenging, given that our participants had significant exposure to a wildlife research organisation and external management interventions. However, we found that the games were well received by the community, with players rapidly understanding and engaging with the NetLogo interface. Our study thus adds to previous work demonstrating the value of experimental games for studying conservation conflicts (Janssen *et al.*, 2014; Redpath *et al.*, 2018; Baynham-Herd *et al.*, 2020; Rakotonarivo *et al.*, 2021b).

Our findings suggest that incentive-based instruments are conducive to pro-conservation behaviour in this conservation conflict setting, but that the amount and the level at which these incentives are provided is important. Future work could focus on identifying realistic thresholds for such payments and the opportunity costs experienced by individuals and communities that participate in conservation initiatives. Non-lethal scaring appeared to be the preferred mitigation strategy and assisting with the cost of provisioning and upkeep would likely increase their use. We highlight the importance of engaging with the entire community and ensuring that all stakeholders' opinions and traditions are respected when developing conservation initiatives. We also echo previous calls for a shift in focus from human attitudes to behaviour to better guide conservation management and assess program effectiveness (Nilsson *et al.*, 2020).

Games offer one method that can lead to improved understanding where little is known about stakeholder perspectives and decision-making. This approach is highly adaptable and applicable across a wide range of conflict contexts (Bell *et al.*, 2016; Rakotonarivo *et al.*, 2021b). Ultimately, to achieve success in managing conservation conflicts, it is necessary to go beyond understanding the ecological system, to develop inclusive approaches that lead to genuine stakeholder participation and improved social outcomes (Redpath *et al.*, 2017).

Field assistant Kambona Kanayaah demonstrates use of the tablet to Mzee Saidi, a Barabaig elder.

Myself and field assistant, Elias Charles, with participants in Isele village. Photo taken by Kambona Kanayaah.

Chapter 6. General Discussion

Sleeping lion. Samburu National Reserve, Kenya.

6.1 Key findings and contributions to knowledge

The African lion (*Panthera leo*) exemplifies the challenges associated with the conservation of large, wide-ranging, potentially dangerous wildlife in the face of widespread land use change and habitat fragmentation. While lions feature prominently on many global wildlife treaties and the key threats to the species are well documented (Hodgetts *et al.*, 2018; Bauer *et al.*, 2020), lion populations have continued to decline (Bauer *et al.*, 2016). This suggests that there is insufficient data to develop clearly defined targets which translate to adequate conservation action (IUCN, 2018a). To understand the potential of human-modified landscapes, which increasingly dominate our world, to support free-roaming lion populations we need to evaluate the main determinants of habitat suitability and understand interactions with people and livestock.

Management to support conservation and facilitate human-lion coexistence in matrix landscapes requires the co-development of collaborative solutions, which must be adaptive to a range of local contexts (Redpath *et al.*, 2017). A combination of different methods is needed to untangle the complexities of human-lion conflict (Pooley *et al.*, 2017) and an important attribute of this thesis is its broad focus and multidimensional approach, using a range of research techniques to improve our understanding of the dynamics of human-lion interactions. Below I return to three objectives outlined in Chapter 1 in order to reflect on the ability of the landscape matrix to support free-roaming lion populations. I synthesize my key findings and contextualise them within the wider literature before outlining future research needs that can build on my work.

6.1.1 Objective 1. *To synthesise current understanding of lion habitat use and suitability*

To determine the extent to which lions can utilise human-dominated landscapes and which conservation actions can facilitate this process, it is first necessary to understand how lions use existing habitats and any key habitat requirements. In Chapter 2, I examined the literature to critically evaluate current understanding of habitat attributes associated with lion presence and develop a framework for conceptualising key drivers of lion habitat use. My findings indicate that space use and habitat selection by lions is highly context- and scale-dependent and this is likely, at least in part, to be responsible for the variability in conflict drivers presented in Chapter 4. Prey abundance and proximity to water appear to be consistently important drivers of habitat use across contexts. However, lions adapt their behaviour in response to anthropogenic pressures, leading to altered patterns in space use such as more frequent use of increased vegetation cover and avoidance of water. This behavioural flexibility may indicate that lions have the potential to adapt to increasingly human-dominated environments. However, my work also reveals a surprising lack of evidence on the species' habitat use for large parts of its geographic range and for landscapes outside of protected areas. Only 31 papers documented evidence of lion habitat use and there was a significant bias in study locations, with the majority of study sites located inside protected areas in Kenya, Tanzania, Zimbabwe, and South Africa. Thus, given the complexity of lion-human-environment interactions, the development of conservation strategies based on this limited evidence base must be approached with caution. My literature review and conceptual framework can be used to guide future research towards filling these data gaps and highlight the key variables which should be considered when examining drivers of habitat use.

6.1.2 Objective 2. *To identify ecological and anthropogenic variables associated with livestock depredations events across contexts*

Loss of livestock can impose significant social and economic costs on communities living alongside lions and often results in retaliatory killing and negative perceptions towards conservation (Dickman *et al.*, 2014; Hazzah *et al.*, 2017; Loveridge *et al.*, 2017a). To effectively manage the negative impacts of lions on local stakeholders requires detailed understanding of where and why depredation happens. Identification of key drivers of depredation risk may allow for the targeting of mitigation measures towards high-risk households, the visualisation of risk across landscapes for land use planning, and the monitoring of interventions' effectiveness (Abade *et al.*, 2014a; Miller, 2015). In the face of limited resources and data deficiency, the use of comparable research techniques and approaches which can be transferred in time and space is valuable for identifying variables which are consistently important in predicting conflict risk. However, thus far, spatial risk mapping studies for African carnivores have not been species-specific and have used a wide variety of different modelling approaches (Abade *et al.*, 2014a; Mpakairi *et al.*, 2018; Kuiper *et al.*, 2021).

In chapter 3, I demonstrated the use of two modelling techniques, Linear Discriminant Analysis (LDA) and Integrated Nested Laplace Approximation (INLA), to identify the landscape features associated with lion attacks on livestock in the Ruaha landscape of Tanzania. My results suggest that livestock depredation exhibits predictable patterns in space and that measures of vegetation productivity, tree cover and distance to rivers are key environmental drivers of lion attack risk, while distance to villages and human population represent important anthropogenic influences. Both modelling approaches had high predictive ability and enabled the generation of predictive risk maps which offer a simple visual interpretation of risk distribution and can be used to stimulate discussion and guide decision-making over conflict mitigation. The use of multiple modelling approaches enabled the examination of differences and uncertainties to avoid underestimation of risk.

In chapter 4, I examined the utility of the LDA approach for predicting livestock depredation across multiple landscapes by testing the transferability of the Ruaha-derived model and implementing the same approach with landscape-specific models. While the Ruaha-derived models were not successful in predicting conflict locations in new landscapes, landscape-specific models derived using the same predictor variables were successful in identifying conflict locations in two Kenyan study sites. However, no variation of the modelling approach led to accurate discrimination of conflict events in a Zimbabwean study site. Distance to water and precipitation appear to be consistently important factors in determining conflict risk. However, context-specific factors such as differences in land use and livestock density are likely to have impacted on model accuracy. Overall, these results support my Chapter 2 finding that lion habitat use is primarily driven by water and prey but is highly context-specific.

The LDA method displays potential as a simple, scalable approach for modelling human-lion conflict. However, locally calibrated models are needed and obtaining accurate data on site-specific variables is crucial. While this is more resource intensive, my findings suggest that the predictor variables used in the models may be widely applicable if landscape attributes such as water points, settlements and livestock presence are accurately digitised.

6.1.3 Objective 3. *To investigate stakeholder preferences for mitigation interventions*

In high-risk areas, it is vital to implement effective strategies which alleviate human-lion conflict. Effectiveness of mitigation methods is often perceived as the successful reduction of livestock losses (Eklund *et al.*, 2017). However, other factors such as social norms and economic costs affect perceptions of acceptability and, ultimately, uptake of interventions (van Eeden *et al.*, 2018b; Liordos *et al.*, 2020; Nesbitt *et al.*, 2021). Experimental games are emerging as a low risk, low-cost tool in the exploration of conservation conflicts (Redpath *et al.*, 2018; Baynham-Herd *et al.*, 2020; Rakotonarivo *et al.*, 2021b), allowing stakeholders to explore the potential of various mitigation options and to examine behaviour and decision-making in response to conflict.

In chapter 5, I used a tablet-based game in the Ruaha landscape of Tanzania to examine pastoralist decision-making in response to various mitigation methods and incentives. I found that non-lethal scaring was the preferred mitigation strategy and that, while incentive-based instruments promoted the provision of wildlife habitat, these were more effective when rewards were higher and targeted at individuals rather than groups. Player characteristics and attitudes had little influence on game behaviour, suggesting that mitigation options may not need to be targeted at specific social groups. However, there was some evidence that gender, wealth, and perceptions of respect had a weak effect on decision-making. These findings provide some of the first evidence for the use of experimental games in a human-carnivore conflict setting. While there were several limitations of this approach, such as difficulty in establishing external validity and the effects of exposure to a wildlife conservation organisation, I found the game to be well-received, easily understood and readily engaged with. My work thus demonstrates the utility of this novel approach for exploring stakeholder perspectives and encouraging discussion, with the aim of developing collaborative approaches to human-wildlife conflict management.

6.2 Limitations and future directions

Building on existing knowledge, my thesis contributes to our understanding of the social and ecological factors influencing human-lion interactions across Africa. I have highlighted several gaps in our understanding of human-lion conflict and demonstrated the application of a variety of methods that could be used across other landscapes where humans and carnivores share space. However, there are several limitations to this work and many avenues for future research to create better understanding of the relationship between humans and lions and how we examine conservation conflicts more generally.

6.2.1 Missing dimensions

As discussed throughout the thesis, human-lion conflict can be presented as having five dimensions: the lion, the wild prey, the livestock, the human and the environment (Montgomery *et al.*, 2018a). Each of these dimensions plays a role in driving conflict both directly and via interactions with other variables. Perhaps given this complexity, few studies of human-lion conflict concurrently evaluate more than two dimensions (Montgomery *et al.*, 2018a). My literature review (Chapter 2) revealed that these categories can also be used to reflect the key drivers of lion habitat use. Thus, as part of my mapping exercises in Chapters 3 and 4, I attempted to include variables relating to the human, environmental and wild prey dimensions, assuming that these will contribute to lion space use (the lion dimension) and hence, conflict.

