Improving our understanding of the socio-ecological complexity of human-carnivore interactions

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Abstract

Conflicts over the management of large carnivores, and their impacts on humans reduces well-being for human communities and threatens the persistence of large carnivore populations around the world. Improving our understanding of the complex ecological and social systems that create these conservation conflicts is vital if they are to be resolved. In this thesis we investigate ecological and social aspects of human-carnivore interactions in land bordering Ruaha National Park in Tanzania where there are conflicting views on how large carnivores should be managed.

Investigating the spatio-temporal patterns of carnivore attacks on livestock we found higher risk of attacks linked to increased rainfall, wild prey and proximity to protected areas. We found re-enforced wire enclosures to be more effective at protecting livestock compared to those of traditional construction. Using local ecological knowledge to investigate carnivore landscape use in community land we found occupancy of lions, wild dog, leopard and cheetah higher in the wet season, while hyenas are present all year round. However low detection rates and respondent availability during the dry season restricted our model's ability to accurately predict carnivore land use.

Studying tolerance towards lions and hyenas we found perceived benefits and positive beliefs were the most influential variables for both species, while experience of species and perceived risks only influenced tolerance towards hyenas.

Engagements with conservation programs increased tolerance towards lions but had a complex relationship with risk perception for both species, highlighting how conservation interventions can interact with other socio-psychological variables with unexpected consequences. Simulating an African savannah community we found low levels of retaliatory killing of large carnivores drove them to extinction. This, however, had little impact on other simulated populations. We also found small herbivores to be responsible for the most damage to crops compared to large herbivores.

This work contributes to our understanding of some of the drivers of the human-carnivore interactions that conservation conflicts are often centred on. We highlight the complexity of these systems and the broad range of tools and disciplines required to study them.

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Cashew Zuberi and George Sedoyeka, a dream team in the field

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Author Contributions

I declare that this thesis, "Improving our understanding of the socio-ecological complexity of human-carnivore interactions", is my own work. The contribution of other authors is stated below. None of the work included has been submitted, in whole or in part, in any previous application for a degree.

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All photos used were taken by Leejiah Dorward.

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CHAPTER 1

General introduction



Lions are one large carnivore species at the centre of conservation conflicts over how to manage their populations and the impacts they have on the communities they live alongside.

1.1 Carnivores, Culture, Conservation and Conflicts

Large carnivores are iconic, charismatic species with important roles in the cultural traditions of many societies. The positive symbolism human societies have attached to these species throughout history can be seen from stories of Romulus, the founder of Rome, and his brother Remus being suckled by a she-wolf, to elite Aztec military orders being named after the jaguar and taking on the power and protection of the mystical cat by donning its costume (Saunders, 1994; Tennant, 1988). Human's fascination with these species continues to this day with carnivores used widely in product branding (Brown, 2010), species body parts playing important roles in medical practices (Still, 2003), and they are major attractions in the multi-billion dollar a year nature-based tourism industry (Goodwin, 1996; Lindsey et al., 2007b; Maciejewski and Kerley, 2014). These positive associations, however, belie the complexity of humanity's relationship with large carnivores, with a host of other cultural traditions exposing a darker side to how we perceive and interact with these species. The "Big Bad Wolf" in Little Red Riding hood and beliefs surrounding werewolves shows a deep seated fear of wolves in European culture while the rewards offered to Maasai warriors for killing lions demonstrates how lethal persecution of carnivore populations can be instilled in almost sacred cultural institutions (Nie, 2002; Goldman et al., 2010).

This pluralism of views is evidenced in contemporary controversies and conflicts surrounding decisions about the management of carnivore populations and their interactions with human interests. While many people place high value on the existence of large carnivores and are concerned about their declining popula-

tions (Ripple et al., 2014; Nelson, 2009; Macdonald, 2001) other communities who deal with the real and perceived costs of living alongside carnivores would rather see carnivore populations continue to decline or go extinct (Barua et al., 2013; Dickman, 2010; Browne-Nuñez et al., 2015; Inskip et al., 2016). While the costs carnivores impose are generally felt locally, positive attitudes and high existence values often operate on national or international scales (Nelson, 2009; OBryan et al., 2018), creating different experiences and beliefs about carnivores among socially, culturally and politically distinct groups (Bruskotter et al., 2017). As a result disagreements over carnivore management are often much more than just discussions about how to manage the costs carnivores impose but also involve a complex array of other cultural, moral and political issues (Young et al., 2010; Nie, 2002).

Resolving these conflicts over the management of large carnivores is vital for both improving the well being of communities who suffer costs resulting from living alongside carnivores as well as for reducing large carnivore persecution and securing the persistence of their populations. In this thesis we aim to improve our understanding of the ecological and social variables that interact to contribute to conservation conflicts around the management of large carnivores around Ruaha National Park in Tanzania.

1.2 Thesis outline

Following the format of an integrated thesis this dissertation begins with an introduction and literature review followed by four data chapters formatted as journal articles, ending with a discussion and conclusions.

Chapter 2. I outline the existing literature relating to conservation conflicts,

the status of carnivores and their conservation, and the social and ecological implications of human-carnivore impacts.

Chapter 3. I aim to improve our understanding of the variables that influence the risk of livestock being attacked by large carnivores. Using data on livestock attacks collected from 632 interviews conducted over 12 months and remote sensed environmental data I investigate spatial and temporal patterns in attacks on livestock.

Chapter 4. This chapter aims to use local ecological knowledge and occupancy modelling to improve our understanding of large carnivore land-use in community land bordering a protected area. I managed repeat visits over a 12 month period to 160 households where interviews were conducted on the local presence of lions, hyenas, leopards, cheetahs, wild dogs and their prey species. I combine data from these interviews and remote sensed environmental data to build occupancy models that help understand the spatio-temporal factors influencing landscape use of 5 large carnivores across a landscape of approximately 1500 km^2.

Chapter 5. In this chapter I use socio-psychological frameworks to investigate tolerance towards large carnivores in a community subject to the impacts of living alongside large carnivores. I use structural equation models and data from 176 structured interviews to investigate how a range of experiential, psychological and social variables influence tolerance of lion and hyena populations.

Chapter 6. In the final data chapter I investigate the ecological and economic impact of apex predator persecution using a simulated African savannah community. I modelled a stereotypical African savannah community consisting of crops, grasses, livestock, large and small wild herbivores, mesopredators and large carnivores. I used type II functional responses to model trophic interactions, deriv-

ing parameter values from the literature. I investigated the changes in simulated populations as large carnivores are persecuted to extinction as a result of lethal management in retaliation for livestock losses.

Chapter 7. I synthesise our findings, discuss the implications of my results and outline areas of further research that will contribute to our understanding of conservation conflicts surrounding large carnivores.



This lioness was killed in retaliation for attacking cattle. Her removed front paw will bring rewards and respect to the warrior who killed her; demonstrating the important cultural role lions play amongst some cultures despite the costs they impose.

CHAPTER 2

LITERATURE REVIEW



Requiring huge home ranges cheetah's often interact with people and their livestock outside of protected areas.

2.1 People, biodiversity, and conflict

Conflicts surrounding management of wildlife that impose costs on human societies is one of the greatest challenges faced by the conservation movement (Young et al., 2010; Dickman, 2010; Redpath et al., 2013). Damage causing wildlife impart high social and economic costs on the communities they live alongside, who are often politically and economically marginalised and can ill afford the costs wildlife impose on them (Barua et al., 2013; Das and Chattopadhyay, 2011; Naughton-Treves, 1997). In return wildlife and biodiversity often suffer as human communities protect their interests by employing (legal and illegal) management techniques that block wildlife's access to important resources or entails lethal control (Dickman, 2010; Woodroffe and Frank, 2005).

Situations where "an action by either humans or wildlife has an adverse effect on the other" (Conover, 2001) are frequently framed as "human-wildlife conflicts" (HWC). However, the use of this terminology can be misleading as arguably animals are unable to consciously enter conflict with humans (Peterson et al., 2010; Redpath et al., 2014), thus most HWC is in reality "human-human conflict", between those who prioritise species conservation against those whose interests wildlife threaten (Peterson et al., 2010; Redpath et al., 2014; Marshall et al., 2007). Re-framing HWC as human-human conflict re-focuses mitigation strategies away from technological approaches that separate wildlife and human-interests to one which tries to understand and reconcile the different human attitudes towards wildlife (Redpath et al., 2014). There is increasing recognition that the terminology describing "human-wildlife conflicts" inadequately and inaccurately describes the complex social and ecological dynamics present in these systems (Redpath et al., 2014). Some authors continue to use HWC terminology while either adding

additional components to their definition of HWC to include "conflicts between humans themselves over how to manage the impacts between humans and wildlife" (Kansky et al., 2016) or recognising the unsatisfactory and reductive nature of the phrase (Montgomery et al., 2018). However there is also a range of new, and more fit for purpose, terminology entering the literature to describe situations where the actions of humans or wildlife threaten the well-being or existence of the other, or where there is disagreement over how these impacts should be managed.

"Human-wildlife interactions" is being used by some authors as a less value driven phrase replacing HWC in describing situations where the actions of humans and wildlife have some impact on the other. The renaming of the "Journal of Human-Wildlife Conflict" to the "Journal of Human-Wildlife Interactions" in 2010 highlights the desire for HWC to be re-framed in a way that draws attention to mutuality between humans and wildlife, while still describing situations where humans and wildlife are in competition or imposing cost upon each other (Peterson et al., 2010; Conover, 2010). Human-wildlife coexistence is another phrase being used to change the framing of how HWCs are perceived (Madden, 2004). Peterson et al. (2010) contend that conflict terminology dichotomises humans and nature, framing wildlife as something that threatens humanity while failing to recognise the contributions nature makes to human welfare. They argue for the more positive framing of human-wildlife coexistence which highlights the potential for mutualism between humans and nature. Many of the situations where humans and wildlife cause harm on the other result from competition over resources, predominantly food and space (Distefano, 2005; Treves and Naughton-Treves, 2005; Treves and Karanth, 2003), thus human-wildlife competition is another value free term used to describe some HWC situations (Matthiopoulos et al., 2008).

Conservation conflicts, or biodiversity conflicts, is another framing used to

describe conflicts between people over wildlife or other aspects of biodiversity (Young et al., 2010; Redpath et al., 2013). Under this framing what are traditionally defined as human-wildlife conflicts are split into two components. Firstly, human-wildlife impacts (HWI), which are defined as "circumstances where people, consciously or unconsciously, impact negatively on biodiversity, or alternatively, where wildlife or other aspects of biodiversity impact negatively on the well-being or livelihoods of people" (Young et al., 2010; Young et al., 2005). Secondly, conservation conflicts, which are centred on interactions between human groups seeking to conserve species or biodiversity and those with other interests (Young et al., 2010; Redpath et al., 2013). The separation of these two aspects is critical as each will be understood and managed differently. HWIs can be resolved through legislative or technical solutions, for instance, fencing that separates wildlife from human interests or compensation for damage caused by wildlife. While resolving conservation conflicts requires a broader and more complex array of political and social tools (Redpath et al., 2013; Madden and McQuinn, 2014; Nie, 2002).

2.1.1 Human-Wildlife Impacts

While not the only, or even the main, factor driving conservation conflicts around the world, understanding and reducing HWIs (or human-wildlife interactions, or human-wildlife competition) is an important step in reducing the negative impacts human communities and wildlife have on each other. HWIs are a global problem occurring in low, middle, and high income countries (Manfredo and Dayer, 2004) with examples from every continent with major human habitation (Dickman et al., 2014; Musiani et al., 2005; Palmeira et al., 2008; Bagchi and Mishra, 2006; Prowse et al., 2015; Thirgood et al., 2000). These impacts come in many different forms such as: crop consumption (Arlet and Molleman, 2007); infrastructure damage

(Su and Scheffrahn, 1998); competition for prey species, land, and water (Johnson et al., 2006; Ripple et al., 2014; Hoare, 1999); timber damage (Messmer, 2000); livestock predation (Dickman et al., 2014; Santiago-Avila et al., 2018), and fishery predation (Matthiopoulos et al., 2008); disease transmission (Ottichilo et al., 2001); and human-injuries, and deaths (Löe and Röskaft, 2004). HWI involves wildlife from a range of taxonomic groups, e.g. terrestrial and marine mammals (Löe and Röskaft, 2004; Butler et al., 2015), birds (Redpath and Thirgood, 1997), reptiles (Chaves et al., 2015), fish (Freitas et al., 2016) and insects (Cease et al., 2015), and while rural societies are the historically most affected, HWI increasingly affects urban societies (Messmer, 2000). The range of human groups affected is immense; from subsistence pastoralists (Dickman et al., 2014) and agriculturalists (Arlet and Molleman, 2007) in low income countries to metropolitan residents (Conover, 1997) and landed nobility in high income countries (Redpath and Thirgood, 1997).

Competition between humans and wildlife has existed throughout history, driving many species to local or global extinction (Graham et al., 2005; Woodroffe et al., 2005). Historically HWI were resolved by legal or illegal persecution of problem species (Woodroffe et al., 2005; Treves and Naughton-Treves, 2005). This aimed to solve the problem by reducing or obliterating wildlife populations that had negative impacts on human well-being (or at least the well-being of those with political power). These actions have had huge impacts on biodiversity: contributing to the extinction of populations and species (e.g. large carnivores in Great Britain (Mitchell-Jones, 1996) and Tasmania's thylacine (Prowse et al., 2013)), the destruction of natural habitat (e.g. the conversion of wildebeest calving grounds to arable land to reduce their populations and disease transmission to cattle (Ottichilo et al., 2001)), the introduction of invasive species (e.g. the cane toad in Australia (Phillips et al., 2007)), or the modification of habitat through the persecution of keystone

species (e.g. elephants and prairie dog (Woodroffe et al., 2005; Kotliar et al., 1999)) and apex predators (e.g. wolves (Sinclair, 1995; Ripple et al., 2001)). More recently the recognition of the benefits of biodiversity and an increasingly powerful and vocal conservation movement has made the widespread eradication or persecution of wildlife a politically costly course of action, leading to disagreements in how HWIs should be managed (Treves and Karanth, 2003).

2.1.2 Conservation Conflicts

Widespread persecution of wildlife has historically been accepted as wildlife management was considered a "rural or agricultural problem" (Messmer, 2000) with wildlife managers mainly responsible for destroying wildlife that threatened human interests (Treves and Naughton-Treves, 2005). However, as the wider economic, social and cultural benefits of wildlife are increasingly recognised and valued the pressure on managers to protect wildlife has increased (Treves and Naughton-Treves, 2005), creating conservation conflicts between those who want wildlife protected and those whose interests wildlife threaten. While the relationships between people and the natural environment often appear central to conflicts around human-wildlife impacts these are often proxy issues, with conservation conflicts representing an array of underlying social issues (Dickman, 2010). While those calling for the conservation of biodiversity often represent the interests of national and international communities HWIs involve local rural communities and the species they are in competition with (Thirgood et al., 2005; Nelson, 2009; OBryan et al., 2018). Increasingly these communities are trapped between damaging wildlife and a myriad of local, national and international institutions that attempt to dictate or control their relationship and interactions with their local environment (Naughton-Treves and Treves, 2005). Young et al. (2010) outlines

six broad categories of conservation conflicts, highlighting the number of different social processes that can result in conflict over wildlife:

- Conflicts over beliefs and values;
- Conflicts of interest, when multiple human groups want different things from a habitat or species;
- Conflicts over process, where there are different opinions over decision-making and fairness in relation to managing biodiversity;
- Conflicts over information, where stakeholders have different access, understanding or perceptions of data;
- Structural conflicts referring to social, legal, economic and cultural arrangements;
- Inter-personal conflicts, where there are personality differences between individuals or groups which can include issues surrounding communication and mistrust.

The species around which conservation conflicts are centred highlights how these conflicts are not primarily about the severity of human-wildlife impacts but are culturally constructed around value judgements regarding which species and who's interests should be protected. The majority of research into HWI and conservation conflicts focuses on iconic species of conservation concern (Peterson et al., 2010; Redpath et al., 2014), with charismatic taxa given their own sub-disciplines within HWC research, e.g. human-elephant or human-carnivore conflict (Hoare, 1999; Treves and Karanth, 2003). Focusing on charismatic species means other species who may be involved in more severe HWIs are often overlooked (Peterson et al., 2010). There is little work that crosses the divide between the agricultural literature, focusing "pests" such as rodents and invertebrates, and the HWI conservation literature, focusing on iconic species (Naughton-Treves and Treves, 2005).

However, a number of studies suggest that in areas adjoining protected areas where rodents and large herbivores are present the most severe HWI are caused by rodents (Arlet and Molleman, 2007; Harich et al., 2013; Gillingham and Lee, 2003; Hawkes, 1991). Rodents and invertebrates can also be important vectors of disease, with deaths from plague and malaria vastly outweigh deaths caused by large carnivores and herbivores (Meerburg et al., 2009; Löe and Röskaft, 2004; WHO, 2017; Worrall et al., 2004). Not only do rodents and invertebrates impose costs on humans but they are also widely persecuted with large industries built around their lethal control (Stenseth et al., 2003; Berg et al., 2012), which can have wide-reaching ecological impacts (Howarth, 1991; Innes and Barker, 1999). Understanding the array of HWIs, how to manage them, and why some create conservation conflicts and others do not requires a wider consideration of overlooked taxa and the social and economic damage they cause.

The diversity of causes and drivers behind conservation conflicts means they cannot be understood by just one scientific discipline. Approaches from the natural sciences, social sciences and humanities are required to understand and manage the various elements that combine to produce conservation conflicts (Redpath et al., 2013). Despite its challenges, resolving these conflicts will require a broad interdisciplinary approach (Dickman, 2010; Montgomery et al., 2018; Nie, 2002).

2.2 Large carnivores; conservation and conflict

Large carnivores are an ecologically, economically and socially important group of animals (Wolf and Ripple, 2016; Ripple et al., 2014). Through a number of top down ecological mechanisms, for example mesopredator release (Brashares et al., 2010; Crooks and Soulé, 1999; Ripple et al., 2013), direct predation and landscapes

of fear (Ripple and Beschta, 2004; Schmitz et al., 1997), carnivores can have wide ranging impacts on the ecological systems they exist in. Through these ecological processes carnivores can also provide economically valuable ecosystem services, e.g. controlling populations of pest animals (Brashares et al., 2010; Prowse et al., 2015; Packer et al., 2005), increasing carbon storage (Strickland et al., 2013), removing waste (Levi et al., 2012) and reducing human exposure to zoonotic diseases (Braczkowski et al., 2018). In many areas large carnivores also offer direct economic benefits as highly sought after animals, and thus a primary driver, for photographic tourism (Lindsey et al., 2007b; Maciejewski and Kerley, 2014). The importance of this economic contribution can be magnified as wildlife based tourism is often prominent in less economically developed areas that lack other economic opportunities (Ashley et al., 2000). There is, however, evidence that the economic benefits from tourism are subject to high levels of elite capture and often do not reach the communities who suffer as a result of living alongside wildlife (Nepal, 1997; Ferraro, 2002). The opportunity costs of protected areas which host tourists are also often not fully accounted for (Bluwstein, 2016). Large carnivores are also socially important species, playing central roles in a number of different cultures (Hazzah et al., 2009; Shen et al., 1982; Coggins, 2003; Kellert et al., 1996; Goldman et al., 2010), and many people derive pleasure purely from the knowledge that large carnivores exist, an existence value that exists independently from viewing or "consuming" the species (Nelson, 2009; Macdonald, 2001). As a result of these ecological and social values placed on carnivores there is significant political will and pressure to protect and conserve these species around the world.

Despite their importance large carnivore populations are under intense pressure around the world and many are threatened with extinction (Ray et al., 2013; Wolf and Ripple, 2016; Ripple et al., 2014). Of the 31 largest species of Carnivora

(excluding pinnipeds) 24 are decreasing in number and 19 are classed as vulnerable, endangered or critically endangered (Ripple et al., 2014). Large carnivore's place at the top of the food chain means they require large home ranges containing large bodied prey, exist at low densities, and have low reproduction rates making them naturally rare species (Ripple et al., 2014). These factors mean they also come into competition with humans for space and prey and are thus especially at risk from human activities such as habitat destruction, human induced prey depletion and persecution (Woodroffe and Ginsberg, 1998; Treves and Karanth, 2003).

The high existence values and conservation effort given to large carnivores by national and international audiences are not always shared locally by communities who pay high social and economic costs for living alongside carnivores (Dickman et al., 2011; Abade et al., 2014a; Nelson, 2009; OBryan et al., 2018). The economic costs of living alongside carnivores can be severe (Loveridge et al., 2010). In parts of Botswana livestock owners lose on average 5.5% of their livestock to predators, with some respondents losing 100% of their stock (Hemson et al., 2009), in northern Tanzania and Bhutan villagers report losing on average over two thirds of their annual cash income to carnivores (Holmern et al., 2007; Wang and Macdonald, 2006) while on Brazilian ranches predators were responsible for 19% of cattle mortality, making up loses of 4.2% of commercialised meat (Palmeira et al., 2008). Alongside these direct costs carnivores also impose a range of intangible and hidden costs (Barua et al., 2013; Treves and Karanth, 2003). Predated livestock often hold intangible value far beyond that of their direct economic value (Kansky et al., 2014). In communities where there is little or no access to formal credit and insurance institutions livestock can provide an investment and safety net that are used to fulfil this role (Kurosaki, 1995; Andrew et al., 2003). Live-

stock can also have high cultural value, for instance the Maasai of East Africa value their cattle for social, political, religious and cultural reasons and much of the Maasai's cultural identity is defined through their relationship with livestock (Galaty, 1982). Even when no livestock losses occur guarding livestock from attack can impose high opportunity costs (Woodroffe et al., 2005; Barua et al., 2013), for instance children may miss school to protect their household's animals (Admassie, 2003) or where livestock guarding takes place at night it may increase exposure to vectors of disease such as malaria (Hoare, 2000; Dixon et al., 2009) or cause physical and mental ill-health as a result of lack of sleep (Hoare, 2000; Barua et al., 2013). Human injuries and fatalities are another cost imposed by a range of large carnivores across the globe (Löe and Röskaft, 2004), and can have far reaching consequences for the health and well-being of affected families and communities who may not have access to health care or the support of social safety nets that help cope with the emotional and economic costs of deaths and injuries (Barua et al., 2013).

The severity and impact of these costs are often magnified by other social, economic or political factors (Naughton-Treves, 1997; Young et al., 2010). Those living alongside carnivores often live in poor, remote, rural areas that border protected areas and may lack economic opportunities outside of livestock keeping. Reliance on livestock and weak economic positions makes people particularly vulnerable to the economic shock of livestock loses (Bagchi and Mishra, 2006). The unpredictable and potentially catastrophic nature of carnivore attacks (for instance a household suffering a "surplus killing" where a carnivore kills many stock in one attack) make it hard for households to plan for and protect themselves economically from these blows (Dickman et al., 2011; Musiani et al., 2005) and the stochastic nature of these losses can be instrumental in pushing people into poverty traps

and keeping them there (Lybbert et al., 2015). These poverty traps can become inter-generational where livestock loses means families are unable to afford school fees or where children forgo schooling in order to protect livestock (Dickman et al., 2011). While social capital can help buffer people from these heavy economic shocks, in many areas where carnivores occur there are high levels of wealth inequality. The most socially and economically vulnerable households may also be more likely to experience losses as they have fewer resources to implement measures to protect their livestock and may be forced to live or graze their stock in higher risk areas where loses to carnivores are more likely (Naughton-Treves, 1997).

People's risk of injury or death to large carnivores also has a political and economic element with those killed by wildlife often from less privileged socio-economic backgrounds (Das and Chattopadhyay, 2011). The distribution of attacks on humans highlights discrepancies between the experiences of urban societies (who place high existence values on carnivores) and rural societies in their dealings with large carnivores. In urban societies most attacks occur when people are engaged in recreational outdoor activities and thus choose to place themselves in risky situations whereas in rural societies most attacks occur during unavoidable everyday domestic activities (Löe and Röskaft, 2004). This not only highlights some of the uneven and inequitable dynamics surrounding who bears the highest costs of large carnivore populations around the world but also may explain differing levels of tolerance among different populations as people are often less willing to tolerate risks they have less control over or feel imposed upon them (Wachinger et al., 2013).

These complex interactions and the costs they impose on human communities means carnivores are frequently persecuted (Dickman, 2010; Dickman et al., 2013;

Loveridge et al., 2010; Woodroffe and Frank, 2005), often eliciting disproportionately harsher responses compared to other damage causing wildlife (Kansky et al., 2014; Dickman, 2010), which contributes to declines in many carnivore populations (Ripple et al., 2014). As well as retaliatory killings occurring as a direct result of livestock losses (Woodroffe and Frank, 2005; Kissui, 2008) carnivores are also killed opportunistically or pre-emptively to reduce carnivore populations and the potential for future losses (Thirgood et al., 2005; Baker et al., 2008). Carnivore killing also plays social or traditional roles in some societies, for instance among the Barabaig and Maasai ethnic groups in East Africa the killing of lions is associated with rights of passage into manhood and one's status as a warrior (Borgerhoff Mulder et al., 1989; Goldman et al., 2010) while carnivores are highly valued trophies among safari hunters (Packer et al., 2011; Lindsey et al., 2007a). Human persecution is one of the greatest threats faced by large carnivores and even within protected areas humans are usually the biggest cause of adult mortality (Woodroffe and Ginsberg, 1998). As a result reducing HWIs and mitigating carnivore persecution has been highlighted as one of the most pressing concerns for large carnivore conservation globally (Woodroffe and Ginsberg, 1998; Ray et al., 2005).

2.3 Spatial and temporal dynamics of human-carnivore impacts

Reducing the numbers of carnivore attacks on livestock is a priority for two reasons. Firstly, to reduce the costs of living alongside carnivores among communities who can often ill afford the economic and social shocks associated with carnivore attacks. Secondly, as even though livestock loses are only one factor of many that

influence people's attitudes towards carnivores (Dickman, 2010; Inskip et al., 2016; Bruskotter and Wilson, 2014) livestock depredations can trigger long lasting negative attitudes towards carnivores as well as increase levels of, and support for, lethal control of carnivore populations (Marker et al., 2003; Dickman et al., 2014; Woodroffe and Frank, 2005; Kissui, 2008; Baker et al., 2008). A wide range of ecological, social, spatial and temporal factors influence the risk of livestock being attacked by carnivores (Miller, 2015). Predator-prey dynamics can play an important role in depredation risk, with density of both livestock and wild prey important determinants of risk (Valeix et al., 2012; Zarco-González et al., 2013; Valeix et al., 2012), however different studies have found wild prey density to be positively (Kolowski and Holekamp, 2006; Treves et al., 2004; Zarco-González et al., 2013) and negatively (Valeix et al., 2012) associated with depredation risk. The age and type of livestock can also influence the overall risk of attack; the carnivore species livestock are at risk from; and the time, day and place where attacks might occur (Azevedo and Murray, 2007; Ogada et al., 2003; Rigg et al., 2011; Loveridge et al., 2017). A variety of landscape features have been linked to changing attack risks such as: distance to forests (Azevedo and Murray, 2007; Rigg et al., 2011); proportion of crop lands, coniferous forest, herbaceous wetlands, and open water (Treves et al., 2004); over-all vegetative cover, and altitude (Zarco-González et al., 2013); and distance to rivers, elevation, and percentage tree-cover (Abade et al., 2014a). Climatic conditions also play a role with evidence that season and localised rainfall interact with carnivore species and livestock husbandry to influence predation risk (Kissui, 2008; Abade et al., 2014a; Butler, 2000; Kolowski and Holekamp, 2006; Loveridge et al., 2017). A number of human land-use factors are also important with roads, protected areas, farm sizes, population densities and the structure of human settlements all influential factors (Holmern et al., 2007;

Treves et al., 2004; Zarco-González et al., 2013; Miller, 2015).

Livestock husbandry has been found by some studies to be highly influential in mediating risk of attack. Woodroffe et al. (2006) found presence of men and dogs as well as the design of livestock enclosures reduced attack risk while presence of scarecrows increased risk of attack. Rigg et al. (2011) report reduced losses and reduced levels of surplus killings among sheep herds protected by livestock guarding dogs. Ogada et al. (2003) found enclosure construction and the presence of watchdogs and human activity all reduced losses to predators. Loveridge et al. (2017) found livestock bells increased livestocks risk of being attacked, and that most livestock were attacked away from the "safety" of their enclosure. Conversely, while Kolowski and Holekamp (2006) found different types of enclosures to influence risk of attack from different carnivores, non-traditional fences, dogs and human activity did not influence the overall risk of attack. Abade et al. (2014a) also found husbandry techniques did not influence predation risk. Factors that influence attack risk also differ by carnivore species with the risk of attack from different carnivore species in the same landscapes affected by time of day and season (Kissui, 2008; Loveridge et al., 2017); distance to protected areas (Holmern et al., 2007), livestock husbandry (Woodroffe et al., 2006; Kolowski and Holekamp, 2006) and the structure of human settlements (Kolowski and Holekamp, 2006).

Improving our understanding of the specific factors that underlie carnivore landscape use and attack risk in different environments and human societal structures will be fundamental in helping communities to protect their livestock from attacks and promoting human-carnivore co-existence.

2.4 Attitudes and tolerance towards damage causing wildlife

Conservation biologists and wildlife managers often make three assumptions about HWI's: (A) the level of wildlife damage is directly related to the level of conflict engendered; (B) the level of conflict elicits a proportionate response; and (C) that altering the response to conflict will have proportionate conservation effects (Dickman, 2010). This, however, ignores many of the attitudinal factors that also come into play and influence peoples perceptions of wildlife and their interactions with them (Dickman, 2010). Recent studies show that with a number of species the damage they cause is not directly proportional to people's attitudes or tolerance towards them or the responses they elicit (Dickman, 2010; Kansky and Knight, 2014; Kansky et al., 2014; Kansky et al., 2016), carnivores in particular elicit disproportionately negative attitudes (Kansky et al., 2014) and in some systems species are discriminated against despite having an overall positive impact on peoples livelihoods (Dickman, 2010; Prowse et al., 2015).

There is a growing literature on attitudes and tolerance towards problem species (Kansky and Knight, 2014; Kansky et al., 2014; Inskip et al., 2016; Carter et al., 2012b) however much of this literature has been guided by conservationist's intuition and not psychological theory, thus there is much confusion and cross-over between the similar but different concepts of tolerance, acceptance and attitudes towards wildlife (Bruskotter et al., 2015). Bruskotter and Fulton (2012) define tolerance as "passive acceptance of a wildlife population" and intolerance as "when an animal or population becomes unacceptable". Bruskotter et al. (2015) and Treves (2012) further define intolerance as made up of two aspects: "prejudicial" attitudes and "discriminatory" behaviour. This multidimensional view of intolerance is sup-

ported by Ajzen's theory of planned behaviour (Ajzen, 1991) which highlights that prejudicial attitudes do not always lead to discriminatory behaviour. Despite these conceptual differences Bruskotter et al. (2015) found strong correlation between attitudinal and behavioural measures of intolerance. Thus in some cases the use of attitudinal measures to assess tolerance and intolerance may be the most suitable method in areas where behavioural measures are likely to be misreported or overly sensitive (Bruskotter et al., 2015).

A large number of socio-psychological factors have been found to influence attitudes, tolerance or acceptance of wildlife. Perceived risks and benefits associated with a species have been identified as important drivers of tolerance in a number of studies covering a range of species and geographies (Carter et al., 2012b; Inskip et al., 2016; Slagle et al., 2012; Riley and Decker, 2000; Zajac et al., 2012; Struebig et al., 2018). Social trust in those tasked with managing wildlife and belief in ones personal ability to manage the risks posed by hazardous wildlife can also decrease perceptions of the risk posed by dangerous wildlife and thus increase tolerance towards them (Struebig et al., 2018; Wachinger et al., 2013; Bruskotter and Wilson, 2014; Bruskotter et al., 2009; Carter et al., 2012b; Zajac et al., 2012; Kleiven et al., 2004). Direct and indirect experience of a species can also influence tolerance (Bruskotter et al., 2015; Kansky et al., 2016; Inskip et al., 2016). Education about hazards and dangerous wildlife can also have the opposite of the intended effect, increasing perceptions of risks and thus reducing tolerance (Slagle et al., 2012; Bruskotter and Wilson, 2014). Tolerance towards species will also be mediated by an array of local cultural factors (Parathian et al., 2018) such as religious beliefs (Hazzah et al., 2009; Bagchi and Mishra, 2006) or traditional associations and beliefs about species (Goldman et al., 2010).

There are a number of different socio-psychological frameworks that attempt

to explain how different psychological, social and economic factors interact to contribute to tolerance towards species (Kansky et al., 2016; Bruskotter and Wilson, 2014; Inskip et al., 2016). For example Kansky et al. (2016)'s tolerance framework outlines an inner model, consisting of variables influencing how a person perceives the costs and benefits of living alongside the species, and an outer model, made up of the experiences a person has had with a species. Bruskotter and Wilson (2014)'s hazard-acceptance model and Inskip et al. (2016)'s tolerance model share similar variables (perceptions of risk; experience of the species; and costs, and benefits, which Inskip et al. (2016) include in "beliefs") however Bruskotter and Wilson (2014) include people's feeling of control over the risks that arise from the species and their trust in the ability of those charged with managing the species. While there is a deep psychological literature on how humans perceive and relate to risks and hazards, the application of psychological theory to HWIs and how people perceive the threats posed by "problem" species is relatively under explored (Bruskotter and Wilson, 2014). Frameworks such as these, offer great potential in understanding the drivers of tolerance and intolerance towards wildlife, a vital step in understanding and moving towards resolutions of conservation conflicts.

2.5 Influence of human-carnivore impacts on ecosystems

HWIs often take place in complex and poorly understood ecological systems. This has led to instances where species are persecuted due to perceptions of the economic damage they cause while actually offering a range of ecosystem services with an overall positive impact on livelihoods (Dickman, 2010; Prowse et al., 2015). For example persecution of prairie dogs throughout the 20th century due to per-

ceived competition with cattle reduced populations by around 98% (Kotliar et al., 1999; Whicker and Detling, 1988), this decimated black-footed ferret populations (Kotliar et al., 1999) and has been linked to reduced nutritional quality of rangeland vegetation for large herbivores and livestock (Whicker and Detling, 1988). Prowse et al. (2015) & Allen (2015) investigated the ecological and economic consequences of dingo control in Australian rangelands, they found dingo's can increase forage availability to cattle by controlling kangaroo numbers with the economic gains from increased forage outweighing the costs of calves lost to dingo predation. Lastly, the endangered Zanzibar red colobus monkey is perceived to negatively impact coconut harvests by eating immature fruit, however studies have shown colobus fruit consumption is positively correlated with harvests, likely due to a pruning effect (Siex and Struhsaker, 1999). If we are to address the negative aspects of HWI it is important to improve our understanding of how these complex ecosystems function and the potential outcomes of human perturbation.

The human-carnivore conflict literature generally focuses on the costs borne by humans living alongside carnivores and the impacts of human actions on carnivore populations with little attention given to the ecosystem services that carnivores offer (Ripple et al., 2014). Few studies link the rich literature on the top-down impacts carnivores have on ecosystems and the cascades that can result in their eradication (Ripple et al., 2014; Crooks and Soulé, 1999; Ripple et al., 2014; Berger et al., 2001) with population declines resulting from human-carnivore impacts (Kuijper et al., 2016). A number of studies investigate the impacts of carnivores on carbon sequestration (Wilmers et al., 2012; Schmitz et al., 2014), water quality (Beschta and Ripple, 2012), and nutrient cycling (Wilmers et al., 2003). However, there are relatively few studies that investigate ecosystem services that have a more direct impact on the well-being of local communities, such as disease

prevalence in livestock (Packer et al., 2003), rangeland quality (Prowse et al., 2015; Allen, 2015) or herbivore crop consumption (Brashares et al., 2010). Improving our understanding of the ecological aspects of human-carnivore interactions will allow us to better understand the true costs and benefits of living alongside carnivores and how these are divided among different sectors of society.

2.6 The Rungwa-Ruaha Landscape in Tanzania

Tanzania holds six species of large carnivore all with globally declining populations (Table 2.1) (Winterbach et al., 2013). Despite the charismatic nature of these species and the importance of the Tanzanian populations (e.g. Tanzania holds over 40% of the world's remaining lions (Riggio et al., 2013)) little is known about their distribution and trends across the country apart from at a handful of well studied populations (TAWIRI, 2009). Negative interactions with humans and subsequent persecution is listed as a major threat to these species across the African continent and within Tanzania (IUCN, 2016; Ray et al., 2005; TAWIRI, 2009). Their ongoing conservation is important for the Tanzania economy with large carnivores acting as major attractants of international tourists who provide almost a quarter of the countries foreign exchange (Bank of Tanzania, 2016). However, these species also impose severe costs on the communities they live alongside (Packer et al., 2005; Dickman, 2009; Kissui, 2008).

Tanzania's Rungwa-Ruaha landscape (Figure 2.1) epitomises many of the issues surrounding large carnivore conservation in Tanzania and globally. Centred around the 23,000 km^2 Ruaha National Park (RNP) the landscape contains a mix of land-uses such as game reserves, wildlife management areas and village land, encompassing a total area of approximately 43,000 km^2, stretching from 33.5° to

Table 2.1: Where available the global population and range declines, IUCN status and level of protection current populations receive for the six large East African carnivores (Löe and Röskaft, 2004; Woodroffe and Sillero-Zubiri, 2012; IUCN/SSC, 2007; Bauer et al., 2016; Jacobson et al., 2016; Abi Said and Dloniak, 2015; Bohm and Höner, 2015; IUCN, 2016; Ray et al., 2005; Durant et al., 2015).

Species	IUCN Status	Population decline	% of historical range	Level of protection of current populations
Lion (*Panthera leo*)	Vulnerable	43% in two decades	8%	–
Leopard (*Panthera pardus*)	Near threatened	–	33-52%	17% of current range protected
Cheetah (*Acinonyx jubatus*)	Vulnerable	–	10%	76% of current range protected
Wild dog (*Lycaon pictus*)	Endangered	17% between 1997 & 2012	6%	–
Spotted hyena (*Crocuta crocuta*)	Least concern	–	73 %	–
Striped hyena (*Hyaena hyaena*)	Near threatened	10% expected over next 3 generations	62%	–

35.7° East and 5.8° to 8.7° South. The landscape is a valuable site for African carnivores, with globally important populations of lions, cheetahs, wild dogs, leopards and hyenas living alongside large human populations, many of which rely on livestock for their livelihoods (Dickman et al., 2014).

The area has wider ecological importance, being the only protected area system covering the transition between the east African acacia-commiphora zone (broadly on the eastern side of the landscape) and the southern African brachystegia or Miombo zone (broadly on the west of the landscape) (Dickman et al., 2014). Within these eco-zones exist a range of woodlands, grasslands, and cultivated or grazed land. The area's climate is semi-arid with approximately 600mm of annual rainfall with the rains split into two peaks; in December to January and March to April (Sosovele and Ngwale, 2002). However, with no functioning weather stations in

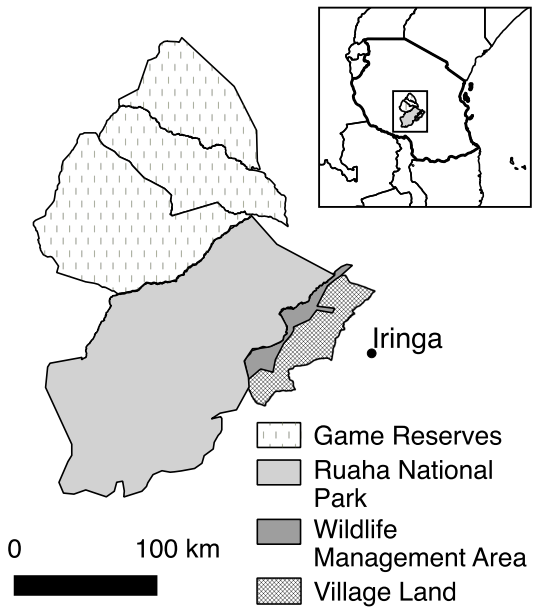


Figure 2.1: Map of the Rungwa-Ruaha landscape showing the study area in village land to the east of Ruaha National Park.

the landscape there is a lack of accurate long-term climate data. The main water source for the area is the Ruaha River that flows from uplands in the west through the south of Ruaha National Park before forming the north-eastern park boundary. The river is a vital water source for both wildlife and livestock, however, changing land-use in the river's catchment area means the river has started to stop flowing during the dry season (Kashaigili et al., 2007).

Around 40,000 people live in community land on the north-eastern border of Ruaha National Park and within the Rungwa-Ruaha landscape (Figure 2.1). These culturally complex communities are made up of at least 35 different ethnic groups containing a mixture of pastoralists and agriculturalists (Abade et al., 2014a). Pastoralists are predominantly from Maasai and Barabaig ethnic groups and are relatively recent migrants into the landscape. The first Maasai families settled in the area within living memory (Cashew Zuberi, personal communication, 2017) with Barabaig families arriving following the loss of access to much of their tra-

ditional grazing lands in the north as a result of large-scale agricultural development progammes in the 1960s and 1970s (Lane and Pretty, 1990; Fratkin, 1997). A number of agriculturalist communities are also relatively new, following forcible evictions that occurred during the creation of Ruaha National Park in the 1950s and resettlements that occurred as a result of the state imposed "villagisation" process in the 1970s (Walsh, 2007). Relationships between these pastoralist and agriculturalist groups are often strained due to long standing social prejudices and conflicts over land-use (Fratkin, 1997). Much of the most fertile land in the landscape is occupied by agriculturalist villages with pastoralists often living in less fertile land that borders the national park, this not only restricts their access to the best grazing but can also put their livestock at greater risk of predation from wild carnivores who live in protected areas. Tungamalenga village is an example of pastoralist displacement where the Maasai community were moved from their original settlements in what is now the village centre into land closer to the national park following conflict over land-use and agriculturalists complaining of cattle damaging their crops (Cashew Zuberi, personal communication, 2017).

2.7 The Ruaha Carnivore Project

Through the killing of livestock, and sometimes people, Ruaha's carnivore populations impart economic and social costs on these local communities who respond through retaliatory and pre-emptive killings (Dickman, 2010). Lions, cheetahs, leopards, African wild dog and spotted hyenas are all cited by those living around the park as being problem animals (Dickman et al., 2014). The impacts these species impose means many community members around the park want populations of these carnivores to decline or become locally extinct (Dickman, 2009). While a number of international conservation NGOs and Tanzanian government

agencies work in the landscape promoting the conservation and protection of large carnivores and other wildlife. The importance of Ruaha's carnivore populations, the complexity and intensity of the interactions between those living in the villages surrounding the park and carnivores, and the plurality of views of how carnivores should be managed highlight the importance of continued research into human-carnivore impacts and conservation conflicts in the Ruaha landscape.

The Ruaha Carnivore Project (RCP) is one of the international conservation organisations that works in and around Ruaha National Park on carnivore conservation by improving our understanding of carnivore ecology in the Ruaha landscape and reducing levels of human-carnivore impacts around the park. RCP started working in the landscape in 2009 and currently runs programmes in 11 villages on the north eastern edge of RNP. RCP runs a range of conservation and research programmes with a mix of aims and objectives. Environmental education programmes such as DVD nights and park trips aim to increase community members exposure to large carnivores in non-threatening environments and improve their understanding of carnivore behaviour and ecology. Other programmes, such as livestock guardian dogs and reinforced wire boma building aim to reduce levels of livestock killing in the landscape by carnivores, reducing the costs carnivores impose on community members. The last programme type are benefit programmes, such as the community camera trapping programme that provides village level benefits based on numbers of carnivores and prey species detected on camera traps in village land. This thesis has been planned and written in collaboration with RCP staff and builds on existing RCP research in the landscape and their relationship with local communities, government agencies and other conservation organisations.



Wild ranging wild dogs often use space outside of protected areas.

CHAPTER 3

SPATIO-TEMPORAL FACTORS AFFECTING CARNIVORE ATTACKS ON LIVESTOCK



Cattle killed by a pride of lions.

3.1 Abstract

Large carnivores impose a range of costs on the communities they live alongside through the real and perceived threats they pose to livestock. The direct and hidden costs that carnivores impose often contribute to intolerance of carnivores and support for lethal management of their populations. Livestock's risk of being attacked by carnivores is mediated by an array of spatial and temporal environmental variables as well as livestock husbandry practices. The effective deployment of limited conservation resources aimed at reducing carnivore's negative impacts on communities and the number of retaliatory carnivore killings requires detailed understanding of the variables influencing carnivore attacks on livestock. We use binomial GLMs to investigate spatial and temporal patterns of carnivore attacks on livestock in community land border Ruaha National Park in Tanzania. Our models show temporal patterns in attacks on livestock with higher risk of attacks likely linked to higher rainfall. The presence of wild prey species was positively associated with risk of attack as was distance to protected areas. Comparing risk of attack at a household's boma with attacks within 2 km of their boma, owning a reinforced wire boma decreased the risk of household's livestock being attacked at their boma while distance to roads increased household's livestock's risk of attack at their boma. Our study highlights the effectiveness of wire bomas over those of traditional construction in protecting livestock from predation and highlights certain areas and times of year where efforts to reduce attacks on livestock should be focused.

3.2 Introduction

Large carnivores around the world are frequently at the center of conservation conflicts (Ripple et al., 2014). The tangible and intangible costs that carnivores impose on local communities (Barua et al., 2013; Treves and Karanth, 2003) can lead to intolerance and lethal management that puts the ongoing existence of many carnivore populations at risk (Ripple et al., 2014; Dickman et al., 2014). While the social, economic and ecological benefits that carnivores provide means there are many advocates for their conservation and protection (Ripple et al., 2014; Lute et al., 2018; OBryan et al., 2018). These different experiences and views of carnivores, their impacts, and their values often interact with a multitude of social and political processes to produce severe conflicts between human groups over how carnivores and their impacts should be managed (Young et al., 2010; Redpath et al., 2014). Resolving these conflicts and finding policies for managing large carnivore populations and their impacts that are acceptable to all stakeholders involved is key to both improving the well-being of communities affected by carnivores and for the ongoing survival of carnivore populations.

Carnivores impose a range of costs on the communities they live alongside, and can contribute significantly to reductions in these communities' well-being (Barua et al., 2013; Dickman et al., 2011). The direct economic costs that result from carnivore attacks on livestock can be severe with some studies reporting average losses equivalent to over two-thirds of households annual income (Holmern et al., 2007; Wang and Macdonald, 2006). These losses and their impacts are not evenly spread throughout communities with carnivores sometimes inflicting large and potentially catastrophic losses on a single household in one event while other households suffer minimal losses (Musiani et al., 2005; Dickman et al., 2014; Baker et

al., 2008). Socially and economically vulnerable households may be more likely to suffer losses as they are less able to implement measures to protect their livestock and may be forced to live on less desirable land where loses to wildlife are more likely (Naughton-Treves, 1997). The impacts of livestock losses are also not felt equally, with poorer households more vulnerable to the stochastic economic shocks associated with losses, which can be instrumental in pushing people into poverty traps and keeping them there (Lybbert et al., 2015). Alongside direct economic impacts, carnivores also impose a range of intangible or hidden costs on communities (Barua et al., 2013). The opportunity costs of guarding livestock from carnivores can be high, with children missing school to protect their households animals (Admassie, 2003). Where livestock guarding takes place at night it may increase exposure to vectors of disease such as malaria (Hoare, 2000; Dixon et al., 2009) or cause physical and mental ill-health as a result of lack of sleep (Hoare, 2000; Barua et al., 2013). While the costs carnivores impose are not the only challenges faced by these communities, and may be directly or indirectly caused or magnified by other social, economic or political factors (Naughton-Treves, 1997; Young et al., 2010), reducing attack rates can play an important role in improving the well-being of affected communities.

As well as improving human well-being, reducing the costs carnivores impose on communities is also important for the ongoing survival of carnivore populations. Understanding the factors that lead to tolerance and intolerance of carnivores is an increasingly important aspect of conservation research aiming to protect carnivore populations from human threats (Kansky et al., 2016; Treves and Bruskotter, 2014; Bruskotter and Wilson, 2014). Intolerance of carnivore populations and predator killing behaviour can be influenced by a complex array of social and cultural factors (Dickman, 2010). Social factors such as perceived norms surrounding

carnivore killing (Marchini and Macdonald, 2012), religious beliefs (Bagchi and Mishra, 2006; Hazzah et al., 2009), or pre-existing conflict between authorities and local communities (Naughton-Treves and Treves, 2005) have been shown to influence attitudes and behaviours towards carnivores and other damage causing wildlife. While direct costs can influence tolerance of damage causing wildlife (Kansky et al., 2014) there is strong evidence that intangible costs, positive beliefs and perceived benefits can be stronger drivers of tolerance than direct costs (Inskip et al., 2016; Kansky et al., 2016; Carter et al., 2012b) (Chapter 5, this thesis). While not always a primary factor influencing tolerance, direct costs can influence how carnivore populations are managed, with attacks on livestock increasing the likelihood of, and support for, lethal control (Ogada et al., 2003; Kissui, 2008; Holmern et al., 2007; Treves and Naughton-Treves, 2005; Inskip et al., 2014; Swanepoel et al., 2015; Baker et al., 2008; Woodroffe and Frank, 2005). As a result reducing carnivore attacks on livestock, and the associated costs (both direct and intangible), can play an important role in reducing carnivore deaths, and conserving their populations.

Understanding the factors that increase livestock's risk of predation is an important first step in planning interventions aimed at reducing livestock losses (Miller, 2015). A number of ecological variables are known to influence predation risk; vegetation cover and type (Abade et al., 2014a; Ogada et al., 2003; Rigg et al., 2011; Miller et al., 2015), rainfall and season (Kolowski and Holekamp, 2006; Abade et al., 2014a; Kissui, 2008; Butler, 2000; Loveridge et al., 2017), and the distribution of carnivores (Kolowski and Holekamp, 2006; Valeix et al., 2012) and wild-prey (Kolowski and Holekamp, 2006; Valeix et al., 2012). Human land-use can also play a role, with distance to protected areas (Holmern et al., 2007; Miller et al., 2015), proportion of land under pasture or crop land (Treves et al., 2004)

and distance to infrastructure such as roads or villages (Treves et al., 2004; Miller et al., 2015) influencing livestock predation risk. Studies have also found evidence that attacks are affected by husbandry practices (Ogada et al., 2003; Woodroffe et al., 2006; Rigg et al., 2011; Kolowski and Holekamp, 2006; Loveridge et al., 2017) and the distribution and behaviour of livestock in relation to carnivore populations (Valeix et al., 2012; Sundararaj et al., 2012). While the impact of some variables (e.g. livestock and carnivore density) is almost universal across study sites (Miller, 2015) the influence of other variables are highly site specific, differing by carnivore species, geographic location and husbandry practices (Miller, 2015; Loveridge et al., 2017). Therefore, creating effective management plans for reducing livestock losses to carnivores requires site specific knowledge of the variables influencing carnivore predation risk.

The Rungwa-Ruaha landscape in Tanzania is an example of a landscape containing severe conservation conflicts over the management of a number of large carnivore species. Pastoralist communities and their livestock frequently come into contact with large carnivores on the edges of Ruaha National Park, resulting in the deaths of livestock and retaliatory and traditional killing of carnivores (Abade et al., 2014a; Dickman et al., 2014). In this study we evaluate the spatial and temporal variables that influence livestock's risk of attack by large carnivores in community land on the edge of Ruaha National Park in Tanzania.

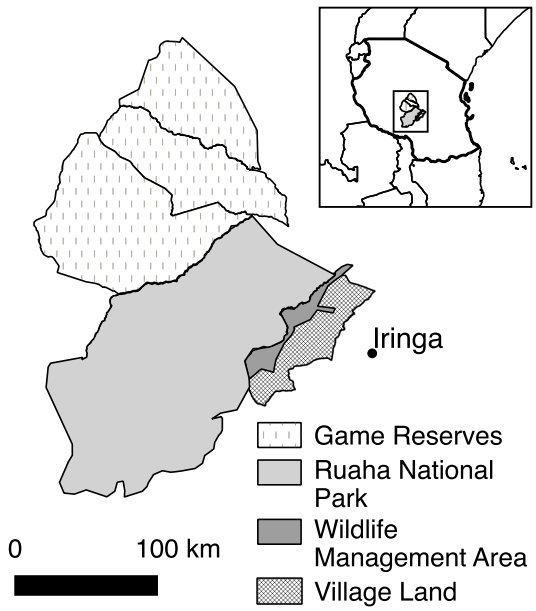


Figure 3.1: Map of the Rungwa-Ruaha landscape showing the study area in village land to the east of Ruaha National Park.

3.3 Methods

3.3.1 Study Area

The Rungwa-Ruaha landscape in Tanzania contains internationally important populations of lions (*Panthera leo*), cheetahs (*Acinonyx jubatus*), African wild dogs (*Lycaon pictus*), leopards (*Panthera pardus*) and spotted hyenas (*Crocuta crocuta*). The interactions between these carnivores, local communities, wildlife management authorities and conservation NGOs epitomises the problems at the heart of conservation conflicts globally (Dickman et al., 2014). The landscape is centred on the 23,000 km^2 Ruaha National Park (RNP) with the rest of the roughly 45,000 km^2 made up of game reserves, community managed protected areas called wildlife management areas (WMAs) and community land (Figure 3.1). Significant proportions of the entire landscape forms habitat for large carnivores and potentially provides valuable connectivity with other protected areas (Abade et al.,

2014a). The area has wider ecological importance as the only protected area system that covers the transition between the east African acacia-commiphora zone and the southern African brachystegia or Miombo zone (Dickman et al., 2014). The area's climate is semi-arid with approximately 600mm of annual rainfall with the rains split into two peaks; in December to January and March to April (Sosovele and Ngwale, 2002). The main water source for the area is the Ruaha River that flows from uplands in the west through the south of Ruaha National Park before forming the north-eastern park boundary. The river is a vital water source for both wildlife and livestock, however, changing land-use in the river's catchment area means the river frequently stops flowing during the dry season (Kashaigili et al., 2007).

Approximately 40,000 people live in village land on the south west border of RNP many of whom rely predominantly or solely on livestock for their livelihoods (Abade et al., 2014a). The majority of pastoralist households in the landscape live in permanent settlements, however, still engage in seasonal migrations. During the wet season, when grazing is abundant, livestock are kept at the household's permanent boma. However, when forage becomes scarce in the dry season many households move the majority of their livestock to seasonal grazing lands outside of the study area, returning once the rains and fresh grazing have arrived.

Killing and injuring livestock, and infrequently people, Ruahas carnivore populations impart economic and social costs on local communities who respond through retaliatory and preemptive killings (Abade et al., 2014a; Dickman et al., 2014). The Ruaha Carnivore Project (RCP) has been conducting ecological and social research and running conservation programmes in the Ruaha landscape since 2009, aiming to improve human-carnivore co-existence in the landscape. Improving our understanding of the factors that increase carnivore attack risks on livestock in

this area is vital to maximising these programmes effectiveness in improving the well-being of communities in the landscape and reducing carnivore mortalities.

3.3.2 Household interviews

We wrote a questionnaire that gathered data on carnivore attacks on respondent's livestock over the previous 30 days and if those attacks occurred at the livestock enclosure (boma) or within 2 km of the boma. We define an attack as any instance where a carnivore injured or killed a respondent's livestock. See Appendix A for interview questions. We did not consider attacks occurring further than 2 km from bomas in our analysis as it is not possible to attribute spatially explicit environmental data to those events. Respondents were also asked about the presence of prey species within 1 km of their boma over the same time period. The interview was written in English and translated to Swahili by two Tanzanian field assistants who also enumerated the interviews in the field. A third translator back translated the Swahili interview to check the accuracy of the initial translation. Interviews were conducted primarily in Swahili, however as not all Maasai and Barabaig (the predominant pastoralist ethnic groups in the survey area) are fluent in Swahili interview questions were further elaborated in Maasai or Barabaig by field assistants if necessary. We used Google Nexus 7 tablets and the Open Data Kit system (Brunette et al., 2013) to conduct interviews and record responses. We piloted the interview and adapted it in response to issues raised. We conducted interviews at livestock owning households, selected to provide an even geographical spread across the landscape. Respondents were all male due to cultural sensitivities towards male enumerators conducting interviews with female respondents, and as male household members are those responsible for livestock husbandry. We revisited households roughly every two months over a 12 month period to cover the

landscape's seasonality. Where possible, we interviewed the same household member. On repeat visits households were visited at least three times to try and find a respondent, if after three visits nobody suitable could be found for interviewing that household was removed from that round's list.

3.3.3 Ethical considerations

Interviews and fieldwork protocols were assessed and approved by the Oxford University ethical committees (ref. R36599/RE001). Before the first interview with each respondent they were verbally informed of the research project's scope and aims, what their involvement would entail, their freedom to refuse to be interviewed and their freedom to leave the research project at any future point. After this explanation we gained informed consent verbally from respondents, with further consent gained before each subsequent interview with a shorter statement reminding the respondents of the project's aims and their freedom to refuse to engage with the project at any point.

3.4 Analysis

3.4.1 Independent variables

We considered a number of environmental variables likely to influence carnivore presence and behaviour, and therefore attack risk (Table 3.1). Human pressures and land-use that may influence carnivore behaviours and presence were modelled using distance to road, distance to RNP, distance to WMA, converted agricultural land and population density. Water availability was modelled using average rainfall over the preceding 30 days and distance to all rivers and large rivers (those that flow all year round). We also included elevation as it has previously been

Table 3.1: Environmental covariates included in GLMs.

Environmental Covariate	Resolution	Source
Digital elevation model	1 arc second 30m	STRM (Jarvis et al., 2008)
Distance to roads	100m	Open Street Map (OpenStreetMap contributors, 2017) & RCP data
Distance to all rivers	100m	Hydrosheds (Lehner et al., 2006)
Distance to major rivers*	100m	Hydrosheds (Lehner et al., 2006)
Distance to Ruaha National Park	100m	TANAPA
Distance to wildlife management area	100m	TANAPA
Population density	3 arc second 100m	Afripop (Linard et al., 2012; *Worldpop* 2013)
Converted agricultural land	30m	MEaSUREs (Xiong et al., 2015)
Precipitation†	0.1 degree 10 km	GPM (Huffman et al., 2015)
Enhanced vegetation index†	500m	MODIS (Didan, 2015)

*The Great and Little Ruaha rivers that are the last rivers to stop flowing in the dry season. †Mean for each household over the 30 days preceding each interview.

shown to influence attack risk (Abade et al., 2014a). Enhanced vegetation index (EVI) was included as a measure of vegetation productivity which influences carnivore behaviour (Schuette et al., 2013b) and can be used as a proxy for prey availability (Pettorelli et al., 2011). We drew a 2 km buffer around each household's location and calculated the average value across that polygon for each environmental variable using R's (R Core Team, 2017) raster package (Hijmans and Etten, 2014). As EVI and average rainfall change during the survey period we used Google Earth Engine (Gorelick et al., 2017) to calculate the average rainfall and EVI for the 30 days preceding interviews across each household's 2 km buffer. We also included the reported presence or absence of small (dik dik, duiker, impala, bushbuck, wild pigs and warthog) and large prey (eland, zebra, buffalo, waterbuck, kudu). We included the month the interview was conducted as a variable to capture other seasonal differences not modelled by other variables. The tribe of the

respondent and the type of boma they own (reinforced boma made from metal poles and wire, or a traditional boma made from wooden poles and cut thorn bushes [Fig. 3.2]) were included as measures of husbandry practices. We scaled all continuous variables and to avoid issues of collinearity compared covariates in a correlation matrix and removed strongly correlated variables ($|r|>0.7$) from the same analysis (Dormann et al., 2012).

3.4.2 Generalised Linear Models

We ran binomial generalised linear models (GLM) in R (R Core Team, 2017) to investigate the variables that influence the probability of a household suffering carnivore attacks in a given 30 day period. Due to low numbers of attacks reported by species other than hyenas, and the difficulty in accurately attributing attacks to specific species (as multiple species signs may be apparent at a single attack site (Abade et al., 2014a)) we did not attempt to model attack risks by individual carnivore species. We modelled attack risk in two steps. Firstly, we combined attacks at the boma and within 2 km of the boma into a single binary variable representing if a household's livestock was attacked (0) or not attacked (1) over the previous 30 days (attack risk). We then used a binomial GLM to investigate the effect of a number of socio-ecological variables (Table 3.1) on the probability of each household suffering attacks on livestock. For the households who experienced attacks on their livestock we used a second binomial GLM to investigate which variables effected the probability of carnivores attacks on livestock occurring at either the household's boma (0) or within 2 km of their boma (1) (attack location). We checked model convergence and fit with an initial global model containing all variables, after we ran models with all possible combinations of explanatory variables and compared fit with AIC values. We conducted full model averaging (Symonds and

Moussalli, 2011) over the most parsimonious models (Δ AIC < 2) (Burnham and Anderson, 2001) using the MuMIn package (Barto, 2018).

3.5 Results

3.5.1 Interviews

632 interviews were conducted at 167 households between 27th April 2016 and 27th April 2017 at 167 bomas. The majority of interviews were conducted at pastoralist households (n=519) (Maasai, n=342; Barabaig, n=177), with the remaining interviews at agriculturalist households (n=113) predominantly Mhehe (n=39), Mgogo (n=35), and Sukuma (n=30). A drought across the study site, and much of Tanzania, during the early wet season (September-December 2016) (National Food Security Division, 2016) resulted in low forage availability for livestock during much of the study period. Many pastoralists, including large numbers of respondent households, moved their livestock to seasonal grazing sites outside the study area and did not return until the following rains in March 2017, causing lower numbers of interviews than anticipated between October 2016 and March 2017 (Figure 3.3). Out of the 632 interviews 135 recorded carnivore attacks on their livestock over the 30 days preceding the interview, of these 83 were attacks at their bomas while 66 occurred within 2 km of the households boma. The vast majority of attacks were attributed to hyenas, however all five carnivore species were associated with some attacks on livestock (Table 3.2). Attack events were widespread throughout the landscape, with reports from households between <10m and 15.5 km away from the nearest protected area (Fig. 3.2).

3.5.2 Model Covariates

Distance to RNP and WMA are strongly correlated (r=0.73), as the WMA lies between the park and community land and thus is the closest protected area across the entire study site we removed distance to RNP from the analysis. Due to low

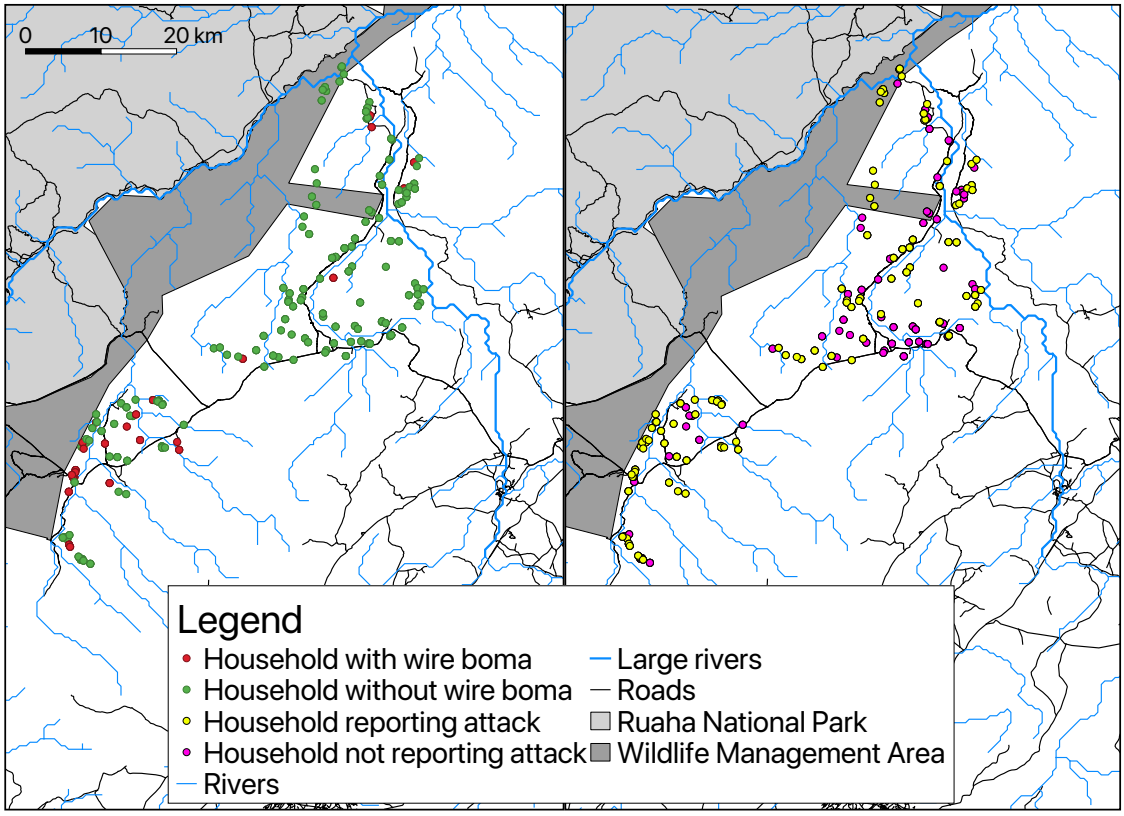


Figure 3.2: Map of households interviewed, showing locations of those who reported carnivore attacks on livestock and those with and without reinforced wire bomas.

numbers of some agriculturalist tribes and similarities in their farming practices, households from Mgogo, Mhehe, Mbena, Mtengeleko and Nyamwezi tribes were consolidated into a single agriculturalist category, Maasai, Barabaig and Sukuma were left as separate categories as they are relatively distinct cultural groups. An interaction between distance to large and all rivers, and rainfall was included in models as the importance of different water bodies is likely to be influenced by general water availability in the landscape and levels of recent rain.

Table 3.2: Carnivore species associated with attacks on livestock over 30 day periods reported during interviews.

Species	Interviews recording attacks on livestock
Hyena	121
Lion	16
Leopard	4
Cheetah	2
Wild dog	2
Total*	135

*Interviews may report multiple attack events attributed to different carnivore species, thus the sum of events attributed to species is greater than the total number of interviews reporting attacks.

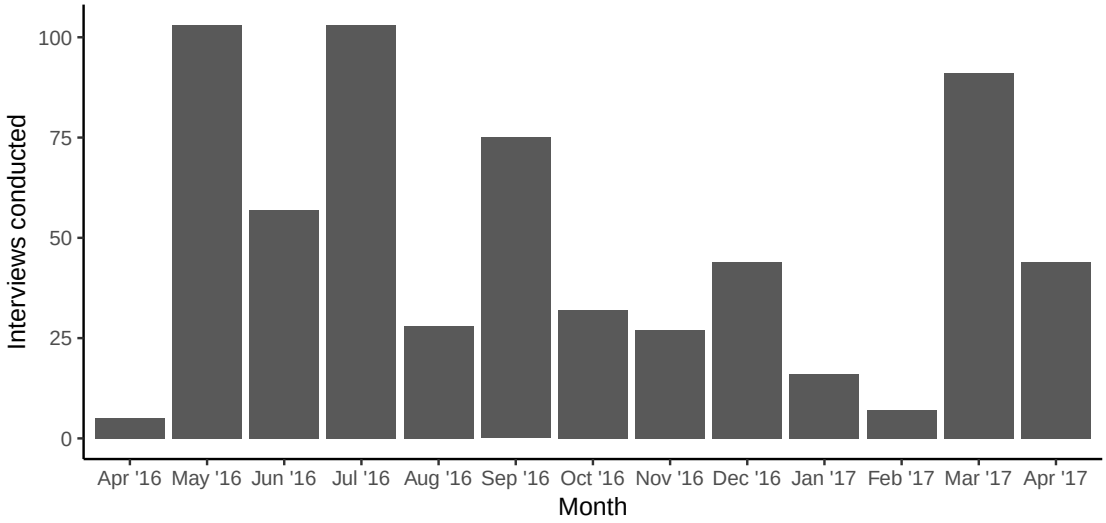


Figure 3.3: Interviews conducted each month of the study period. Low numbers of interviews from October 2016 to February 2017 are due to unusually low rainfall during these months resulting in a general migration of pastoralists out of the study area to dry-season grazing lands.

3.5.3 Binomial GLMs

Global models for both attack risk and attack location show acceptable fit to the data (Nagelkerke pseudo R^2 = 0.317 and 0.305 respectively (Nagelkerke, 1991)) and no evidence of over-dispersion ($\hat{c}$ = 1.01 and 1.16). After running all combi-

nations of variables there was no clear "best" model with 22 strongly supported attack risk models and 18 strongly supported attack location models (Δ AIC < 2). Nagelkerke pseudo R^2 values for the strongly supported attack risk models range from 0.292 - 0.313 and for attack location models from 0.107 - 0.144.

Attack risk. All variables appear in the top ranked models for attack risk (Appendix B Table B.1) while the interaction between large rivers and precipitation is in some top ranked models the interaction between all rivers and precipitation is not included in any top ranked models. Presence of small prey, distance to WMA, presence of a reinforced wire boma and month all have a relative variable importance (RVI) of 1.00 meaning they are present in all top ranked models, suggesting they are useful variables in understanding livestock's risk of attack (Figure 3.4). Presence of small prey species and presence of a reinforced boma increases the risk of attacks by carnivores while distance to WMA has a negative impact on risk of attack. Month's high RVI value is driven by the increased attack risk associated with the month of may, however, 95% confidence intervals (CI) of the coefficients for the other months overlap zero and so we cannot infer too much about their impact on attack risk, although the small negative lower 95% CI for June and August suggest a potential positive risk of attack associated with these months. Average precipitation and distance to large rivers also have high RVI values (0.92 and 0.85 respectively) however their 95% CI overlap zero, although the small level of overlap suggest that precipitation may be associated with an increased risk of attack while higher distances from the larger rivers may decrease risk of attack. See Appendix B for full model averaged results.

Attack location. Fewer variables were represented in the top ranked models for attack location (Appendix B Table B.1), with no models containing tribe, month or interactions between precipitation and rivers selected. Distance to roads and

the presence of a reinforced boma are the only variables with an RVI of 1.00 and 95% CI that do not cross zero, both variables increasing the likelihood of carnivore attacks within 2 km of the household over attacks at the boma (Figure 3.4). The only other variable with a relatively high RVI is distance to WMA which has a positive impact on the risk of attacks away from the boma, however its 95% CI overlap zero so again we cannot infer too much about it's influence. See Appendix B for full model averaged results.

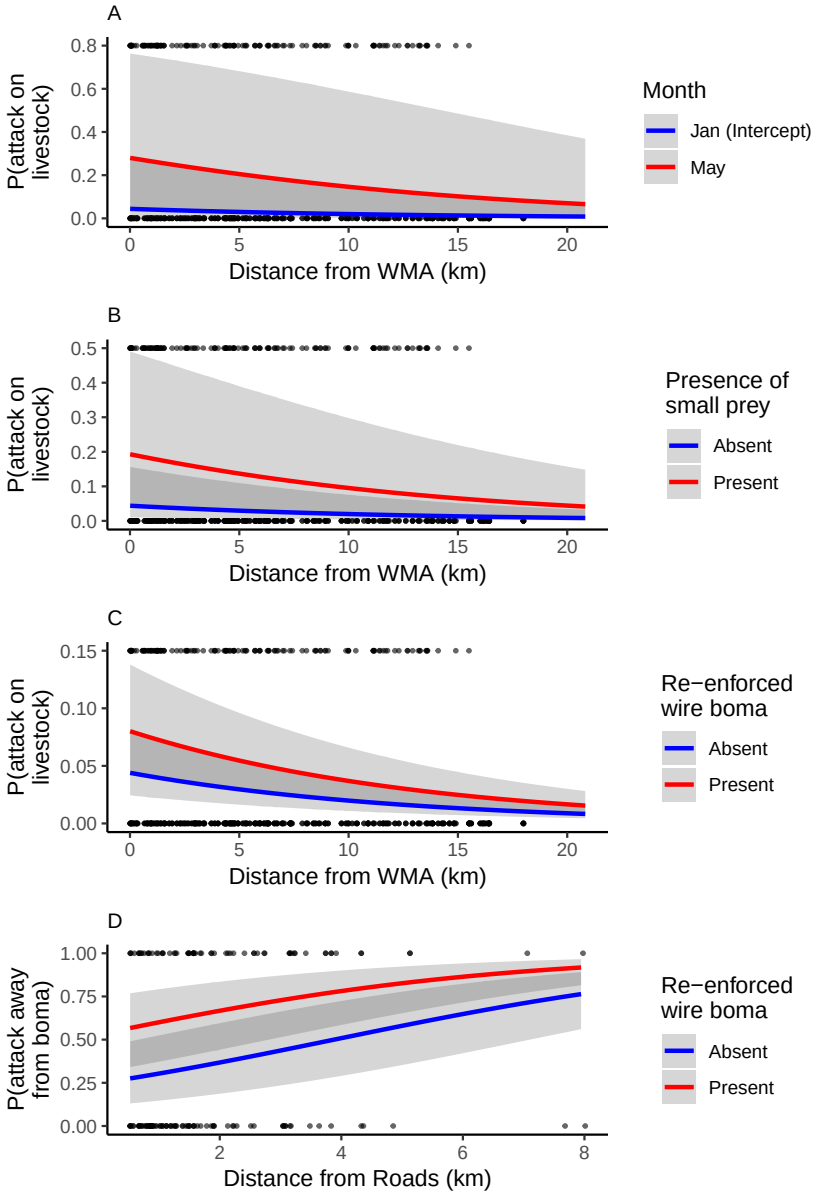


Figure 3.4: Important variables explaining probability of livestock being attacked (graphs A, B and C) and probability of attacks occurring within 2 km of the boma over at the boma (graph D). All plotted variables have RVI = 1 and 95% confidence intervals that do not cross 0 (shaded grey in figure).

3.6 Discussion

Generalized linear models show both environmental variables and husbandry practices influence the likelihood and location of carnivore attacks on livestock. With models showing reinforced wire bomas, time of year, presence of small prey and the distance to a protected area and roads influencing either the overall risk of attacks on livestock or the location that attacks are likely to occur.