However, the lack of available data on wild prey distributions and densities necessitated the use of net primary productivity as a proxy variable in the models. Many studies have demonstrated consistent scaling laws for consumer-producer relationships based on energy availability and primary productivity (Coe *et al.*, 1976; Pettorelli *et al.*, 2009; Hatton *et al.*, 2015), particularly in African ecosystems (Fløjgaard *et al.*, 2021). Furthermore, due to the difficulty of obtaining data on all five dimensions, ecogeographical variables are frequently used as proxies for predator and prey presence (Packer *et al.*, 2013; Abade *et al.*, 2014a; Miller, 2015). However, the collection of real-world data on prey biomass and distribution is vital for improving model outputs and enhancing our understanding of conflict risk. Despite wild prey depletion being ranked as a key threat to lion populations, a causal factor for lions targeting livestock, and a key driver of lion habitat use (Bauer *et al.*, 2020; Sargent *et al.*, 2022), this dimension is the least well-studied in the literature (Montgomery *et al.*, 2018a), perhaps due to a lack of widely available data.

Similarly, the livestock dimension is rarely assessed in the conflict literature, and I was unable to include variables relating to livestock density in my models as data were unavailable at appropriate scales. Livestock distributions may affect lion space use either as an attractant, through accessing livestock as secondary prey (Patterson *et al.*, 2004; Valeix *et al.*, 2012a; Mkonyi *et al.*, 2018), or a repellent due to the risk of persecution associated with the use of pastoralist areas (Everatt *et al.*, 2019), and this may vary seasonally based on cattle herding practises and wild prey availability (Schuette *et al.*, 2013; Kuiper *et al.*, 2015).

I therefore highlight the pressing need to collect fine-scale data on wild prey and livestock abundance and dynamics in human-dominated landscapes. This would require site-specific monitoring and therefore may be resource intensive, however it is crucial to enable these dimensions to be considered more widely in the literature. Methods such as placing GPS collars on livestock and wild herbivores (Owen-Smith *et al.*, 2020; Kuiper *et al.*, 2021), and the use of camera trapping technology (Abade *et al.*, 2019; Beattie *et al.*, 2020) can allow for detailed understanding of prey space use and calculation of prey abundance and density (Palmer *et al.*, 2018). These technological tools are becoming increasingly important in the study of ecology and conservation. However, they are costly and can be labour intensive. A first step for assessing herbivore presence in a given study landscape may therefore be to conduct count and spoor transects (Cromsigt *et al.*, 2009; Everatt *et al.*, 2019), or participatory mapping exercises (Basupi *et al.*, 2017; Pearson *et al.*, 2017). Spoor and dung counts represent a simple, low-effort approach for revealing which species are present in an area. In comparison to aerial and observational counts, spoor surveys have been shown to result in similar population estimates, achieve higher encounter rates, and better capture species diversity (Cromsigt *et al.*, 2009; Keeping *et al.*, 2018). Another method, participatory mapping, involves the use of maps as tools to acquire indigenous knowledge (Basupi et al. 2017). For example, through focus groups and/or transect walks, pastoralists can identify key landscape features and grazing areas (Wario *et al.*, 2015; Rojas *et al.*, 2021). Based on herders' knowledge, a landscape-scale picture of the pastoral system is developed. This understanding of space use and seasonal grazing areas could then be used, for example, to generate 'true' absence data for conflict mapping exercises (i.e., locations where cattle are present but no predator attacks occur).

In conjunction with this, as highlighted in Chapters 2 and 4, the scope of anthropogenic variables considered could also be broadened. While the common focus in the literature is on distance to human structures, site-specific attributes such as land management practises, seasonal movement of people and livestock, and creation of artificial water points may all result in differences in drivers of conflict across landscapes.

6.2.2 Livestock husbandry

In Chapter 3 I identified landscape features associated with increased risk of depredation for livestock corralled inside bomas. One caveat of this work was that we were unable to examine the influence of boma quality and other husbandry practises in determining boma attack risk. Individual features of livestock enclosures such as wall height and material, visibility of stock and number of entrances may make some bomas more vulnerable to attacks by carnivores (Ogada *et al.*, 2003; Woodroffe *et al.*, 2007). Furthermore, the use of other deterrents such as dogs, lights and scarecrows may also affect depredation risk (Broekhuis *et al.*, 2017; Lesilau *et al.*, 2018).

In the Ruaha landscape, husbandry practices are of a low average standard, with weakly constructed bomas, and typically no additional guarding strategies other than the presence of untrained dogs (Abade *et al.*, 2014a). Of participants interviewed in Chapter 4, 96% used traditional thorn bush bomas and 87% stated that they did not use any non-lethal scaring techniques. However, further work examining different boma constructions and the use of additional deterrent techniques at both attack and non-attack locations would allow for the investigation of other factors such as: effectiveness of different techniques, changes in depredation risk following implementation of mitigation strategies, and possible displacement of conflict to other areas.

6.2.3 Conservation conflicts and power dynamics

Human-wildlife conflict (HWC) is an inherently interdisciplinary issue (White and Ward, 2010; Montgomery *et al.*, 2019), representing a coupled human and natural system in which people and nature are inextricably linked (Liu *et al.*, 2007). Thus, a variety of different research techniques and perspectives are required to address the social and ecological components of the problem (Beck *et al.*, 2019). It is also important to acknowledge that HWC includes human-human conflicts between groups of stakeholders with different goals and values (Peterson *et al.*, 2010; Redpath *et al.*, 2015) and that wider societal issues exist within the management of conflict (Bond and Mkutu, 2018; Fletcher and Toncheva, 2021). I therefore acknowledge that this research was conceived and framed by authors from the global north who hold the view that carnivores should be conserved. Hence, while I attempt to remain objective, I recognise that my cultural and disciplinary background may have resulted in unconscious biases and beliefs which affect my interpretation of this issue.

Conservation scientists are often positioned as impartial bystanders attempting to resolve conflict between people and wildlife. However, it must be recognised that they also represent a stakeholder group invested in pro-conservation outcomes (Redpath *et al.*, 2015). Furthermore, conservation practitioners and researchers frequently originate from high-income countries with ‘Western’ perspectives and may be considered ‘outsiders’ in the communities in which they work (Beck *et al.*, 2021). Hence, there are inevitable structural inequalities and unbalanced power dynamics when researchers from the global north work with local stakeholders from historically colonised and marginalised communities (Muhammad *et al.*, 2015; LaRocco *et al.*, 2020). An extensive literature exists examining the involvement of the disciplines of ecology and conservation in both historical and neo-colonial practises (Nelson, 2003; Garland, 2008; Mbaria and Ogada, 2016; Asase *et al.*, 2021; Trisos *et al.*, 2021), and this is a particularly relevant consideration for the study of HWC (Bond and Mkutu, 2018; Kamau and Sluyter, 2018).

In Chapter 5 of this thesis, I conducted interviews with local pastoralists who hold strong cultural identities and are typically disenfranchised from political and conservation decision-making (Dickman, 2008; Yurco, 2017; Woodhouse and McCabe, 2018). Pastoralists across Africa have suffered a history of oppression and continue to be economically and socially vulnerable (Fratkin, 1997; López-i-Gelats *et al.*, 2016). We must therefore consider this positionality, alongside other intersectional issues such as gender, age and race, and the resulting dynamics between the researcher and the researched in order to better understand conservation conflicts.

Previous work in the Ruaha landscape found that communities in this region held highly negative attitudes towards wildlife, particularly carnivores, and that retaliatory killing was common (Dickman *et al.*, 2014). This suggests that individuals are willing to admit their desire for wildlife populations to decrease in the presence of international researchers. My findings in Chapter 5, along with other more recent work in this landscape (Dorward, 2018), indicate that these perceptions may have changed, with respondents reporting more positive attitudes towards lions. However, I cannot rule out the possibility that participants may have been adapting their responses due to the presence of a foreign observer. Since the original interviews were conducted (Dickman, 2008), communities in this landscape have had significant exposure to a wildlife conservation organisation. This is likely to have impacted on behaviour and tolerance towards wildlife, possibly explaining this apparent change in attitudes. However, it may also have affected how respondents perceive and interact with international researchers (Clark, 2008; LaRocco *et al.*, 2020).

Further research is needed to explore the power dynamics at play between local, national, and international actors in conservation conflicts. To advance the study of human-wildlife conflict and coexistence, conservationists must begin to define their positionality and practice reflexivity to assess their influence on the scientific process and foster transparency and collaboration (Sultana, 2007; Beck *et al.*, 2021). This requires collaborative, interdisciplinary partnerships between diverse sets of stakeholders and increased training regarding the associated methodological and communication challenges (Pooley *et al.*, 2014; Beck *et al.*, 2019; Beck *et al.*, 2021). Reflexivity may be defined as a process of critical self-reflection to inspect the entire research process for bias in our own values and perspectives, how we establish relationships with others, and the consideration of historical contexts and future impacts (Schwandt, 2007; Beck *et al.*, 2021). Practical techniques to stimulate this critical awareness could include: the writing of positionality statements regarding researchers' background, motivations, and expectations (Moon *et al.*, 2019; LaRocco *et al.*, 2020); brainstorming sessions and workshops with collaborators and stakeholders to establish dialogue and discuss methods and risks (Coreau, 2020); and improved ethics training and review procedures (Brittain *et al.*, 2020).

6.3 Towards human-lion coexistence

My thesis aimed to assess the viability of the human-dominated landscape matrix for supporting free-roaming lion populations and highlighted the complexity of the processes that drive human-lion interactions. Ultimately, successful coexistence relies on adaptation and a wide variety of both ecological and sociological factors contribute to the ability of lions and people to adapt to each other's presence. There is evidence to suggest that the flexibility and variability of lion behaviour and habitat use may enable them to persist in matrix landscapes (Chapter 2), however there are still large gaps in our understanding of habitat use across their full geographic range and of the fitness consequences of using human-dominated areas. Interactions between lions, people and livestock are complex, and models of conflict risk must be locally calibrated (Chapters 3 & 4). Key drivers of both lion habitat use and livestock depredation risk appear to be water and prey availability, therefore future research should focus on more targeted approaches to monitoring these variables and developing management strategies for protecting livestock in high-risk areas. Appropriate mitigation methods are likely to be context-specific and must be developed collaboratively with stakeholders who suffer the costs of sharing landscapes with lions. The use of experimental games is one approach which could be used to engage communities and provide a relaxed environment within which to express preferences and perspectives (Chapter 5). Developing a framework for human-lion coexistence requires detailed understanding of all the dimensions involved and, therefore, we must utilise holistic, interdisciplinary approaches to investigate conflict across contexts and develop solutions which both ensure the persistence of lion populations and the well-being of the communities they live alongside.