While previous studies in this area have found no evidence that different traditional husbandry practices influence attack risks (Abade et al., 2014a) we found reinforced bomas are effective at protecting livestock housed within (Sutton et al., 2017; Ogada et al., 2003). The counter-intuitive correlation between boma ownership and a higher overall attack risk likely occurs as households with a higher risks of attacks are more likely to invest in a reinforced boma. The cost of installing reinforced bomas is shared between RCP and the household, those living in areas with higher risks of attacks may be more likely to request reinforced bomas from RCP and be more willing to pay the associated costs - in households we surveyed those with reinforced bomas were significantly more likely to live nearer to the WMA than those without $t(166.07) = 7.16$, $p<0.001$, which we found to be associated with increased risk of attacks. Larger herds may be more likely to suffer losses to carnivores, particularly while grazing away from the boma when managing and protecting larger herds is more difficult (Ogada et al., 2003), so these households may also be more willing to invest in protecting their larger holdings, while also better able to afford the costs. As Maasai and Barabaig are generally wary of sharing the size of their livestock holdings data on herd sizes was not collected and so we are not able to test the effect of herd size on attack risk.

As mentioned above our models show that risk of carnivore attacks on livestock

reduces the further a household lives from the WMA, concurring with the findings of a number of other studies that show risk of livestock predations decreasing with distance to protected areas (Holmern et al., 2007; Miller, 2015). While hyenas, the most commonly cited predator of livestock, occur throughout the study area (Chapter 4, this thesis) the increased risk of attacks closer to the WMA border may result from either higher predator densities nearer protected areas or predator behaviour in less disturbed habitat that increases their predation of livestock. The lower risk of attacks occurring at bomas nearer the WMA shown in our attack location models is most likely driven by the increased likelihood of households living near the WMA owning reinforced bomas which offer more effective protection than those of traditional construction. While other studies found links between vegetation type (Abade et al., 2014a) and other land-use types (such as amount of pasture or crop land) (Treves et al., 2004) and livestock predation neither EVI or proportion of land converted to agriculture were important variables in either our attack risk or attack location models. The low intensity agriculture and highly mixed and fragmented mosaic of land-use across our study area may explain why levels of converted land do not influence predation risks as much of the landscape is still accessible to predators like hyena that are well adapted to living among relatively dense human communities (Boydston et al., 2003a; Abay et al., 2011; Schuette et al., 2013b; Woodroffe, 2000). The attack location models showed average distance to road to be an important factor influencing where attacks occur, with households further from roads less likely to suffer attacks at their boma. This may be because the presence of roads and associated human activity causes carnivores to become more active at night, which is when livestock are generally kept in bomas, and when boma predation events generally occur (Abade et al., 2014a). However, higher human population densities is likely to have a similar influence

on carnivore behaviour but was not an important variable in any of our models, therefore there may be other reasons for the impact of roads on attack location.

The positive association between the month of May and overall attack risk is likely to be associated with the end of the 2016 rainy season, with the last heavy rains falling in April and May, with our models also suggesting a potential positive association between average rainfall and attack risk. However, the unusual rainfall patterns that occurred during our study may have masked or exaggerated normal seasonal impacts on carnivore predations of livestock. Studies show the relationship between rainfall and livestock losses to carnivores differs between systems and predator species, with a positive associations between rainfall and attack risk in some African systems (Kolowski and Holekamp, 2006; Abade et al., 2014a; Kissui, 2008; Woodroffe and Frank, 2005; Loveridge et al., 2017), while the reverse has been found in areas of Zimbabwe with greater risk of losses to predators in the dry season (Butler, 2000). Kissui (2008) also found seasonal changes in attacks by hyenas and lions, while leopards attack risk was constant throughout the year. There are a number of hypothesis behind these different dynamics, Butler (2000) suggest less vegetation cover in the dry season makes hunting wild prey more difficult so predators switch to domestic prey. Kissui (2008) hypothesises that carnivores follow wild prey as they migrate into community lands during the wet season which increases their opportunities to predate livestock. While Loveridge et al. (2017) propose that in the wet season carnivores switch to domestic prey as wild prey are less congregated around water and in better condition so are less vulnerable to predation. We found the reported presence of smaller prey species is positively associated with attack risks which supports dynamics similar to those proposed by Kissui (2008), however the vast majority of livestock predations in our study were carried out by hyenas which are widespread in community

land throughout the year (Chapter 4, this thesis). Suggesting that either the relationship between attack risk, season, and the presence of prey species occurs on finer scales than just the general presence of absence of prey and carnivores in community land or is mediated by other factors not included in our models. Seasonal changes in grazing patterns may also influence attack risk with grazing conducted in areas more vulnerable to attack by carnivores at different times of year (Loveridge et al., 2017), this, however, is unlikely to influence our results as we only considered attacks near bomas.

Our study has highlighted several areas where further research should be focused to improve our understanding of attacks on livestock. Firstly, by collectively analysing our data we are unable to investigate how the impact of variables differs by carnivore species (Ogada et al., 2003; Loveridge et al., 2017). As the most widespread large carnivore species, and reportedly responsible for the majority of attacks, our findings are likely to reflect the high proportion of hyena attacks in our data. However, building a species specific understanding of attack risk will allow better protection of livestock in areas where different carnivore species are more prevalent. Secondly, the relationship between seasons, prey availability and attack risk appears to be site specific with numerous different relationships reported in the literature (Miller, 2015; Woodroffe and Frank, 2005; Butler, 2000; Kissui, 2008), understanding how season and prey density influence attack risk may allow more effective pre-emptive measures to protect livestock, for instance avoiding grazing cattle in areas with fresh rainfall or areas with high densities of wild prey. Finally, our study focused on broader landscape level variables, using average values in a relatively large buffer area around attack locations, while this gives a broad image of where livestock are at greater risk of attack it does not provide information on what fine scale variables can trigger predation events (Miller

et al., 2015), for example the immediate vegetation type and density, amount of clear ground, length of grass, time of attack, presence of trails etc which may provide useful information on types of habitat to avoid grazing livestock in, or building bomas near. We also recommend further research into which aspects of wire boma design leads to effective carnivore deterrence, for instance; if their effectiveness is due to the standardized fence heights or door construction methods (potential weak points in traditional designs) then these design elements may be transferable to bomas made of cheaper traditional materials.

3.7 Conclusions

Our study shows the importance of a number of environmental and social variables in understanding carnivore attacks on livestock in the Ruaha landscape. We found reinforced wire bomas to be more effective than traditionally construction bomas in protecting livestock from carnivores and recommend the continued construction of these structures. We also found seasonal patterns in attacks likely driven by rainfall patterns with increased carnivore attacks during the rainy season. Distance to protected area was the most important spatial variable with livestock from households living closer to the WMA more likely to be attacked. The high numbers of attacks reported, 21.4% of all interviews reported attacks by carnivores over the preceding 30 days, demonstrates the importance of reducing the pressures living alongside carnivores imposes on these communities. Our study shows how spatial predation risk modelling can play an important role in understanding the complex dynamics of these systems with an aim of informing how conservation programmes working on the ground can best deploy their resources to help reduce the negative impacts large carnivores impose and promote human-carnivore co-existence.

3.8 Acknowledgements

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Livestock protected by a traditional thorn bush boma.

CHAPTER 4

USE OF INTERVIEW-BASED OCCUPANCY MODELS TO ASSESS LARGE CARNIVORE SITE USE IN A HUMAN-DOMINATED LANDSCAPE



Maasai respondents identifying large carnivore tracks.

4.1 Abstract

Interactions between large carnivores and humans can reduce human well-being and threaten the persistence of wild carnivore populations. Understanding the spatial variables that cause carnivores populations to come into contact with human communities is paramount if we are to reduce the intensity of these interactions. We use interview-based occupancy models to understand the spatial and temporal factors influencing land-use by 5 carnivore species in land bordering Ruaha National Park in Tanzania. The distribution of lions, wild dog, leopard and cheetah in community land outside of protected areas appears to be highly seasonal with higher land-use in the wet season, while hyenas are present all year round. However, our model's ability to predict carnivore land-use was restricted by low respondent availability during the dry season and low detection rates for some carnivore species. Combining local ecological knowledge with occupancy models can be a useful tool in inferring ecological knowledge about carnivore distributions, however it is not a methodology suited to all species, cultures and landscapes.

4.2 Introduction

Large carnivores are an ecologically, economically and socially important group of animals (Wolf and Ripple, 2016; Ripple et al., 2014). Through a number of top down ecological mechanisms (for example mesopredator release (Ripple et al., 2013; Crooks and Soulé, 1999), direct predation and landscapes of fear (Ripple and Beschta, 2004; Schmitz et al., 1997)) carnivores can have wide ranging impacts on the ecological systems they exist in, in turn providing ecosystem services to human communities (OBryan et al., 2018). There is evidence carnivores increase agricultural output by controlling pest animals (Prowse et al., 2015), increase ecosystem carbon storage (Strickland et al., 2013), reduce human exposure to zoonotic diseases (Braczkowski et al., 2018; Levi et al., 2012) and remove organic waste (irovi et al., 2016). As highly sought after animals for photographic tourism, large carnivores can also provide direct economic benefits to areas lacking other economic opportunities (Lindsey et al., 2007b; Maciejewski and Kerley, 2014). Different societies also place important cultural roles and values on carnivores (Hazzah et al., 2009; Shen et al., 1982; Kellert et al., 1996) and many people derive pleasure purely from the knowledge that large carnivores exist (Nelson, 2009; Macdonald, 2001). However, despite their ecological, economic and cultural importance, large carnivores also impart significant direct and indirect costs on human-communities (Barua et al., 2013; Treves and Karanth, 2003), which may result in human-carnivore interactions that reduce human well-being and threaten carnivore populations around the globe (Ripple et al., 2014).

Large home ranges put carnivores in frequent contact with human communities and their livestock (Ripple et al., 2014; Treves and Karanth, 2003); as many large carnivores are specialist predators of ungulates, and have high metabolic

requirements (Carbone et al., 1999) this contact can lead to the predation of domestic livestock and attacks on humans (Löe and Röskaft, 2004). While the loss of livestock and human fatalities have direct economic and social impacts, carnivores also impose wider hidden costs (Barua et al., 2013). Examples of these hidden costs are the opportunity costs involved with protecting livestock, poor mental and physical health, reduced food security, and social conflict (Barua et al., 2013). Many of the human communities who suffer loses to carnivores are marginalised and economically poor rural societies who can ill-afford the tangible and intangible costs carnivores impose on them (Dickman et al., 2014; Ripple et al., 2014; Kansky and Knight, 2014). This can result in human communities adopting management practices (legal and illegal) that impose severe costs on carnivores by blocking their access to important resources or lethal control (Treves and Naughton-Treves, 2005; Baruch-Mordo et al., 2013; Dickman, 2010; Woodroffe and Ginsberg, 1998).

Carnivores are naturally rare species, existing at low densities and with low reproduction rates, which makes their populations especially susceptible to the pressures that result from negative human-carnivore interactions (Hazzah et al., 2009; Watts and Holekamp, 2009; Balme et al., 2009; Ripple et al., 2014). Promoting human-carnivore coexistence is vital if we are to improve the well-being of the human-communities who live alongside carnivores and ensure the taxa's ongoing survival (Dickman, 2010; Redpath et al., 2014; Ripple et al., 2014). Understanding predator's distributions and landscape use is important in planning and implementing programmes to increase human-carnivore coexistence. Occupancy models are one methodology used to study species' distributions and habitat preferences (MacKenzie et al., 2002; Bailey et al., 2014; MacKenzie et al., 2002). Using occurrence data from multiple surveys conducted in the same sampling unit, occupancy models can be used to estimate the probability of a species being detected

at that site if present, and the probability of a species occurring at sites with no detections given the detection probability. Including covariate information allows for the modeling of site specific differences in detection and occupancy (MacKenzie et al., 2002; MacKenzie et al., 2002).

While occurrence data, compared to density data or abundance, is relatively easy to collect, using conventional methods to gather ecological data on species with large home ranges, low densities, and secretive habits, such as carnivores, can be resource intensive. However, as culturally important species that interact with human interests there often exists a wealth of local ecological knowledge (LEK) on carnivore ecology (Zeller et al., 2011; Martínez-Martí et al., 2016). There is increasing recognition that using LEK allows the rapid gathering of data over large spatial and temporal scales (Turvey et al., 2014a; Pillay et al., 2013; Danielsen et al., 2005) where conventional methods are infeasible or expensive (Meijaard et al., 2011; Danielsen et al., 2005). As well as gaining useful ecological data the use of LEK can also increase dialogue between different stakeholders (Danielsen et al., 2000), lead to better understanding of threats to species (Abram et al., 2015) and improved decision making and natural resource management (Danielsen et al., 2010; Silvano and Valbo-Jørgensen, 2008).

As with ecological data collected by any method, the use of interviews and LEK is not free from biases and inaccuracies (White et al., 2005; Moller et al., 2004; Danielsen et al., 2005). For example, recall biases affecting respondent's ability to accurately remember information (Bradburn et al., 1987), the mis-identification of cryptic species (Danielsen et al., 2005), the use of different species concepts and taxonomy by respondents and interviewers (Turvey et al., 2014b), and the intentional provision of false information by respondents due to real or perceived conflicts of interests between respondents and other stakeholders (Danielsen et al.,

2005). Despite these biases the use of robust methodologies means data gathered from interviews can be comparable with that of conventional methods (Jones et al., 2008; Danielsen et al., 2005; Meijaard et al., 2011; White et al., 2005). Combining occupancy models and interviews of LEK have been shown to be an effective method of surveying endangered species (Brittain et al., 2018) and communities (Karanth et al., 2009; Pillay et al., 2011) and can provide information over long time periods (Pillay et al., 2011) and across large spatial scales (Martínez-Martí et al., 2016; Karanth et al., 2009; Pillay et al., 2011).

In this study we combine structured interviews with pastoralists and occupancy models to study the spatial and temporal factors that influence carnivore occurrence in community land to the east of Ruaha National Park (RNP) in Tanzania. This chapter has a number of aims, firstly, to test how effective pastoralist's LEK and interview-based occupancy models are at understanding large carnivore landscape use. Secondly, to test the application of a novel method of defining the spatial extents over which respondents report species detection. Thirdly, to improve our understanding of the spatial and seasonal patterns that determine how large carnivores use land outside protected areas. Improving our understanding of carnivore occurrence in land shared with pastoralists is vital to the planning and implementation of programmes aimed at reducing negative human-wildlife interactions in the landscape.

4.3 Methods

4.3.1 Study Area

Containing internationally important populations of lions *Panthera leo*, cheetahs *Acinonyx jubatus*, African wild dogs *Lycaon pictus*, leopards *Panthera pardus* and spotted hyenas *Crocuta crocuta* (hereafter hyenas), Tanzania's Rungwa-Ruaha landscape is a priority area for African carnivore conservation and epitomises the problems caused by negative human-carnivore interactions globally (Dickman et al., 2014). The 23,000 km^2 RNP forms the core of the landscape with the rest of the roughly 45,000 km^2 comprising a mosaic of game reserves, wildlife management areas and community land (Figure 4.1) with much of this land forming habitat for large carnivores and potentially providing valuable connectivity with other protected areas (Abade et al., 2014a). The area is the only protected area system covering the transition between the east African acacia-commiphora and the southern African brachystegia or Miombo zone (Dickman et al., 2014) containing a mix of woodlands, grasslands, and cultivated or grazed land within these broader eco-zones. The climate is semi-arid with approximately 600mm of annual rainfall, generally split into two peaks; in December to January and March to April with little to no rain falling during the dry season from May to October(Sosovele and Ngwale, 2002). The main water source for the area is the Ruaha River that flows through the south of Ruaha National Park before forming the north-eastern park boundary. The river is a vital water source for both wildlife and livestock, however, changing land-use in the river's catchment area means the river has started to stop flowing during the dry season (Kashaigili et al., 2007).

Around 40,000 people live in village land on the south west border of RNP and within the Ruaha landscape. These communities are culturally complex contain-

ing at least 35 different ethnic groups, a number of whom rely predominantly or solely on livestock for their livelihoods (Abade et al., 2014a). Through the killing of livestock, and sometimes people, Ruahas carnivore populations impart economic and social costs on local communities who respond through retaliatory and pre-emptive killings (Abade et al., 2014a; Dickman et al., 2014), indeed many community members want populations of carnivores to decline or become locally extinct (Dickman, 2009). Despite it's ecological importance the Ruaha landscape has received relatively little research attention and there is little known about the ecology of carnivores in the landscape and particularly about their spatial ecology in village land (Abade et al., 2014a; Cusack et al., 2015; Cusack et al., 2016; Abade et al., 2014b). The Ruaha Carnivore Project (RCP) has been working in the Ruaha landscape since 2009 conducting ecological and social research and running conservation programmes aiming to improve human-carnivore co-existence. Increasing our understanding of carnivore landscape use in this area is paramount if we are to maximise the effectiveness of these programmes.

4.3.2 Sampling approach

We chose to use a grid of 6 x 6 km squares as our sampling units with each interview conducted in a sampling unit acting as a survey replicate to create each unit's detection history. The sampling unit size is based on the home range size of hyenas (Gittleman and Harvey, 1982; Boydston et al., 2003b), which are cited as the most widespread carnivore species and perceived to cause the most problems in the landscape (Dickman et al., 2014). Combining the expert opinion of RCP staff, as to the likely average occupancy and detection probabilities for each carnivore species, and the equations presented by Mackenzie and Royle (2005) we estimated the optimum number of surveys required in each sampling unit for each

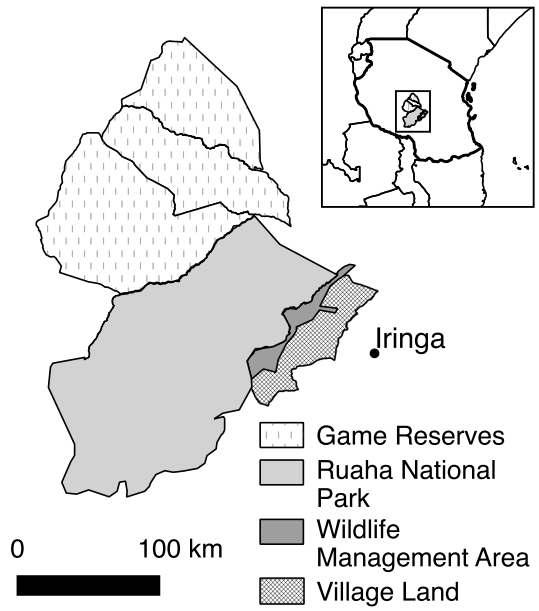


FIGURE 4.1. Map of the Rungwa-Ruaha landscape showing the study area in village land to the east of Ruaha National Park.

carnivore species (Table 4.1), we aimed for a minimum of 5 surveys per sampling unit as the 11 surveys required for surveying leopards were logistically impossible to achieve. To achieve as even a distribution of surveys in each sampling unit as possible we placed a grid of 6 x 6 km squares across the landscape, the origin of this grid was then moved 60 times by 0.1 km increments in three directions; $x + 0.1km, y$; $x, y + 0.1km$ and $x + 0.1km, y + 0.1km$. These grids were then combined with an existing RCP database of the locations of all the livestock owning households collected in 2012. We selected the grid placement that contained the most grid squares containing a minimum of 5 households. Where possible we then selected 7 households per grid square to be interviewed with the expectation that not all households would be available to be interviewed. If a household had moved, did not want to partake in the study or did not contain any suitable household members for interviewing the nearest suitable boma was selected to replace the unavailable household. Pastoralist households were picked in preference over

other ethnic groups where possible due to their higher knowledge of wildlife (Dickman et al., 2014). To investigate seasonal changes in carnivore landscape use we conducted 6 rounds of interviews roughly every two months from 27 April 2016 to 28 April 2017 (Table 4.2).

TABLE 4.1. The optimum number of surveys per site that minimises survey costs while maintaining acceptable precision in estimates of occupancy, given a standard survey design; where all sites are surveyed an equal number of times, and that the costs of initial surveys is approximately equal to the cost of repeat surveys (Mackenzie and Royle, 2005). Detection and occupancy probabilities estimated using expert opinion of RCP staff

Species	Occupancy probability (ψ)	Detection probability (p)	Optimum number of surveys to conduct at each site.
Lion	0.40	0.50	3
Leopard	0.70	0.20	11
Hyena	0.70	0.90	2
Cheetah	0.25	0.30	5
Wild Dog	0.25	0.40	4

TABLE 4.2. Summary of dates and interview numbers for each round of surveys

Round	Dates	Interviews Completed
One	27 April 15 June 2016	158
Two	5 July 5 August 2016	120
Three	5 September 25 October 2016	98
Four	31 October 31 December 2016	81
Five	17 January 10 February 2017	45
Six	4 March 28 April 2017	122

4.3.3 Area of Knowledge Mapping

One of the challenges of using LEK to collect occupancy data is defining the geographical area over which species detections are reported in a way that is interpretable for respondents and researchers. Previous interview based occupancy analysis has either been conducted on a national spatial scale (Karanth et al., 2009); sampled well known, pre-determined areas, i.e. forest reserves, national

parks or forestry blocks (Pillay et al., 2011; Pillay et al., 2013; Brittain et al., 2018); or been conducted in areas where interviewees and researchers are able to interpret and define spatial extents on a drawn map (Taubmann et al., 2015; Zeller et al., 2011; Petracca et al., 2013; Martínez-Martí et al., 2016). Our study site, covering approximately 1500 km^2, is not divided into widely recognised and appropriately sized areas and the majority of pastoralist's are not familiar with drawn maps, requiring a novel methodology for defining survey sites.

We refer to the area a respondent reports wildlife detections as their "Area Of Knowledge" (AOK) (Zeller et al., 2011). We defined the AOK as a circle centred on the respondent's boma with radius of 1 km. To define each respondent's AOK the respondent and interviewer used a GPS unit to find a recognisable and memorable landmark (i.e. a large tree, another household's boma, a farm, a river, a road etc.) that was between 900 and 1100 meters from the respondent's boma, the primary landmark. The respondents were then asked to describe at least 3 other secondary landmarks the same distance away from their boma as the primary landmark but in other directions, the primary and secondary landmarks were recorded on a map and form the boundaries of the respondent's AOK. Where possible the distances of the secondary landmarks to the boma cross checked by measuring their distance to the homestead with a GPS unit.

4.3.4 Occupancy Interviews

We developed a questionnaire that gathered detection/non-detection data on lions, hyenas, cheetahs, leopards, wild dogs and a number of potential prey species. The questionnaire was initially written in English and then translated into Swahili, a back translation was performed to check the initial translation's accuracy. We conducted interviews using the Open Data Kit system (Brunette et al., 2013) and

Google Nexus 7 tablets. We piloted interviews prior to data collection and adapted the questionnaire in response to issues raised. We selected interviewees from members of the household who spend significant amounts of time herding livestock and thus more likely to detect wildlife. For cultural reasons we excluded women and children under 16 from being interviewed. To ascertain interviewee's wildlife knowledge they were required to undergo a two step wildlife identification process (Zeller et al., 2011). They were first asked to describe the bodily appearance of the 5 large carnivores as well as their tracks and vocalisations, following this they were asked to identify images of the 5 large carnivores and their tracks. We required interviewees to be able to describe and identify at least one carnivore species and its tracks to be included in the survey, and if they failed to correctly identify a species or its tracks their detections were removed from that species' analysis. We then asked respondents to report which species they detected in their AOK over the last 30 days, and for species detected if the detection was a direct sighting and/or tracks and signs.

We re-visited households roughly every two months over a 12 month period to cover the landscape's seasonality. During repeat interviews respondents were reminded of the landmarks defining the boundaries of their AOK and again asked about species detections. Where possible, we interviewed the same household member, if they were not available and another household member was, they were replaced as long as the new respondent was familiar with the landmarks defining the AOK and also undertook the wildlife test. On repeat visits households were visited at least three times to try and find a respondent, if after three visits nobody suitable could be found for interviewing that household was removed from that round's list. See Appendix A for interview questions.

4.3.5 Occupancy Assumptions

Our methods require relaxing a number of the assumptions of standard occupancy models. Firstly, using 36 km^2 squares as sampling units means we cannot assume population closure for species such as lions, cheetah and wild dog who have much larger home ranges (Gittleman and Harvey, 1982). MacKenzie and Nichols (2004) state that this assumption can be relaxed if changes to the populations are random over the survey period, changing the interpretation of the occupancy parameter, ψ, from "proportion of area occupied" to "proportion of area used" (MacKenzie and Nichols, 2004). As we are ultimately interested in understanding carnivore landscape use this interpretation is sufficient for our study.

Secondly, where AOKs overlap the assumption that detections are independent may be violated if respondents share knowledge regarding wildlife detections, which is likely to happen for carnivore species that threaten people's livestock. To minimise the impact of knowledge sharing we ensured respondents were aware that the interview only referred to detections they themselves had witnessed. However, to minimise confusion we did not attempt to exclude detections that a respondent had seen as a result of being informed by somebody else. Thirdly, where households are on the edge of sampling units AOKs may overlap into neighbouring sampling units, meaning detections between samplings sites are not always independent. However the lack of suitably sized and widely recognised geographic boundaries meant using AOK's defined as buffers around households was the only suitable way of defining the spatial extents of surveys.

4.4 Analysis

4.4.1 Site use and detection covariates

We considered a number of environmental covariates to explain heterogeneity in carnivore site use (Table 4.3). We modelled human pressures that may influence carnivore site use using distance to road, distance to RNP, distance to wildlife management area (WMA), converted agricultural land, population density and pastoralist households per sampling unit. Water availability was modelled by rainfall over the survey period and distance to all rivers and large rivers for the wet and dry seasons respectively. We included enhanced vegetation index (EVI) as a measure of vegetation productivity which can be used as a proxy for prey availability (Pettorelli et al., 2011). We modelled detection probability using interviewee-specific variables such as their age and tribe, as well as habitat covariates. We converted spatial covariates to raster layers where appropriate using raster package (Hijmans and Etten, 2014) in programme R (R Core Team, 2017) and calculated average pixel values for each sampling unit. We compared covariates in a correlation matrix and strongly correlated variables ($|r|>0.7$) were not included in the same analysis (Dormann et al., 2012).

4.4.2 Occupancy Models

We calculated estimates for detection probability (p) and site use (ψ) using single species single season occupancy models in the unmarked package (Fiske and Chandler, 2011) in programme R (R Core Team, 2017). We fitted a global model containing all p and ψ covariates and assessed goodness of fit using the MacKenzie and Bailey (2004) goodness-of-fit bootstrap test. Where a global model would not converge we removed covariates that individually explained the least variance

TABLE 4.3. Environmental covariates included in occupancy models.

Environmental Covariate	Resolution	Source
Distance to roads	100m	Open Street Map (OpenStreetMap contributors, 2017) & RCP data
Distance to all rivers	100m	Hydrosheds (Lehner et al., 2006)
Distance to major rivers*	100m	Hydrosheds (Lehner et al., 2006)
Distance to Ruaha National Park	100m	TANAPA
Distance to wildlife management area†	100m	TANAPA
Population density	3 arc second 100m	Afripop (Linard et al., 2012; *Worldpop* 2013)
Pastoralist households per sampling unit	-	RCP data
Converted agricultural land	30m	MEaSUREs (Xiong et al., 2015)
Average precipitation for survey period‡	0.1 degree 10 km	GPM (Huffman et al., 2015)
Average Enhanced vegetation index for survey period‡	500m	MODIS (Didan, 2015)

*The Great and Little Ruaha rivers that are the last rivers to stop flowing in the dry season †The wildlife management area is the closest protected area to the whole study area (Figure 4.2). ‡From 30 days before the first survey of the round until the day of the last survey of the round, data was accessed and averages calculated using Google Earth Engine (Gorelick et al., 2017)

in a stepwise manner until the model converged. Where there was evidence of over-dispersion ($\hat{c} > 1$) we used QAICc to rank models (Richards, 2008). We used a two step model selection process. First, to identify which covariates best explained detection probability, we modelled p using all detection co-variates with ψ held constant. We then ranked models using ΔQAICc, and considered them strongly supported if ΔQAICc < 2 (Burnham and Anderson, 2001). Secondly, we modelled ψ using the strongly supported detection models and all possible combinations of site use covariates.

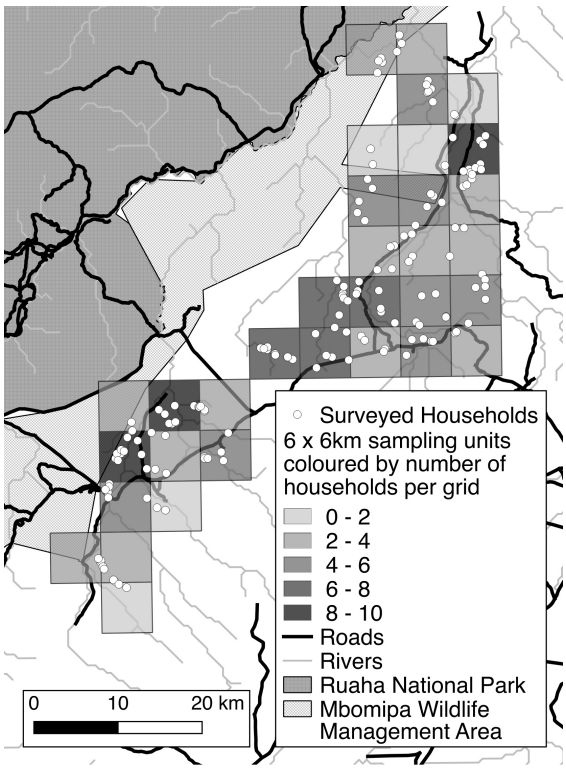


FIGURE 4.2. Map showing study area to the east of Ruaha National Park and locations of households interviewed.

4.5 Results

4.5.1 Interviews

From the 188 originally selected households, 106 had either moved or were not suitable for interviewing, of these 67 were replaced with a nearby household and 39 could not be replaced, 11 new households were added as a result of new pastoralist settlements not included in the 2012 RCP survey, leaving a sample of 160 households. These households were spread across 33 sampling units with a mean of 4.81 households per unit. (Figure 4.2).

A total of 624 interviews were carried out between 27th April 2016 and 28 April 2017 (Table 4.2) with 170 different respondents. Mean respondent age was

30 and ranged between 16 and 75, the majority of respondents were from pastoralist tribes, Maasai (n=76), Barabaig (n=60) and Sukuma (n=8), with the remaining agriculturalists predominantly Hehe (n=12) and Gogo (n=11). Rainfall across the study site, and much of Tanzania, was very low during the early wet season (September to December) causing widespread drought, low vegetation productivity and a lack of forage for livestock (National Food Security Division, 2016). As a result many pastoralist households, including large numbers of respondent households, moved their livestock to seasonal grazing sites in highlands outside the study area. This resulted in very low numbers of interviews during the dry season, particularly in rounds four and five (Table 4.2). As a result of low numbers of interviews and low detection rates during the dry season rounds two to five were combined and analysed as a single season.

Respondent knowledge of lion and hyena identification was generally high, while knowledge of leopard, cheetah and wild dog identification was relatively poor (Table 4.4). Respondents were least able to correctly identify cheetahs and their tracks, however the majority of those with good knowledge of cheetah identification lived in the north west of the study area, an area cheetahs are anecdotally known to reside. Distances from 24 landmarks to the respondent's homestead were measured to check the accuracy of respondent's distance estimates. The real distances for landmarks estimated to be 1 km away from the respondent's household ranged from 0.98-1.87 km, with a mean of 1.13 km (σ=0.303).

4.5.2 Covariates

Distance to RNP and distance to WMA were strongly correlated (r = 0.737). As RNP is a more strongly enforced protected area distance to RNP was kept in the analysis and distance to WMA removed. Rainfall in round 6 was strongly corre-

TABLE 4.4. Number of respondents reporting detections across entire study and the number of respondents whose knowledge of that species was high enough for their reported detections to be included in analysis.

Species	Total detections	Knowledgeable respondents
Lion	68	153
Hyena	362	118
Leopard	22	64
Cheetah	9	32
Wild dog	15	67

lated to population density (r = 0.727), and so neither were included in the same models. Naive and estimated site use for the most common prey species (monkeys, dikdik, kudu and impala) was near 100% across all survey periods (Figure 4.3). As suitable sized prey for all the carnivore species occurred across the study area and throughout the study period prey site use was not included as a co-variate in carnivore models.

4.5.3 Occupancy Models

4.5.3.1 Lions

Lions were widely detected during most of the study period (Figures 4.3 & 4.4). Estimates of constant detectability were highest in rounds 1, p=0.32 (95% CI 0.21-0.44), and 6, p=0.43 (95% CI 0.23-0.66), with lower estimate in round 2-5, p=0.15 (95% CI 0.089-0.23). In the most parsimonious models average EVI over the study period had a positive impact on detectability in round 1 while distance to RNP had a negative impact on detectability during round 1 but a positive impact in round 6. Estimates of lion site use was highest in round 1, ψ(.)=0.70 (95% CI 0.42-0.89), and fell through rounds 2-5, ψ(.)=0.53 (95% CI 0.29-0.76), and 6, ψ(.)=0.24 (95% CI 0.10-0.46)(Figure 4.3). Despite a number of site use covariates appearing in the most parsimonious models none of them confidently predicted lion site use

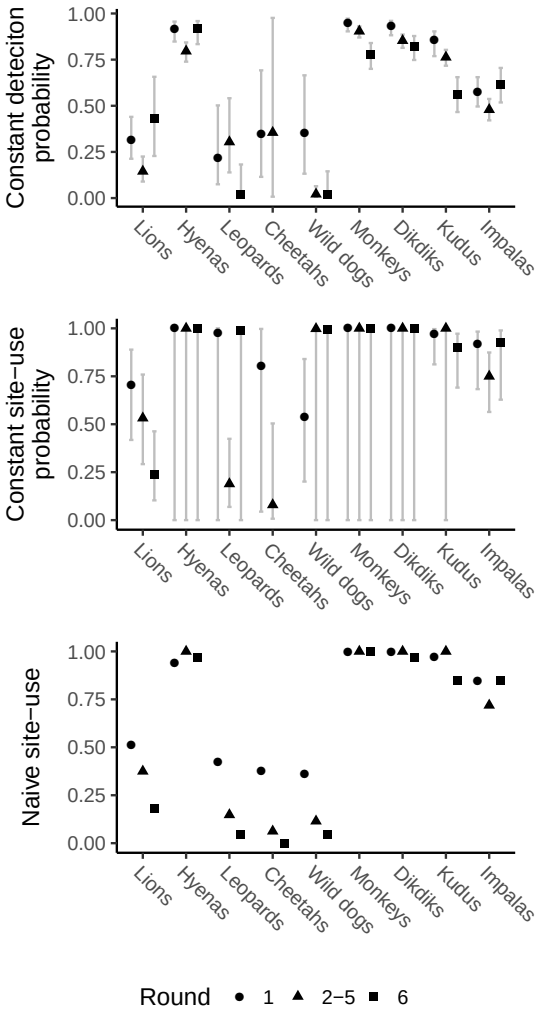


FIGURE 4.3. Estimates of constant detection and site use, and naive occupancy for 5 carnivore species and the most common herbivores for rounds 1, 2-5 combined and 6. As naive occupancy for hyenas, monkeys, dikdiks and kudu are high the large ψ confidence intervals are likely caused by boundary issues (See Appendix C for estimates of naive site use for all rounds and species).

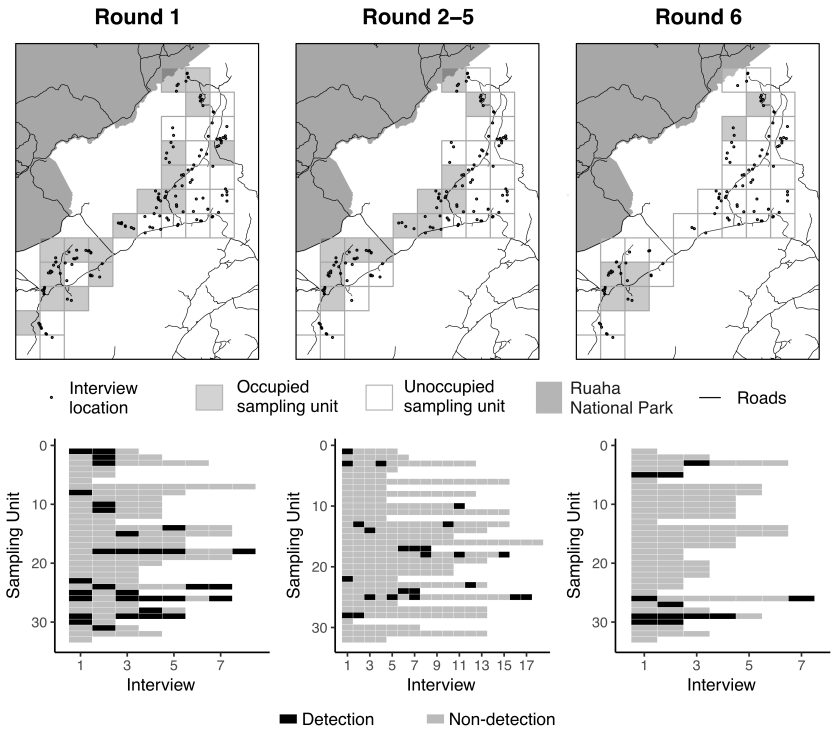


FIGURE 4.4. Seasonal lion detection histories and maps of sampling units where detection occurred.

during any of the survey rounds (Table 4.5). Goodness of fit tests of the most parameterised models showed no evidence for lack of fit (P=0.53) or over-dispersion ($\hat{c}$=0.89) for round 1, however, models for round 2-5 and 6 showed evidence of lack of fit (P_{2-5}=0.048, P_6=0.11) and over-dispersion ($\hat{c}_{2-5}$=3.83, $\hat{c}_6$=2.24).

4.5.3.2 Hyena

Hyenas were the most widely reported of the carnivore species (Table 4.4), with very high detection and site use probabilities across the three survey periods (Figures 4.3 & 4.5). Estimates of hyena detectability followed a similar pattern to that of lions, with highest detectability estimates during rounds 1, p(.)=0.92 (95% CI 0.85-0.96), and 6, p(.)=0.92 (95% CI 0.83-0.96) and the lowest in round 2-5, p(.)=0.80 (95% CI 0.74-0.84) (Figure 4.3). In the best fitting models distance to all

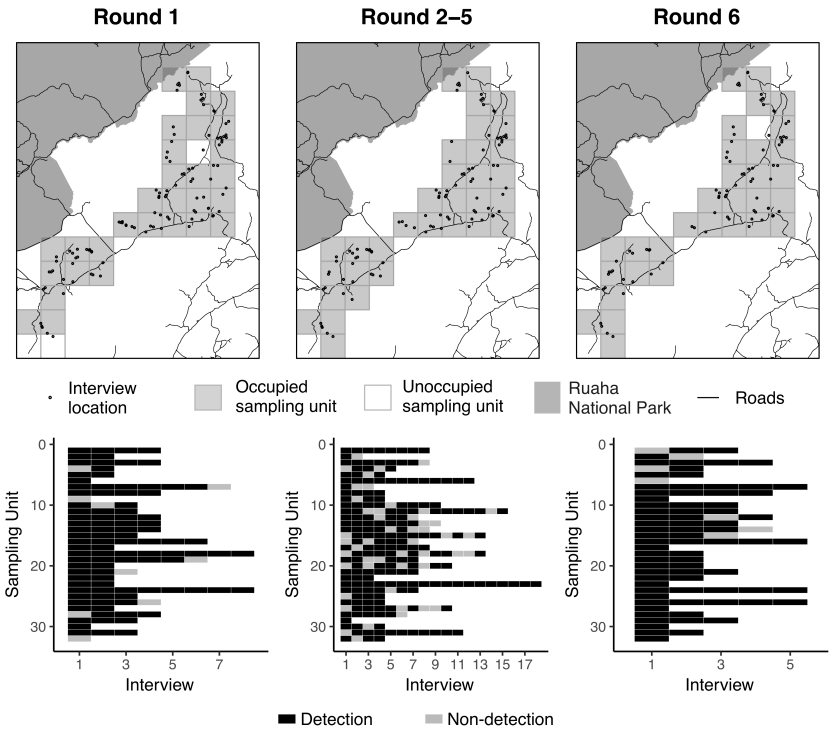


FIGURE 4.5. Seasonal hyena detection histories and maps of sampling units where detection occurred.

rivers had a positive impact on detectability in round 1, respondent age and distance to major rivers had a negative impact on detectability in round 2-5 and EVI had a positive impact on detectability in round 6. Estimates of site use were 1.00 (95% CI 0.00-1.00) for all three survey periods (large confidence intervals a result of boundary issues) and no covariates confidently predicted changes in site-use (Table 4.5). Goodness-of-fit tests for all of the survey periods showed no evidence for lack of fit (P_1=0.35, P_{2-5}=0.63, P_6 = 0.70) or over-dispersion ($\hat{c}_1$=0.82, $\hat{c}_{2-5}$=0.28, $\hat{c}_6$=0.55).

4.5.3.3 Leopard

Detection estimates for leopards were similar in rounds 1, p(.)=0.22 (95% CI 0.075-0.50), and 2-5, p(.)=0.30 (95% CI 0.14-0.54), while a single detection in round 6

prevents the fitting of meaningful models. The only covariates that predict detection were human population density and distance to major rivers that both have a positive impact on detectability in the best fitting model for round 2-5 (Table 4.5). Site use estimates were very high for round 1, $\psi(.)$=0.98 (95% CI 0.00-1.00) (as occupancy estimates are relatively high, the large confidence intervals are likely a result of boundary issues) and much lower for round 2-5 $\psi(.)$=0.19 (95% CI 0.069-0.42). No models showed any evidence of lack of fit (P_1=0.25, P_{2-5}=0.48). While there is no evidence of over-dispersion for models for round 2-5 ($\hat{c}_{2-5}$=0.52) models for round 1 showed mild over-dispersion ($\hat{c}_1$=1.3) (See Appendix C for detection histories and maps of detections).

4.5.3.4 Wild dog and cheetah

Wild dogs were recorded across all survey periods, however round 1 contained the highest detection estimate, $p(.)$=0.35 (95% CI 0.13-0.67), and the only meaningful occupancy estimate, $\psi(.)$=0.54 (95% CI 0.20-0.84). Low numbers of detections in round 2-5 and 6 did not provide enough data to fit meaningful models. Cheetahs recorded the lowest number of detections of any of the carnivore species with no detections in round 6 and only one in round 2-5. Low numbers of detections prevent the fitting of meaningful models for any rounds, however naive site use was highest in round 1 and lower in proceeding months (See Appendix C for detection histories and maps of detections).

Table 4.5: Most parsimonious models with untransformed estimates of β covariates. A, respondent age; P, average distance to Ruaha National Park; O, average distance to road; C, proportion of land converted to agriculture; E, average EVI during survey period; W, average rainfall during survey period; D, human population density; RW, wet season rivers; RD, dry season rivers; H, households per sampling unit. (See Appendix C for all top ranked models (Δ QAICc < 2))

Species	Round	Variables	β	LCI	UCI
Lions	1	p intercept	-1.25	-1.85	-0.661
		E	0.893	0.320	1.47
		P	-1.10	-1.79	-0.413
		ψ intercept	34.3	-93.2	161
		C	26.2	-88.9	141
		P	-41.7	-193	109
	2-5	p intercept	-1.82	-2.25	-1.39
		ψ intercept	7.54	-55.8	70.8
		RD	18.8	-60.2	97.7
		P	-48.0	-243	147
	6	p intercept	3.11	0.362	5.86
		P	4.19	1.14	7.24
		ψ intercept	-43.5	-209	122
		W	19.9	-56.4	96.2
		P	-78.5	-366	209

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Species	Round	Variables	β	LCI	UCI
Hyenas	1	p intercept	3.04	1.96	4.12
		RW	1.11	0.113	2.10
		ψ intercept	38.5	-119	196
		C	-17.7	-89.5	54.2
	2-5	p intercept	1.48	1.13	1.82
		A	-0.262	-0.560	0.0369
		RD	-0.367	-0.665	-0.0697
		ψ intercept	10.2	-46.6	66.9
	6	p intercept	2.77	1.75	3.78
		E	0.916	0.0810	1.75
		ψ intercept	11.6	-113	136
Leopards	1	p intercept	-0.838	-1.49	-0.187
		ψ intercept	93.3	-171	357
		H	-46.3	-180	86.9
		O	152	-284	587
	2-5	p intercept	-3.43	-5.66	-1.19
		D	2.00	0.716	3.29
		RD	2.79	-0.652	6.23
		ψ intercept	-13.0	-52.6	26.6
		H	-45.8	-175	83.4
	6	p intercept	-3.82	-6.14	-1.50
		ψ intercept	4.62	-117	126
Cheetah	1	p intercept	-0.118	-1.07	0.835

Continued on next page

Table 4.5 – continued from previous page

Species	Round	Variables	β	LCI	UCI
		ψ intercept	3.62	-56.7	64.0
		D	-28.22	-231	175
	2-5	p intercept	-0.597	-4.90	3.71
		ψ intercept	-2.45	-4.91	0.0157
	6	No detections			
Wild dog	1	p intercept	-0.599	-1.88	0.685
		ψ intercept	0.145	-1.38	1.67
	2-5	p intercept	-2.76	-3.93	-1.59
		ψ intercept	-42.9	-184	98.9
		P	-142	-598	313
	6	p intercept	-3.85	-5.92	-1.77
		ψ intercept	5.31	-119	129

4.6 Discussion

4.6.1 Carnivore Site use and detection

Large carnivores are a globally valued and threatened taxa which frequently come into competition with human communities for space and other resources (Ripple et al., 2014). Promoting co-existence between large carnivores and humans is paramount for the ongoing survival of local and global carnivore populations and improving the well-being of affected human communities (Dickman et al., 2014; Redpath et al., 2014). Improving our understanding of the status and habitat use of large carnivores in human-modified landscapes is vital for the planning and implementing of conservation projects aimed at promoting human-carnivore co-existence. In this study we show how interviews and occupancy models can be a cost effective method of inferring information on the occurrence of large carnivores in a human-modified landscape that borders a national park.

Lions were widely reported across the landscape in round 1 with lower estimates of site use in subsequent survey periods, while the difference in site use estimates between survey periods was not significant our results suggest seasonal changes in lion site use. Schuette et al. (2013a) found lions seasonally shift their spatial distribution to avoid pastoralists and their livestock, however in our study the highest estimates of lion site use in round 1 coincide with the period of time when numbers of pastoralists in the study area were also at their highest. Given the high costs lions often face when in contact with pastoralist communities (Kissui, 2008) this suggests other ecological factors causing lions to move into community land during the wet season. Changing prey availability can drive seasonal changes in lion movements (Loveridge et al., 2009; Druce et al., 2004), while our study did not detect seasonal changes in prey occupancy or site-use, we did not as-

sess prey abundance which is likely to be higher in or near RNP due to decreased competition for forage from livestock and access to water in the Ruaha river which flows in the park or along the the park boundary. There is little support for any environmental covariates predicting lion site use, however a number of covariates had an impact on detection probability. The positive impact EVI has on detection in round 1, may be because pastoralists living in areas with higher vegetation productivity are able to spend more time grazing their livestock around their bomas, effectively increasing the survey effort within the 1 km AOK and increasing detection rates. Distance to RNP had a negative impact on lion detection in round 1, suggesting lions may adapt their behaviour and become more secretive in more human-dominated landscapes (Schuette et al., 2013a). The opposite seems to occur in round 6 however poor model fit and over-dispersion questions the validity of those results.

Hyenas have previously been reported as the carnivore species that causes the most problems for residents around Ruaha due to the threat they pose to livestock (Dickman et al., 2014), despite this they were the by far the most common species reported by pastoralists. High occupancy estimates during all rounds suggest hyenas are resident throughout the study area, a finding supported by RCP camera trapping data that has recorded denning sites in village land (unpublished data). This concurs with other studies that show hyena populations are able to adapt to live in human-dominated landscapes (Boydston et al., 2003a; Abay et al., 2011; Schuette et al., 2013b; Woodroffe, 2000). The co-existence of humans and hyenas in this landscape despite high perceptions of hyenas as a problem species (Dickman et al., 2014) highlights the fact that negative human-wildlife interactions and high levels of wildlife persecution result from other processes than just levels of economic damage caused by wildlife (Dickman, 2010; Peterson et al., 2010). High

occupancy estimates mean there was little support for any environmental covariates predicting hyena occupancy at the spatial scales over which our analysis was conducted. Environmental detection covariates; EVI in round 6 and distance to major rivers in round 2-5, may act as proxies for survey effort (similarly to lions), with increased detection probabilities in areas with more vegetation and access to dry season water as pastoralists are able to spend more time within their 1 km AOK.

High estimate of leopard site use in round 1, ψ=0.98, fits that of other studies that suggest leopards are well adapted to living in human modified landscapes (Woodroffe, 2000; Strampelli et al., 2018). However, lower estimates of site-use in round 2-5, ψ=0.19, suggests seasonal differences in leopard home ranges. Availability of domestic food sources are likely higher in areas closer to water and with higher population density (Athreya et al., 2016), particularly in the dry season, which may be why these covariates had a positive leopard detection probability during rounds 2-5. Low numbers of wild dog and cheetah detections limit the inferences that can be made about their spatial and temporal patterns of site use, however naive site-use and estimates of site-use where meaningful models could be constructed suggest similar patterns of landscape use to lions and leopards with higher site use during round 1 than the proceeding survey periods. While changing prey availability influences seasonal changes in home ranges in cheetahs and leopards (Odden and Wegge, 2005; Bailey, 1993; Marker, 2002; Houser et al., 2009) other factors, such as denning in wild dogs (Pomilia et al., 2015) and offspring care in cheetah and leopard may also influence temporal changes in ranging behaviour (Houser et al., 2009; Odden and Wegge, 2005). A lack of respondents knowledgeable in cheetah identification in areas we suspect cheetah do not occur means our study likely overestimates naive site-use for cheetah, however these biases are

likely to be constant throughout the study period so do not impact comparisons made across seasons.

4.6.2 Use of local ecological knowledge

Respondent's abilities to identify different carnivores agrees with previous studies that found LEK to be highest for culturally iconic (lion) and common species (hyena) (Nyhus and Tilson, 2003; Gilchrist et al., 2005). Poor respondent knowledge of the other carnivore species, and in particular the spatial distribution of knowledge about cheetah identification, highlights one limitation in the use of LEK with occupancy models; where knowledge of a species identification positively correlates with exposure to that species then reliable data is only available from areas of high site use or high detection probability. This not only restricts where data collection can be conducted but may lead to over estimates in site use or occupancy as areas where the species do not occur and respondent's knowledge are poor are omitted from models.

Our study highlights one of the inherent disadvantages of using LEK over traditional monitoring techniques, with the spatial and temporal distribution of data collection reliant on the availability of suitable respondents. In contrast to other studies that used maps (Taubmann et al., 2015; Zeller et al., 2011; Petracca et al., 2013; Martínez-Martí et al., 2016) or pre-existing land boundaries to define AOKs (Pillay et al., 2011; Pillay et al., 2013; Brittain et al., 2018) we deemed defining AOKs as areas around respondent's households the most appropriate given the culture and landscape use of pastoralists in our study area. This, however, restricts the range of covariate values represented in our models to those covered by households in the landscape, and may be one reason why we found little support in our models for environmental covariates which are highly likely to have

a strong impact on carnivore site-use, such as distance to RNP or human population density (Woodroffe and Ginsberg, 1998; Schuette et al., 2013b; Everatt et al., 2014). The temporal distribution of interviews was impacted by unusually low rainfall which led to larger than normal numbers of pastoralists migrating out of the study site for a longer period of time, severely reducing the availability of data in the dry season.

Another disadvantage of using an AOK that is so closely tied to areas of human habitation is that it is difficult to disentangle the social and ecological factors that influence detection and site-use probability. While other studies are able to use detection covariates to infer changes in species behaviour (Schuette et al., 2013b; O'Connell Jr et al., 2006) as pastoralist behaviour and site-use also changes in response to environmental covariates, e.g. water and forage availability, it is not always possible to disentangle the effects changing behaviours of pastoralists or wildlife on detection probabilities.

4.7 Conclusions

While interview data is subject to a number of constraints and biases (White et al., 2005; Moller et al., 2004; Danielsen et al., 2005) we demonstrate that interview data and LEK can be used with occupancy models to infer information on the landscape use of a range of large carnivores in human-dominated landscapes. While landscape use by most species appears highly seasonal with higher use of community land in the wet season, hyenas were permanently recorded across the whole study area suggesting a high ability for them to coexist alongside human communities despite being cited as a problem species in the landscape (Dickman et al., 2014).

We use a novel method of defining AOK's as buffers around households which allows the collection of spatially explicit data in the absence of pre-determined geographic extents or where respondents are unfamiliar with maps (Zeller et al., 2011; Martínez-Martí et al., 2016). However, defining AOK's in relation to household locations reduces what we can infer regarding the impact of environmental covariates on detection and site use probability by restricting the spatial distribution of data collection and tying data collection to areas of human landscape use. The ability of our models to predict carnivore site use was also reduced due to low respondent availability in the dry season and low respondent knowledge of some carnivore species. The limitations of our study highlight that while interview based occupancy models can be used to infer useful information on seasonal species distributions it is not suitable method across all cultures, landscapes, species and questions.

4.8 Acknowledgements

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This cow's poor condition at the beginning of the wet season is testament to the harsh dry season it just endured

CHAPTER 5

USING SOCIO-PSYCHOLOGICAL FRAMEWORKS TO UNDERSTAND TOLERANCE TOWARDS LARGE CARNIVORES



An RCP DVD night showing wildlife documentaries at a Barabaig household.

5.1 Abstract

Understanding the factors that drive human tolerance towards species at the centre of conservation conflicts is vital if we are to improve the well being of human communities and reduce the negative impacts of these interactions on carnivore populations. Drawing on psychological theory and pre-existing socio-psychological frameworks we create a theoretical tolerance framework for lions and hyenas around Ruaha National Park in Tanzania. Interviews with 176 livestock owners were analysed using structural equation models to test the tolerance framework's variables and pathways. Our models show tolerance towards carnivores is mediated by a complex mix of variables. Perceived benefits and positive beliefs were the most influential variables influencing tolerance for both species while experience of species and perceived risks only influenced tolerance towards hyenas. Engagements with conservation programmes increased tolerance towards lions, however, they had a complicated relationship with risk perception for both species. Highlighting that care is needed when planning conservation interventions aimed at increasing tolerance towards wildlife, as their interaction with other socio-psychological variables can have unexpected and potentially unintended consequences. Our findings show the utility of socio-psychological frameworks in understanding how living alongside dangerous wildlife influences peoples perceptions and tolerance towards those species.

5.2 Introduction

Large carnivores' extensive home ranges and high metabolic requirements frequently put them in competition with human communities for space and resources (Ripple et al., 2014; Carbone et al., 1999). Human communities bear economic and social costs related to the real and perceived threats carnivores pose to the lives of domestic livestock and humans (Dickman et al., 2014; Treves and Karanth, 2003; Löe and Röskaft, 2004). Direct costs are caused by attacks on humans and livestock while the indirect costs carnivore pose include the opportunity costs involved with protecting livestock, poor mental and physical health, reduced food security, and social conflict (Barua et al., 2013). These costs often result in lethal retaliatory action from human communities which is widely associated with declines and extinctions in carnivore populations (Ripple et al., 2014; Woodroffe and Frank, 2005; Woodroffe and Ginsberg, 1998).

Despite the costs they impose on some communities, many large carnivores are ecologically, economically and culturally important species (Wolf and Ripple, 2016; Ripple et al., 2014). Large carnivores can influence ecological community structures through a number of top-down mechanisms (for example mesopredator release (Ripple et al., 2013; Crooks and Soulé, 1999), direct predation and landscapes of fear (Ripple and Beschta, 2004; Schmitz et al., 1997)). Through these ecological impacts carnivores can provide ecosystem services to human communities (OBryan et al., 2018), e.g. increasing agricultural output (Prowse et al., 2015), increasing carbon storage (Strickland et al., 2013), and reducing human exposure to zoonotic diseases (Braczkowski et al., 2018; Levi et al., 2012). Large carnivores also offer direct economic benefits to some communities as drivers of photographic tourism (Lindsey et al., 2007b; Maciejewski and Kerley, 2014). This is driven in

part by the important cultural roles carnivores play in many societies (Hazzah et al., 2009; Shen et al., 1982; Kellert et al., 1996) and many people derive pleasure purely from the knowledge that large carnivores exist (Nelson, 2009; Macdonald, 2001).

The different experiences and perceptions of the costs and benefits of large carnivores amongst different human groups often leads to intense conservation conflicts between stakeholders over how large carnivores, and human-carnivore interactions should be managed (Treves and Bruskotter, 2014; Redpath et al., 2014). Resolving these conflicts is important for both improving the well being of the human communities who bear the costs of living alongside these species as well as for ensuring the long-term survival of the carnivore populations involved (Dickman et al., 2014; Bruskotter and Wilson, 2014). There is increasing recognition that much of the literature mis-conceptualises this "human-wildlife conflict" as being between wildlife and humans and not, as is the case, between different human values and views of how wildlife should be managed (Redpath et al., 2014; Young et al., 2010; Peterson et al., 2010). Dickman (2010) also outlines a number of widely held assumptions about these conflicts, firstly, the intensity of the conflict is directly proportional to levels of damage caused by wildlife, secondly, the intensity of conflict elicits a proportional human response, thirdly, altering the human response to the conflict will have a proportionate conservation effect . The mis-conceptualisation of conflict and these assumptions have led to a focus on addressing the impacts of interactions between humans and carnivores through scientific, technical or legislative solutions without recognising the socio-cultural contexts that have given rise to different human values of wildlife and views towards their management (Young et al., 2010).

Improving our understanding of the human-dimensions of these conflicts and

the diversity of opinions, and their drivers, amongst different stakeholder groups is vital if these conflicts are to be resolved to the satisfaction of all involved parties. Building an understanding of the extent of conflict within and between stakeholder groups is important in ensuring that the full ranges of interests and concerns are considered when attempting to find resolutions (Kansky et al., 2016). There has been an increase in research focused on improving our understanding of the complex range of factors that influence human attitudes towards wildlife (Kansky et al., 2014; Kansky and Knight, 2014; Dickman, 2010; Struebig et al., 2018). In a meta-analysis of attitudinal studies Kansky and Knight (2014) found that the costs of living alongside wildlife were more important than the benefits in driving attitudes towards wildlife, and counter to the assumptions outlined in Dickman (2010), intangible costs, such as psychological costs of fear, danger or risk, outweighed the impact of tangible costs and were the single most important category influencing attitudes. Socio-psychological frameworks (such as Ajzen (1991)'s Theory of Planned Behaviour) have been widely used to study relationships between attitudes, social structures and individual behaviours (Miller, 2017; St. John et al., 2018). Recently there has been increasing interest in using tolerance frameworks based on socio-psychological theory to improve our understanding of the factors that drive tolerance of wildlife with the aim of resolving conservation conflicts (Bruskotter et al., 2015; Bruskotter and Wilson, 2014; Treves and Bruskotter, 2014; Inskip et al., 2016; Kansky et al., 2016; St. John et al., 2018; Carter et al., 2012b).

Tolerance for wildlife can be defined as "passive acceptance of a wildlife population" while intolerance is often described as having both attitudinal (e.g. negative feelings or judgements towards a species) and behavioural (e.g. undertaking active behaviours with the intent of killing an animal or reducing it's population)

components (Brunette et al., 2013; Bruskotter and Wilson, 2014; Inskip et al., 2016). A range of socio-psychological factors have been identified as potentially influencing people's tolerance of wildlife: perceived risks and benefits associated with a species; attitudes and beliefs towards a species and its impacts (Lischka et al., 2008; Bruskotter et al., 2009; Inskip et al., 2016; Carter et al., 2012b), social trust of those tasked with managing wildlife (Bruskotter et al., 2009; Carter et al., 2012b; Struebig et al., 2018), belief in ones own ability to control risk (Bruskotter et al., 2009; Zajac et al., 2012; Kleiven et al., 2004) and direct and indirect experiences with the species (Bruskotter et al., 2015; Kansky et al., 2016).

Reviewing literature regarding tolerance of carnivores and placing it within psychological theory Bruskotter and Wilson (2014) propose a number of variables likely to influence people's tolerance of large carnivores. In their hazard-acceptance model tolerance for a species is predicted by the individual's perceptions of the risks and benefits that the species provides, as well as the individual's affect (an emotive response based on prior experience) for the species. Risk-benefit perception is in turn influenced by the individual's affect, their social trust in those responsible for managing wildlife and their perception of their own ability to control the hazards the species poses. A similar framework is proposed and tested by Inskip et al. (2016) who investigated the variables that influence tolerance for tigers in the Sundarbans. Their model includes a number of related variables to that of Bruskotter and Wilson (2014), e.g. tiger-related experience, and perception of risks and benefits (positive beliefs), however excludes variables related to social trust and personal control over hazards.

In this manuscript we investigate the application of a theoretical socio-psychological framework to understand tolerance towards carnivores (Fig. 5.1). Building on the frameworks proposed by Inskip et al. (2016) we include variables from Bruskotter

and Wilson (2014) related to social trust in the agencies responsible for wildlife management and perceived personal control over hazards carnivores impose on respondents. We include perceptions of household and village level benefits provided by carnivores as well as positive belief statements similar to those used by Inskip et al. (2016). We also consider the role that engagement with conservation programmes that aim to reduce negative human-carnivore interactions may have on tolerance towards carnivores, hypothesising that they play a similar role to "positive" indirect experience of carnivores, and could influence beliefs, perceptions of risk and indirectly overall tolerance. We use this adapted tolerance framework to investigate tolerance towards two carnivore species, lions and hyenas, that are at the centre of conservation conflicts in community land on the edges of Ruaha National Park in Tanzania (Dickman et al., 2014).

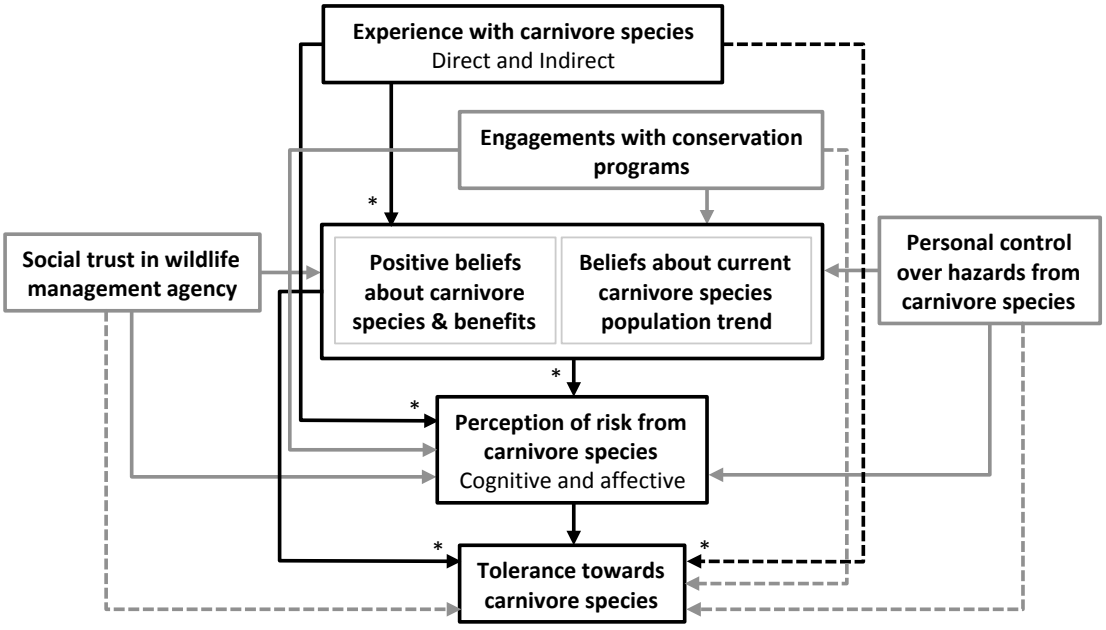


FIGURE 5.1. Theoretical tolerance model adapted from Inskip et al. (2016) & Bruskotter and Wilson (2014). Boxes represent variables that have a direct (solid arrows) or indirect (dashed arrows) impact on tolerance for carnivore species. Black boxes and arrows represent variables and relationships proposed and tested by Inskip et al. (2016), stars mark relationships that Inskip et al. (2016) found at least partial support for. Grey boxes and arrows represent additional variables and relationships mostly adapted from Bruskotter and Wilson (2014)'s proposed tolerance framework

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5.3 Methods

5.3.1 Study Site

The 45,000 km^2 Rungwa-Ruaha landscape in Tanzania contains a wide mixture of protected and unprotected land-use types; centred on the the 23,000 km^2 Ruaha National Park (RNP) the rest of the landscape contains a mixture of game reserves, wildlife management areas and community land (Figure 5.2). The landscape contains internationally important populations of lions *Panthera leo*, cheetahs *Acinonyx jubatus*, African wild dogs *Lycaon pictus*, leopards *Panthera pardus* and spotted hyenas *Crocuta crocuta* (hereafter hyenas) (Dickman et al., 2014; Abade et al., 2014a). The landscape also contains culturally complex human communities containing approximately 35 different ethnic groups, including pastoralists who are heavily reliant on livestock for their livelihoods (Abade et al., 2014a). Pastoralists are predominantly from Maasai and Barabaig ethnic groups and are relatively recent migrants into the landscape. The first Maasai families settled in the area within living memory (Cashew Zuberi, personal communication, 2017) with Barabaig families arriving after loosing access to traditional grazing lands in the north to large-scale agricultural development progammes in the 1960s and 1970s (Lane and Pretty, 1990; Fratkin, 1997). Relationships between pastoralist and agriculturalist groups are often strained due to long standing social prejudices and conflicts over land-use (Fratkin, 1997). Much of the most fertile land in the landscape is occupied by agriculturalist villages with pastoralists often living in less fertile land bordering the national park, this not only restricts their access to the best grazing but can also put their livestock at greater risk of predation from wild carnivores who live in protected areas. These carnivores impose conservation impacts on the communities bordering the national park through the killing

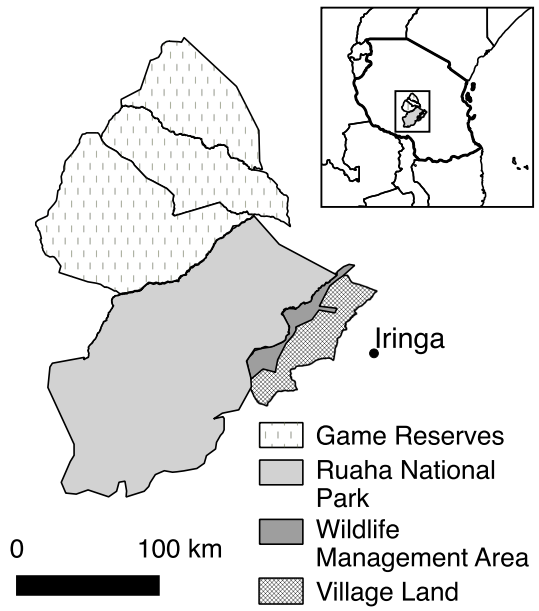


FIGURE 5.2. Map of the Rungwa-Ruaha landscape showing the study area in village land to the east of Ruaha National Park.

of livestock, and infrequently people, resulting in conservation conflicts over the management of these species (Dickman et al., 2014). Traditional and retaliatory killings of large carnivores, particularly lions and hyenas, occur alongside extensive conservation efforts by national and international organisations (NGO's and government wildlife authorities) aiming to reduce carnivore deaths.

The Ruaha Carnivore Project (RCP) is one internationally managed and funded NGO working in the landscape to reduce numbers of livestock killed by carnivores and carnivores killed by communities. RCP started working in the landscape in 2009 and currently runs programmes in 11 villages on the north eastern edge of RNP. RCP programmes range from providing free trips into RNP for community members who live near the park, to building predator proof livestock enclosures and the provision of village and household level benefits dependent on the numbers of carnivores and prey species detected on camera traps in village land.

5.3.2 Interviews

We collected data during 176 structured interviews conducted between 5 July 2016 and 26 April 2017. Interviews were written in English and then translated into Swahili by two Tanzanian field assistants who were also the interview enumerators. A back translation was conducted by a field assistant not involved in the initial translation to check accuracy of the initial translation. Field assistants conducted interviews primarily in Swahili, however, as not all Maasai and Barabaig (the predominant pastoralist ethnic groups in the survey area) are fluent in Swahili interview questions were further elaborated in Maa or Barabaig if necessary. We used the Open Data Kit system (Brunette et al., 2013) to conduct interviews on Google Nexus 7 tablets, for a list of questions see Appendix A. We piloted interviews prior to data collection and adapted the questionnaire in response to issues raised. We conducted interviews at livestock owning households which were selected to provide an even geographical spread across the landscape. Respondents were all male due to cultural sensitivities towards male enumerators conducting interviews with female respondents, and as male household members are those responsible for livestock husbandry and those who engage in carnivore killing amongst the pastoralist tribes living around RNP.

5.3.3 Ethical Considerations

Interviews and fieldwork protocols were assessed and approved by the Oxford University ethical committees (ref. R36599/RE001). Prior to being interviewed we verbally informed respondents of the research projects scope and aims, what their involvement would entail, how the data would be used, their freedom to refuse to be interviewed and the confidentiality of all responses. Due to high rates of illiteracy amongst pastoralist groups in the landscape, we verbally gained free, prior

and informed consent from respondents.

5.3.4 Tolerance framework

We measured tolerance for lions and hyenas using the Wildlife Acceptance Capacity (WAC) concept, this postulates that people's preference for the population size, or change in population size of a species, indicates their acceptance, or tolerance, for that species (Bruskotter et al., 2015; Decker and Purdy, 1988). We assessed tolerance for large carnivores by asking respondents "What would you like to see happen to the numbers of hyenas/lions in the area?". Recording responses on a 5 point scale from "disappear" to "increase a lot" with a mid-point of stay the same. We investigated tolerance towards lions and hyenas, despite the presence of three other large carnivore species in the landscape, as lions and hyenas are reported to cause the most problems for communities living in the study area (Dickman et al., 2014).

We asked respondents about carnivores seen within 2 km of their homestead over the previous 30 days and if any of the respondent's livestock had been attacked by that carnivore species within the previous 30 days, responses were combined to create a "direct experience score" (1 = no direct experience; 2 = seen species species; 3 = species attacked small stock (goats, sheep); 4 = species had attacked large stock (cows, donkeys)). We measured indirect experience by the respondent's knowledge of any other attacks on livestock by that carnivore species in their village over the previous 30 days (no = 1; yes = 2).

We asked respondents if they had engaged with a number of RCP conservation programmes all aiming to promote human-carnivore co-existence across the landscape. These programmes have a range of aims and objectives; environmental edu-

cation programmes aimed at raising awareness of the benefits of large carnivores (DVD nights), offering direct assistance to livestock owners with living alongside large carnivores (assistance building carnivore proof livestock enclosures, provision of noise-makers to chase away large carnivores, lion defender programme), and providing other benefits to livestock owners linked to the existence of large carnivores in village land (veterinary medicines and benefits from community camera trapping). Due to the number of different engagements their overall impact on respondent tolerance was assessed, with each respondent receiving a score from 0-9 depending on the number of programmes they had engaged with.

We drew a number of positive belief statements from previous RCP surveys in the area; "Lions/hyenas benefit people by attracting tourists", "I feel that lions/hyenas are beautiful animals' and "Lions/hyenas deserve protection", with responses given on a five point scale from "strongly disagree" to "strongly agree" with a "neutral" midpoint. Positive views towards the species were also assessed by asking respondents about the benefits they perceive lions and hyenas provide on a household level and village level, and if they perceived there to be benefits what these were.

Risk perception can be split into cognitive risk perception, reflecting the perceptions of the probability of a negative experience occurring, and affective risk perception, reflecting emotional response to risk, for instance the level to which one worries about negative experiences with carnivores (Sjöberg, 1998). We created cognitive risk perception indexes for lions and hyenas by combining respondent's perceived trend in livestock attacks by each species with their perceived frequency of livestock attacks (Trend x Frequency) (Inskip et al., 2016). This produces an index ranging from 0-15, with lower scores indicating lower perception of risk (0 indicating a perception that livestock attacks never occur, while 15 in-

dicates attacks occur frequently and increasingly). We assessed affective risk perception; respondent's emotional concern about the risk lions and hyenas pose, with the question "Living alongside lions/hyenas is one the hardest challenges you face" with responses on a five point scale from "strongly disagree" to "strongly agree".

To assess social trust in authorities in charge of wildlife management we asked respondents the level to which they agreed with the statement "The organisations responsible for managing wildlife are able to protect people and livestock from carnivores". Respondent's perception of their own control over carnivores as a hazard was assessed with the statement "You are able to stop lions/hyenas from attacking your livestock", responses to both of these statements was on a five point scale from "strongly disagree" to "strongly agree".

5.3.5 Structural Equation Modelling

We used structural equation modelling (SEM) in AMOS (Arbuckle, 2017) to analyse the interview data. SEM is well suited to studying socio-psychological frameworks as it allows the exploration of relationships between multiple independent and dependent variables, and allows the assessment of latent variables (factors that are not measured but assessed indirectly using measured variables, e.g. "positive beliefs"). We used a two step SEM process (Gallagher et al., 2008), initially using confirmatory factor analysis to construct measurement models investigating how positive beliefs and perceived benefits observed variables loaded onto "positive belief" and "benefit" latent (unobserved) variables. We then created structural models representing the hypothesized tolerance framework (Fig. 5.1), including the measurement models constructed in the previous stage. Questions respondents refused to answer or questions respondents did not know the answers to were classed as missing values. As SEM requires no missing values we used maxi-

mum likelihood estimation to impute missing values in the dataset (Byrne, 2016).