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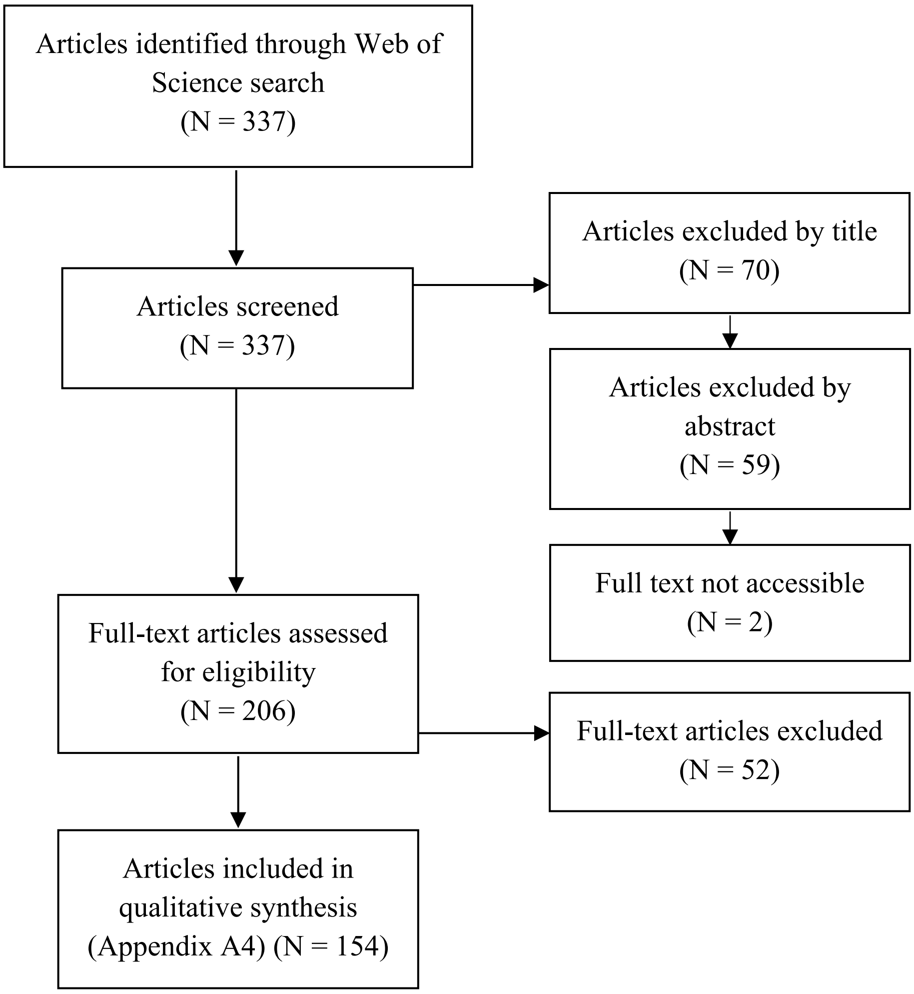
Appendix A

Appendix A1. PRISMA flow diagram of article selection (adapted from Moher *et al.* (2009)).



Appendix A2. Coding of habitat types used in literature review.

Table A2. Descriptors of habitat types used in the review: based on MCD12Q1 International Geosphere-Biosphere Programme (IGBP) classes (Sulla-Menashe & Friedl 2018), habitats described in the articles were grouped into broad categories.

Habitat type as stated in literature review	**Examples of descriptions from articles**	**MCD12Q1 categories and definitions**
Grassland	Long and short grass plains; Wooded grassland; Mixed grassland; Bushed grassland; Savanna grassland	Grassland *(herbaceous annuals <2m)*
Savanna	Acacia savanna; Tree savanna; Open savanna; Savanna plains; Wooded savanna; Bushland savanna	Savannas Woody Savannas *(tree cover 10-60%, canopy >2m)*
Woodland	Riverine forest; Acacia forest; Closed and open woodland; Sand forest; Deciduous woodland; Miombo woodland	Evergreen Broadleaf Forests Deciduous Broadleaf Forests Mixed Forests *(tree cover >60%, canopy >2m)*
Shrubland	Bushland; Thicket; Open scrub; Low shrub; Dense bushland; Wooded bushland	Closed Shrublands Open Shrublands *(woody perennials 10-60%, height 1-2m)*
Wetland/Floodplain	Palm swamps; Swamps and marshes; Large floodplains	Permanent Wetlands *(30-60% water cover, >10% veg. cover)*
Mosaic	Grassland and woodland with crops	Cropland/Natural Vegetation Mosaic *(cultivation 40-60%)*
Cropland	Cultivated agriculture; Rain-fed agriculture; Fields	Croplands *(cultivation >60%)*
Urban		Urban and Built-up Lands *(>30% impervious surfaces)*
Barren	Bare ground	Barren *(>60% non-vegetated)*

Appendix A3. Validation exercise comparing Earth observation data to data extracted from the literature.

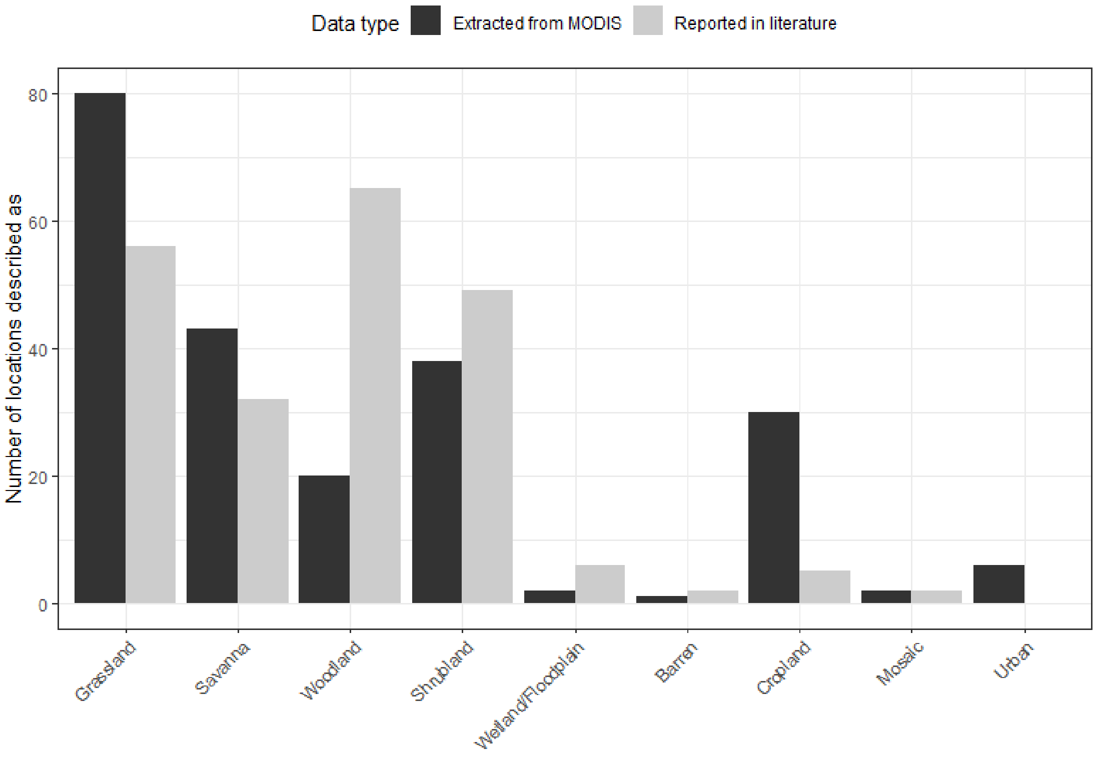


Figure A3. Habitat types as reported in the literature compared to data from the same locations extracted from a 200 km^2 area of MODIS MCD12Q1 (IGBP). If the literature and MODIS data were equivalent, we would expect bars of roughly equal size for each habitat type. Number of locations = 84.

For quality control ('did the authors use consistent habitat terminology') and data filling ('no documented data on habitat type'), we extracted land cover type for each study from MODIS MCD12Q1 IGBP 500m (Friedl & Sulla-Menashe 2019), including all habitats mapped within a buffer around the study coordinate. Lion home ranges vary in size between populations based on prey abundance, pride size and physical barriers (Orsdol et al. 1985, Loveridge et al. 2009). Home ranges may be as small as 25 km^2 in locations such as Nairobi NP and Manyara NP in East Africa (Orsdol et al. 1985) or reach up to 1000 km^2 in locations such as Waza NP, Cameroon (Tumenta et al. 2013). We therefore first extracted habitat from the smallest possible range using a 2.8 km buffer, equivalent to an area of ~25 km^2. We then extracted habitats from 5.6 km (100 km^2) and 8 km (200 km^2) buffers.

Of studies that stated habitat type, the MODIS data from the 2.8 km buffer matched with at least one of the described habitats in 77% of study locations. This increased to 84% for the 5.6 km buffer, and 86% for the 8 km buffer. Of the 14% that did not align in the largest buffer, 74% were mismatches between grassland and savanna. This could be due to differences in definitions between these habitat types or the resolution at which MODIS measures habitat. If we ignored the discrepancies between grassland and savanna, MODIS results from the 8 km buffer matched with at least one of the habitat descriptions for 96% of study locations. Therefore, we considered the 8 km buffer sufficient for broadly capturing habitat type in a given study area.

Comparing the reported habitat types to the habitats extracted from MODIS revealed that there are some discrepancies between the author descriptions and the remotely sensed data. There is a higher representation of grassland across locations based on the MODIS data and a large decrease in the presence of woodland in comparison to the author descriptions (Figure A3). This could indicate confusion in reporting and classifying of habitat type, and even within study areas, there appeared to be a lack of consensus on how to describe the habitats occurring there. It may also suggest that using remotely sensed data is not accurate enough for fine-scale habitat classification due to the scale and resolution of sensors. Another limitation is the difference in the scale of reporting. In most cases, the literature is describing habitat across the whole study area, of which each is a different size. MODIS data has been extracted from around a central coordinate of the study area and may or may not be larger than the area described by the authors. This could lead to some habitats being missed in the MODIS extraction if they are present in other areas of the landscape, or additional habitats being captured by MODIS because it is encompassing a larger area than described by the authors.

As described in the methods, where possible we used the literature to determine habitat information. MODIS data was used only for the 29 studies, which had no information in the articles.

Appendix A4. The 154 studies included in the qualitative synthesis in Chapter 2

Abade L, Macdonald DW, Dickman AJ (2014a) Assessing the relative importance of landscape and husbandry factors in determining large carnivore depredation risk in Tanzania's Ruaha landscape. *Biological Conservation* 180: 241-248.

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Abade L, Cusack J, Moll RJ, Strampelli P, Dickman AJ, Macdonald DW, Montgomery RA (2019) The relative effects of prey availability, anthropogenic pressure and environmental variables on lion (Panthera leo) site use in Tanzania's Ruaha landscape during the dry season. *Journal of Zoology* 310: 135-144.