While SEM is relatively robust to non-normal data, high degrees of non-normality can bias goodness of fit statistics and standard error estimates (Finney and DiStefano, 2006), to address potential issues with non-normal data we used bootstrapping using maximum-likelihood estimation and 95% bias-corrected confidence intervals to calculate model parameters (Byrne, 2016). We used a number of model fit indices to assess model fit; Comparative Fit Index (CFI; acceptable fit threshold > 0.95), root mean square error of approximation (RMSEA; acceptable fit threshold < 0.10), and standardised root mean square residual (SRMR; acceptable fit threshold < 0.08) (Byrne, 2016; Hooper et al., 2008). To improve model fit we used model trimming (Gallagher et al., 2008); with non-significant pathways and variables with standardised residual covariances above 2 removed where appropriate.

5.4 Results

5.4.1 Socio-demographics of respondents

80.1% of respondents were from pastoralist tribes (48.3% Maasai, 31.8% Barabaig), with Hehe (6.8%), Gogo (6.2%), and Sukuma (5.1%) making up the majority of respondents from agriculturist tribes. Respondent ages ranged from 16-75 years old with a mean of 30.19. Most respondents had no formal education (50.6%) while 36.4% had a primary education and 13.1% a secondary education.

5.4.2 Components of tolerance frameworks

Experience with hyenas and lions. Respondents were significantly more likely to have encountered a hyena (83.0% of respondents) over the proceeding 30 days than a lion (11.4%) ($\chi^2(1) = 178.13$, $p < 2.2 \times e^{-16}$) (Table 5.3). There is a significant difference in the frequency of hyena and lion attacks on different livestock ($\chi^2(2) = 22.1$, $p = 1.6 \times e^{-5}$), with 1.7% of respondents suffering attacks on their livestock from lions in the 30 days proceeding the interview, while 15.9% of respondents suffered attacks from hyenas. Lion attacks were evenly spread between cows (1.1%) and small stock (1.1%) (goats and sheep) while hyena attacks on small stock were more common (11.9%) than on cows (5.1%). There is a significant difference in respondent's "direct experience scores" for lions and hyenas ($W = 3944$, $p < 2.2 \times e^{-16}$, $n_a = n_b = 176$) with respondents more likely to have to have direct experience with hyenas. There is a significant difference in the numbers of respondents reporting indirect experience of lions (5.1%) or hyenas (14.8%) ($\chi^2(1) = 8.1$, $p = 4.4 \times e^{-3}$).

Beliefs about hyenas and lions and their population trend The majority of respondents either agreed or strongly agreed that lions (78.4%) and hyenas (73.3%) benefit people by attracting tourists, with no significant difference

in responses between the species (W = 16512, p = 0.25, $n_a = n_b = 176$). While the majority of respondents agree or strongly agree with the statement that lions (62.5%) are beautiful animals, fewer respondents gave the same responses for hyenas (48.3%), with a significant difference in responses between species (W = 17604, p = 0.023, $n_a = n_b = 176$). Similarly there was a significant difference in responses to the statement that lions or hyenas should be protected (W = 18360, p = 0.0018, $n_a = n_b = 176$) with respondents more likely to agree or strongly agree that lions should be protected (70.5%) than they were for hyenas (54.0%) .

The majority of respondents saw no benefits to their own household from the presence of lions (72.7%) or hyenas (81.3%) in the land surrounding their village. There was, however, a significant difference in the perceived benefits offered by lions and hyenas (W = 13246, p = $3.9 \times e^{-5}$, $n_a = 156, n_b = 148$) with respondents more likely to report benefits to their household from lions (15.9%) than hyenas (2.8%). A similar pattern is true for village level benefits, with a significant difference in perceived benefits from the two species (W = 7155, p = 0.037, $n_a = 111, n_b = 114$), with 23.3% of respondents reporting village level benefits from lions compared to 15.9% for hyenas. There is a significant difference in perceptions of household and village level benefits for both species (lions: W = 6915, p = $2.6 \times e^{-4}$, $n_a = 156, n_b = 1111$; hyenas: W = 6619.5, p = $2.2 \times e^{-7}$, $n_a = 148, n_b = 114$) with respondents reporting more benefits at the village level for both species. Respondents were, however, less knowledgeable of village level benefits with 34.4% and 33.6% of respondents unsure if lions and hyenas respectively offered any village level benefits compared to 6.8% and 13.0% for household level benefits.

The most commonly cited benefits lions provided on a household level were benefits from conservation programmes (n = 13) (for instance veterinary medicines from RCP), employment (n = 7), and seeing lions (n = 7) (Table 5.1). While reported

TABLE 5.1. Types of household and village level benefits respondents perceived hyenas and lions provide

Benefit type	Hyena		Lion	
	Household	Village	Household	Village
None	143	86	128	70
Employment	–	–	6	2
Money from tourists/attracts tourists	2	25	1	36
Benefits from conservation projects	2	2	13	3
Personally seeing the species	1	–	7	–
Belief that the presence of lions can increase cattle numbers	–	–	1	–
Don't know	28	63	20	65

household benefits from hyenas were money from tourists (n = 2), benefits from conservation programmes (n = 2) and seeing hyenas (n = 1). Attracting tourists and the money they provide was the most commonly cited village level benefit provided by both hyenas (n = 25) and lions (n = 36) with benefits from conservation projects also mentioned for both species (n = 2, n = 3) and employment for lions (n = 2).

There is a significant difference in respondent's perceived population trends for lions and hyenas (W = 8724, p = $4.9 \times e^{-12}$, $n_a = 170, n_b = 176$) with respondents more likely to perceive lion populations as decreasing (33.5%) than increasing (26.7%) while hyenas were more likely to be perceived as increasing (55.1%) than decreasing (8.0%).

Risk perceptions. Respondents reported a significant difference in the frequency at which the two species attacked livestock in their village (W = 2933, p = $2.2 \times e^{-16}$, $n_a = 168, n_b = 175$), with lions mostly reported attacking livestock "rarely" (yearly) (48.3%) while hyenas were mostly reported as attacking livestock "commonly" (weekly) (52.8%). The trend in hyena attacks on livestock was also perceived to be significantly different to that of lions (W = 9474.5, p = $3.1 \times e^{-9}$,

n_a = 168, n_b = 175) with hyena attacks most likely to be perceived as staying the same (39.8%) or increasing (48.9%) while lion attacks were perceived as mostly staying the same (36.9%) or decreasing (34.1%). Hyena's mean cognitive risk perception index (10.3) was significantly higher than lion's (3.9) (t = -14.8, df = 333.9, p = $2.2 \times e^{16}$). There is no significant difference in affective risk perception between the two species (W = 15712.5, p = 0.79, $n_a = n_b$ = 176) with nearly all respondents agreeing or strongly agreeing that living alongside lions (89.2%) or hyenas (87.5%) was one of the hardest challenges they faced.

Beliefs about social and personal management of carnivores. Respondents were more more likely to agree or strongly agree that they were personally able to defend their livestock from lions (56.8%) and hyenas (63.1%) than agree or strongly agree that those responsible for wildlife and carnivore management are able to protect people and livestock from carnivores (40.3%), a significant difference for both species (lions: W = 13047, p = $8.5 \times e^{-3}$, $n_a = n_b$ = 176; hyenas: W = 11662, p = $3.9 \times e^{-5}$, $n_a = n_b$ = 176). However there was no significant difference in the respondents belief in their ability to protect their livestock from lions or hyenas (W = 13804, p = 0.068, $n_a = n_b$ = 176).

Engagements with RCP The majority of respondents (72.7%) have had some engagement with RCP programmes, with a median number of engagement types of two. Receiving veterinary medicines, receiving household visits and attending DVD nights were the most common engagements respondents had with RCP (Table 5.2.

Acceptance capacity Respondent's wildlife acceptance capacity for lions and hyenas are significantly different (W = 19646, p = $1.9 \times e^{-7}$, n_a = 171, n_b = 175), with a majority of respondents wanting hyenas to decrease or disappear (58.0%)

TABLE 5.2. Percentage of respondents who reported engaging with different RCP programmes

Engagement	Yes	No
Received veterinary medicines	41.4	58.5
Received household visit	41.4	58.5
Attended DVD night	39.2	60.8
Received help from Lion Defenders	17.0	83.0
Received reinforced boma	14.2	85.8
Received benefits from community camera trapping	14.2	85.8
Attended park visit	7.4	92.6
Received noise-maker	4.5	95.5
Other (e.g. hospital transport)	15.9	84.1

while a majority want lion populations to stay the same or increase (62.0%).

Table 5.3: Summary of variables used in tolerance framework showing response options and the percentage of respondents who selected each option.

Variable	**Responses**				
Acceptance capacity	**Disappear**	**Decrease**	**Stay the same**	**Increase**	**Don't know**
Lions	10.2	25.0	31.3	30.7	2.8
Hyenas	30.1	27.8	27.8	13.6	0.6
Livestock attacked	**Large-stock**	**Small-stock**	**None**		
Lions	1.1	1.1	98.3		
Hyenas	5.1	11.9	84.1		
Seen	**Yes**	**No**			
Lions	17.0	83.0			
Hyenas	88.6	11.4			
Direct experience	**None**	**Seen**	**Small stock attacked**	**Large stock attacked**	
Lions	81.8	16.5	0.6	1.1	

Hyena	8.5	75.6	10.8	5.1	
Indirect experience	**Yes**	**No**			
Lions	5.1	94.9			
Hyenas	14.8	85.2			
Beliefs	**Strongly disagree**	**Disagree**	**Neutral**	**Agree**	**Strongly agree**
Lions deserve protection	8.5	19.7	11.4	33.0	37.5
Hyenas deserve protection	20.5	14.2	11.4	24.4	29.5
Lions are beautiful	15.9	14.8	6.8	29.5	33.0
Hyenas are beautiful	24.4	17.0	10.2	21.0	27.2
Lions benefit people by attracting tourists	6.8	2.8	11.9	33.0	45.5
Hyenas benefit people by attracting tourists	9.7	6.3	10.8	31.2	41.5

Benefits	**None**	**Small benefits**	**Big benefits**	**Very big benefits**	**Don't know**	
Lions benefit to household	72.7	4.0	5.1	6.8	11.4	
Hyenas benefit to household	81.3	0.6	2.3	0	15.9	
Lions benefit to village	39.7	2.8	7.4	13.1	36.9	
Hyenas benefit to village	48.9	2.8	5.1	8.0	35.2	
Population trends	**Decreasing a lot**	**Decreasing**	**Staying the same**	**Increasing**	**Increasing a lot**	**Don't know**
Lions	20.5	13.1	36.4	12.5	14.2	3.4
Hyenas	1.1	6.8	36.4	16.5	38.6	0.6
Livestock attack frequency	**Commonly (weekly)**	**Occasionally (monthly)**	**Rarely (yearly)**	**Never**	**Don't know**	
Lions	4.5	14.8	48.3	28.4	4.5	

Hyenas	52.8	38.1	7.4	1.1	0.6	
Livestock attack trend	**Decreasing a lot**	**Decreasing**	**Staying the same**	**Increasing**	**Increasing a lot**	**Don't know**
Lions	19.9	14.2	36.9	13.1	11.4	4.5
Hyenas	3.4	7.4	39.8	22.7	26.1	0.6
Affective Risk Perception	**Strongly disagree**	**Disagree**	**Neutral**	**Agree**	**Strongly agree**	
Lions	3.4	2.8	4.5	34.7	54.5	
Hyenas	5.1	3.4	4.0	33.5	54.0	
Social trust	**Strongly disagree**	**Disagree**	**Neutral**	**Agree**	**Strongly agree**	
	21.6	10.2	27.8	26.1	14.2	
Personal locus of control	**Strongly disagree**	**Disagree**	**Neutral**	**Agree**	**Strongly agree**	
Lions	9.1	18.8	15.3	39.2	17.6	
Hyenas	10.8	13.6	12.5	33.5	29.5	

TABLE 5.4. Observed variable factor loading on latent variables in measurement models

Latent Variable	Observed Variable	Hyena loadings	Lion loadings
Positive belief	Deserve protection	0.83 ($p < 0.001$)	0.88 ($p < 0.001$)
	Beautiful animals	0.94 ($p < 0.001$)	0.87 ($p < 0.001$)
	Benefit people by attracting tourists	0.55 ($p < 0.001$)	0.47 ($p < 0.001$)
Benefits	Household benefits	0.18 ($p = 0.69$)	0.87 ($p < 0.001$)
	Village benefits	1.9 ($p = 0.69$)	0.70 ($p < 0.001$)

5.4.3 Structural Equation Models

5.4.3.1 Belief measurement models

We tested a measurement model with three observed belief statements (related to tourism, protection and benefits) loaded onto a "positive belief" latent variable and the two benefit statements (household and village level benefits) loaded onto a "benefits" latent variable.

Hyenas. In an initial measurement model the three observed belief statements all had adequate factor loadings (>0.5) onto the positive belief latent variable (Gallagher et al., 2008) (Table 5.4). Household and village benefit loadings onto the "benefit" latent variable (factor loading greater than 1) suggest an improper solution caused by issues with data or model structure (Chen et al., 2001). As perceptions of household benefits from hyenas is highly skewed it was removed along with the "benefit" latent variable, leaving village level benefits as an observed variable. The observed "positive belief" factor loadings in the re-specified measurement model were all adequate (hyenas deserve protection = 0.83; hyenas are beautiful animals = 0.94; hyenas benefit people by attracting tourists = 0.55) and significant at $p < 0.001$ with the model showing acceptable fit to the data (SRMR: 0.030, CFI: 0.989, RMSEA: 0.089).

Lions. Nearly all the observed variables loaded adequately in the initial measurement model for the "positive belief" and "benefits" latent variables for lions (Table 5.4). As all variables were significant and only a single factor loading (for the statement "lions benefit people by attracting tourists") was marginally inadequate (0.47) the model was not re-specified, and all observed variables were kept. The initial model showed acceptable fit to the data (SRMR: 0.026, CFI:0.99, RMSEA: 0.078).

5.4.3.2 Tolerance frameworks

Hyenas. The hyena tolerance model had 11 significant direct and 7 significant indirect pathways (Table 5.5, for standardised regression weights for all direct and indirect pathways see Appendix D), and showed acceptable fit to the data (SRMR: 0.059, CFI:1.00, RMSEA: 0.005).

The hyena structural equation model showed support for a number of elements of our theoretical tolerance framework (Fig. 5.3). Direct experience with hyenas had a direct positive effect on beliefs about hyena population trends, while indirect experience had a direct negative effect on perceived village level benefits that hyenas provide. Direct and indirect experience with hyenas both had a small indirect negative impact on respondent's acceptance capacity of hyenas.

Higher levels of engagement with RCP programmes had a direct positive effect on beliefs about hyena population trends, and a direct negative effect on positive beliefs about hyenas. Engagement with RCP programmes also had direct and indirect positive effects on respondent's affective risk perception. While not a proposed indirect pathway in the theoretical model higher engagements also had an indirect positive effect on cognitive risk perception, mediated by the belief in higher population trends.

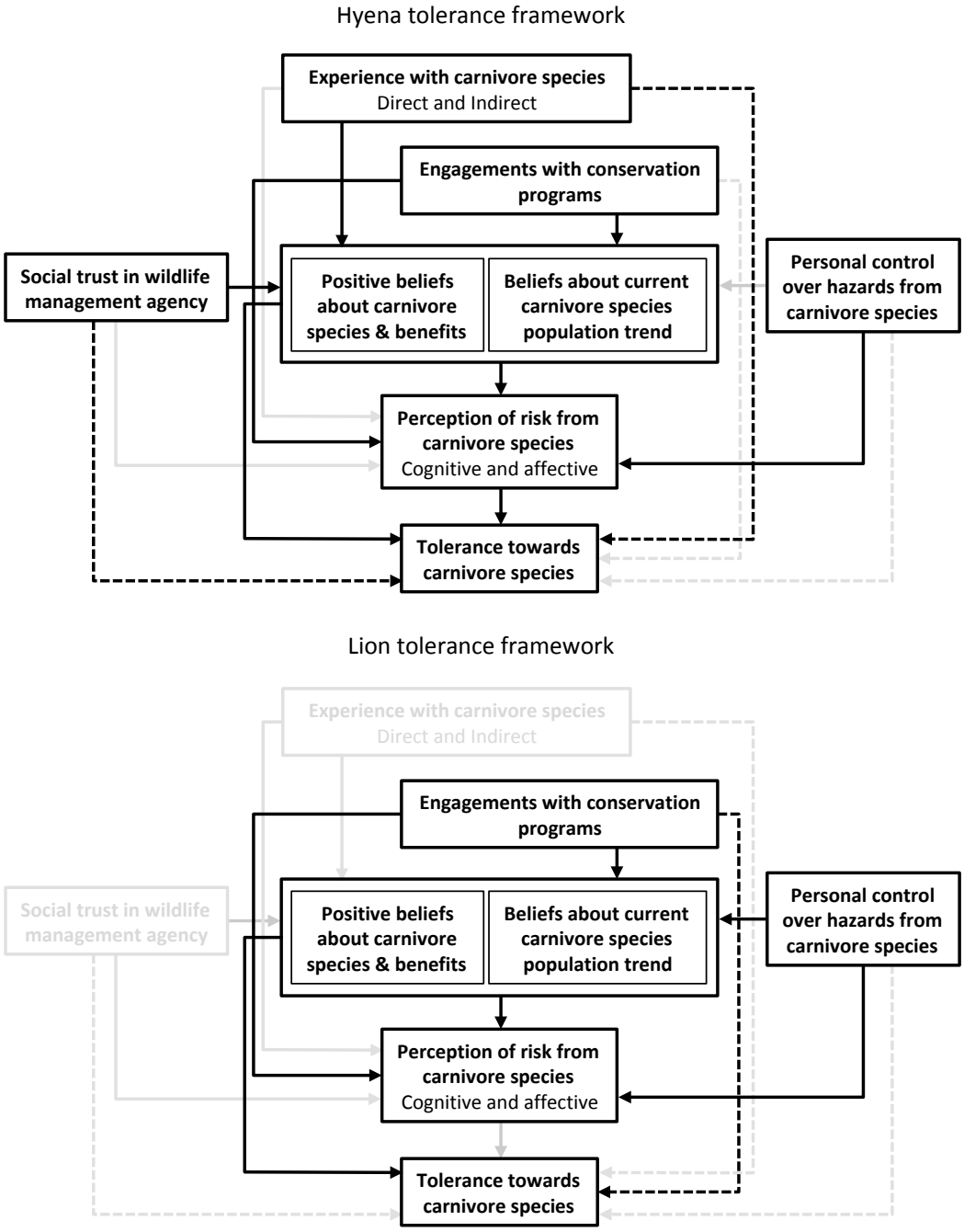


FIGURE 5.3. Pathways from theoretical tolerance model supported by structural equation models for hyenas and lions. Solid lines represent direct effects and dashed lines indirect effects. Black lines represent pathways with significant effects ($p < 0.05$), while grey lines represent pathways with no effect or non-significant effects. For pathways standardised regression weights see Table 5.5, for weights and significance of all pathways see Appendix D

TABLE 5.5. Significant pathways in lion and hyena structural equation models.

Dependent Variable	Independent variable	Effects		
		Direct	Indirect	Total
Hyenas				
Population trend	Direct experience	0.30***	–	0.30***
	RCP engagements	0.33**	–	0.33**
Positive beliefs	Social trust	0.24**	–	0.24**
	RCP engagements	-0.20*	–	-0.20*
Village benefits	Indirect experience	-0.16**	–	-0.16**
Affective risk perception	Personal locus of control	0.42***	–	0.42***
	RCP engagements	-0.27**	-0.024*	-0.30**
Cognitive risk perception	Direct experience	–	0.22***	0.22***
	Population trend	0.73**	–	0.73**
	RCP engagements	–	0.24**	0.24**
Acceptance capacity	Village benefits	0.33***	–	0.33***
	Positive beliefs	0.20*	–	0.20*
	Direct experience	–	-0.047**	-0.047**
	Indirect experience	–	-0.064**	-0.064**
	Social trust	–	0.11**	0.11**
	Population trend	–	-0.16**	-0.16**
	Cognitive risk perception	-0.21**	–	-0.21**
Lions				
Population trend	Personal locus of control	–	0.044*	0.044*
	Positive beliefs	-0.27***	–	-0.27***
	RCP engagements	0.33***	–	0.33***
Positive beliefs	Personal locus of control	-0.16*	–	-0.16*
Benefits	RCP engagements	0.58***	–	0.58***
Affective risk perception	Personal locus of control	0.19*	-0.039*	0.15
	Positive beliefs	0.24***	–	0.24***
	RCP engagements	-0.23**	–	-0.23**
Cognitive Risk perception	Personal locus of control	-0.072	0.052*	-0.020
	Positive beliefs	-0.15*	-0.17***	-0.32***
	RCP engagements	–	0.28***	0.28***
	Population trend	0.65**	–	0.65**
Acceptance capacity	Benefits	0.33**	-0.023	0.31***
	Positive beliefs	0.28**	0.016	0.30***
	RCP engagements	–	0.20***	0.20***

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Levels of social trust in wildlife management authority's ability to protect respondents from carnivore species had a direct positive effect on positive beliefs about hyenas and as a result had an indirect positive effect on respondent's acceptance capacity for hyenas. While respondent's personal locus of control (belief in their own ability to protect their livestock from hyenas) had a positive direct effect on affective risk perception.

Beliefs about increasing hyena population trends had a direct positive impact on cognitive risk perception, which in turn had a negative direct effect on respondent's acceptance of hyena populations. As a result beliefs about hyena population trends had an indirect negative affect on acceptance of hyena populations. Positive beliefs about hyenas and perceived village level benefits both had a direct positive affect on respondent's acceptance capacity.

Lions. In the lion tolerance model the social trust, direct experience, and indirect experience observed variables all had standardised residual covariances above 2 and were removed to improve model fit. The final model had 11 significant direct and 6 significant indirect pathways (Table 5.5, for standardised regression weights for all direct and indirect pathways see Appendix D), and showed acceptable fit to the data (SRMR: 0.049, CFI:0.95, RMSEA: 0.068).

Respondent's beliefs about lion population trends were positively effected by higher levels of engagement with RCP programmes, leading to an indirect positive effect on cognitive risk perception, while levels of engagements with RCP programmes had a direct negative affect on affective risk perception. Perceptions of the benefits lions provide was directly positively affected by RCP engagements in turn leading to RCP engagements having an indirect positive affect on respondent's acceptance capacity for lion populations.

Respondent's personal locus of control had a direct negative effect on respondent's positive beliefs about lions. Locus of control also had a direct positive effect on respondent's affective risk perception, as well as a smaller negative indirect effect. There are also minor indirect positive effects of respondent's personal locus of control on beliefs about lion population trends and cognitive risk perception.

Beliefs about lion population trends had a positive direct effect on respondent's cognitive risk perception. Positive beliefs about lions had a direct negative effect on beliefs about lion population trends, mediating an indirect negative effect, as well as a direct negative effect, on cognitive risk perception. Positive beliefs about lions had a direct positive effect on both affective risk perception and acceptance capacity.

5.5 Discussion

Our study supports the argument that tolerance of carnivores is driven by a complex range of socio-psychological factors (Inskip et al., 2016; Bruskotter and Wilson, 2014; Kansky et al., 2016; Struebig et al., 2018). Perceived benefits and positive beliefs were among the most influential variables affecting tolerance for both hyenas and lions, agreeing with previous studies on tigers in Nepal (Carter et al., 2012b), Bangladesh (Inskip et al., 2016) and Indonesia (Struebig et al., 2018), and wolves in the USA (Slagle et al., 2012). While direct and indirect experience of hyenas influenced various aspects of our tolerance model (e.g. beliefs about population trends, benefits, and cognitive risk perception), experience (direct and indirect) of hyenas only had a small affect on tolerance, and their inclusion in lion models worsened model fit, agreeing with the assertions of Dickman (2010), that conservation conflicts are driven by more than just damage caused by wildlife. However, we only measured experience over the preceding 30 days, which is likely to have missed some of the dynamics involved in respondent's direct and indirect experience with lions and hyenas (Dickman et al., 2014).

Higher levels of engagement with RCP programmes is associated with higher perceptions of the benefits lions offer, resulting in an indirect positive effect on acceptance of lion populations. The positive effect of RCP programmes on respondent's perceptions of the benefits lions provide is likely to arise for two reasons. Firstly, the most frequently reported household level benefit provided by lions were benefits from conservation programmes. Suggesting the direct provision of benefits from RCP to pastoralists related to the presence of lions and other carnivores on village land (e.g. the provision of veterinary medicines) are of a level that positively influences respondent's acceptance of lions, but not hyenas. Secondly,

a number of RCP programmes have an element of environmental education (e.g. DVD nights) which inform participants about the work RCP does in the area and the wider economic and ecological benefits carnivores offer, these may increase respondent's perceptions of the benefits lions provide. The difference in perceived household level benefits and village level benefits for both hyenas and lions suggests that while respondents perceive benefits from these species do exist they themselves are not necessarily receiving them. This is particularly true of income from tourism; 14% and 20% of respondents reported income from tourism as a village level benefit from hyenas and lions respectively, while only 1% of respondent's reported household level income from tourism as a result of either species, suggesting that while income from tourism is widely reported to benefit local communities, and communities themselves may hold this view, the actual economic impact of protected area tourism on local households may be minimal (Nepal, 1997; Ferraro, 2002).

Counter-intuitively positive beliefs about hyenas were negatively associated with RCP engagements. While we cannot infer causality from this relationship it suggests more detailed research into the impacts of conservation interventions on peoples perceptions of species is required. One potential cause of this relationship could be strong pre-existing negative attitudes towards hyenas (Goldman et al., 2010; Kesby, 2003) interacting with confirmation biases (Nickerson, 1998). In this case engagements with RCP programmes could increase salience of hyenas which in turn reinforces negative beliefs.

Engagements with RCP programmes is also linked to risk perceptions. There is a significant positive relationship between engagements with RCP programmes and perceptions of hyena and lion population trends, with a resulting indirect positive effect of engagements on respondent's cognitive risk perceptions for both

species. As we cannot infer causal relationships from SEM analysis it is not possible to decipher if this effect is, firstly, a result of individuals who perceive carnivores to be a greater risk being more likely to seek support from RCP, or, secondly, a result of higher levels of engagements causing respondents to perceive hyenas and lions to be more prevalent and thus pose a greater risk. Education and indirect experience of risks can increase risk perception (Wachinger et al., 2013; Slagle et al., 2012; Bruskotter and Wilson, 2014), and the framing of interventions as mediating conflict between humans and carnivores may cause attendees who previously saw carnivores as a fact of life to re-frame these species into problems requiring solutions (Pooley et al., 2017). Whatever the cause of higher cognitive risk perception among engaged respondents the negative relationship between engagements and affective risk perceptions, for both species, suggest that despite respondents with higher levels of engagements with RCP having higher cognitive risk perception this does not translate into a higher levels of emotional concern over the risks these species pose, in fact emotional concern is lower for more engaged individuals.

While our study finds evidence that conservation interventions may increase tolerance towards certain species, the use of conservation interventions to influence tolerance of dangerous species must come with a number of ethical caveats. Firstly, if providing benefits, it is vital to ensure equitable distribution of benefits amongst the effected communities as elite capture of benefits may lead to apparent support for programmes at the expense of the weakest and potentially most affected members of the community (Dickman et al., 2011). Secondly, if using environmental education programmes it is important to acknowledge that these are often based on promoting a specific (and frequently external) belief system about the environment and human relations with it, over a myriad of local beliefs systems (Whitehouse, 2015). This may result in the promotion of environ-

mental knowledge and beliefs that erode communities existing relationships with nature (Pooley et al., 2017) and lead to mistaken beliefs about the benefits wildlife provide. We also found correlations between engagements with conservation programmes and increased risk perceptions. Improving our understanding of any potential mechanism by which conservation programmes may increase risk perceptions is paramount to ensuring conservation interventions are not unwittingly causing stress to participants.

Trust in authorities charged with managing hazards is known to reduce people's perception of risk (Wachinger et al., 2013; Bruskotter and Wilson, 2014). While social trust was removed from our lion tolerance model there was a significant positive effect of social trust on positive beliefs about hyenas, mediating a positive indirect effect of social trust on acceptance of hyena populations. This concurs with previous work that has found low levels of trust in government ability to manage tiger-related risks linked to lower levels of tolerance for tiger populations (Carter et al., 2012b; Struebig et al., 2018). Individuals perceived control over a hazard is another important factor influencing their perception of risk from that hazard (Bruskotter and Wilson, 2014; Kahan et al., 2007). Counter to previous studies (that found a negative relationship between perceived risks posed by black bears and perceived control (Zajac et al., 2012), and a positive relationship between acceptability of wolves and personal control (Kleiven et al., 2004)) we found a positive relationship between respondent's locus of control and affective risk perception for both species. Fatalist beliefs (associated with low locus of control) have been linked to low levels of risk perception (Kouabenan, 1998). Our findings may be because higher perceptions of personal control lead to an increased sense of responsibility to protect themselves, their households and their livestock from that risk, which raises affective risk perception, without influenc-

ing cognitive risk perception. This increase in affective risk perception may also explain the negative relationship between personal control and positive beliefs.

While studies have found significant links between respondent's perceived risk of harm or damage from carnivores and tolerance of those species (e.g. cougars (Riley and Decker, 2000) and black bears (Zajac et al., 2012) in the USA), Inskip et al. (2016) and Carter et al. (2012b) found no significant effect of cognitive or affective risk perception on tolerance for tigers in Bangladesh or Nepal respectively. While we found beliefs about increasing population trends had a positive effect on cognitive risk perception for both hyenas and lions the positive effect of cognitive risk perception on tolerance was only significant for hyenas, and we found no evidence for affective risk perception influencing tolerance of either species.

The different role risk perceptions play mediating tolerance towards carnivores in different locations and for different species, highlights the need to place socio-psychological frameworks into local cultural context (Parathian et al., 2018). Research into tolerance towards carnivores in Europe and North America often takes place in the context of returning or increasing carnivore populations (Zajac et al., 2012; Riley and Decker, 2000), thus carnivores represent a novel hazard that people may perceive to be involuntarily imposed upon them, two factors that can increase risk perception, or willingness to accept risk, of a hazard (Slovic, 1987; Wachinger et al., 2013). While perceptions of risk may play a smaller role mediating tolerance in communities that have lived alongside carnivores for centuries and have internalised those risks as facts of life (Inskip et al., 2016; Pooley et al., 2017).

The different views respondents hold on hyenas and lions may also be explained by the cultural traditions that most respondents hold. Positive beliefs, per-

ceived benefits, and acceptance capacity were significantly higher for lions than hyenas while perceived population trends and cognitive risk perceptions were higher for hyenas, all indicating more favourable attitudes towards lions than hyenas. These different attitudes may be explained by more direct experiences, and in particular livestock losses, for hyenas, and RCP programmes which often have a focus on lions over hyenas. However, lions and hyenas play very different cultural roles for Maasai and Barabaig pastoralists who made up the majority of respondents. Attitudes towards lions amongst Maasai are complex and nuanced, often combining elements of fear, fascination, admiration and respect (Goldman et al., 2010), the complexity of this relationship may explain the positive association we found between positive beliefs and affective risk perception for lions. Even lion attacks on cattle may be perceived in a positive light, with one respondent reporting that lion attacks on cattle result in increased cattle births and a larger herd in the long run. Lions are also perceived to be respectful when they attack livestock, only killing what they need, while hyenas are seen as disrespectful and greedy; devastating herds by killing more than they can consume (Goldman et al., 2010). While hyenas are viewed scornfully lions are viewed as a respected enemy and traditional killing of lions forms an important part of Maasai and Barabaig culture, providing prestige and wealth to the warriors involved (Borgerhoff Mulder et al., 1989; Goldman et al., 2010). While socio-psychological frameworks built on quantitative data are useful in understanding factors that may influence tolerance placing these frameworks within wider cultural beliefs is important if tolerance towards carnivores is to be truly understood.

Socio-psychological frameworks and measures can play a useful role in improving our understanding of the array of complex and interrelated factors that mediate acceptance and tolerance of large carnivores. However, tolerance, and the fac-

tors that influence it, are often culturally defined and differ by society, geography, and species. While general frameworks provide useful starting points in understanding tolerance, it is important to acknowledge the importance of local cultural contexts and that much psychological theory is grounded in research conducted by and in American and European societies (Henrich et al., 2010; Parathian et al., 2018), which do not cover the spectrum of societies involved in conservation conflicts.

5.6 Acknowledgements

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Spotted hyenas are widespread and widely disliked

CHAPTER 6

USING MATHEMATICAL MODELS TO UNDERSTAND THE SOCIO-ECOLOGICAL COMPLEXITY OF HUMAN-WILDLIFE INTERACTIONS



A lion defends its kill from a black-backed jackal

6.1 Abstract

The complexity of the social and ecological systems that combine to cause negative human-wildlife interactions are not always considered when investigating the impacts of these interactions on human communities and wildlife populations. We used a simulated African-savannah system containing multiple classes of carnivores and herbivores as well as domestic livestock and crops to investigate the potential ecological impacts of lethal control of large carnivores in retaliation for attacks on cattle. In our simulations very low levels of retaliation resulted in the extinction of large carnivores, however, as a result of strong bottom-up ecosystem regulation populations of mesopredators, rodents, large herbivores, livestock, and patterns of crop consumption by wildlife were relatively unaffected by the loss of large carnivores. Our simulated rodent populations also caused the most damage to crops compared to large herbivores. Our study shows the need for more research into the complex interactions of social and ecological systems and the importance of considering the impact of non-charismatic species on human well-being.

6.2 Introduction

Human-wildlife co-existence is a one of the greatest challenges facing the global conservation movement (Dickman, 2010; Redpath et al., 2014). Negative human-wildlife interactions, commonly referred to as human-wildlife conflict (HWC), are a global problem occurring in low, middle, and high income countries (Manfredo and Dayer, 2004) with examples from every continent with major human habitation (Dickman et al., 2014; Musiani et al., 2005; Palmeira et al., 2008; Bagchi and Mishra, 2006; Prowse et al., 2015; Thirgood et al., 2005). These interactions come in innumerable different forms such as: crop consumption; infrastructure damage; competition for prey species, land, and water; timber damage; livestock, and fishery predation; disease transmission; and human-injuries, and deaths (Arlet and Molleman, 2007; Conover, 1997; Messmer, 2000; Woodroffe et al., 2005; Thirgood et al., 2005). They also involve wildlife from a range of taxonomic groups (e.g. terrestrial and marine mammals (Butler et al., 2015; Dickman et al., 2014), birds (Thirgood and Redpath, 1997), reptiles (Chaves et al., 2015), fish (Freitas et al., 2016) and insects (Cease et al., 2015) and while rural human societies are the historically most affected, negative human-wildlife interactions are an increasing problem in urban societies (Messmer, 2000). The range of human groups affected is immense; from subsistence pastoralists (Dickman et al., 2014) and agriculturalists (Arlet and Molleman, 2007) to metropolitan residents (Conover, 1997) and landed nobility (Thirgood and Redpath, 1997). However, despite the wide body of work on HWC there has been relatively little work considering the complex wider ecological systems within which many of these interactions take place.

In the conservation literature many studies of human-wildlife co-existence

have been conducted under a human-wildlife conflict framing. HWC is commonly defined as "situations occurring when an action by either humans or wildlife has an adverse effect on the other" (Conover, 2001). The terminology surrounding human-wildlife conflict is problematic for a number of reasons and has led to issues in how human-wildlife interactions are perceived and researched. Firstly, animals are, arguably, unable to consciously enter conflict with humans, and so most conflict is "human-human" conflict, between those who prioritise species conservation against those whose interests wildlife threaten (Peterson et al., 2010; Redpath et al., 2014). Acknowledging that human interests and values exist on both sides of the conflict explain why much of the HWC literature is focused on charismatic species of conservation concern (e.g. elephants and large carnivores) while less charismatic species that may have greater negative impacts on human well-being (e.g. insects and rodents (Arlet and Molleman, 2007; Cease et al., 2015)) are relatively under-represented (Peterson et al., 2010). Secondly, the HWC framing posits two opposing sides, humanity and wildlife (Peterson et al., 2010; Redpath et al., 2014), this leads to a focus on the direct impact species have on people's well-being and the impact of lethal control or other management on wildlife populations. As a result a lot of HWC research does not integrate human interests and actions into the ecological systems within which these negative interactions take place, resulting in relatively little work on the two-way interactions between human actions and interests and the ecological functions of some of these systems (Kuijper et al., 2016).

The majority of HWC research focuses on charismatic species of conservation concern (Peterson et al., 2010; Redpath et al., 2014); human-elephant (Hoare, 1999) and human-carnivore (Treves and Karanth, 2003) conflict being examples of sub-disciplines to which much conservation and research effort is devoted. This

focus results in other species that cause more harm to human societies being overlooked (Peterson et al., 2010). Small rodents are an example of a taxa that imposes severe economic and social costs around the world but are under-represented in HWC literature (Arlet and Molleman, 2007). Rodents are among the worlds most important global pests (Stenseth et al., 2003), in Tanzania average annual yields of maize lost to rodent damage are estimated to be 5-15% (Leirs, 2003), but can be as high as 48% during an outbreak (Mwanjabe et al., 2002), and an estimated 17% of Indonesia's rice harvest is lost to rodents each year (Singleton and Petch, 1994). While there is a lack of research quantifying yield losses to different taxa (Naughton-Treves and Treves, 2005), a number of studies suggest that in areas adjoining protected areas rodents may be a primary cause of crop damage when compared to large charismatic herbivores (Arlet and Molleman, 2007; Harich et al., 2013; Gillingham and Lee, 2003; Hawkes, 1991). These studies may also underestimate the impact of rodents by not taking into account post-harvest damage caused to food stores (5-14% for smallholder farmers (Swanepoel et al., 2017)) and using interviews with farmers to assess damage, who may be less likely to notice widespread insidious damage caused caused by rodents against localised catastrophic damage caused by larger species (Harich et al., 2013; Arlet and Molleman, 2007; Naughton-Treves and Treves, 2005). As well as imposing economic costs Meerburg et al. (2009) list over 60 rodent-borne diseases that cause severe illness and death in humans - and at a rate much higher than many of the most dangerous larger species. Globally between 2010 and 2015 rat borne plague alone infected 3248 people and killed 584 (116.8 people yr^{-1}) (WHO, 2017), an annual death rate marginally under that attributed to tigers during the 20th century (125.99 people yr^{-1}) but much greater than that attributed to wolves (6.07 people yr^{-1}) (Löe and Röskaft, 2004). If we are to truly understand the wide array of negative human-

wildlife interactions and how to deal with them then it is important to integrate overlooked taxa, such as rodents, and the social and economic damage they cause into how we study and conceive human-wildlife interactions.

Large carnivores are one example of a charismatic taxa that has received a lot of research attention, this research, however, has generally failed to look at the impact of carnivore-human interactions on wider ecological and social processes (Kuijper et al., 2016). Large carnivore's high metabolic needs (Carbone et al., 1999) and large home range requirements (Ripple et al., 2014) mean they frequently come into contact with, and lethally threaten, human communities and their livestock (Ripple et al., 2014; Dickman et al., 2014) many of which can ill-afford the tangible and intangible costs carnivores impose on them (Dickman et al., 2014; Ripple et al., 2014; Kansky and Knight, 2014). This often leads to lethal control (Thirgood et al., 2005; Baker et al., 2008) to which large carnivores are particularly vulnerable due to their slow life histories and low population densities (Woodroffe et al., 2005; Bodmer et al., 1997; Cardillo et al., 2004). As well as being involved in often severe negative human-wildlife interactions carnivores also play important roles in regulating top-down ecological processes (Ripple et al., 2014; Wallach et al., 2015) and mediating trophic cascades throughout the food web (Terborgh, 2001; Thébault and Loreau, 2005). For instance direct predation and landscape of fear effects can limit herbivore populations and impact their behaviour (Ripple and Beschta, 2004; Schmitz et al., 1997), in turn influencing vegetation type and growth (Kuijper et al., 2013; Winnie and Creel, 2017). Interference competition and intra-guild predation can suppress mesopredator populations (Crooks and Soulé, 1999; Ripple et al., 2013) and lead to increases in small vertebrates (Ritchie and Johnson, 2009). Despite the fact that in many parts of the world carnivores exist in, or are returning to, human modified and dominated landscapes (Kuijper et al., 2016; Crooks et al.,

2011; Carter et al., 2012a) the majority of studies on carnivore ecology have taken place in relatively intact conservation areas (Kuijper et al., 2016; Dorresteijn et al., 2015) while the majority of studies on human-carnivore interactions have not taken into account the wider ecological roles carnivores play.

Carnivore persecution is often perceived to benefit pastoralists and ranchers by reducing loses to livestock (McManus et al., 2014; Treves and Karanth, 2003; Baker et al., 2008), though it has been shown that under certain conditions carnivores can have a positive economic impact by controlling herbivore populations thus improving range-lands for livestock grazing (Prowse et al., 2015). Agriculturalists on the other hand suffer crop losses to a range of herbivore species, from small rodents to large herbivores such as elephants and other large ungulates (Naughton-Treves, 2008; Conover, 2001; Arlet and Molleman, 2007). While vegetation growth and populations of large and small herbivores are all known to be affected by carnivores in relatively intact conservation systems (Ritchie and Johnson, 2009; Ripple and Beschta, 2012; Kuijper et al., 2013) there has been little work on their role in trophic cascades in human modified landscapes (Kuijper et al., 2016). While imposing costs on livestock owners large carnivores also perform some ecosystem services (Prowse et al., 2015; OBryan et al., 2018). For example limiting large herbivore populations may reduce crop raiding and competition for grazing, however, if small herbivores (e.g rats and mice) cause more damage to crops than large herbivores (Arlet and Molleman, 2007) then by controlling mesopredators large carnivores may indirectly impose costs by contributing to higher rodent abundance.

The changes to ecosystem structure that results from negative human-wildlife interactions is more complicated than just a question of the different economic costs and benefits to agriculturalists versus pastoralists and ranchers. These com-

plex ecological systems are linked to complex social systems. Livestock often have more than just an economic value to their owners, for instance providing insurance against future losses or social status (Kurosaki, 1995; Andrew et al., 2003). There are also complex political relationships between the different human groups, in many farming systems agriculturists, ranchers and pastoralists come from different economic, social and ethnic backgrounds, each with its own political and cultural history (Fratkin, 1997). For instance pastoralists have a history of persecution with governments often forcing them into more sedentary lifestyles, while ranchers may have controversially acquired land from both subsistence agriculturalists and pastoralists (Fratkin, 1997; Kantai, 2007). Human-wildlife interactions occur at an intersection between complex human and ecological systems, and improving our understanding of the ecological implications of these interactions will allow us to gain a better understanding of the real costs and benefits associated with living alongside different wildlife to different societal groups.

In this chapter we use type II functional responses (Holling, 1959) to simulate predator-prey interactions in a multi-species model that represents the wild and domestic elements of an African savannah ecosystem. We aim to investigate the ecological and social impacts that result from negative human-wildlife interactions across multiple taxa and trophic levels. We hypothesise small herbivores cause more damage to crops than larger herbivores, however, as apex predator populations are reduced by human persecution top-down ecosystem regulation will cause shifts in herbivore populations potentially influencing rates of crop consumption by different herbivore guilds.

6.3 Methods

6.3.1 Model overview

We constructed an ordinary differential equation model simulating a multi-trophic level ecosystem containing interacting wild and domestic components using the deSolve package (Soetaert et al., 2010) in R (R Core Team, 2017). The model simulates a 10,000 km^2 area containing a mixture of crops (C) and natural vegetation (V) which are fed on by small (R) and large (U) herbivores with livestock (L) only feeding on natural vegetation. Small carnivores (M) predate the small herbivores, while large carnivores (A) predate large herbivores, livestock and small carnivores (Fig. 6.1). Large carnivores predating livestock are controlled through retaliatory human behaviour, undergoing lethal control in relation to the numbers of livestock they kill.

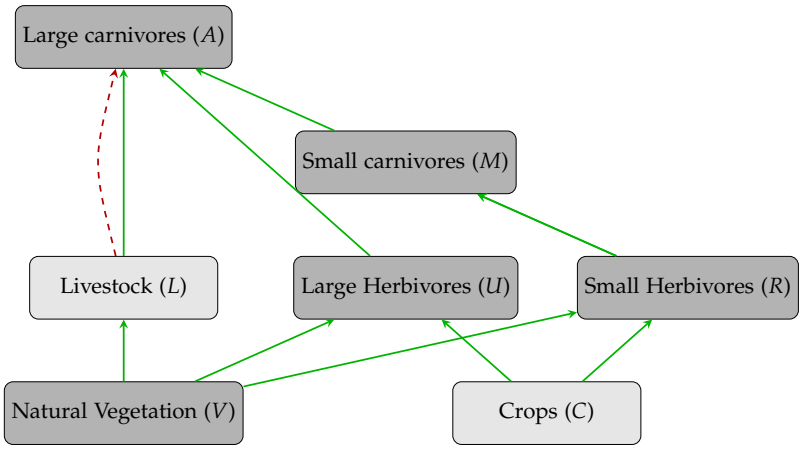


FIGURE 6.1. Flow diagram showing model components and their interactions. Solid green arrows denote predations in the form of Hollings type II functional responses with energy flowing in the direction of the arrow, dashed red arrows represent costs inflicted by humans in retaliation for predation of domestic guilds.

6.3.2 Model Equations

Increases in crop and natural vegetation mass ($kg\,dry\,matter\,day^{-1}$) are defined as:

$$\frac{dJ}{dt} = f(J) = q_J.a.l_J.r \tag{6.1}$$

Where J is the plant productivity, q_J is the plants growth rate ($kg\,dry\,matter\,km^{-2}\,mm^{-1}$), a is the area the model covers (km^{-2}), l_J is the proportion of the area under that vegetation type ($l_C + l_V = 1$), and r is rainfall ($mm\,day^{-1}$).

Population recruitment for all other nodes and losses to predation are simulated by Type II functional responses based on Holling's disc equation (Holling, 1959), in the form:

$$\frac{dP}{dt} = g(P|P,N) = \frac{P.c.\alpha.N}{1+\alpha.\beta.N} \tag{6.2}$$

where P is the predator population, N is the prey population, c is the efficiency with which predators convert food into offspring, α is the effective search area ($km^2\ day^{-1}$) calculated by multiplying the width of path an individual can effectively search by the speed of movement and the probability of success per attack (Fryxell et al., 2007), and β is the predator's handling time for each prey item ($days$). For functional responses simulating changes in prey populations as a result of predation c is set to one as for every attack the prey lose an individual population unit irrespective of the predator's energy assimilation efficiency.

For predators with multiple prey the following functional response adapted from Holling (1959) is used (Cock, 1978; Murdoch, 1973):

$$\frac{dP}{dt} = g(P|P, N_1 ... N_n) = \frac{P.c_1.\alpha_1.N_1}{1 + \alpha_1.\beta_1.N_1 + ... + \alpha_n.\beta_n.N_n} \tag{6.3}$$

Death rates were simulated via a sigmoidal function. In a type II functional response $\frac{1}{\beta}$ is a predator's maximum possible nutrient intake. Defining S as the fraction of a species maximum possible intake below which starvation occurs then $\frac{S}{\beta}$ is the level of nutrient intake below which predator populations suffer food shortages and start to starve. Rearranging the disc equation allows us to calculate the size of prey population per predator below which starvation begins (N_{min}):

$$N_{min} = \frac{S}{(1 - S).\bar{\alpha}.\bar{\beta}} \tag{6.4}$$

Where $\bar{\alpha}$ and $\bar{\beta}$ are the predator's respective mean effective search area and handling time for all it's prey populations.

We can create a sigmoidal function that for values of ΣN (the sum of all a predator's prey populations) above N_{min} returns a species non-food constrained death rate (K) and for values of ΣN below N_{min} returns an increasing death rate peaking at 1 (100% daily mortality) when ΣN is 0:

$$\frac{dP}{dt} = h(P|P, N) = \left(\frac{(1 - K)}{1 + e^{\frac{10.\Sigma N}{N_{min}.P} - 5}} + K\right).P \tag{6.5}$$

Small carnivores were not included in large carnivores death rate function as they are not a primary food source.

Human persecution of wildlife in retaliation for predation of a domestic guild is modeled with the following:

$$\frac{dP}{dt} = i(P|N) = f(P|P,N).\gamma_{P,N} \tag{6.6}$$

Here $f(P|P,N)$ is a type II functional response simulating the rate at which (P) predates (N) and $\gamma_{P,N}$ is a constant that controls the level and success rate of human retaliation for attacks on N by P.

The equations for each model node are as follows

$$\frac{dC}{dt} = f(C) - g(R|C) - g(U|C) \tag{6.7}$$

$$\frac{dV}{dt} = f(V) - g(R|V) - g(U|V) - g(L|V) \tag{6.8}$$

$$\frac{dR}{dt} = g(R|V,C) + g(R|C,V) - g(M|R) - h(R|C,V) \tag{6.9}$$

$$\frac{dU}{dt} = g(U|V,C) + g(U|C,V) - g(A|U,L,M) - h(U|C,V) \tag{6.10}$$

$$\frac{dL}{dt} = g(L|V) - g(A|L,U,M) - h(L|V) \tag{6.11}$$

$$\frac{dM}{dt} = g(M|R) - g(A|M,U,L) - h(M|R) \tag{6.12}$$

$$\frac{dA}{dt} = g(A|L,U,M) + g(A|U,M,L) + g(A|M,L,U) - i(A|L) - h(A|L,U) \tag{6.13}$$

Where:

C = Crops (in Kg)

V = Natural vegetation (in Kg)

U = Large herbivores

R = Small herbivores

L = Livestock

M = Small carnivores

A = Large carnivores

6.3.3 Model Parameterisation

We initially parameterised the model as an African savannah system as they are frequently involved in complex human-wildlife interactions that have negative impacts on the wildlife and human communities involved (Dickman et al., 2014; Kissui, 2008; Ogada et al., 2003). We chose relatively well studied savannah species that are stereotypical of their guild as functional types to represent each node (Table 6.1). This allowed initial parameterisation of the model from existing published data on these species' traits (Table 6.2). Where data on these specific species were not available we used data on similar species from a different ecosystem, for instance we used data on coyote (*Canis latrans*) to approximate black backed jackal traits, where data on comparable species were not available

TABLE 6.1. Species chosen as functional types for each node and estimates of their population densities in the wild

Node	Species	Population Density km^{-2}
Large carnivore (A)	Lion (*Panthera leo*)	0.08 to 0.13 (Creel and Creel, 1997)
Small carnivore (M)	Black backed jackal (*Canis mesomelas*)	4 to 7 (McKenzie, 1993)
Large herbivore (U)	Cape buffalo (*Syncerus caffer*)	3.3 to 5.6 (Jolles, 2007)
Small herbivore (R)	Natal multimammate mouse (*Mastomys natalensis*)	3,120 (Linzey and Kesner, 1997) to 90,000 (during an outbreak year in agricultural land) (Mwanjabe et al., 2002)
Livestock (L)	Cattle (*Bos taurus*)	2.44 to 52.12 (Ottichilo et al., 2001)
Natural vegetation (V)	Savannah grasses	–
Crops (C)	Maize (*Zea mays*)	–

we made best estimates of those parameters. Table 6.3 outlines the calculation of parameters that could not be directly extracted from the literature.

Table 6.2: Initial model parameters, adjusted parameters used in the final model and the data from which parameters were calculated. g_x denotes growth rate for plant x. $c_{N\to P}$, $\alpha_{N\to P}$, $\beta_{N\to P}$ respectively denote the energy conversion efficiency, effective search area, and handling times of P feeding on N. S_P is the fraction of species P's maximum possible nutrition intake below which death rates begin to increase due to starvation. K_P is the non-starvation death rate of species P.

	Parameters from the literature	**Adjusted Parameters used in stable model**	**Values used to calculate parameter**		
Growth rates ($kg\,km^{-2}\,mm^{-2}$)					
g_C	3702 (Farré and Faci, 2006)	4072			
g_V	336.9 (Higgins et al., 2000)	404.3			
Energy conversion efficiency ($Offspring\,per\,unit\,food\,consumed$)			**Female reproductive contribution** ($year^{-1}$)	**Units of prey eaten** ($indiviual^{-1}\,year^{-1}$)	**Proportion of population fertile and female**
$c_{C\to R}$, $c_{V\to R}$	3.674	2.572	43.45 (Oliff, 1953)	1.423 (Green and Rowe-Rowe, 1987)	0.1204 (Oliff, 1953)
$c_{V\to L}$	9.387×10^{-5}	1.877×10^{-2}	0.656 (Roderick et al., 1998)	2376 (Oyenuga and Olubajo, 1975)	0.34 (Roderick et al., 1998)

$c_{C\to U}$, $c_{V\to U}$	4.214×10^{-5}	8.427×10^{-3}	0.6154 (Groves et al., 2011)	5110 (Groves et al., 2011)	0.3499 (Jolles, 2007)
$c_{R\to M}$	1.336×10^{-4}	1.736×10^{-4}	3 (Bingham and Purchase, 2002)	5615(Bekoff, 1977; Oliff, 1953) [1]	0.25 (Ferguson et al., 1983)
$c_{U\to A}$, $c_{L\to A}$	3.616×10^{-2}	3.616×10^{-3}	0.825 (Sunquist and Sunquist, 2009)	8.821 (Owen-Smith and Mills, 2008; Scheel, 1993)	0.3867 (Stander, 1991)
$c_{M\to A}$	1.266×10^{-3}	1.266×10^{-4}	0.825 (Sunquist and Sunquist, 2009)	252.0 (Owen-Smith and Mills, 2008; Walton and Joly, 2003)	0.3867 (Stander, 1991)
Effective Search Area ($km^2\,day^{-1}$)			**Search path** (km)	**Travel velocity** ($km\,day^{-1}$)	**Probability of successful attack**
$\alpha_{C\to R}$, $\alpha_{V\to R}$	5.000×10^{-5}	1.000×10^{-5}	0.002 [2]	0.025 [2]	1 [2]
$\alpha_{V\to L}$	1.020	15.31	0.1 [2]	10.20 (Raizman et al., 2013)	1 [2]
$\alpha_{C\to U}$, $\alpha_{V\to U}$	7.553×10^{-1}	11.33	0.1 [2]	7.553 (Bennitt et al., 2014)	1 [2]
$\alpha_{R\to M}$	1.752×10^{-1}	8.762×10^{-2}	0.05 [2]	10.62 (Ferguson et al., 1988)	0.33 (Nel, 1984)
$\alpha_{U\to A}$	1.160	7.540×10^{-2}	0.4 (Fryxell et al., 2007)	10 (Fryxell et al., 2007)	0.29 (Fryxell et al., 2007)
$\alpha_{L\to A}$	8.000×10^{-1}	5.200×10^{-2}	0.4 (Fryxell et al., 2007)	10 (Fryxell et al., 2007)	0.2 (Kolowski and Holekamp, 2006)
$\alpha_{M\to A}$	2.000×10^{-1}	2.000×10^{-3}	0.4 (Fryxell et al., 2007)	10 (Fryxell et al., 2007)	0.05 [2]

[1] Captive coyote dietary intake used to calculate black backed jackal prey requirements.
[2] Author estimate.

Handling time (day^{-1})			**Attacking and subduing** (day^{-1})	**Consuming and digesting** (day^{-1})
$\beta_{C\to R}$, $\beta_{V\to R}$	9.970×10^{-1}	7.976×10^{-1}	0[2]	0.9970[3] (Hadj-Chikh et al., 1996)
$\beta_{V\to L}$	1.543×10^{-2}	3.858×10^{-2}	0[2]	0.01543 (Laca et al., 1994)
$\beta_{C\to U}$, $\beta_{V\to U}$	1.543×10^{-2}	3.858×10^{-2}	0[2]	0.01543 (Laca et al., 1994)
$\beta_{R\to M}$	1.531×10^{-2}	1.531×10^{-2}	8.367×10^{-3} [2]	6.944×10^{-3} [2]
$\beta_{U\to A}$, $\beta_{L\to P}$	4.055	2.028	0.045 (Fryxell et al., 2007)	4.01 (Fryxell et al., 2007)
$\beta_{M\to A}$	2.129×10^{-1}	4.259×10^{-1}	6.944×10^{-3} [2]	0.1435 [2]
Fraction of a species maximum possible intake below which starvation begins				
S_R	0.75[2]	0.9		
S_U	0.75[2]	0.525		
S_L	0.75[2]	0.525		
S_M	0.75[2]	0.6		
S_A	0.75[2]	0.8625		
Non starvation mortality rates (day^{-1})				
K_R	6.635×10^{-3} (Oliff, 1953)	7.299×10^{-3}		
K_L	2.438×10^{-4} (Roderick et al., 1998)	2.926×10^{-4}		
K_U	5.479×10^{-4} (Slade et al., 1998)	5.753×10^{-4}		

[3]Grey squirrel consumption times rates used to calculate Natal multimammate mouse consumption

K_M	8.219×10^{-4} (Slade et al., 1998)	9.863×10^{-4}
K_A	3.288×10^{-4} (Mosser and Packer, 2009)	3.288×10^{-4}
Other parameters		
Area (km^2)	1×10^4	1×10^4
Proportion of Area under farmland	0.1	0.1
Rainfall ($mm\,day^{-1}$)	2.740 (Higgins et al., 2000)	2.740

TABLE 6.3. For parameters required in a Hollings type II functional response that could not be extracted directly from literature the above equations and data were required. Here c is the energy conversion efficiency, α effective search area and b handling time

Parameter	Data required	Equation
c	daily births per female (d), units of prey eaten per individual per day (e), percentage of population fertile females (f)	$c = \frac{f.d}{e}$ (Fay and Greeff, 1999)
α	search path (s), travel velocity (v), probability of success per attack (j)	$\alpha = s.v.j$ (Fryxell et al., 2007)
b	time to attack and subdue prey ($b1$), time to consume and digest prey ($b2$)	$b = b1 + b2$ (Fryxell et al., 2007)

TABLE 6.4. Population sizes for each node from models of increasing complexity using unadjusted literature derived parameters

Nodes included	Small herbivores (R)	Large herbivores (U)	Livestock (L)	Small carnivores (M)	Large carnivores (A)
CVR	68,235,944	-	-	-	-
CVU	-	284,731	-	-	-
VL	-	-	128,195	-	-
CVRU	68,229,826	25.82	-	-	-
CVRL	68,231,893	-	17.22	-	-
CVRM	64,385,350	-	-	58,564	-
CVUA	-	4.776×10^{-3}	-	-	2.0855×10^{-3}
VLA	-	-	9.667×10^{-3}	-	7.334×10^{-3}
CVRUM	64,379,089	27.98	-	58,559	-
CVRUMA	64,402,519	3.000	-	58,292	4.637
CVRULMA	64,453,888	9.539×10^{-26}	13.44	57,474	17.51

6.3.4 Simulation Studies

We ran initial simulations with retaliation for carnivore predation of livestock set to 0 to establish baseline parameters and populations without carnivore persecution. Simulations using literature derived parameters resulted in model instability with large herbivores, livestock, and large carnivores all going extinct or existing at very low numbers at the end of the 20 year simulation time frame (Table 6.4). We ran a series of simplified simulations containing subsets of nodes to investigate if there were specific guilds, parameters or interactions that were leading to model instability (Table 6.4).

To calculate parameter values that produced biologically sensible populations (Table 6.1) we ran simulations using 100,000 parameter sets where each parameter was drawn from normal distributions with means of the parameter's literature derived value and standard deviations a sixth of the mean. We used the summed square of the percentage error between the simulated models and population densities from the literature to select parameter sets that produced the most biologically reasonable population sizes. These parameter sets were used alongside information from the simplified simulations to inform manual adjustments of parameters to produce a set of adjusted parameters that simulated biologically realistic population sizes (Table 6.2). To investigate the impact of carnivore persecution on the modeled populations we ran multiple simulations increasing the retaliation constant ($\gamma_{P,N}$) incrementally from zero until large carnivores were unable to persist.

To investigate the model's robustness to different model parameterisations we conducted two sensitivity analyses. Firstly, to investigate the sensitivity of the baseline model without carnivore persecution, we generated 100,000 parameter

sets where $\gamma_{P,N}$ was set to 0 and all other parameters were generated from a normal distribution with a mean of its adjusted value (Table 6.2) and standard distribution a sixth of the mean, with all negative values discarded. To keep values of $S_{R,L,U,M,A}$ less than one a standard deviation of a sixth of $1-\bar{x}$ was used and values over 1 discarded. Secondly, to investigate how the outcomes of carnivore persecution may change under different scenarios we generated a second set of 100,000 random parameter sets using the same methods as above. Simulations then investigated the impact of increasing carnivore persecution on the populations these parameter sets simulated.

6.4 Results

Simulations using literature derived parameters for the full model produced low population sizes for large herbivores, livestock and large carnivores, while small herbivores and small carnivore populations were within the bounds of real population densities (Table 6.4). Simulations using a subset of nodes show that while small herbivores, large herbivores and livestock populations persist independently, large herbivores and livestock populations do not persist in the presence of small herbivores suggesting small herbivores out-compete other herbivorous populations under this parameterisation. Running repeated simulations where large herbivore and livestock competitiveness was improved by incremental increases to their energy conversion efficiency in the presence of small herbivores shows livestock and large herbivores require 168 and 369 factor respective increases in their energy conversion efficiency to persist at realistic levels in the presence of small herbivores (51,035 for livestock and 159,773 for large herbivores) (Fig. 6.2).

The introduction of large carnivores to simulations containing large herbivores or livestock results in the extinction of the herbivorous species as well as the carnivores (Table 6.4). The ability of very low populations of large carnivores to suppress herbivore populations suggests the large carnivore's effective search area are too high to allow both populations to persist. Reducing large carnivore effective search area on large herbivores from 1.16 to 0.00752 (km^2day^-1) while holding all other parameters constant produces biologically reasonable populations of large herbivores (7.653×10^4) and large carnivores (801) (Fig 6.2), similarly reducing large carnivores effective search area on livestock from 0.8 to 0.0148 produces realistic populations of livestock (4.262×10^4) and large carnivores (865) (Fig 6.2). Combining this information with that gained from simulations with the lowest

TABLE 6.5. Simulated populations produced using adjusted parameters (Table 6.2)

Node populations	
Node	Population
Small herbivore	47,296,817
Large herbivore	38,007
Livestock	28,967
Small carnivore	44,127
Large carnivore	1,195
Fluxes between nodes containing domestic species	
Flux	Population units consumed
Crops to small herbivores	1.062×10^7
Crops to large herbivores	5.395×10^5
Natural vegetation to small herbivores	8.772×10^6
Natural vegetation to large herbivores	4.457×10^5
Natural vegetation to livestock	7.508×10^5
Livestock to large carnivores	2.020×10^2

summed square percentage error from 100,000 simulations with random parameters allowed manual parameter adjustment to find a parameter set that produced reasonable populations for the full model (Table 6.2 & Table 6.5).

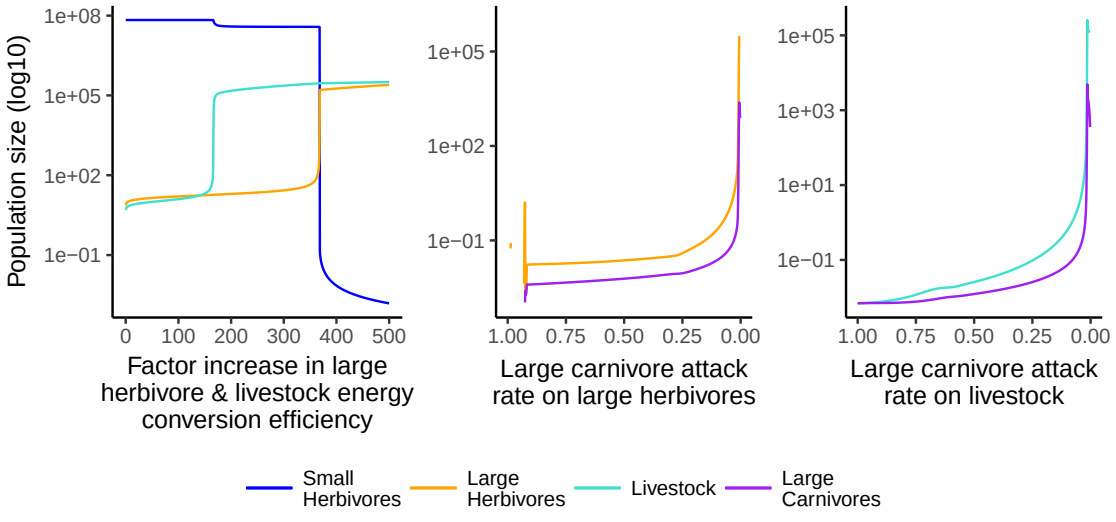


FIGURE 6.2. The impact of adjusting herbivore energy efficiencies and large carnivore effective search areas on the persistence of populations in simplified model structures.

In simulations run with the adjusted parameters small herbivores consume 91.784% of the models total primary productivity, with large herbivores consuming 4.663% and livestock 3.554%. Small herbivores also dominate crop consumption, consuming 95.17% of total crop productivity with the remaining 4.835% consumed by large herbivores. Levels of predation on livestock by large carnivores is high with 0.6982% of livestock eaten by large carnivores in each daily time step.

Introducing retaliation against large carnivore populations for attacking livestock causes immediate declines in large carnivore populations, with extinction (N<1) occurring at $\gamma_{P,N}$ values above 0.01412 ($lions killed per livestock predation$), approximately equating to one lion death for every 71 cattle killed (Fig 6.3). Other simulated population sizes do not change drastically as large carnivores go extinct, large herbivores and livestock populations change the most, increasing by 0.9872% and 0.5526% respectively. There is a small mesopredator release effect as small carnivore populations increase by 0.1899%, with a resulting decrease in small herbivores of 0.08759%. Total crop consumption does not change as large carnivores go extinct, however there is a shift in levels of crop consumption by node. As large herbivore populations increase their crop consumption increases by 1.008% while small herbivore crop consumption decreases by 0.05120%, a shift in consumption which represents 0.04872% of total crop productivity.

Sensitivity analysis of the baseline model without carnivore persecution suggests the model is relatively robust to different parameterisations. While the ranges of populations simulated from 100,000 random parameter sets are large (Fig 6.4) the interquartile ranges of simulated populations are biologically reasonable. The interquartile ranges of small herbivore (3.739-5.503$\times 10^7$) and livestock (2.143-4.104$\times 10^4$) populations falls within ranges from the literature (Table 6.1). While those of large herbivores (2.915-5.207$\times 10^4$), small carnivores (2.999-5.511$\times 10^4$)

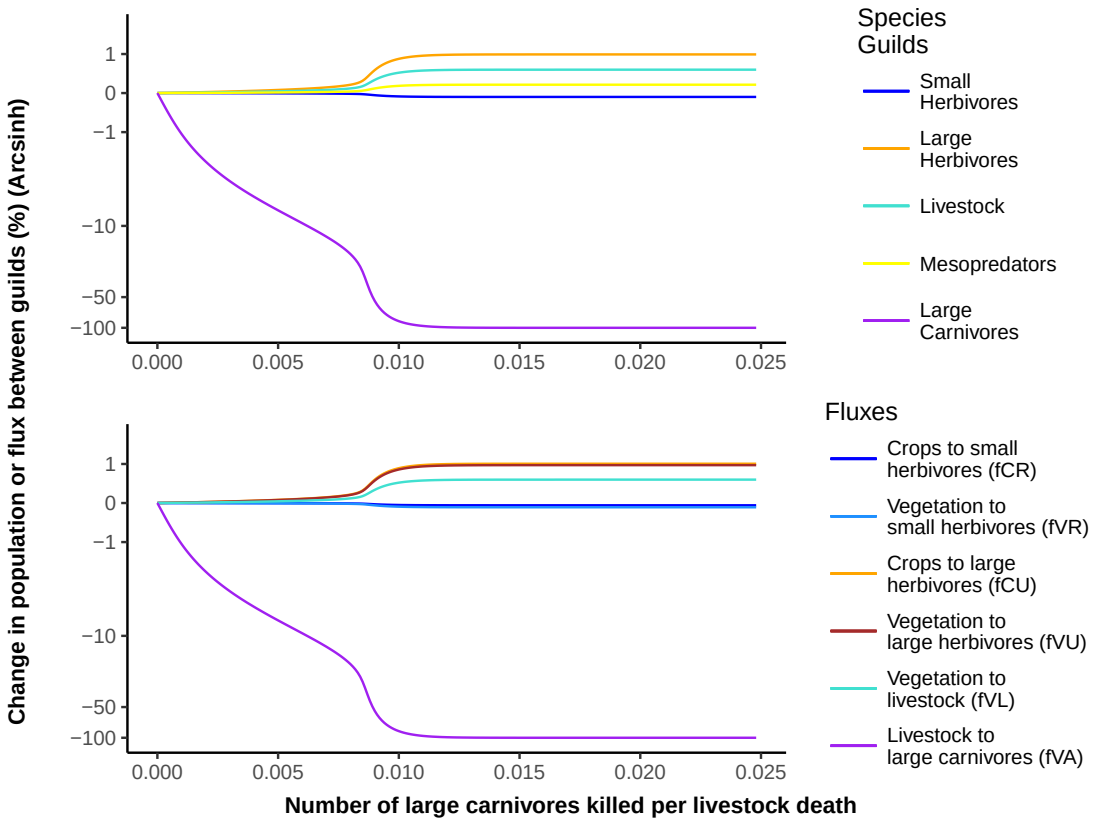


FIGURE 6.3. Changes in populations and fluxes as levels of retaliation against large carnivores for killing livestock is increased

and large carnivores (9.142-16.67$\times 10^2$) only fall marginally outside of population densities from the literature. Median population sizes from the sensitivity analysis were also very similar to populations simulated by the baseline parameters (Fig 6.4).

Fig. 6.5 & 6.6 show the percentage changes in populations and fluxes as carnivore persecution is increased on 100,000 random parameter sets. As large carnivores were persecuted to extinction livestock populations increased by a small amount under all parameter sets (median of 0.5781, IQR = 0.4714 to 0.7061). As small herbivore populations fell in all simulations (median of -0.09824, IQR = -0.1355 to -0.07203) crop consumption by small herbivores also fell (median of -

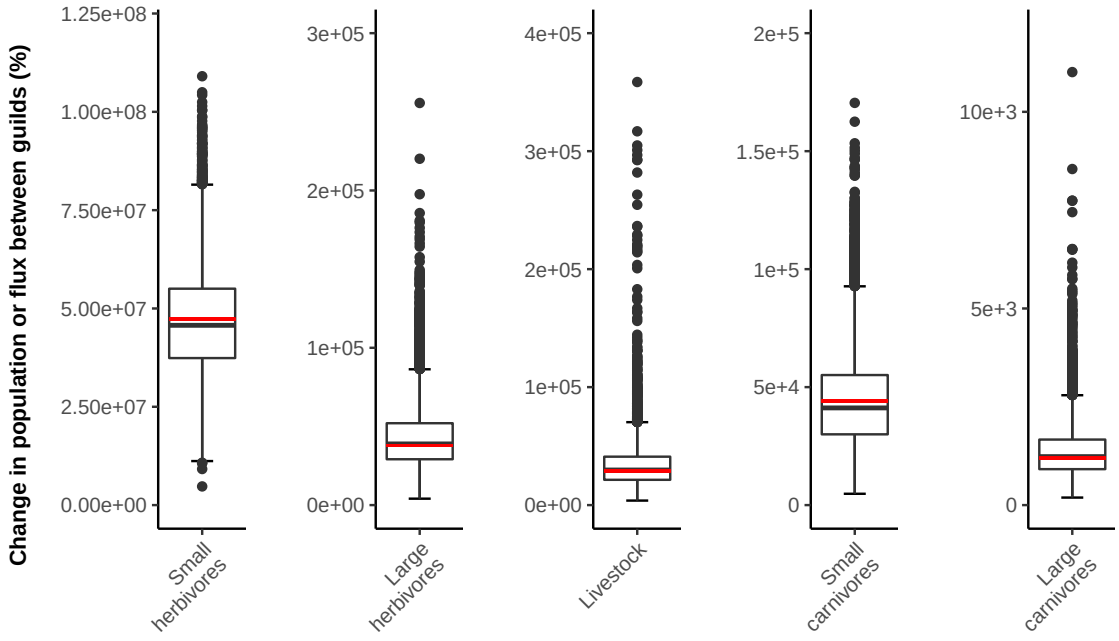


FIGURE 6.4. Populations from 100,000 simulations run with random parameter sets. Red lines denoting populations from simulations run with baseline parameters.

0.05442, IQR = -0.08208 to -0.03676). Large herbivore populations increased in the majority of cases (median of 0.9754, IQR = 0.8030 to 1.177) and large herbivore consumption of crops increased in all cases (median of 1.006, IQR = 0.8276 to 1.214). However, there were three cases where large herbivore populations decreased in the face of large increases in livestock populations. Despite small carnivore populations increasing on average (median of 0.1700, IQR = 0.1091 to 0.2403) there were 321 cases where their populations fell, these decreases are likely caused by decreasing small herbivore populations as they compete for food with increasing large herbivore and livestock populations.