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Appendix A5. Coding of study topics used in literature review

Table A5. The broad study topics of the articles categorised based on aims and key words

Study topic	Key words	Example aims
Demography	- Demography - Group size/pride size/social organisation - Territorial behaviour/ competition - Population dynamics/ reproductive success	"To determine demographic variables that influence the persistence of lion prides" "To assess the effects of environmental, social and prey factors on pride size and reproductive rates" "To evaluate the impact of trophy hunting on lion survival, recruitment and population size"
Density estimates	- Density/population size/relative abundance - Spoor/tracks/camera traps/call-up surveys - Random encounter models/ capture-recapture/monitoring	"Using spoor counts to quantify lion population size in Khutse Game Reserve" "Estimating the density of female lions from a camera trap survey" "Define survey effort required to achieve estimates with known precision"
Diet & Foraging	- Diet/dietary niche/prey base - Predation/prey composition/ predator-prey relationships/ preferences/optimal foraging - Scat analysis/kill site detection - Body weight/biomass	"To estimate lion diet using opportunistic observations, GPS cluster analysis and scat" "To test for spatial differences between kills sites and the effect of water dependency on predation" "To predict the diet of lions in situations of varying predator and prey abundances"
Disease	- Wildlife disease - Transmission modes - Endoparasites/nematodes - Interspecific contacts	"A survey of endoparasites carried by free-ranging lions" "To explore the role of interactions between livestock and wildlife in disease transmission" "To examine transmission pathways in a social carnivore"
Focus on other species	*Varied - Primary aim focussed on other species, but which documented lion presence*	"To investigate habitat preference and effects of lion predation risk on medium-large herbivore species" "To examine the effect of lion predation on Plain's and Grevy's zebra populations" "To test how selection of, attendance at, and proximity to dens by spotted hyenas may be influenced by the risk of predation by lions"
Habitat use	- Habitat/habitat selection/ habitat choice/habitat use - Space use/spatial ecology/landscape - Resource selection functions/ occupancy modelling	"To investigate the drivers of space use by lions" "To examine density vs fitness-based measures of habitat quality" "To investigate the influence of environmental and anthropogenic variables on lion site use"
Human-wildlife conflict	- Human-carnivore conflict - Depredation/livestock/husbandry - Anthropogenic disturbance/ lethal control/trophy hunting/ retaliatory killing - Mitigation/compensation - Attitude/behaviour	"To assess the relative influence of husbandry and environmental factors on livestock depredation risk" "To model the landscape of anthropogenic mortality risk for African lions" "To provide a comprehensive evaluation of predator-proof enclosure efficacy"

Table A5. Continued

Study topic	**Key words**	**Example aims**
Movement & Dispersal	- Movement/dispersal/space use/connectivity/spatial distribution - Behaviour/territoriality/group fission - Seasonal variation/climate change	"To investigate the impact of a severe drought on lion's home ranges size and movement patterns" "To explore how habitat saturation and territory quality influence dispersal decisions" "To compare the movement of African lions in different demographic categories and the influence of rainfall and group size"
Other	*Varied - Several article topics did not fit into the above categories and were only studied in 1-2 papers. These were therefore grouped as 'Other'.*	"To examine the evolutionary and ecological factors influencing the mane of the African lion." "To confirm the lion's continued presence in Mole NP, Ghana" "To relate African lion population densities and population trends to contrasting management practices, explicitly the effectiveness of fencing and management budgets"

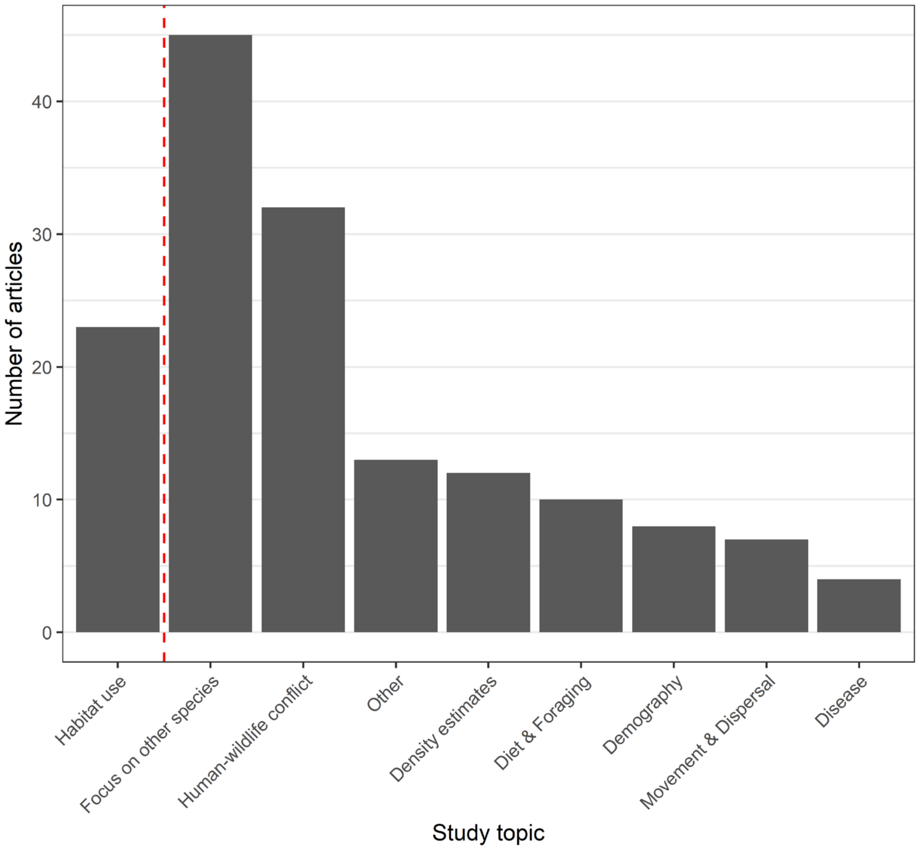

Figure A5. The number of articles from which data was extracted, grouped into broad study topics. Ordered from most frequent to least frequent, with the exception of 'habitat use' (separated by dashed line). Topics grouped into the 'Other' category were studied in ≤ 2 papers with foci that included interspecific competition, reserve management and confirmation of presence.

Appendix A6. Summary of results for 23 lion habitat use articles, plus a further 8 relevant articles, considered in the literature review.

Table A6. Summary of data extracted for 23 habitat use studies, plus a further 8 studies which documented some lion habitat preference. Only variables measured in more than two studies are included in the table. '•' denotes variable measured, '+' and '-' denote findings of positive and negative significant associations between variable and lion use/occupancy/density. The presence of both signs indicates both relationships were found and were conditional on other variables. N = measure indicating sample size/effort. PA=Protected area, OMA= Other managed area, UA=Unprotected area. See Appendix A4 for full references.

					Human variables			Environmental variables							
Study	Country	Method	N	Land use	Human population density	Distance to settlements / buildings	Land use	Distance to water	Prey abundance	Vegetation cover	Elevation	Slope	Precipitation	Habitat type	Notes
Habitat use studies															
Abade et al. (2014b)	Tanzania	Camera traps, direct observation	59 presence points	PA, OMA, UP		•		-		•	•	•	+		Slight contribution of low elevation & open canopy.
Abade et al. (2019)	Tanzania	Camera traps	157 presence points	PA, OMA, UP	•	•	Village land: no detections	•	+	•					
Cristescu et al. (2013)	South Africa	Direct observation, radio collars	4 lions (1 pride)	PA							-	•		Study area scale: Selected disturbed (old agricultural land). Home range: Selected disturbed & grassland.	
Davidson et al. (2012)	Zimbabwe	GPS Collars	30 lions	PA				-						Home range: Selected bushed grassland Kill sites: Selected thickets.	
Eby et al. (2013)	Tanzania	Direct observation	Not stated	PA										Selected unburned areas where veg. cover was higher.	
Everatt et al. (2015)	South Africa	Camera traps, spoor	664 photos, 55 tracks	PA		•			+						–ve with probability of bushmeat poaching & +ve with riparian area.
Everatt et al. (2019)	Mozambique, South Africa, Zimbabwe	Spoor	Spoor on 215/3759 transects	PA, UP		•	Community land: no detections		+						-ve with occurrence of cattle & bushmeat poaching, +ve with distance to PA centre
Henschel et al. (2016)	Benin, Burkina Faso, Niger	Spoor	Lion spoor in 32/79 sample units	PA, OMA	•			•		•			+		+ve with no. patrol staff/km^2
Hopcraft et al. (2005)	Tanzania	Direct observation, radio collars, kill sites	10,151 observations, 269 kill sites	PA				-						Spent less time and made fewer kills on short grass plains. Preferred areas of good cover.	
Kittle et al. (2016)	Tanzania	GPS collars, direct observation	6 lions	PA				-	+	•	•	•			Some variation seasonally.
Midlane et al. (2014)	Zambia	Spoor	Spoor on 147/1010 sections	PA		•		•	•					Higher probability of use in munga/ termitaria woodland, compared to miombo woodland or grassland/scrub.	
Millspaugh et al. (2015)	South Africa	Direct observation, radio collars	4 lions, 1103 observations	PA										Winter: High probability of occurrence in reedbeds/grassland. Summer: sand forest. Overlap both habitats in spring & autumn.	

Table A6. Continued

					Human variables			Environmental variables							
Study	Country	Method	N	Land use	Human population density	Distance to settlements / buildings	Land use	Distance to water	Prey abundance	Vegetation cover	Elevation	Slope	Precipitation	Habitat type	Notes
Habitat use studies cont.															
Mkonyi et al. (2018)*	Tanzania	Spoor	136 tracks	PA, UP	•	+ inside NP	Communal grazing land: no detections	- /+			•	•		•	Lions associated with water in NP, avoided it in village land.
Mogensen et al. (2011)*	Kenya	Direct observation, radio collar	3 prides	PA, OMA			See notes on habitat type							Reserve lions spent most of their time in open habitat. Ranch lions often occurred in bushland & woodland. Reserve lions ate on open grass plains, ranch lions inside bushes.	
Mosser et al. (2009)**	Tanzania	Direct observation, radio collars	44 prides	PA				-	•	•			+		Variation when considering short vs long term and repro. success vs. density.
Ogutu & Dublin (2004)	Kenya	Direct observation	Lions in 382/1827 grid cells	PA					+	+			•		Lions located mainly in thickets lining drainage pathways.
Oriol-Cotterill et al. (2015)	Kenya	GPS collars	5 lions (5 prides)	UP		Varied w/ human activity, moonlight & rainfall	Avoided pastoral land (preferred commercial ranches)						Interacted with distance to boma		Used pastoral land during high moonlight & low-medium human activity.
Schuette et al. (2013)	Kenya	Direct observation, radio collars	6 lions (3 prides, 2 male coalitions)	OMA		•	see notes	see notes	•	see notes					Increased use of conservation area (CA), closed habitats & further from river when settlements moved nearer to CA.
Snyman et al. (2019)	Botswana, Zimbabwe & South Africa	GPS collars	9 lions	PA, OMA, UP		+ but varied w/ season & scale	95% GPS locations were in PA & OMA.	•			-			•	
Spong et al. (2002)	Tanzania	Direct observation, radio collars	11 prides	PA										Significant preference for riverine & short grass habitat. Avoidance of acacia woodland.	
Suraci et al. (2019)	Kenya	GPS collars	14 lions	UP		Varied w/ time of day & behaviour		•		Varied w/ distance to boma & behaviour		•			
Valeix et al. (2010)	Zimbabwe	GPS collars	19 lions	PA				-							
Yiu et al. (2018)	South Africa	GPS collars	11 lions	PA		Varied w/ sex & time since release		-		Varied w/ sex & time since release	-	-		Varied with time since release, season & intraspecific conflict.	
Other studies															
Broekhuis et al. (2013)	Botswana	GPS collars	5 lions (5 prides)	PA, OMA										Home range: more grassland & mixed woodland, less mopane woodland & swamp than expected. Within home range: preferred mixed woodland over grassland	
Courbin et al. (2016)	Zimbabwe	GPS collars	21 lions	PA				-						Selected grassland & open bushland during day & night. Avoided woodlands at night.	