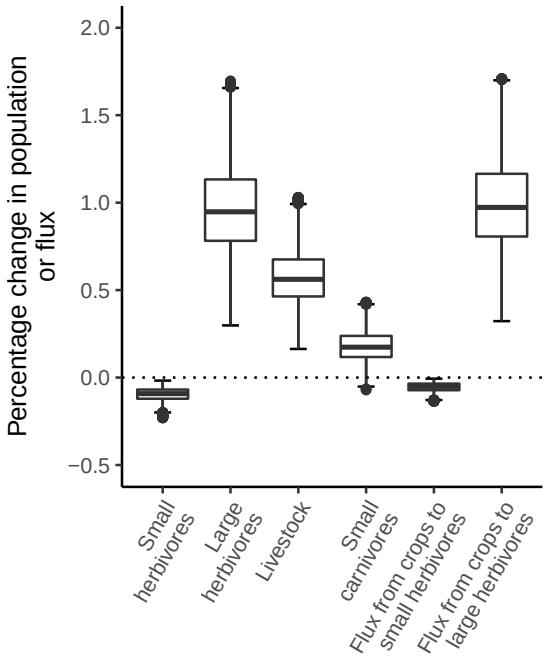


FIGURE 6.5. Percentage change of populations and fluxes for 100,000 random parameter sets as large carnivores go extinct. Outliers that lie beyond 1.5 times the interquartile range have been removed

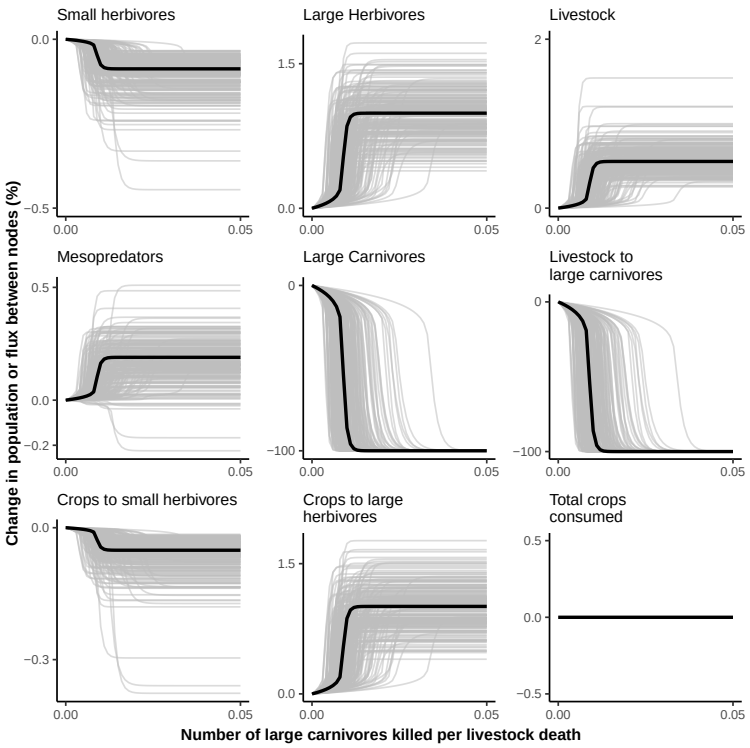


FIGURE 6.6. Impact of increasing large carnivore persecution on the populations simulated by 200 random parameter sets (grey) compared to baseline parameter set (black).

6.5 Discussion

It is widely acknowledged that human-wildlife interactions can have severe negative impacts on human well-being and the populations of wildlife involved, many of which are of conservation concern (Dickman, 2010). While these interactions involve a wide array of species the conservation literature has historically focused on charismatic species such as large carnivores and mega-herbivores (Peterson et al., 2010; Redpath et al., 2014). This focus reflects their high global cultural value and not necessarily their impact on the well-being of the human communities they live alongside (Peterson et al., 2010; Arlet and Molleman, 2007). While some studies suggest less charismatic species, such as rodents, cause more crop damage than larger herbivores (Arlet and Molleman, 2007; Harich et al., 2013; Gillingham and Lee, 2003) there is a lack of research quantifying losses to different taxa (Naughton-Treves and Treves, 2005). There has also been a lack of research integrating wider ecological processes and human-wildlife interactions and how these may interact with and impact human interests (Dorresteijn et al., 2015). Our simulated savannah ecosystem shows the need to consider a wider array of species when conceptualising negative human-wildlife interactions with rodents imposing much greater costs than larger ungulates through crop consumption. Large carnivores also imposed costs through the predation of livestock, however their extinction as a result of persecution by humans had minimal impact on the wider ecosystem causing only marginal shifts in crop consumption by the other species.

6.5.1 Crop Consumption

Our understanding of crop losses to wildlife is limited by a scarcity of empirical data in many farming systems around the world (Naughton-Treves and Treves, 2005). In areas where subsistence agriculture dominates, as is the case on the

edges of many protected areas, this lack of data is compounded by the variability of farming practices, yields and losses, making extrapolating patterns of losses from the meagre data that exists difficult (Yudelman et al., 1998; Naughton-Treves and Treves, 2005). In such instances modelling the mechanisms that impact crop consumption by wildlife may offer useful insights into crop consuming species and the types of farming systems or ecological structures where further research should be focused. Our simulations agree with other studies that show rodents can cause more crop damage than large herbivores in systems where both occur (Arlet and Molleman, 2007; Harich et al., 2013; Gillingham and Lee, 2003) and is consistent with studies that show outbreaks of rodents can have catastrophic impacts on yields with our simulated populations consuming over 95% of crop productivity (Stenseth et al., 2003; Mwanjabe et al., 2002).

It must be noted however that our model considers the percentage crop losses to wildlife which is not always comparable to assessing the impact of wildlife on human well-being as different farmers display different levels of vulnerability to losses (Naughton-Treves and Treves, 2005). While we assume spatial homogeneity in crop losses, distance to protected areas or habitat fragments are known to influence a farm's overall crop losses and losses to different species (Naughton-Treves, 1997; Hill, 1997). Vulnerable immigrant populations can also be disproportionately represented in farmland around protected areas, and thus at higher risk of suffering crop losses to wildlife (Naughton-Treves, 1997). Temporal variability in losses also impacts farmers ability to cope; with regular, incremental losses less damaging than sporadic, catastrophic ones (Barnett et al., 2008). Elephants are one example of a large herbivore known to cause irregular, localised and catastrophic damage that subsistence farmers are particularly vulnerable to (Hawkes, 1991; Naughton et al., 1999; Gillingham and Lee, 2003; Naughton-

Treves and Treves, 2005). As residents of agricultural land (Massawe et al., 2007; Caro, 2002) rodents cause widespread insidious damage (Hawkes, 1991), though they also have the ability to cause catastrophic damage during outbreak years (Stenseth et al., 2003; Mwanjabe et al., 2002). It is possible, however, to predict rodent outbreaks as they are linked to climatic conditions, and given the required infrastructure exists forecasts can allow the early implementation of protection measures (Mwanjabe et al., 2002). Improving our understanding of the spatial and temporal distribution and variability of crop consumption by different taxa and how this interacts with farmer's vulnerability is vital in improving our understanding of how best to minimise the impacts of crop losses on farmer's well-being.

6.5.2 Impact of large carnivores and their extinction

In our simulated ecosystem large carnivores imposed severe costs on livestock owners, predating 0.6982% of livestock every day, predation rates real cattle populations are unlikely to be able to sustain. Levels of livestock losses this high represents severe economic hardship to poor pastoralist communities, Holmern et al. (2007) found a 4.5% annual loss of livestock represented a loss equal to 19.2% of households annual cash income. The impact of these loses on human well-being may be magnified beyond the upfront economic cost as livestock often hold cultural and social value beyond their upfront economic value (Andrew et al., 2003; Kurosaki, 1995). Despite the high rates of livestock predation carnivore extinction did not cause large increases in livestock numbers with livestock owners only benefiting a 0.5525% increase in livestock populations. This suggests that despite high levels of livestock losses to carnivores, if predation by large carnivores is not a population's limiting factor then expending large amounts of effort reducing predation may result in negligible increases in the numbers of livestock that ecosystem

is able to hold. It is important to note though that predation pressure is not evenly distributed between households (Dickman et al., 2014) and not all households are equally able to cope with the consequences of livestock losses (Naughton-Treves and Treves, 2005), as a result small average gains and losses across a landscape may be catastrophic for the most vulnerable and affected households.

Our model agrees with the literature that large carnivore populations are highly susceptible to persecution with land on the edge of protected areas potentially acting as population sinks (Woodroffe and Ginsberg, 1998; Ripple et al., 2014). Simulated populations of lions became extinct when human persecution of lions was greater than one lion killed in retaliation for every 71 cattle predated. A level of retaliation much lower than that reported by Kissui (2008) who found approximately 1 lion killed for every 1.7 cattle attacked. The very low levels of retaliation required to drive our simulated populations to extinction is driven by the high levels of cattle predation our model recorded, which at 0.6982% of cattle killed per day are much higher than those reported in the literature. In northern Tanzania Kissui (2008) report annual loss rates to lions of 1% of cattle and 4% of goats and sheep, while Holmern et al. (2007) reports annual losses 4.5% of all livestock to all carnivores. In community land around Ruaha National Park, Tanzania, Dickman et al. (2014) reports 1.2% monthly losses of all livestock to all carnivores. While in a global review Graham et al. (2005) find predators kill 0.2-2.6% of livestock annually. The high predation rates we find in our model are likely driven by two factors, firstly the model does not take into account husbandry practices that protect livestock from attack. Secondly, our model assumes a homogeneous landscape where livestock, wild herbivores and carnivores mix equally, while many of the studies reported above are on the edges of protected areas where there are likely to be opposing gradients in the density of carnivores and wild herbivores

on one side and livestock on the other - reducing the rate at which carnivores encounter domestic prey.

Our model shows strong bottom up dynamics, with minimal changes to other simulated populations as human persecution drives large carnivores to extinction. While mesopredator release is a widely reported response to decreases in apex predator numbers (Elmhagen and Rushton, 2007; Crooks and Soulé, 1999; Ritchie and Johnson, 2009) our model showed very weak mesopredator release with a 0.1899% increase in small carnivores as large carnivores went extinct. These results match with some studies in human-modified landscapes, Dorresteijn et al. (2015) found a limited evidence of top down suppression of foxes by wolves in a human-dominated landscape in Romania, with bottom up effects of habitat type playing a bigger role influencing mesopredator numbers. They cite two potential explanations for the weak mesopredator release, firstly that foxes are generally suppressed by predators of a closer body size to their own than wolves, or that wolf densities are too low to suppress foxes. Studying historical predator populations in Sweden Elmhagen and Rushton (2007) found fox populations grew rapidly in response to declining apex predator numbers in productive ecosystems, while in low productivity areas there was negligible mesopredator release. By only modelling a small subset of species present in African savannahs our study may be replicating low productivity systems with relatively low densities of both mesopredators and large carnivores reducing the strengths of interactions between them (Elmhagen and Rushton, 2007).

Herbivore populations also showed weak top-down regulation. As large carnivores become extinct herbivore populations changed by less than 1% with similarly low changes in levels of crop consumption by large and small herbivores. Sinclair et al. (2003) show that ungulate prey size and diversity of predators influence

strengths of top-down and bottom-up process in the Serengeti. Smaller ungulates fall within the dietary niches of many predators which results in high levels of predation and top-down regulation. Larger ungulate species have fewer predators and so are more likely to be regulated by bottom-up processes which matches the dynamics found in our models.

6.5.3 Model limitations

Functional response models have been used widely to improve our understanding of predator-prey relationships and how they influence ecosystems (Holling, 1959; Fryxell et al., 2007; Murdoch, 1973; Fay and Greeff, 1999; Anderson, 2005). However, as this study shows, there are a number of challenges in their application to complex systems. Despite selecting widespread and iconic or economically important species as functional types for each node we struggled to find data on many of these species' traits. As a result a number of parameters and traits had to be estimated and the rest collected from multiple studies, under the assumption that a species' behavioural traits are relatively constant across landscapes and ecosystems. These models show how we can use information on basic species biology to understand complex ecosystems and interactions, however for many species and systems, including very well studied ones, a paucity of data restricts our ability to accurately model them (Tewksbury et al., 2014; Botkin et al., 2007).

The degree to which some parameters had to be changed from those derived from the literature to achieve realistic populations suggests the model is missing some ecological processes, particularly those that influence competition between herbivores and predation of herbivores by large carnivores. Our model is likely to inflate rodent populations and their competitive advantage over large herbivores for two reasons. Firstly, our model assumes rodents are able to access 100% of

crop and vegetation productivity, while in reality their ability to derive nutrition from the seeds, leaves and stems of plants differs drastically (Taylor and Green, 1976), for instance savannah ungulates and rodents display resource partitioning, with rodents feeding on species and parts of plants that are less palatable to ungulates which will impact their relative competitiveness (Delany, 1986). Secondly, many rodent populations, particularly in the tropics, are susceptible to seasonally cyclic population dynamics, with rapid population growth when environmental conditions are suitable and population declines when these resources are no longer available (Stenseth et al., 2003; Mwanjabe et al., 2002; Delany, 1986). In seasonal ecosystems, such as African savannahs, large herbivores undergo seasonal migrations which offer them a competitive advantage over sedentary rodent populations (Senzota, 1983; Delany, 1986), dynamics not represented in our model.

The adjustments required to parameters defining large carnivore predation on ungulates may be as a result of simplifying complex systems with numerous species into a small number of functional type species. This means our model assumes large carnivores only predate large bodied herbivores, however large carnivores predate a wide range of prey whose body sizes can differ by an order of magnitude (Sinclair et al., 2003), which is likely to have a significant impact on energy conversion, attack rates and handling times.

In assessing the impacts of different species on human well-being our model also fails to take into account the complexities of many human-wildlife interactions. Firstly, carnivores offer ecosystem services excluded from our model (OBryan et al., 2018), for instance jackals remove organic waste (irovi et al., 2016) and leopards control feral dog populations (Braczkowski et al., 2018) with positive impacts on human health by reducing disease transmission. While the presence of large carnivores can provide economic benefits to communities through wildlife based

tourism (Lindsey et al., 2007b; Maciejewski and Kerley, 2014), there is often a disparity between those who incur costs from wildlife and those who receive benefits from tourism (Wang and Macdonald, 2006; Dickman et al., 2011). Secondly, we have not accounted for the different tangible and intangible costs associated with defending crops or livestock from different wildlife. Crop guarding is a common tactic for defending crops from large (and potentially dangerous) herbivores which imposes a range of tangible and intangible costs on farmers e.g. increased malaria risk, increased alcohol consumption, fatigue, mental illness, lack of schooling (Barua et al., 2013), while trapping or poisoning for small herbivores can incur financial costs (Mwanjabe et al., 2002). Damage causing wildlife may also play important cultural roles for local communities which are hard to quantify or compare to other tangible and intangible costs or benefits. Maasai attitudes towards lions for instance are complex and nuanced, often combining elements of fear, fascination, admiration and respect (Goldman et al., 2010), while tigers play important spiritual roles for the Kerincinese and Minangkabau people in Sumatra despite killing people and livestock (Struebig et al., 2018). While it would be near impossible to include the myriad of different impacts wildlife have on different communities it is important to acknowledge these different experiences, how they influence well-being, and how they shape people's attitudes to different species.

6.6 Conclusions

Ecological models are one tool that can help us improve our understanding of the complex interactions that occur as a result of human-wildlife interactions and how we can reduce the negative impacts these interactions can have on wildlife populations and human well-being. However, the complexity of these systems and a paucity of data on the biology of the species they contain poses severe challenges in the formulation of robust models of these systems. Our simulations showed large carnivore populations to be highly susceptible to extinction as a result of persecution in retaliation for attacks on livestock, however, strong bottom-up regulation meant the extinction of large carnivores resulted in minimal changes to populations of mesopredators, rodents, large herbivores, livestock, or patterns of crop consumption by wildlife. Our model found rodents consumed the most crops relative to large herbivores, and we recommend a greater research focus on levels of crop consumption by non-charismatic species that have historically been overlooked by conservation literature on human-wildlife interactions.

6.7 Acknowledgements

Many thanks to Mike Heath, Dougie Speirs David Greenhalgh and Nigel Mottram for training in ODE models and help with the conceptualizing and coding of an early iteration of the model. Thanks to Chris Terry for many useful insights into functional responses and their mathematical representation.



Overlapping tracks of hyena, leopard, cattle and people in community land bordering Ruaha National Park.

CHAPTER 7

General discussion and conclusions



Cattle grazing near the border of Ruaha National Park.

7.1 Contribution to knowledge

In this thesis we use a range of social and ecological research methods to improve our understanding of the dynamics of conservation conflicts around large carnivores in the Rungwa-Ruaha ecosystem in Tanzania. We start by investigating the ecological factors that lead to a number of large carnivore species' negative impacts on communities living near the park. We then investigate the socio-psychological factors that influence local community's tolerance of the two most prominent carnivore species; lions and hyenas. Finally, we use mathematical models to investigate how the negative impacts of large carnivores compare to those of other species and the ecological and economic consequences of lethal management of large carnivore populations.

7.1.1 Chapter 3

Investigating variables influencing livestock's risk of attack from carnivores in village land near Ruaha National Park, I found temporal patterns in stock losses with higher risk of losses likely linked to increased rainfall. Presence of certain wild prey species and distance to protected areas are positively associated with risk of losses. Livestock housed in reinforced wire bomas are less likely to be attacked in the boma than those housed in traditionally constructed bomas while the closer households lived to roads the more likely they are to suffer losses from their boma than while livestock are grazing nearby. My results highlight the effectiveness of wire bomas over those of traditional construction in protecting livestock from predation and recognise certain areas and times of year where efforts to reduce livestock losses should be focused.

7.1.2 Chapter 4

I used detections of carnivores and prey species reported in interviews with livestock owning households to construct occupancy models to understand the spatial and temporal factors that influence land use by the five largest carnivore species. Lion's, wild dog's, leopard's and cheetah's use of community land appears to be highly seasonal with higher occupancy estimates in the wet-season, while hyenas are widespread in community land all year. However, low respondent availability in the dry season and low detection rates for leopards, cheetahs and wild dogs restricted my study's ability to construct reliable models predicting carnivore land-use. I conclude that combining local ecological knowledge with occupancy models can be a useful tool in inferring ecological knowledge about carnivore distributions. However, restrictions in defining spatially explicit survey sites over which respondents can report detections, respondent availability and familiarity with species, and low detection rates for cryptic or rare species means the use of local ecological knowledge is not suited to all species, cultures or landscapes.

7.1.3 Chapter 5

I found tolerance towards lions and hyenas is most strongly mediated by the perceived benefits they offer and positive beliefs about the species, while experience of the species and perceived risks only influences tolerance towards hyenas. Tolerance towards lions is positively influenced by engaging with RCP programmes, these however have a complicated relationship with risk perception for both species. This highlights the care required when planning conservation interventions, as they can interact with other socio-psychological variables with unexpected and potentially harmful consequences.

7.1.4 Chapter 6

I found simulated large carnivore populations to be highly susceptible to extinction in the face of low levels of lethal management. However, strong bottom-up ecosystem regulation mean the loss of large carnivores has minimal impacts on populations of mesopredators, rodents, large herbivores, livestock, and patterns of crop consumption by wildlife. Comparing crop consumption between herbivore groups, our simulated rodent population causes the most crop damage compared to large herbivores highlighting the importance of considering the impact of non-charismatic species on human well-being.

7.2 Limitations and Future directions

Building on an existing body of literature on HWIs this thesis contributes to our knowledge of the social and ecological factors influencing human-carnivore interactions and conservation conflicts around Ruaha National Park. It has also demonstrated the application of methods that could be used further afield to study other systems where humans and carnivores share space. There are however a number of limitations to the findings in this thesis and much still to learn about the relationships between carnivores and humans in the Rungwa-Ruaha ecosystem and more generally about how we conceive and study HWIs and conservation conflicts around the world.

7.2.1 Attacks on livestock

Chapter three focused predominantly on environmental variables, with boma construction the only husbandry variable considered. However, further work on the impact of other husbandry techniques, for instance the use of guardian animals

of different species, breeds and with different training (Rigg, 2001), or different predator deterrents (Miller et al., 2016), and their effectiveness in the Rungwa-Ruaha landscape may find other cost effective methods of protecting livestock and reducing the severity of HWIs. Further research into different boma constructions, and the specific aspects of reinforced wire bomas that result in their effectiveness may also show cost-effective methods of improving traditionally constructed boma's ability to protect livestock (Ogada et al., 2003). This study also was not able to disentangle the effect of reinforced bomas on attack risk from the fact that households owning bomas lived in more risky areas. I recommend further work that controls for these confounding variables, for instance studies tracking attack risk at households before and after the construction of a wire boma, or the use of statistical matching techniques. While this study found reinforced bomas to be effective at protecting livestock at a household level they may displace carnivore attacks to other households thus not reducing attack risk on a landscape level. Further research into the impact of wire bomas on attack risk at a landscape level and at households with traditional bomas is vital to ensure they do not increase livestock losses for poorer households who are unable to afford the costs associated with constructing a wire boma.

This study also focused on broad scale environmental and ecological effects; considering environmental variables over a 2km buffer and including attacks by all carnivore species in the same analysis. Finding methods of accurately validating carnivore species responsible for attacks, and gathering more data on attacks by species other than hyena will allow for more detailed analysis of the variables influencing attack risk by different carnivore species (Abade et al., 2014a; Ogada et al., 2003; Loveridge et al., 2017). It is also important to improve our understanding of how environmental variables on a finer scale influence livestock attack

risk (Miller et al., 2015). This not only requires accurate remote sensing data but will also require accurate measurements of attack locations when they occur away from the boma, a challenging prospect when many attacks occur deep in the bush away from roads and paths.

7.2.2 Large carnivore landscape use

Low availability of respondents and poor respondent knowledge of some species resulted in a lack of data that hampered the predictive ability of the occupancy models constructed in chapter four. While able to deduce broad seasonal patterns in carnivore landscape use the models did not find any meaningful impact of specific environmental variables on carnivore landscape use. While all fieldwork comes with logistical challenges researchers have little or no control over the actions and behaviour of respondents, meaning interview based occupancy methods may be more likely to produce lower quantities of data than expected when compared to other methods of data collection.

Future work that compares the use of LEK in occupancy models with traditional methods of detecting species occupancy (Polfus et al., 2013; Gilchrist et al., 2005) or models that account for multiple detection methods (Nichols et al., 2008), would be useful in assessing the accuracy of LEK in predicting carnivore site use, as well as it's cost effectiveness and different risks of low data returns. However, in these comparisons it is important to recognise other benefits that the use of LEK offers over other methods that may be hard to quantify from a conservation perspective, such as the potential to engagement with large numbers of community members throughout a study area, and combine occupancy research with research into the social elements of human-wildlife interactions.

With access to more comprehensive and robust data, investigating the use of multi-season and multi-species occupancy models would allow a better understanding of carnivore land-use compared the single-species models used here (Nichols et al., 2008). With better data I would also recommend exploring occupancy models that account for false positive detections, the importance of which are being increasingly recognised (Berigan et al., 2018; Pillay et al., 2014; Miller et al., 2011; Royle and Link, 2006).

One of the challenges of using LEK to collect occupancy data is defining the spatial extent in which species detections are reported. There have been a number of different methods used to define AOKs, for instance; using well defined state level administrative areas (Karanth et al., 2009); using well known pre-determined areas, i.e. forest reserves, national parks or forestry blocks (Pillay et al., 2011; Pillay et al., 2013; Brittain et al., 2018); or using a drawn map in areas where interviewees and researchers are both able to interpret and define spatial extents on maps (Taubmann et al., 2015; Zeller et al., 2011; Petracca et al., 2013; Martínez-Martí et al., 2016). Our study area, covering approximately $1500km^2$, was too large to accurately map using participatory methods and available resources, is not divided into widely recognised and appropriately sized areas and the majority of pastoralist's are not familiar with drawn maps. These constraints required a novel methodology for defining AOKs in a way that was relevant and understandable to both the research team and respondents. However, our solution, to restrict AOKs to a 1km buffer around respondent's bomas, is likely to have introduced a number of biases in species detection and occupancy probabilities due to the proximity of the AOK to human habitation and how respondents are likely to spend different amounts of time in their AOK during different seasons. While in this landscape and cultural context there was no better way of collecting spatially explicit detection data it is

worth noting the variety of methods used to define AOKs and that there is little work done comparing their accuracy.

7.2.3 Tolerance towards large carnivores

Chapter five focuses on the human aspects of human-carnivore impacts, assessing the drivers of tolerance and intolerance of large carnivores among livestock owning households. While this study found direct and indirect experience influences tolerance towards hyenas we found no evidence that experience influenced tolerance towards lions, however we only measured experience over a short time frame. Further work that explores how the cumulative impact of different experiences of carnivores interacts with other factors to influence changes in tolerance through time would improve our understanding of the longer term implications of human-carnivore interactions. Similarly our assessment of the impact of engagements with RCP interventions did not consider the impact that repeated exposure to programmes or the time since last exposure to programmes has on tolerance. Understanding how engagements with interventions, tolerance and time interact will allow more effective and efficient planning of where and when programmes should be implemented and repeated. This analysis also grouped all RCP interventions together, while the various programmes have different aims and attempt to increase tolerance towards large carnivores via different means - for instance through environmental education, benefits as a result of carnivore presence or reducing the severity of HWIs. Further study of how these different programmes influence perceptions of benefits, risks and therefore tolerance towards carnivores will not only improve the intervention's effectiveness but also ensure interventions are not having unintended impacts on respondent's risk perceptions.

It is also important to acknowledge the cultural context within which this re-

search has taken place. It is important to question how relevant and cross-cultural socio-pyschological frameworks are likely to be when the majority of psychological theory has been developed in North American and European contexts (Henrich et al., 2010; Parathian et al., 2018). Encouraging a broader scholarship around socio-pyschological theory and its impacts on tolerance and attitudes towards wildlife is likely to capture more of the differences in how cultures engage with and perceive different risks and hazards such as large carnivores. Pastoralist communities in Tanzania, who made up the majority of respondents, are in a state of cultural flux, between their strong traditional cultural identities and greater access to technology which increases their exposure to global cultures and pressures (Hodgson, 2001). Understanding how this mixing of cultural pressures influences tolerance towards large carnivores and traditional beliefs around carnivore killing will not only help us understand aspects of contemporary system but also potentially help predict the future direction and implications of human-carnivore interactions (Bruskotter et al., 2017).

Recent work by Struebig et al. (2018) has also shown the importance of ecological variables that predict risk of tiger encounter in understanding tolerance to tigers in Indonesia, with ecological variables providing a 32 fold improvement in models compared to those using just social variables. Combining data on the environmental variables that influence carnivore occupancy and attack risk across the Rungwa-Ruaha landscape with social data could not only improve our understanding of the drivers of tolerance but also allows geographic areas to be ranked by risk of attacks and risk of retaliatory killings, allowing better prioritisation of conservation resources (Struebig et al., 2018).

7.2.4 Modelling human-wildlife interactions

Chapter 6 demonstrates many of the difficulties of accurately modelling human-carnivore impacts. Our relatively poor ecological understanding of many of these systems and the species involved adds to the challenges of modelling systems containing a wide array of species with complex interactions. The use of functional responses in continuous models required large numbers of model parameters which were not all derivable from the literature, requiring the use of parameters derived from different study sites, substitute species or best guesses. This difficulty was compounded by the relative complexity and species richness of African savannah systems compared to other systems where human-carnivore interactions occur. I would recommend further work exploring the use of other modelling frameworks (e.g. structured population models (De Roos et al., 1992)) that are less challenging to parameterise. Parameterising models of less complex and better understood ecosystems (e.g. temperate systems where wolves predate deer and livestock), may also offer fewer challenges.

The difficulties in finding literature to parameterise this model highlights how poorly understood the ecology of many of these systems are. Parameterising type II functional responses requires very basic data on species behaviour (Fay and Greeff, 1999; Fryxell et al., 2007), a number of which were not available for common savannah species, for instance daily food requirements for black backed jackal or food consumption rates for natal multimammate mouse. This highlights the importance of fundamental research into species behavioural ecology and how the publication of this, seemingly basic, information can contribute to answering complex questions in socio-ecological systems (Tewksbury et al., 2014; Botkin et al., 2007).

7.2.5 Large carnivores and conservation conflicts

This thesis has focused on the social and ecological complexity of human-wildlife impacts, it has not, however, addressed the wider political complexity that exists within conservation conflicts that surround the management of large carnivores (Redpath et al., 2013; Young et al., 2010). Here it must be acknowledged that the research questions and framing were conceived by authors who hold the moral view that in general conserving carnivores is correct. Therefore in discussing conservation conflicts, while we attempt to be objective, we must recognise that we are not impartial bystanders, but actors invested in the outcome of the conflict.

Chapter five investigated tolerance towards carnivores among community members living alongside Ruaha National Park; many of those interviewed wanted carnivore populations to decrease or disappear (Table 5.3) representing one view in the conservation conflict over carnivore management in this landscape. Counter to this view is that of international NGOs and Tanzanian government authorities who are working to protect and conserve carnivore populations (Ruaha Carnivore Project, 2018; TAWIRI, 2009). The mainstream discussions of HWIs still uses human-wildlife conflict framing (Dickman, 2010; Peterson et al., 2010; Redpath et al., 2014), positioning conservationists as neutral bystanders attempting to mediate a conflict between wildlife and humans, focusing research on attitudes of the local human communities who are "in conflict" with wildlife. However, many conservation biologists would not accept resolutions that threaten conservation outcomes and so are not in fact interested in resolving conflicts as much as winning them (Redpath et al., 2013). If we consider conservationists as antagonists in these conflicts then it is vital that we also understand their views and motivations if we are to find resolutions of this conflict that are acceptable to all involved parties.

Once we acknowledge that these conflicts are between human groups then as well as considering the attitudes and motivations of all parties it is also important to acknowledge the power dynamics at play if we are to truly understand how conflict is manifested and can be resolved. A significant proportion of conservation organisations, practitioners and funding originate in high-income countries (many with colonial pasts), while many prominent conservation conflicts involve communities who were historically colonised and continue to experience neo-colonial treatment (e.g. (Rust and Taylor, 2016)). This pits powerful national and international elites with the skills to lever economic and political power against often marginalised local communities. While there exists a literature examining the wider global conservation movements roots and role in historical and neo-colonial processes (Neumann, 1998; Garland, 2008; Mbaria and Ogada, 2016) this critique is especially relevant to conservation conflicts. All conflicts are about power and understanding the power dynamics between two groups and their historical context is an important step if the conflict is to be truly resolved.

Pastoralists in East Africa have suffered a history of oppression, with the loss of much of their traditional grazing lands to settlers, ranchers, agriculturalists and national parks, and concerted efforts by colonial and post-colonial governments to exclude them from state sponsored development (Hodgson, 2002; Fratkin, 1997). As well as this material marginalisation, pastoralists have suffered social disenfranchising, labelled second-class citizens and disparaged as backwards and culturally conservative (Hodgson, 2002; Hodgson, 2001). Our understanding of conservation conflicts involving pastoralists must take into account this historical and contemporary oppression and their social and political power in relation to those who create policy that decides where pastoralists are allowed to live or that dictates how pastoralists are allowed to engage with carnivores they encounter. Fur-

ther research that explores the local, national and international power dynamics between different actors in conservation conflicts in the Rungwa-Ruaha Ecosystem and further afield, and how these actors use the different levels and types of power at their disposal to further their aims is vital in understanding and resolving these conflicts.

7.3 Conclusions

This thesis has cast some light on the complexity of the ecological and social processes that interact to create conservation conflicts over the management of large carnivores and their impacts. Many communities suffer a range of costs as a result of sharing land and other resources with large carnivores, with the presence of carnivores and risk of losses influenced by a range of temporal, spatial and social variables (Chapters 3 & 4). Alongside an array of social and psychological variables, these interactions can influence tolerance of the large carnivores (Chapter 5), and in situations where intolerance leads to lethal control this can put carnivore populations at risk of extinction (Chapter 6). The negative impact of intolerance and lethal control of carnivore populations puts these communities in conflict with those who perceive large carnivores as charismatic species with important ecological and social roles (Chapter 6). If we are to resolve these conflicts and ensure the persistence of large carnivore populations and the well being of the communities they live alongside, we must continue to improve our understanding of the complex interplay of factors that influence human-carnivore impacts and place these within the wider social and political contexts that mediate relations between human groups with different interests.

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APPENDIX A

INTERVIEWS

A.1 Questionnaire

Interviews were conducted using the ODK (Brunette et al., 2013) system on google nexus tablets. While conditional logic was used in the interviews it has not been included in this Appendix for clarity.

name	label::english
start_time	
today	
boma_number	Boma number
survey_number	Survey number
location	Where are you?
interview_gps	Record GPS location of the household's Boma
s_gps	What are the boma's GPS south co-ordinates?
n_gps	What are the boma's GPS east co-ordinates?
same_boma	Has this boma been interviewed before?
boma_avail	Is it possible to do an interview at this boma this month?
boma_emp	Why was it not possible to conduct an interview?
	Read the following to the respondent: I am a research assistant with the Ruaha Carnivore Project. We are researching carnivores and other wildlife in village land. Would you be interested in being involved? We want to learn where carnivores live at different times of the year so we can reduce the numbers of attacks on livestock. However we will not be able to stop all attacks from happening. I want to speak to livestock herders and vijana who spend time in the bush and see the tracks and signs of animals. If you choose to be a part of this, here is what will happen: I will ask you a few questions and then we will need walk about 1km from your homestead for a mapping exercise. Then I will ask you about wildlife around your homestead. The interview will take about one hour. We will want to return throughout the next year to ask questions about wildlife around your homestead, these repeat interviews will take about 15 minutes and will not involve walking anywhere. I will record the answers you give me on this tablet. This research is anonymous, which means that in any reports, your name will not be used. This is completely voluntary and we can stop any time you like. This research has been approved by Oxford University's ethics committee. If you would like to speak to the University directly, I can give you their postal address or their email address. Do feel free to contact me also. My mobile is [Local number will be provided]. You don't have to say yes to the project; you can ask me any questions you want before or throughout; you can also withdraw at any stage.
ethics	Are you still willing to take part?
boma_name	Boma (mzee) name
respondent_name	Respondent name
same_respondent	Is it the same respondent as before?
interviewers	Interviewer or interviewers
one_year	Have you lived here more than one year?
years	How many years have you lived here?

months	How many months have you lived here?
lion_desc	Can you describe what a lion looks like?
lion_track	Can you describe or draw on the ground what a lion's track looks like?
lion_call	Can you describe or imitate the noise a lion makes?
leopard_desc	Can you describe what a leopard looks like?
leopard_track	Can you describe or draw on the ground what a leopard's track looks like?
leopard_call	Can you describe or imitate the noise a leopard makes?
cheetah_desc	Can you describe what a cheetah looks like?
cheetah_track	Can you describe or draw on the ground what a cheetah's track looks like?
cheetah_call	Can you describe or imitate the noise a cheetah makes?
wilddog_desc	Can you describe what a wild dog looks like?
wilddog_track	Can you describe or draw on the ground what a wild dog's track looks like?
wilddog_call	Can you describe or imitate the noise a wild dog makes?
hyaena_desc	Can you describe what a hyaena looks like?
hyaena_track	Can you describe or draw on the ground what a hyaena's track looks like?
hyaena_call	Can you describe or imitate the noise a hyaena makes?
species_sheet	Can you name these animals?
sp_one	Species one correct?
sp_two	Species two correct?
sp_three	Species three correct?
sp_four	Species four correct?
sp_five	Species five correct?
sp_six	Species six correct?
sp_seven	Species seven correct?
sp_eight	Species eight correct?
tracks_sheet	Can you name the species that made these footprints?
track_one	Species one correct?
track_two	Species two correct?
track_three	Species three correct?
track_four	Species four correct?
track_five	Species five correct?
knowledge	Does the respondent have an acceptable knowledge of local wildlife and their tracks to be a part of the study?
age	Respondent age
gender	Respondent gender
tribe	Respondent tribe
phone	If this is a boma we have interviewed before check that the phone numbers on the mapping sheet are correct, if they are incorrect then correct them on the mapping sheet
phone1	First phone number respondent can be contacted on
phone2	Second phone number respondent can be contacted on
phone3	Third phone number respondent can be contacted on
education	What is your highest education level?
dry_season_house	Does your household have a dry season boma elsewhere?
dry_season_month	Last season which months did you spend at your dry season bomas?

dry_season_entire_household	When you are moving with your livestock do you take them all or leave some?
start_mapping	Start mapping exercise
lacking_knowledge	Thank the respondent for their time, but inform them that we need to use someone with better knowledge of the wildlife
ack_one_1km	Find the initial interview sheet and maps for this boma in the folder. Remind the respondent of the distance to the landmark that is 1km from their boma, read the description of the landmark to the respondent and show them the map of landmarks that are 1km from the boma.
_1km_map	Show the respondent the 1km map
ack_two_1km	Read the following to the respondent: I am going to ask you about any animals or signs of animals that you have seen or heard in the area around your boma shown on the map. You must only tell me about animals or signs of animals you yourself have seen or heard. If somebody else has told you about an animal being around but you yourself have not seen it, its tracks or heard it then please say that you have not seen it.
lion_1km_30	Have you seen or heard any signs of lions that have been inside the area shown on the map in the last 30 days?
lion_detection_1km	Did you see a lion or see its tracks or hear it call?
lion_number_1km	How many lions do you think were inside the area on the map in the last 30 days? More or less than 20?
leopard_1km_30	Have you seen or heard any signs of leopards that have been inside the area shown on the map in the last 30 days?
leopard_detection_1km	Did you see a leopard or see its tracks or hear it call?
leopard_number_1km	How many leopards do you think were inside the area on the map in the last 30 days? More or less than 20?
hyena_1km_30	Have you seen or heard any signs of hyenas that have been inside the area shown on the map in the last 30 days?
hyena_detection_1km	Did you see a hyena or see its tracks or hear it call?
hyena_number_1km	How many hyenas do you think were inside the area on the map in the last 30 days? More or less than 20?
cheetah_1km_30	Have you seen or heard any signs of cheetahs that have been inside the area shown on the map in the last 30 days?
cheetah_detection_1km	Did you see a cheetah or see its tracks or hear it call?
cheetah_number_1km	How many cheetahs do you think were inside the area on the map in the last 30 days? More or less than 20?
wilddog_1km_30	Have you seen or heard any signs of wild dogs that have been inside the area shown on the map in the last 30 days?
wilddog_detection_1km	Did you see a wild dog or see its tracks or hear it call?
wilddog_number_1km	How many wild dogs do you think were inside the area on the map in the last 30 days? More or less than 20?
jackal_1km_30	Have you seen or heard any signs of jackals that have been inside the area shown on the map in the last 30 days?
jackal_detection_1km	Did you see a jackal or see its tracks or hear it call?
jackal_number_1km	How many jackals do you think were inside the area on the map in the last 30 days? More or less than 20?
kudu_1km_30	Have you seen or heard any signs of kudus that have been inside the area shown on the map in the last 30 days?
kudu_detection_1km	Did you see a kudu or see its tracks or hear it call?
kudu_number_1km	How many kudus do you think were inside the area on the map in the last 30 days? More or less than 20?