Table A6. Continued

Study	Country	Method	N	Land use	Human variables			Environmental variables							Notes
					Human population density	Distance to settlements / buildings	Land use	Distance to water	Prey abundance	Vegetation cover	Elevation	Slope	Precipitation	Habitat type	
Other studies cont.															
Cozzi et al. (2013)	Botswana	GPS collars, direct observation	14 lions (6 prides)	PA, OMA		- for lodges/ camps		•						Almost complete absence in mopane woodland. High density on floodplains & adjacent grassland & woodland.	
Elliot et al. (2014b)	Zimbabwe	GPS collars	50 lions	PA, OMA, UP	-		Avoided agro-pastoral land			-				Bushed grassland & shrubland selected by adult males & females. Dispersing males avoided these & selected woodlands.	
Loveridge et al. (2017b)	Zimbabwe	GPS collars	84 lions	PA, OMA, UP		- for hunting camps	Avoided communal land	-		•					
Miller et al. (2018)	South Africa	Camera traps	2011 captures	PA	•				+					Occupancy probability of lions decreased with increasing hideable habitat (woodland, open/closed shrubland)	
Tambling et al. (2013)	South Africa	GPS collars, kill sites	4 lions	PA										Lions avoided dense thicket	
Valeix et al. (2012a)	Botswana	GPS collars	9 lions (9 prides)	PA, OMA		+ but varied w/ time of day & season									Migratory prey period: avoided <3km to cattle-posts. Resident prey period: selected 1-6km from cattle-posts.

*these are the only articles which make a direct comparison between habitat use inside and outside protected areas **this is the only article considering fitness-based measures of habitat quality

Appendix A. References

Friedl M, Sulla-Menashe D (2019) MCD12Q1 MODIS/Terra+Aqua Land Cover Type Yearly L3 Global 500m SIN Grid V006. NASA EOSDIS Land Processes DAAC.

Loveridge AJ, Valeix M, Davidson Z, Murindagomo F, Fritz H, Macdonald DW (2009) Changes in home range size of African lions in relation to pride size and prey biomass in a semi-arid savanna. *Ecography* 32: 953-962.

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Appendix B

Appendix B1. Description of the Integrated Nested Laplace Approximation method.

Integrated Nested Laplace Approximation (INLA) is an approach which can be used to compute hierarchical models that include a spatial component. It utilises interpolation to create an image of the whole study area surface based on point-level information. In effect the surface is assumed to be a gaussian random field (GRF). A GRF assumes that there are probability density functions for the key variables across the whole surface and that these additively (by way of the Central Limit Theorem) can be assumed to be gaussian in form (Krainski *et al.* 2019). A Delauney triangulation through the data points creates a mesh capturing the distances between points. The analysis then calculates the Matérn correlation across the mesh to define the covariance between points, given their separation in space as quantified by vectors joining points in the mesh (Blangiardo and Cameletti 2015). This effectively captures the spatial dependence in the response variable. A Laplacian model is used to take the spatial variation between points and interpolate values between the known points assuming steady state conditions. In 2 dimensions the Laplacian is an example of an elliptical partial differential equation (PDE) in the x and y directions. A stochastic partial differential equation (SPDE) is an extension to the Laplacian idea in that it assumes that the spatial process captured in the model is also susceptible to gaussian random noise, i.e., there is stochasticity amongst the measurements at the points (Lindgren and Rue 2015). Measures of putative predictor variables at the points can be used as fixed effects, with the Matérn correlation providing estimates of spatial dependence and its decline in space. Given that there is no analytical solution possible for most PDEs and none for an SPDE these models are usually solved by numerical integration. The R-INLA package uses Finite Elements approaches (Rue *et al.* 2009; Lindgren and Rue 2015).

For further technical explanation see:

Blangiardo, M. and M. Cameletti. (2015). *Spatial and spatio-temporal Bayesian models with R-INLA.* John Wiley & Sons.

Krainski, E.T. et al. (2019) *Advanced Spatial Modeling with Stochastic Partial Differential Equations Using R and INLA.* Boca Raton, FL: Chapman & Hall/CRC Press.

Lindgren, F. and Rue, H. (2015) 'Bayesian Spatial Modelling with R-INLA', *Journal of Statistical Software*; 63(19), pp. 1-25.

Appendix B2. Summary plots showing characteristics of bush attack and absence sites.

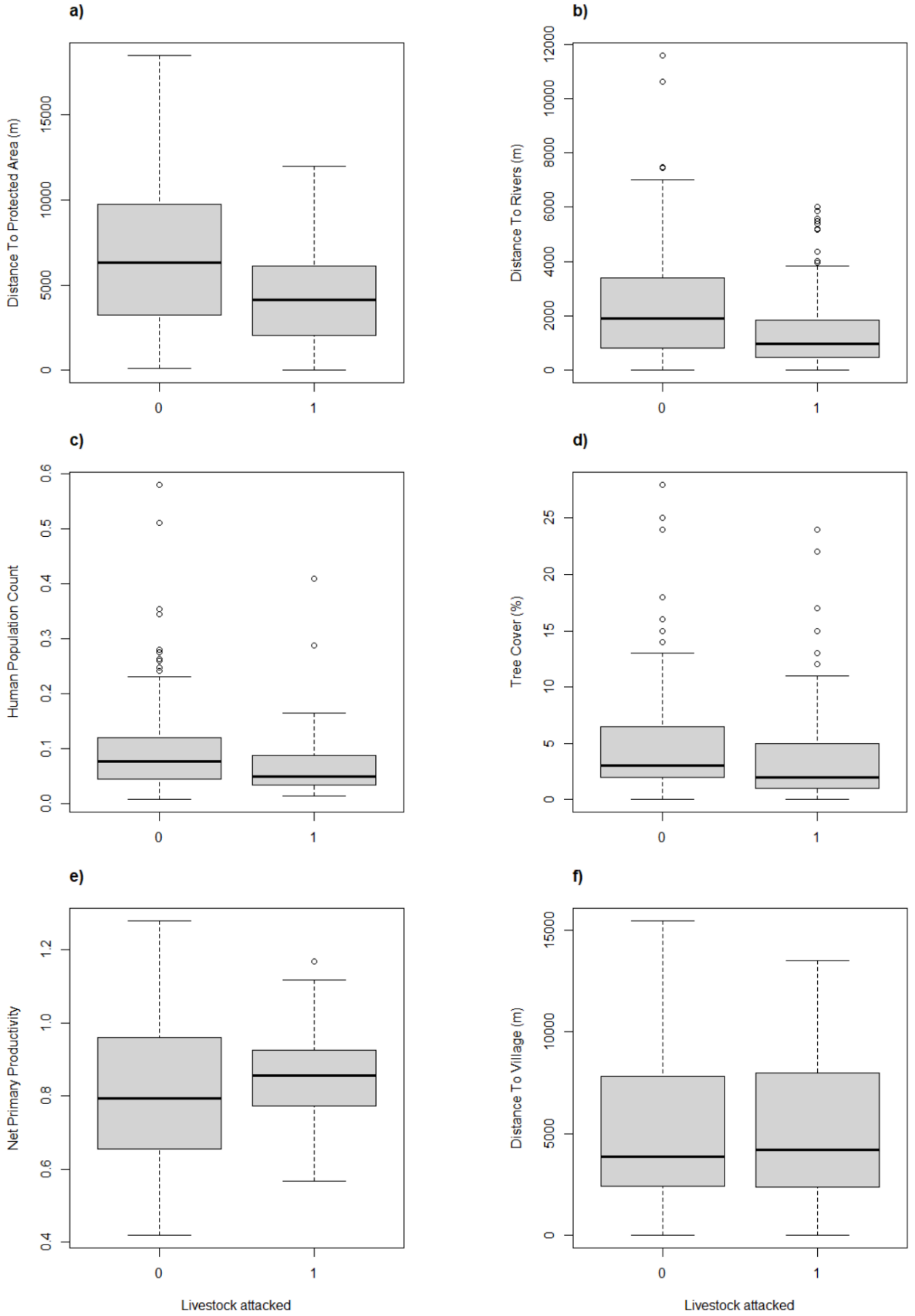

Figure B2. The distribution of bush attack events and absences in relation to distance to PA (a), distance to rivers (b), human population count (c), tree cover (d), net primary productivity, and distance to village (f).

Appendix B3. Results of the Linear Discriminant Analysis (LDA) using square root transformed variables.

Several of the predictor variables, with the exception of net primary productivity and annual rainfall, had skewed distributions. We therefore square root transformed the predictor variables that were not normally distributed and ran the LDA analysis with the transformed data.

For bush attacks, five of the six predictor variables that were included in the final model (Table 3.2) were also significant in distinguishing between attack and non-attack events using transformed data (Table B3.1). However, distance to village was no longer included in the model using the transformed data.

Table B3.1 Wilk's lambda and discriminating ability of the square root transformed variables at each stage of forward stepwise variable selection for bush attacks. Variables retained show significance in separating attack and non-attack events.

Variable	Wilk's lambda	F	p-value	F difference	p difference
Distance to PA	0.913	19.245	p<0.001	19.245	p<0.001
Distance to Rivers	0.848	17.939	p<0.001	15.266	p<0.001
Population Count	0.805	16.051	p<0.001	10.560	p<0.01
Tree Cover	0.762	15.430	p<0.001	11.118	p<0.01
NPP*	0.710	16.067	p<0.001	14.432	p<0.001

*not transformed as raw data were normally distributed

Bootstrapped LDA, based on 500 repeat random samples of 90% of the transformed data indicated that bush attack events occurred in areas closer to the PA, closer to rivers and with lower human population counts (Table B3.2). The values of the linear discriminants were similar to those of the final model and the directions of the relationships remained the same (Table 3.3).

Table B3.2 Mean coefficients and confidence intervals of linear discriminants obtained from bootstrapped LDA of bush attack locations, based on 500 repeat random samples of 90% of the square root transformed data.

Variable	Mean LD	95% CI
Distance to PA	-1.29E-02	-1.60E-02, -9.81E-03
Distance to Rivers	-1.62E-02	-2.12E-02, -1.19E-02
Population Count	-6.18	-6.96, -5.40
Tree Cover	-0.91	-1.02, -0.79
NPP*	4.29	3.55, 5.03

*not transformed

On average, 75.8% (95% CI [72.8, 78.8]) of the bush attack data were correctly classified and the average area under the curve score (AUC) was 0.82 (95% CI [0.80, 0.85]).

For boma attacks, the same five predictor variables that were included in the final model (Table 3.4) were also significant in distinguishing between attack and non-attack events using transformed data (Table B3.3).

Table B3.3 Wilk's lambda and discriminating ability of the square root transformed variables at each stage of forward stepwise variable selection for boma attacks. Variables retained show significance in separating attack and non-attack events.

Variable	Wilk's lambda	F	p-value	F difference	p difference
Distance to Village	0.702	95.605	<0.001	95.605	<0.001
Population Count	0.658	58.247	<0.001	14.958	<0.001
Tree Cover	0.645	40.875	<0.001	4.376	<0.05
NPP*	0.603	36.579	<0.001	15.639	<0.001
Annual Rainfall*	0.584	31.486	<0.001	7.097	<0.01

*not transformed as raw data were normally distributed

The bootstrapped LDA, based on 500 repeat random samples of 90% of the transformed data indicated that boma attack events occurred in areas further from villages, with lower human population and lower tree cover (Table B3.4). The values of the linear discriminants were similar to those of the final model and the directions of the relationships remained the same (Table 3.5).

Table B3.4 Mean coefficients and confidence intervals of linear discriminants obtained from bootstrapped LDA of boma attack locations, based on 500 repeat random samples of 90% of the square root transformed data.

Variable	Mean LD	95% CI
Distance to Village	2.88E-02	2.60E-02, 3.12E-02
Population Count	-3.44	-4.08, -2.80
Tree Cover	-0.71	-0.83, -0.59
NPP*	6.12	5.30, 6.91
Annual Rainfall*	-0.009	-0.01, -0.006

*not transformed

On average, 78.3% (95% CI [76.0, 80.7]) of the boma attack data were correctly classified and the average area under the curve score (AUC) was 0.90 (95% CI [0.88, 0.91]).

Appendix B4. Summary plots showing characteristics of boma attack and absence sites.

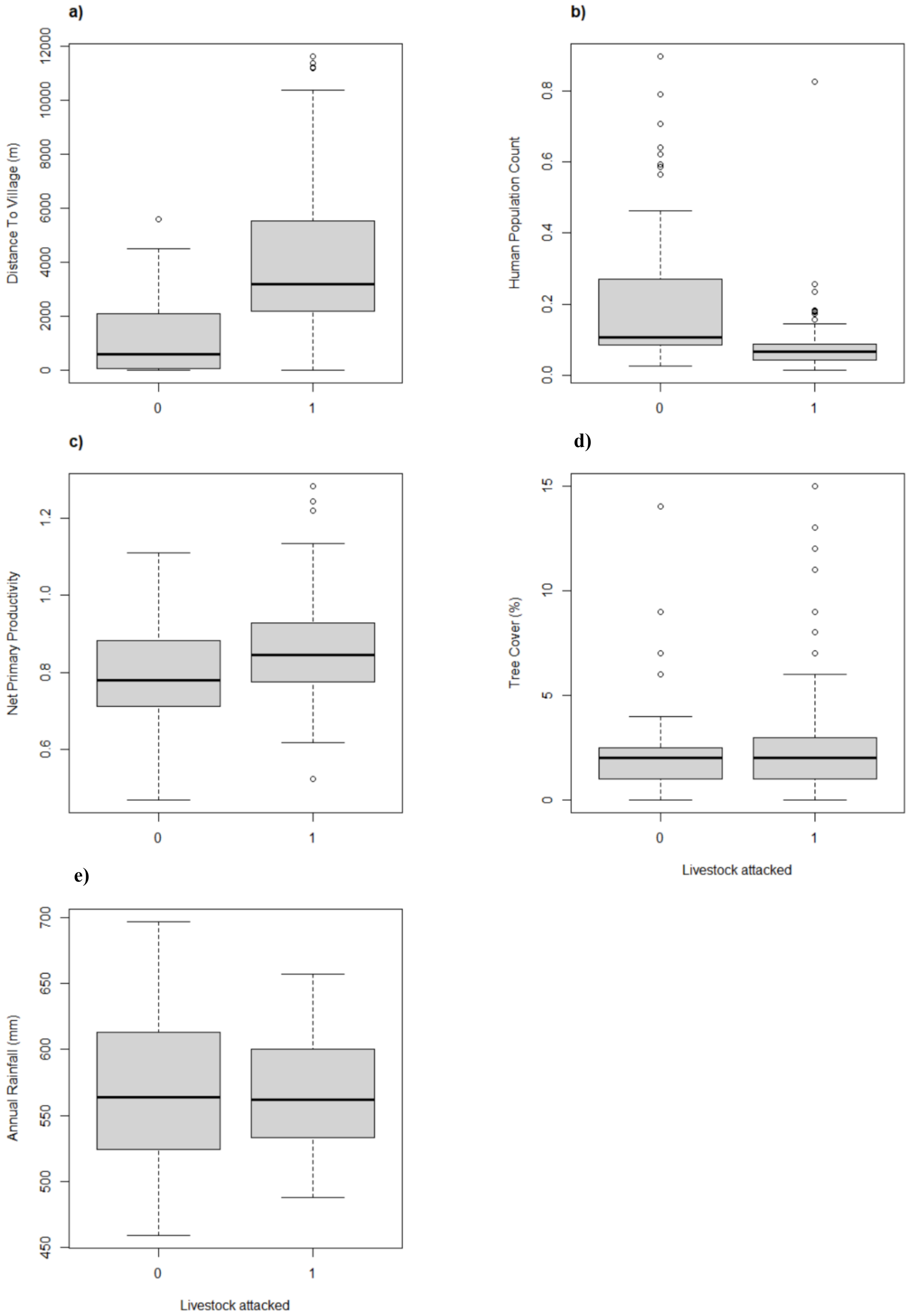

Figure B4. The distribution of boma attack events and absences in relation to distance to village (a), human population count (b), net primary productivity (c), tree cover (d), and average annual rainfall (e).

Appendix B5. Testing for spatial dependence in bush and boma depredation events.

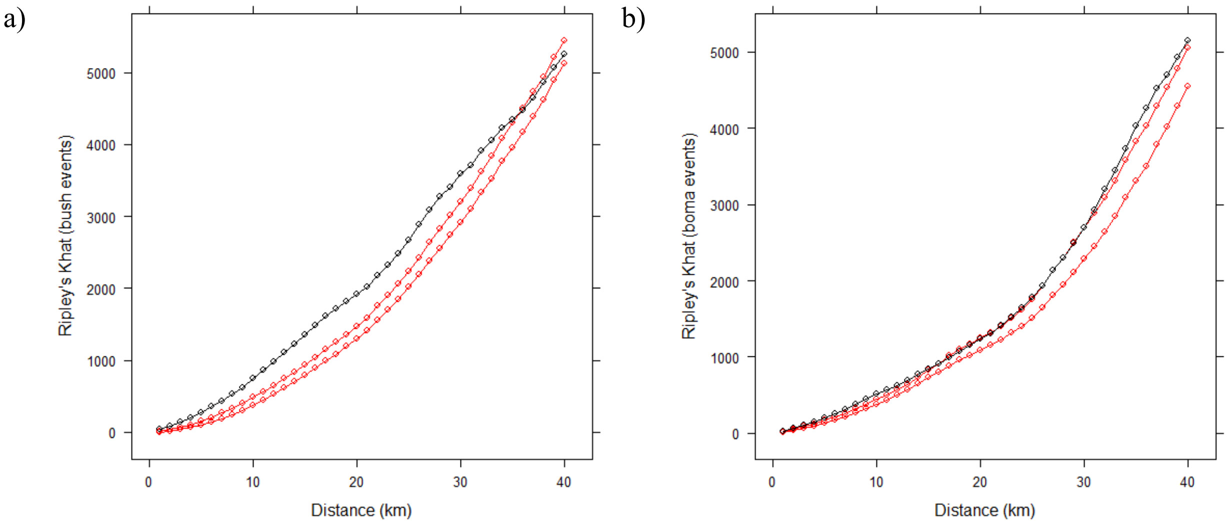

Figure B5. *K* function analysis showing the extent to which lion attacks on livestock in the bush (a) and at bomas (b) are spatially clustered. The observed (black line) represents a mean count of the number of attack events within fixed distances of an event. Higher values of $\hat{k}$ show stronger clustering. Upper and lower 95% confidence intervals are shown for estimates of $\hat{k}$ derived by allocating attacks to randomly selected locations and repeating 100 times (red lines). Where the observed values are greater than those derived from random resampling, we can conclude that lion attacks on livestock are nearer to each other than we would expect by chance at those distances.

Appendix B6. Testing for spatial dependence in boma placement.

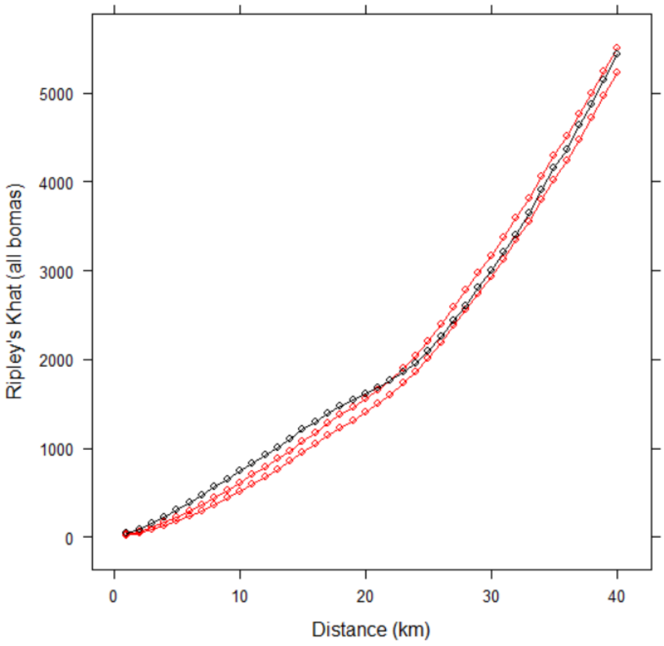

Figure B6. *K* function analysis showing the extent to which bomas are spatially clustered. The observed (black line) represents a mean count of the number of bomas within fixed distances of a boma location. Higher values of $\hat{k}$ show stronger clustering. Upper and lower 95% confidence intervals are shown for estimates of $\hat{k}$ derived by allocating bomas to randomly selected locations and repeating 100 times (red lines). We can conclude that bomas are nearer to each other than we would expect by chance up to a distance of ~ 20km.

Appendix C

Appendix C1. Land cover composition for each of the four study landscapes.

Table C1. Percentage of study area covered by each vegetation type, based on Copernicus Global Land Cover Product*

	Shrubland	Herbaceous	Open woodland	Closed woodland	Cropland	Other**
Ruaha, Tanzania	35.9	3.3	35.8	4.03	20.4	0.6
Hwange, Zimbabwe	23.7	0.5	55.7	5.4	14.5	0.2
Laikipia, Kenya	73.6	13.3	10.1	0.4	2.5	0.1
Samburu, Kenya	69.9	27.4	1.2	0	1.2	0.2

*Buchhorn, M., Smets, B., Bertels, L., De Roo, B., Lesiv, M., Tsendbazar, N.-E., Herold, M. and Fritz, S. (2020) 'Copernicus Global Land Service: Land Cover 100m: Collection 3 Epoch 2019, Globe', Version V3.0.1.

**includes built up, water, wetland and bare ground

Appendix D

Appendix D1. Summary of results of the questionnaire survey. Number of participants = 172.

PARTICIPANT

Age	Mean	32.6
	Range	14-67
Gender	Men	153 (89%)
	Women	19 (11%)
Ethnic group	Barabaig	69 (40%)
	Maasai	97 (44%)
	Other	27 (16%)
Years of formal education	Mean	3.2
	Range	0-15

INCOME

How many livestock do you currently own? *(summarised as Tropical Livestock Units*; 1 player did not own any livestock)*	Mean	30.4
	Range	0-241.6
How many sources of income do you have?	1	6 (3%)
	2	154 (90%)
	3	12 (7%)
What is the primary source of income for your household?	Livestock	159 (92%)
	Crops	13 (8%)
Do you receive any income from tourism?	Yes	9 (5%)
	No	163 (95%)

CONFLICT

Which wild animal do you think causes the biggest problem in your area? *('Other' responses included leopard, cheetah and elephant)*	Lion	41 (24%)
	Hyena	125 (72%)
	Other	3 (2%)
	Don't know	3 (2%)
How many livestock have you lost to lions over the last 12 months? *(excluding 1 participant who owned no livestock)*	Mean	0.68
	Range	0-6
In past 12 months have you used any non-lethal scaring techniques to protect your livestock?	Yes	23 (13%)
	No	148 (87%)
Have you or anyone you know ever used lethal techniques to protect your livestock?	Yes	14 (8%)
	No	157 (91%)
	Prefer not to say	1 (1%)
In the past 12 months have you received any assistance from: Ruaha Carnivore Project (RCP), National Parks Authority, Other government authority, Other NGOs.	RCP	95 (55%)
	None of the above	77 (45%)

** a reference unit which allows for the aggregation of different livestock species based on average weights (Otte and Chilonda, 2002)*

Otte, M.J. and Chilonda, P. (2002) *Cattle and small ruminant production systems in sub-Saharan Africa : a systematic review*. Rome : FAO.

PERCEPTIONS AND BELIEFS

To what extent do you agree with the following statements:	Not at all	Little	Don't know	Somewhat	Very much
"Lions harm my well-being"	46%	10%	1%	19%	24%
"Lions are beneficial to my well-being"	41%	3%	5%	19%	32%
"The presence of lions benefits my village"	27%	3%	11%	12%	47%
"Killing a lion for status/prestige is acceptable"	79%	4%	2%	3%	12%
"Killing a lion to protect family/livestock is acceptable"	63%	3%	0%	11%	23%
"Carnivore conservation is important for future generations"	9%	1%	3%	12%	75%
"The government has a responsibility to compensate local people for the negative impacts of wildlife"	10%	2%	3%	15%	70%

MANAGEMENT OPTIONS

In your opinion, to what extent are the options below ACCEPTABLE with regard to mitigating conflict between carnivores and pastoralists:	Not at all	Little	Don't know	Somewhat	Very much
Non-lethal techniques (dogs, fences, lights)	3%	0%	2%	11%	84%
Lethal techniques	88%	2%	0%	1%	9%
Provision of wildlife habitat	3%	1%	0%	11%	85%
Compensation and subsidies	6%	1.5%	1.5%	13%	78%
Ecotourism	1%	0%	0%	8%	91%
Hunting tourism	93%	1%	0%	1%	5%

INSTITUTIONAL TRUST

Do you trust the following organisations to make balanced decisions about land and wildlife management?	Not at all	Little	Don't know	Somewhat	Very much
Tanzanian government	4%	1%	17%	22%	56%
National parks service	2%	2%	23%	17%	56%
International organisations and NGOs, e.g., RCP	2%	1%	16%	12%	69%

COMMUNITY TRUST

	Not at all	Little	Don't know	Somewhat	Very much
Would you say that most of the time people in your community are trying to help each other?	6%	2%	1%	20%	71%
Would you say that most people in your community are honest and can be trusted?	6%	1%	2%	23%	68%
Do you feel you are respected in this community?	2%	2%	1%	16%	79%
Do you participate in village activities?	9%	1%	0%	11%	79%

EQUITY

	Not at all	Little	Don't know	Somewhat	Very much
Do you feel able to influence decision making related to wildlife management and farming?	8%	6%	8%	28%	50%
Do you feel that current management schemes respect your local traditions and cultures regarding wildlife, agriculture and access to land?	9%	4%	5%	28%	54%
Would you say that allocation of finances for wildlife management in Tanzania is fairly distributed?	6%	3%	25%	25%	42%

Do feel you have the right to use the land around your village however you wish?	22%	2%	1%	18%	56%
ABOUT THE GAMES					
Please state how familiar you are with each of the other participants on a scale of 1-4 (very limited-very good). *Answers were summed to provide an overall familiarity score for each player (with possible scores between 3-12)*	Mean Range	10 3-12			
What was your main goal in the game?	To win To do what I do in real life To have fun To do what was best for the group			83 (48%) 74 (43%) 8 (5%) 7 (4%)	
	Not at all	Little	Don't know	Somewhat	Very much
Did your choices in the game depend on what others did?	60%	1%	6%	13%	20%
Did you consider the effect of your choices on other players?	61%	1%	10%	8%	20%

Appendix D2. Variables considered in linear mixed effect models and correlations

Table D2. Variables considered in linear mixed effect models and correlations

Variable	Data type	Description
Fixed effects		
Treatment_subsidy	Categorical (8 levels)	• Baseline • Deterrents • Individual Subsidy of 4, 8 or 12 • Community Subsidy of 4, 8 or 12
Rounds	Numeric	Rounds within a game treatment
Habitat_others_previous	Numeric	Sum of number of habitat decisions of 3 other players in previous round
Scare_others_previous	Numeric	Sum of number scare decisions of 3 other players in previous round
Lion_damage_previous	Numeric	No. points lost to lion damage in previous round
Correlation with random effect		
Village	Categorical (9 levels)	Village where game took place
Age	Numeric	Age of participant in years
Gender	Categorical (2 levels)	Gender of participant
Ethnic_group	Categorical (4 levels)	• Maasai • Barabaig • Sukuma • Other (Bena, Hehe)
Education	Numeric	No. years of education
Total_livestock	Numeric	Total no. livestock (Tropical Livestock Index)
Stock_lost_lions	Numeric	No. livestock lost to lions in the past 12 months
Assistance_received	Categorical (2 levels)	Household has received assistance from Ruaha Carnivore Project (Yes/No)
Game_objective	Categorical (4 levels)	• To win • To have fun • To do what I do in real life • To do what is best for the group
Familiarity	Numeric	Sum of familiarity with 3 other players. Participants were asked to rate their familiarity with each player on a scale of 1-4 (very limited-very familiar), resulting in sum familiarity score between 3-12.
Lions_benefit_me	Ordinal	"Lions are beneficial to my well-being"
Lions_benefit_village	Ordinal	"The presence of lions benefits my village"
Trust_Tanzanian_Government	Ordinal	Do you trust X to make balanced decisions about land and wildlife management?
Trust_TANAPA	Ordinal	
Trust_NGOs	Ordinal	
Community_help_each_other	Ordinal	Would you say that most of the time people in your community are trying to help each other?
Community_can_be_trusted	Ordinal	Would you say that most people in your community are honest and can be trusted?
Respected_in_community	Ordinal	Do you feel you are respected in this community?
Management_respects_traditions	Ordinal	Do you feel that current wildlife management schemes respect your local traditions and cultures?
Finances_fairly_distributed	Ordinal	Would you say that allocation of finances for wildlife management in Tanzania is fairly distributed?
Able_to_influence_decisions	Ordinal	Do you feel able to influence decision making related to wildlife management?
Right_to_use_land	Ordinal	Do you feel that you have the right to use the land around your village however you wish?
Likert scale used for all ordinal data: Not at all (-2) – Little (-1) – Don't know (0) – Somewhat (1) – Very much (2)		

Appendix D3. Summary of model selection for linear mixed effects models of game decisions.

Table D3. Summary of model selection. All models also included a correlation structure and a random effect: corr=corAR1(form=~1|GameID/PlayerID), random=~1|GameID/PlayerID. Shaded rows indicate the final model.

A. Habitat choices all rounds (no. observations = 4516)

model 1	log(Habitat_choices+1)~Treatment*Rounds
model 2	log(Habitat_choices+1)~Treatment+Rounds
model 3	log(Habitat_choices+1)~Treatment

Model	**df**	**AIC**	**BIC**	**logLik**	**Test**	**L. Ratio**	**p-value**
model 1	20	5264.49	5392.80	-2612.25			
model 2	13	5365.17	5448.57	-2669.59	1 vs 2	114.69	<0.001
model 3	12	5373.17	5450.16	-2674.59	2 vs 3	10.00	<0.01

B. Habitat choices excluding round 1 (no. observations = 3828)

model 1	log(Habitat_choices+1)~Treatment*Rounds+Habitat_others+Lion_damage
model 2	log(Habitat_choices+1)~Treatment*Rounds+Habitat_others
model 3	log(Habitat_choices+1)~Treatment+Rounds+Habitat_others
model 4	log(Habitat_choices+1)~Treatment+Habitat_others
model 5	log(Habitat_choices+1)~Treatment*Habitat_others
model 6	log(Habitat_choices+1)~Treatment*Habitat_others+Rounds

Model	**df**	**AIC**	**BIC**	**logLik**	**Test**	**L. Ratio**	**p-value**
model 1	22	3880.09	4017.59	-1918.05			
model 2	21	3878.15	4009.40	-1918.07	1 vs 2	0.06	0.809
model 3	14	3874.93	3962.43	-1923.47	2 vs 3	10.79	0.148
model 4	13	3875.69	3956.94	-1924.83	3 vs 4	2.75	0.097
model 5	20	3817.43	3942.43	-1888.71	4 vs 5	72.26	<0.001
model 6	21	3819.20	3950.45	-1888.60	5 vs 6	0.23	0.631

C. Scare choices all rounds (no. observations = 4516)

model 1	log(Scare_choices+1)~Treatment*Rounds
model 2	log(Scare_choices+1)~Treatment+Rounds
model 3	log(Scare_choices+1)~Treatment

Model	**df**	**AIC**	**BIC**	**logLik**	**Test**	**L. Ratio**	**p-value**
model 1	20	6360.88	6489.19	-3160.44			
model 2	13	6374.42	6457.82	-3174.21	1 vs 2	57.54	<0.001
model 3	12	6375.53	6452.51	-3175.77	2 vs 3	3.11	0.078

D. Scare choices excluding round 1 (no. observations = 3828)

Model	
model 1	log(Scare_choices+1)~Treatment*Rounds+Scare_others+Lion_damage
model 2	log(Scare_choices+1)~Treatment*Rounds+Scare_others
model 3	log(Scare_choices+1)~Treatment+Rounds+Scare_others
model 4	log(Scare_choices+1)~Treatment+Scare_others
model 5	log(Scare_choices+1)~Treatment*Scare_others
model 6	log(Scare_choices+1)~Treatment*Scare_others+Rounds

Model	**df**	**AIC**	**BIC**	**logLik**	**Test**	**L. Ratio**	**p-value**
model 1	22	5046.10	5183.60	-2501.05			
model 2	21	5044.13	5175.38	-2501.07	1 vs 2	0.03	0.854
model 3	14	5035.02	5122.52	-2503.51	2 vs 3	4.89	0.674
model 4	13	5033.14	5114.39	-2503.57	3 vs 4	0.12	0.738
model 5	20	5023.03	5148.03	-2491.52	4 vs 5	24.12	<0.01
model 6	21	5024.86	5156.12	-2491.43	5 vs 6	0.17	0.682

Appendix D4. Correlation matrix of individual random effects from linear mixed models of game decisions and questionnaire data

Table D4. Correlation matrix of individual random effects and questionnaire data. Lower half of the table shows r values, upper half details the type of correlation used. PN=Pearson, PS=Polyserial, PC=Polychoric. Highlighted cells show correlations where r exceeds the critical value for a Pearson correlation to be considered significant (r≥ 0.149 (blue), r ≤ -0.149 (red), df=170) AND the 95% confidence intervals do not overlap this value.

	Habitat_ Random_Eff	Scare_ Random_Eff	Village	Gender	Age	Ethnic_ group	Education	Total_ livestock	Stock_lost_ lions	Assistance_ received	Player_ familiarity	Game_ objective	Lions_ benefit_me	Lions_benefit _village	Trust_TZ_ Government	Trust_ TANAPA	Trust_NGOs	Community_ help	Community_ trusted	Respected_in _community	Management _respects	Finances_ fair	Influence_ decisions	Right_to_ use_land
Habitat_Random_ Effect	1.000	PN	PS	PS	PN	PS	PN	PN	PN	PS	PN	PS	PS	PS	PS	PS	PS	PS	PS	PS	PS	PS	PS	PS
Scare_Random_ Effect	-0.287	1	PS	PS	PN	PS	PN	PN	PN	PS	PN	PS	PS	PS	PS	PS	PS	PS	PS	PS	PS	PS	PS	PS
Village	-0.003	0.001	1	PC	PS	PC	PS	PS	PS	PC	PS	PC	PC	PC	PC	PC	PC	PC	PC	PC	PC	PC	PC	PC
Gender	0.268	0.039	-0.039	1	PS	PC	PS	PS	PS	PC	PS	PC	PC	PC	PC	PC	PC	PC	PC	PC	PC	PC	PC	PC
Age	-0.046	-0.052	0.140	-0.109	1	PS	PN	PN	PN	PS	PN	PS	PS	PS	PS	PS	PS	PS	PS	PS	PS	PS	PS	PS
Ethnic_group	-0.096	0.069	-0.064	-0.098	0.248	1	PS	PS	PS	PC	PS	PC	PC	PC	PC	PC	PC	PC	PC	PC	PC	PC	PC	PC
Education	-0.048	0.038	0.094	-0.022	-0.075	0.382	1	PN	PN	PS	PN	PS	PS	PS	PS	PS	PS	PS	PS	PS	PS	PS	PS	PS
Total_livestock	-0.206	-0.047	0.194	-0.097	0.110	0.013	0.104	1	PN	PS	PN	PS	PS	PS	PS	PS	PS	PS	PS	PS	PS	PS	PS	PS
Stock_lost_lions	-0.021	0.145	0.435	0.414	-0.029	-0.192	-0.002	0.323	1	PS	PN	PS	PS	PS	PS	PS	PS	PS	PS	PS	PS	PS	PS	PS
Assistance_received	-0.047	-0.061	0.096	0.199	0.120	0.188	0.217	0.124	0.152	1	PS	PC	PC	PC	PC	PC	PC	PC	PC	PC	PC	PC	PC	PC
Player_familiarity	-0.014	0.133	-0.197	0.098	0.100	0.137	0.062	-0.114	-0.071	-0.125	1	PS	PS	PS	PS	PS	PS	PS	PS	PS	PS	PS	PS	PS
Game_objective	0.038	-0.071	-0.174	0.198	-0.064	-0.241	-0.267	0.051	0.069	-0.088	0.137	1	PC	PC	PC	PC	PC	PC	PC	PC	PC	PC	PC	PC
Lions_benefit_me	0.027	0.061	-0.242	0.058	-0.028	0.057	0.133	-0.003	-0.161	0.048	0.008	-0.133	1	PC	PC	PC	PC	PC	PC	PC	PC	PC	PC	PC
Lions_benefit_ village	0.059	-0.038	-0.125	0.031	0.077	0.144	0.088	0.177	-0.101	0.072	0.030	-0.291	0.691	1	PC	PC	PC	PC	PC	PC	PC	PC	PC	PC
Trust_Tanzanian_ Government	0.046	-0.030	-0.081	-0.187	-0.075	-0.181	0.053	-0.022	-0.140	-0.289	0.277	0.003	0.073	0.130	1	PC	PC	PC	PC	PC	PC	PC	PC	PC
Trust_TANAPA	-0.004	-0.054	-0.086	0.092	-0.040	-0.223	0.036	0.119	-0.073	-0.187	0.199	0.022	0.225	0.234	0.768	1	PC	PC	PC	PC	PC	PC	PC	PC
Trust_NGOs	-0.007	-0.119	-0.117	-0.074	-0.098	-0.293	-0.135	0.049	-0.119	-0.356	0.270	0.182	0.091	0.071	0.661	0.686	1	PC	PC	PC	PC	PC	PC	PC
Community_help_ each_other	0.137	-0.153	-0.009	-0.129	0.012	-0.038	0.052	0.103	-0.035	-0.103	0.224	0.010	0.195	0.176	0.478	0.470	0.386	1	PC	PC	PC	PC	PC	PC
Community_can_be_trusted	0.130	-0.010	0.084	0.148	0.177	0.136	0.105	-0.004	0.070	-0.054	0.267	-0.063	0.293	0.372	0.284	0.250	0.121	0.732	1	PC	PC	PC	PC	PC
Respected_in_ community	0.009	0.230	0.159	-0.180	0.352	0.231	0.188	0.073	0.045	-0.150	0.261	-0.275	0.301	0.388	0.270	0.300	0.161	0.359	0.522	1	PC	PC	PC	PC

Table D4. Continued.

	Habitat_Random_Eff	Scare_Random_Eff	Village	Gender	Age	Ethnic_group	Education	Total_livestock	Stock_lost_lions	Assistance_received	Player_familiarity	Game_objective	Lions_benefit_me	Lions_benefit_village	Trust_TZ_Government	Trust_TANAPA	Trust_NGOs	Community_help	Community_trusted	Respected_in_community	Management_respects	Finances_fair	Influence_decisions	Right_to_use_land
Management_respects_traditions	-0.064	0.248	0.044	-0.093	-0.048	-0.160	-0.063	-0.090	-0.012	-0.279	0.295	-0.007	0.198	0.251	0.654	0.514	0.437	0.399	0.408	0.412	1	PC	PC	PC
Finances_fairly_distributed	-0.039	0.021	-0.181	-0.301	-0.063	-0.146	-0.004	-0.120	-0.242	-0.226	0.223	-0.054	0.373	0.279	0.595	0.488	0.587	0.414	0.368	0.384	0.592	1	PC	PC
Able_to_influence_decision_making	-0.016	0.189	-0.056	-0.203	-0.010	0.056	0.039	-0.045	-0.124	-0.346	0.197	-0.080	0.392	0.215	0.555	0.488	0.465	0.454	0.334	0.389	0.625	0.635	1	PC
Right_to_use_land	0.122	0.007	0.109	0.224	0.209	0.143	-0.021	-0.082	-0.010	0.256	-0.068	-0.045	0.170	0.257	-0.103	-0.107	-0.460	-0.026	0.316	0.193	0.011	0.048	-0.063	1

Appendix D5. Correlation matrix of group random effects from linear mixed models of game decisions and group-level characteristics.

Table D5. Correlation matrix of group random effects and group-level questionnaire data. Numeric variables represent the mean for each game group. Gender and was categorised as 'male-only' or 'mixed'. Ethnic group was categorised as 'mixed' or 'uniform'. Lower half of the table shows r values, upper half details the type of correlation used. PN=Pearson, PS=Polyserial, PC=Polychoric. Highlighted cells show correlations where r exceeds the critical value for a Pearson correlation to be considered significant (r≥ 0.301 (blue), r ≤ -0.301 (red), df=41) AND the 95% confidence intervals do not overlap this value.

	Habitat_Random_Effect	Scare_Random_Effect	Village	Gender	Ethnic_group	Age	Education	Total_livestock	Stock_lost_lions	Player_familiarity
Habitat_Random_Effect	1	PN	PS	PS	PS	PN	PN	PN	PN	PN
Scare_Random_Effect	-0.737	1	PS	PS	PS	PN	PN	PN	PN	PN
Village	-0.004	-0.010	1	PC	PC	PS	PS	PS	PS	PS
Gender	0.137	-0.480	-0.019	1	PC	PS	PS	PS	PS	PS
Ethnic_group	0.218	-0.082	0.093	0.295	1	PS	PS	PS	PS	PS
Age	-0.125	0.018	0.201	0.113	-0.534	1	PN	PN	PN	PN
Education	-0.030	-0.043	0.153	0.181	-0.138	0.070	1	PN	PN	PN
Total_livestock	0.058	-0.183	0.415	-0.031	-0.055	0.199	0.147	1	PN	PN
Stock_lost_lions	0.159	0.0213	0.623	-0.551	0.065	0.018	-0.047	0.553	1	PN
Player_familiarity	-0.365	0.309	-0.277	-0.052	0.029	0.119	0.125	-0.082	-0.123	1