eland_1km_30	Have you seen or heard any signs of elands that have been inside the area shown on the map in the last 30 days?
eland_detection_1km	Did you see a eland or see its tracks or hear it call?
eland_number_1km	How many elands do you think were inside the area on the map in the last 30 days? More or less than 20?
waterbuck_1km_30	Have you seen or heard any signs of Waterbucks that have been inside the area shown on the map in the last 30 days?
waterbuck_detection_1km	Did you see a waterbuck or see its tracks or hear it call?
waterbuck_number_1km	How many Waterbucks do you think were inside the area on the map in the last 30 days? More or less than 20?
zebra_1km_30	Have you seen or heard any signs of zebras that have been inside the area shown on the map in the last 30 days?
zebra_detection_1km	Did you see a zebra or see its tracks or hear it call?
zebra_number_1km	How many zebras do you think were inside the area on the map in the last 30 days? More or less than 20?
buffalo_1km_30	Have you seen or heard any signs of buffalos that have been inside the area shown on the map in the last 30 days?
buffalo_detection_1km	Did you see a buffalo or see its tracks or hear it call?
buffalo_number_1km	How many buffalos do you think were inside the area on the map in the last 30 days? More or less than 20?
impala_1km_30	Have you seen or heard any signs of impalas that have been inside the area shown on the map in the last 30 days?
impala_detection_1km	Did you see an impala or see its tracks or hear it call?
impala_number_1km	How many impalas do you think were inside the area on the map in the last 30 days? More or less than 20?
duiker_1km_30	Have you seen or heard any signs of duikers that have been inside the area shown on the map in the last 30 days?
duiker_detection_1km	Did you see a duiker or see its tracks or hear it call?
duiker_number_1km	How many duikers do you think were inside the area on the map in the last 30 days? More or less than 20?
dikdik_1km_30	Have you seen or heard any signs of dik diks that have been inside the area shown on the map in the last 30 days?
dikdik_detection_1km	Did you see a dik dik or see its tracks or hear it call?
dikdik_number_1km	How many dik diks do you think were inside the area on the map in the last 30 days? More or less than 20?
bushbuck_1km_30	Have you seen or heard any signs of bushbucks that have been inside the area shown on the map in the last 30 days?
bushbuck_detection_1km	Did you see a bushbuck or see its tracks or hear it call?
bushbuck_number_1km	How many bushbucks do you think were inside the area on the map in the last 30 days? More or less than 20?
hogs_1km_30	Have you seen or heard any signs of warthog or bushpigs that have been inside the area shown on the map in the last 30 days?
hogs_detection_1km	Did you see a bushpig or warthog or see their tracks or hear them call?
hogs_number_1km	How many warthog or bushpigs do you think were inside the area on the map in the last 30 days? More or less than 20?
monkey_1km_30	Have you seen or heard any signs of monkeys that have been inside the area shown on the map in the last 30 days?
monkey_detection_1km	Did you see a monkey or see its tracks or hear it call?
monkey_number_1km	How many monkeys do you think were inside the area on the map in the last 30 days? More or less than 20?

baboon_1km_30	Have you seen or heard any signs of baboons that have been inside the area shown on the map in the last 30 days?
baboon_detection_1km	Did you see a baboon or see its tracks or hear it call?
baboon_number_1km	How many baboons do you think were inside the area on the map in the last 30 days? More or less than 20?
giraffe_1km_30	Have you seen or heard any signs of giraffes that have been inside the area shown on the map in the last 30 days?
giraffe_detection_1km	Did you see a giraffe or see its tracks or hear it call?
giraffe_number_1km	How many giraffes do you think were inside the area on the map in the last 30 days? More or less than 20?
elephant_1km_30	Have you seen or heard any signs of elephants that have been inside the area shown on the map in the last 30 days?
elephant_detection_1km	Did you see a elephant or see its tracks or hear it call?
elephant_number_1km	How many elephants do you think were inside the area on the map in the last 30 days? More or less than 20?
ack_one_2km	Remind the respondent of the landmark that is 2km from their boma, read the description of the landmark to the respondent and show them the map of landmarks that are 2km from the boma.
_2km_map	Show the respondent the 2km map
ack_two_2km	Read the following to the respondent: I am going to ask you about any animals or signs of animals that you have seen or heard in the area around your boma shown on the map. You must only tell me about animals or signs of animals you yourself have seen or heard. If somebody else has told you about an animal being around but you yourself have not seen it, its tracks or heard it then please say that you have not seen it.
lion_2km_30	Have you seen or heard any signs of lions that have been inside the area shown on the map in the last 30 days?
lion_detection_2km	Did you see a lion or see its tracks or hear it call?
lion_number_2km	How many lions do you think were inside the area on the map in the last 30 days? More or less than 20?
leopard_2km_30	Have you seen or heard any signs of leopards that have been inside the area shown on the map in the last 30 days?
leopard_detection_2km	Did you see a leopard or see its tracks or hear it call?
leopard_number_2km	How many leopards do you think were inside the area on the map in the last 30 days? More or less than 20?
hyena_2km_30	Have you seen or heard any signs of hyenas that have been inside the area shown on the map in the last 30 days?
hyena_detection_2km	Did you see a hyena or see its tracks or hear it call?
hyena_number_2km	How many hyenas do you think were inside the area on the map in the last 30 days? More or less than 20?
cheetah_2km_30	Have you seen or heard any signs of cheetahs that have been inside the area shown on the map in the last 30 days?
cheetah_detection_2km	Did you see a cheetah or see its tracks or hear it call?
cheetah_number_2km	How many cheetahs do you think were inside the area on the map in the last 30 days? More or less than 20?
wilddog_2km_30	Have you seen or heard any signs of wild dogs that have been inside the area shown on the map in the last 30 days?
wilddog_detection_2km	Did you see a wild dog or see its tracks or hear it call?
wilddog_number_2km	How many wild dogs do you think were inside the area on the map in the last 30 days? More or less than 20?
jackal_2km_30	Have you seen or heard any signs of jackals that have been inside the area shown on the map in the last 30 days?

jackal_detection_2km	Did you see a jackal or see its tracks or hear it call?
jackal_number_2km	How many jackals do you think were inside the area on the map in the last 30 days? More or less than 20?
kudu_2km_30	Have you seen or heard any signs of kudus that have been inside the area shown on the map in the last 30 days?
kudu_detection_2km	Did you see a kudu or see its tracks or hear it call?
kudu_number_2km	How many kudus do you think were inside the area on the map in the last 30 days? More or less than 20?
eland_2km_30	Have you seen or heard any signs of elands that have been inside the area shown on the map in the last 30 days?
eland_detection_2km	Did you see a eland or see its tracks or hear it call?
eland_number_2km	How many elands do you think were inside the area on the map in the last 30 days? More or less than 20?
Waterbuck_2km_30	Have you seen or heard any signs of Waterbucks that have been inside the area shown on the map in the last 30 days?
waterbuck_detection_2km	Did you see a waterbuck or see its tracks or hear it call?
Waterbuck_number_2km	How many Waterbucks do you think were inside the area on the map in the last 30 days? More or less than 20?
zebra_2km_30	Have you seen or heard any signs of zebras that have been inside the area shown on the map in the last 30 days?
zebra_detection_2km	Did you see a zebra or see its tracks or hear it call?
zebra_number_2km	How many zebras do you think were inside the area on the map in the last 30 days? More or less than 20?
buffalo_2km_30	Have you seen or heard any signs of buffalos that have been inside the area shown on the map in the last 30 days?
buffalo_detection_2km	Did you see a buffalo or see its tracks or hear it call?
buffalo_number_2km	How many buffalos do you think were inside the area on the map in the last 30 days? More or less than 20?
impala_2km_30	Have you seen or heard any signs of impalas that have been inside the area shown on the map in the last 30 days?
impala_detection_2km	Did you see an impala or see its tracks or hear it call?
impala_number_2km	How many impalas do you think were inside the area on the map in the last 30 days? More or less than 20?
duiker_2km_30	Have you seen or heard any signs of duikers that have been inside the area shown on the map in the last 30 days?
duiker_detection_2km	Did you see a duiker or see its tracks or hear it call?
duiker_number_2km	How many duikers do you think were inside the area on the map in the last 30 days? More or less than 20?
dikdik_2km_30	Have you seen or heard any signs of dik diks that have been inside the area shown on the map in the last 30 days?
dikdik_detection_2km	Did you see a dik dik or see its tracks or hear it call?
dikdik_number_2km	How many dik diks do you think were inside the area on the map in the last 30 days? More or less than 20?
bushbuck_2km_30	Have you seen or heard any signs of bushbucks that have been inside the area shown on the map in the last 30 days?
bushbuck_detection_2km	Did you see a bushbuck or see its tracks or hear it call?
bushbuck_number_2km	How many bushbucks do you think were inside the area on the map in the last 30 days? More or less than 20?
hogs_2km_30	Have you seen or heard any signs of warthog or bushpigs that have been inside the area shown on the map in the last 30 days?

hogs_detection_2km	Did you see a warthog or bushpig or see their tracks or hear them call?
hogs_number_2km	How many warthog or bushpigs do you think were inside the area on the map in the last 30 days? More or less than 20?
monkey_2km_30	Have you seen or heard any signs of monkeys that have been inside the area shown on the map in the last 30 days?
monkey_detection_2km	Did you see a monkey or see its tracks or hear it call?
monkey_number_2km	How many monkeys do you think were inside the area on the map in the last 30 days? More or less than 20?
baboon_2km_30	Have you seen or heard any signs of baboons that have been inside the area shown on the map in the last 30 days?
baboon_detection_2km	Did you see a baboon or see its tracks or hear it call?
baboon_number_2km	How many baboons do you think were inside the area on the map in the last 30 days? More or less than 20?
giraffe_2km_30	Have you seen or heard any signs of giraffes that have been inside the area shown on the map in the last 30 days?
giraffe_detection_2km	Did you see a giraffe or see its tracks or hear it call?
giraffe_number_2km	How many giraffes do you think were inside the area on the map in the last 30 days? More or less than 20?
elephant_2km_30	Have you seen or heard any signs of elephants that have been inside the area shown on the map in the last 30 days?
elephant_detection_2km	Did you see a elephant or see its tracks or hear it call?
elephant_number_2km	How many elephants do you think were inside the area on the map in the last 30 days? More or less than 20?
depredation	Has any of your households animals been killed or attacked by carnivores in the last 30 days?
carnivore_attack	Which carnivores are responsible for the attack?
livestock_predation_lion	Which type of animals were attacked by lions?
area_attack_lion	Where were your livestock attacked?
cow_deaths_lion	How many cows were killed by lions?
cow_injured_lion	How many cows were injured but not killed?
goat_attack_lion	How many goats were killed by lions?
goat_injured_lion	How many goats were injured but not killed?
sheep_attack_lion	How many sheep were killed by lions?
sheep_injured_lion	How many sheeps were injured but not killed?
donkey_attack_lion	How many donkeys were killed by lions?
donkey_injured_lion	How many donkeys were injured but not killed?
pig_attack_lion	How many pigs were killed by lions?
pig_injured_lion	How many pigs were injured but not killed?
dog_dog_lion	How many dogs were killed by lions?
dog_injured_lion	How many dogs were injured but not killed?
livestock_predation_leopard	Which type of animals were attacked by leopards?
area_attack_leopard	Where were your livestock attacked?
cow_deaths_leopard	How many cows were killed by leopards?
cow_injured_leopard	How many cows were injured but not killed?
goat_attack_leopard	How many goats were killed by leopards?
goat_injured_leopard	How many goats were injured but not killed?
sheep_attack_leopard	How many sheep were killed by leopards?

sheep_injured_leopard	How many sheeps were injured but not killed?
donkey_attack_leopard	How many donkeys were killed by leopards?
donkey_injured_leopard	How many donkeys were injured but not killed?
pig_attack_leopard	How many pigs were killed by leopards?
pig_injured_leopard	How many pigs were injured but not killed?
dog_dog_leopard	How many dogs were killed by leopards?
dog_injured_leopard	How many dogs were injured but not killed?
livestock_predation_cheetah	Which type of animals were attacked by cheetahs?
area_attack_cheetah	Where were your livestock attacked?
cow_deaths_cheetah	How many cows were killed by cheetahs?
cow_injured_cheetah	How many cows were injured but not killed?
goat_attack_cheetah	How many goats were killed by cheetahs?
goat_injured_cheetah	How many goats were injured but not killed?
sheep_attack_cheetah	How many sheep were killed by cheetahs?
sheep_injured_cheetah	How many sheeps were injured but not killed?
donkey_attack_cheetah	How many donkeys were killed by cheetahs?
donkey_injured_cheetah	How many donkeys were injured but not killed?
pig_attack_cheetah	How many pigs were killed by cheetahs?
pig_injured_cheetah	How many pigs were injured but not killed?
dog_dog_cheetah	How many dogs were killed by cheetahs?
dog_injured_cheetah	How many dogs were injured but not killed?
livestock_predation_wild_dog	Which type of animals were attacked by wild dogs?
area_attack_wild_dog	Where were your livestock attacked?
cow_deaths_wild_dog	How many cows were killed by wild dogs?
cow_injured_wild_dog	How many cows were injured but not killed?
goat_attack_wild_dog	How many goats were killed by wild dogs?
goat_injured_wild_dog	How many goats were injured but not killed?
sheep_attack_wild_dog	How many sheep were killed by wild dogs?
sheep_injured_wild_dog	How many sheeps were injured but not killed?
donkey_attack_wild_dog	How many donkeys were killed by wild dogs?
donkey_injured_wild_dog	How many donkeys were injured but not killed?
pig_attack_wild_dog	How many pigs were killed by wild dogs?
pig_injured_wild_dog	How many pigs were injured but not killed?
dog_dog_wild_dog	How many dogs were killed by wild dogs?
dog_injured_wild_dog	How many dogs were injured but not killed?
livestock_predation_hyena	Which type of animals were attacked by hyenas?
area_attack_hyena	Where were your livestock attacked?
cow_deaths_hyena	How many cows were killed by hyenas?
cow_injured_hyena	How many cows were injured but not killed?
goat_attack_hyena	How many goats were killed by hyenas?
goat_injured_hyena	How many goats were injured but not killed?
sheep_attack_hyena	How many sheep were killed by hyenas?

sheep_injured_hyena	How many sheeps were injured but not killed?
donkey_attack_hyena	How many donkeys were killed by hyenas?
donkey_injured_hyena	How many donkeys were injured but not killed?
pig_attack_hyena	How many pigs were killed by hyenas?
pig_injured_hyena	How many pigs were injured but not killed?
dog_dog_hyena	How many dogs were killed by hyenas?
dog_injured_hyena	How many dogs were injured but not killed?
livestock_predation_jackal	Which type of animals were attacked by jackals?
area_attack_jackal	Where were your livestock attacked?
cow_deaths_jackal	How many cows were killed by jackals?
cow_injured_jackal	How many cows were injured but not killed?
goat_attack_jackal	How many goats were killed by jackals?
goat_injured_jackal	How many goats were injured but not killed?
sheep_attack_jackal	How many sheep were killed by jackals?
sheep_injured_jackal	How many sheeps were injured but not killed?
donkey_attack_jackal	How many donkeys were killed by jackals?
donkey_injured_jackal	How many donkeys were injured but not killed?
pig_attack_jackal	How many pigs were killed by jackals?
pig_injured_jackal	How many pigs were injured but not killed?
dog_dog_jackal	How many dogs were killed by jackals?
dog_injured_jackal	How many dogs were injured but not killed?
village_attack	Have you heard of any one elses livestock being attacked by carnivores in last 30 days?
village_attack_carn	Which carnivores have been responsible for attacks on other peoples livestock in the last 30 days?
attitudes	I will now ask you a few questions about your opinion towards carnivores
dvd	Have you experienced a DVD night from RCP?
dvd_when	When was this?
hh_visit	Have you experienced a household visit from RCP? Not including visits made by this research team
hh_visit_when	When was this?
park_visit	Have you ever gone on a park visit with RCP?
park_visit_date	When was this?
noise	Have you been given a noisemaker by RCP?
noise_when	When was this?
wireboma	Have you had a wire boma made by RCP?
wireboma_when	When was this built?
wireboma_use	How useful do you think the wire boma has been?
cct	Have you received any benefits from the CCT programme?
cct_when	When was this?
vet_meds	Have you received any vetinary medicines from RCP?
vet_meds_when	When was this?
other_rcp	Have you received any other help or input from Ruaha Carnivore Project?
other_rcp_info	What was this?
other_rcp_when	When was this?

lion_def	Have you heard of the Lion Defenders or Guardian programme?
lion_def_inv	Have you had any involvement with the lion defenders programme?
lion_def_info	What was this?
lion_def_when	When was this?
other_orgs	Have you had contact or interaction with any other wildlife organisations?
other_org_info	Which organisation was this?
other_org_info2	What was the contact or interaction?
other_org_date	When was this?
lion_pop	What would you like to see happen to the numbers of lion in this area?
cheetah_pop	What would you like to see happen to the numbers of cheetah in this area?
leopard_pop	What would you like to see happen to the numbers of leopard in this area?
hyaena_pop	What would you like to see happen to the numbers of hyena in this area?
wilddog_pop	What would you like to see happen to the numbers of wild dog in this area?
jackal_pop	What would you like to see happen to the numbers of jackal in this area?
lion_per	How much benefit do you and your household receive from the presence of lion in this area?
lion_per_ben	What are these benefits?
lion_vill	How much benefit do you think your village receives from the presence of lions in this area?
lion_vill_ben	What are these benefits?
hyena_per	How much benefit do you and your household receive from the presence of hyena in this area?
hyena_per_ben	What are these benefits?
hyena_vill	How much benefit do you think your village receives from the presence of hyenas in this area?
hyena_vill_ben	What are these benefits?
responsible	Who is responsible for managing large carnivores and other wildlife in your village?
responsible_other	which other organisations?
agree_ack	I am now going to ask you a series of statements, can you tell me how much you agree with each of these
social_trust	The organisations responsible for managing wildlife are able to protect people and livestock from carnivores
lions_tourist	Lions benefit people by attracting tourists
lion_beautiful	I feel that lions are beautiful animals
lion_protection	Lions deserve protection
lion_prestige	Killing a lion for prestige/status is acceptable
lion_dissaprove	Many people important to you would disapprove of you killing lions
lion_kill_cow	If your cow was killed by a lion you will kill the lion
lion_kill_fam	If your family member was injured by a lion you would kill it
lion_kill_boma	If a lion entered you boma you would kill it
lion_kill_bush	When you see a lion in the bush you will kill it
lion_people_control	People are able to completely stop lions from attacking their livestock.
lion_personal_control	you are able to completely stop lions from attacking your livestock.
lion_problem	Living alongside lions is one the hardest challenges you face
hyena_tourist	Hyenas benefit people by attracting tourists
hyena_beautiful	I feel that hyenas are beautiful animals

hyena_protection	hyenas deserve protection
hyena_prestige	Killing a hyena for prestige/status is acceptable
hyena_dissaprove	Many people important to me would disapprove of me killing hyenas
hyena_kill_cow	If my cow was killed by a hyena I will kill the hyena
hyena_kill_fam	If a family member was injured by a hyena I would kill it
hyena_kill_boma	If a hyena entered my boma I would kill it
hyena_kill_bush	When you see a hyena in the bush I will kill it
hyena_people_control	People are able to stop hyenas from attacking their livestock.
hyena_personal_control	You are able to stop hyenas from attacking my livestock.
hyena_problem	Living alongside hyenas is one the hardest challenges you face
lion_vill_land_inc	How frequently do lions enter your village land?
lion_attack_inc	How frequently do lions attack livestock in your village?
lion_trend	What do you think is happening to the numbers of lions entering your village land?
lion_attacks_trend	What do you think is happening to the numbers of lion attacks on livestock in your village?
hyena_vill_land_inc	How frequently do hyenas enter your village land?
hyena_attack_inc	How frequently do hyenas attack livestock in your village?
hyena_trend	What do you think is happening to the numbers of hyenas entering your village land?
hyena_attacks_trend	What do you think is happening to the numbers of hyena attacks on livestock in your village?
thanks	Tell the respondent the interview is over, thank them for their time and remind them that we will visit again in two months, but we will use the phone numbers they provided to arrange the visit

APPENDIX B

CHAPTER 3

B.1 Averaged binomial GLM outputs

Table B.1: GLM model averaged estimates, with standard errors, 95% confidence intervals and relative variable importance. Important variables (RVI = 1 and CI that do not cross 0) highlighted in bold.

	Attack risk					Attack location				
	Estimate	Standard error	95% CI Lower	95% CI Upper	RVI*	Estimate	Standard error	95% CI Lower	95% CI Upper	RVI*
Intercept	-3.64	1.29	-6.17	-1.10	–	-0.563	0.357	-1.27	0.143	–
Precipitation	0.533	0.333	-0.120	1.19	0.92	1.30×10^{-3}	0.0404	-0.0786	0.0812	0.04
EVI	-2.75×10^{-3}	0.0758	-0.152	0.146	0.03	-1.39×10^{-3}	0.0385	-0.0774	0.0747	0.04
Presence of small prey	1.65	0.771	0.133	3.16	1.00	0.0146	0.279	-0.536	0.565	0.04
Presence of large prey	0.0797	0.211	-0.334	0.493	0.22	3.73×10^{-3}	0.0100	-0.195	0.202	0.04
Distance to WMA	-0.416	0.160	-0.730	-0.102	1.00	0.263	0.226	-0.185	0.710	0.75
Distance to roads	0.128	0.127	-0.120	0.376	0.70	0.424	0.191	0.0458	0.801	1.00
Distance to all rivers	-3.51×10^{-3}	0.0321	-0.0664	0.0594	0.04	0.0974	0.169	-0.235	0.429	0.39
Distance to large rivers	-0.267	0.197	-0.653	0.119	0.85	-0.105	0.217	-0.531	0.321	0.31
Precipitation:large rivers	0.0232	0.0767	-0.127	0.174	0.17	–	–	–	–	–
Population density	7.02×10^{-4}	0.0294	-0.0570	0.0584	0.03	3.92×10^{-5}	0.0416	-0.0822	0.0823	0.04
Elevation	1.20×10^{-5}	0.0372	-0.0731	0.0731	0.03	0.121	0.237	-0.346	0.587	0.34
Converted land	-3.36×10^{-3}	0.0509	-0.103	0.0966	0.07	0.0104	0.0715	-0.131	0.151	0.09
Enforced wire boma	0.645	0.311	0.0323	1.26	1.00	1.24	0.474	0.302	2.17	1.00
Maasai	-0.0279	0.222	-0.463	0.407	0.63†	–	–	–	–	–
Sukuma	-0.162	0.487	-1.12	0.794	0.63†	–	–	–	–	–
Agriculturalist	-0.643	0.613	-1.84	0.558	0.63†	–	–	–	–	–
February	-14.3	541	-1080	1050	1.00†	–	–	–	–	–
March	-1.19	1.23	-3.60	1.22	1.00†	–	–	–	–	–
April	-0.755	1.21	-3.13	1.62	1.00†	–	–	–	–	–
May	2.13	1.08	1.18×10^{-3}	4.25	1.00†	–	–	–	–	–
June	1.73	1.20	-0.619	4.08	1.00†	–	–	–	–	–
July	0.492	1.17	-1.80	2.78	1.00†	–	–	–	–	–
August	1.57	1.23	-0.854	3.98	1.00†	–	–	–	–	–
September	0.615	1.21	-1.76	2.99	1.00†	–	–	–	–	–
October	-1.45	1.55	-4.49	1.60	1.00†	–	–	–	–	–
November	0.672	1.24	-1.76	3.11	1.00†	–	–	–	–	–
December	-1.37	1.31	-3.95	1.20	1.00†	–	–	–	–	–

*RVI (relative variable importance) is the sum of AIC weights from all the models including that variable.

† RVI values are constant for all levels within a categorical variable.

APPENDIX C

CHAPTER 4

C.1 Occupancy Models

C.1.1 Naive model outputs

Naive site use and estimates of p and ψ for constant models.

TABLE C.1. Naive site use and estimates of transformed p and ψ probability for constant models for carnivores and most common prey species.

Species	Round	Naive ψ	p(.)	LCI	UCI	ψ(.)	LCI	UCI
Lion	1	0.515	0.316	0.213	0.440	0.706	0.418	0.889
	2-5	0.375	0.145	0.0894	0.225	0.532	0.292	0.759
	6	0.182	0.429	0.228	0.657	0.240	0.103	0.463
Hyena	1	0.938	0.917	0.848	0.956	1.00	0.00	1.00
	2-5	1	0.796	0.739	0.843	1.00	0.00	1.00
	6	0.969	0.916	0.834	0.959	1.00	0.00	1.00
Leopard	1	0.423	0.220	0.0747	0.502	0.976	0.00	1.00
	2-5	0.148	0.304	0.139	0.541	0.189	0.0689	0.424
	6	0.0455	0.0215	0.00216	0.182	0.990	0.00	1.00
Cheetah	1	0.375	0.350	0.115	0.692	0.807	0.0443	0.997
	2-5	0.0625	0.355	0.00736	0.976	0.0797	0.00732	0.504
	6	0	No detections					
Wild dog	1	0.360	0.354	0.132	0.665	0.536	0.201	0.84
	2-5	0.115	0.0212	0.00676	0.0643	0.998	0.00	1.00
	6	0.0435	0.0209	0.00269	0.145	0.995	0.00	1.00
Monkeys	1	1.00	0.948	0.903	0.972	1.00	0.00	1.00
	2-5	1.00	0.904	0.870	0.930	1.00	0.00	1.00
	6	1.00	0.778	0.700	0.840	1.00	0.00	1.00
Dikdik	1	1.00	0.931	0.882	0.960	1.00	0.00	1.00
	2-5	1.00	0.853	0.814	0.886	1.00	0.00	1.00
	6	0.970	0.822	0.748	0.878	1.00	0.00	1.00
Kudu	1	0.970	0.858	0.769	0.903	0.97	0.812	0.996
	2-5	1.00	0.763	0.717	0.803	1.00	0.00	1.00
	6	0.848	0.563	0.466	0.655	0.899	0.691	0.972
Impala	1	0.848	0.577	0.496	0.655	0.919	0.683	0.983
	2-5	0.719	0.479	0.421	0.537	0.750	0.564	0.874
	6	0.848	0.616	0.518	0.705	0.925	0.628	0.989

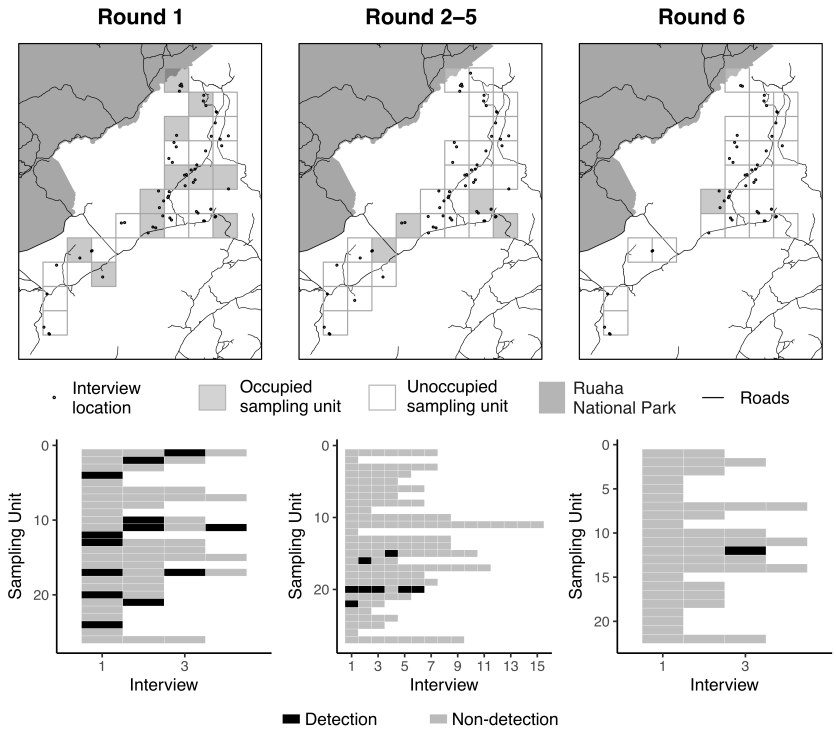


FIGURE C.1. Seasonal leopard detection histories and maps of sampling units where detection occurred.

C.1.2 Detection histories and maps of sampling units

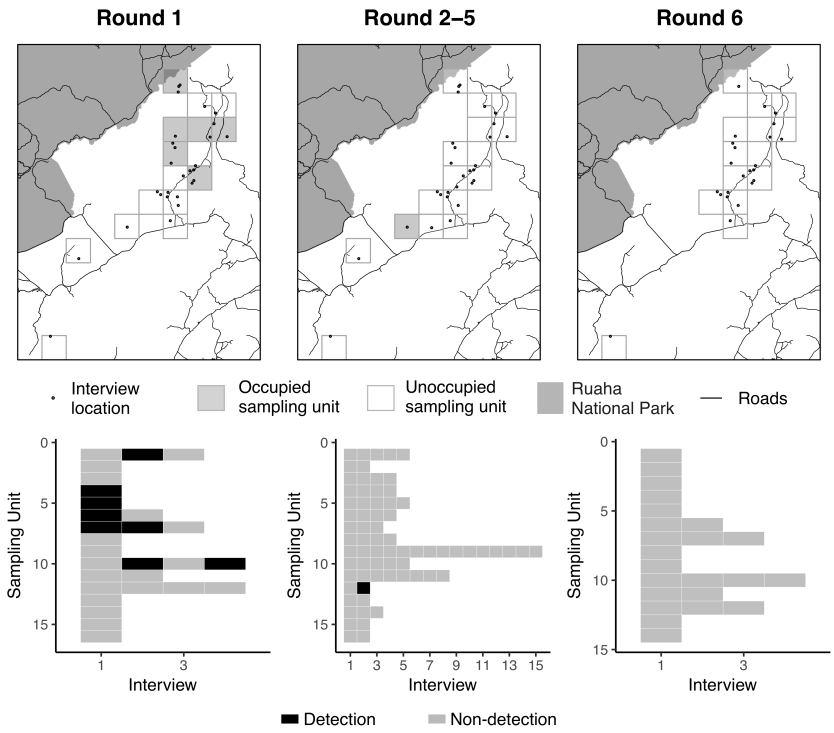


FIGURE C.2. Seasonal cheetah detection histories and maps of sampling units where detection occurred.

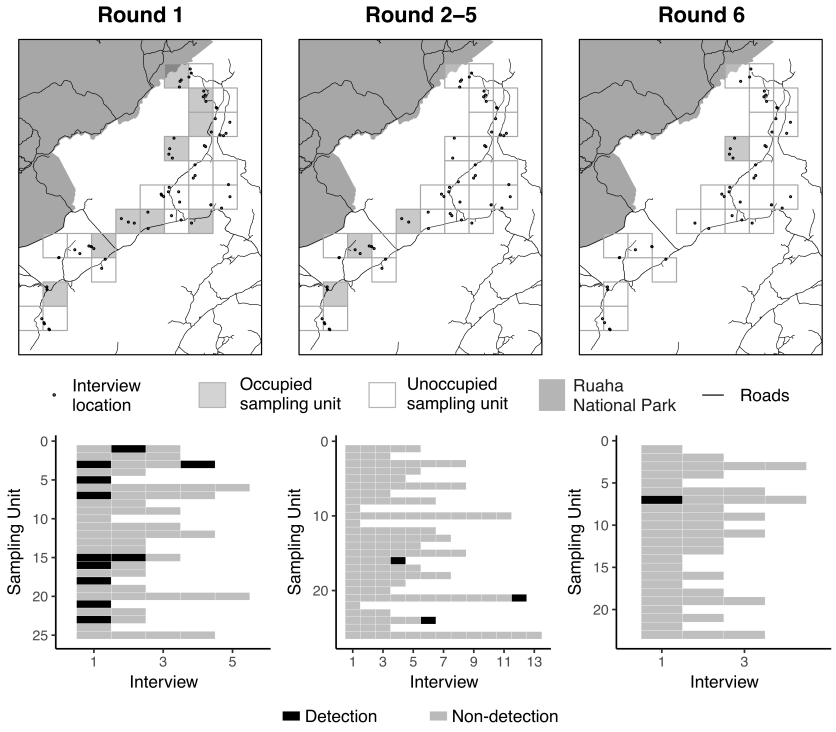


FIGURE C.3. Seasonal wild dog detection histories and maps of sampling units where detection occurred.

C.1.3 Top ranked model outputs

Top ranked models (ΔQAICc <2) for all carnivore species

Table C.2: Top ranked occupancy models (Δ QAICc < 2), w_i is the QAICc model weight, n is the number of parameters in the model and ΔQAICc is the difference in values between the lowest QAICc model and each model. A, respondent age; P, average distance to Ruaha National Park; O, average distance to road; C, proportion of land converted to agriculture; E, average EVI during survey period; W, average rainfall during survey period; D, human population density; RW, wet season rivers; RD, dry season rivers; H, households per sampling unit

Species	Round	Model	QAICc	ΔQAICc	w_i	n
Lion	1	p(E+P)ψ(C+P)	128.1	0.00	0.0196	6
		p(E+P)ψ(E+P)	128.1	0.0356	0.0192	6
		p(D+P)ψ(D+O)	128.7	0.595	0.0145	6
		p(D+A+P)ψ(D+O)	129.0	0.903	0.0125	7
		p(D+P)ψ(W+O)	129.5	1.45	0.00950	6
		p(D+A+P)ψ(W+O)	129.6	1.48	0.00935	7
		p(D+E+P)ψ(C+P)	129.7	1.63	0.00865	7
		p(D+E+P)ψ(E+P)	129.8	1.67	0.00849	7
		p(A+E+P)ψ(E+P)	129.8	1.67	0.00848	7
		p(A+E+P)ψ(C+P)	129.8	1.69	0.00843	7
	2-5	p(.)ψ(RD+P)	57.2	0.00	0.0302	4
		p(.)ψ(P)	58.0	0.890	0.0194	3

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Table C.2 – continued from previous page

Species	Round	Model	QAICc	ΔQAICc	w_i	n
		p(.)ψ(.)	58.6	1.49	0.0143	2
		p(RD+P)ψ(.)	58.9	1.77	0.0125	4
	6	p(P)ψ(W+P)	28.3	0.00	0.0627	5
		p(A+P)ψ(W+P)	29.8	1.43	0.0307	6
Hyena	1	p(RW)ψ(C)	60.2	0	0.0363	4
		p(RW)ψ(H)	60.3	0.0231	0.0359	4
		p(O)ψ(E+O)	61.0	0.728	0.0252	5
		p(O)ψ(W+O)	61.0	0.743	0.0250	5
		p(O)ψ(E+H)	61.0	0.749	0.0250	5
		p(RW+O)ψ(W+H+P+O)	61.4	1.18	0.0202	8
		p(RW+O)ψ(C+E+H+O)	61.5	1.21	0.0198	8
		p(RW+O)ψ(E+O)	61.8	1.53	0.0169	6
		p(RW+O)ψ(W+O)	61.8	1.53	0.0169	6
		p(O)ψ(C+E+H+O)	62.2	1.98	0.0135	7
	2-5	p(A+RW)ψ(.)	238.7	0.00	0.0285	4
		p(RW)ψ(.)	238.0	0.296	0.0245	3
		p(RW+P)ψ(.)	238.0	0.306	0.0244	4
		p(A+RW+P)ψ(.)	238.1	0.380	0.0235	5
		p(A+P)ψ(.)	238.4	0.703	0.0200	4
		p(P)ψ(.)	239.2	1.45	0.0138	3
		p(A+E+RW)ψ(.)	239.5	1.83	0.0114	5
		p(E+RW)ψ(.)	239.7	1.98	0.0106	4
	6	p(E)ψ(.)	49.9	0.00	0.0273	3

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Table C.2 – continued from previous page

Species	Round	Model	QAICc	ΔQAICc	w_i	n
		p(D)ψ(.)	50.2	0.341	0.0230	3
		p(E+O)ψ(.)	51.6	1.76	0.0113	4
		p(C+E)ψ(.)	51.8	1.88	0.0107	4
		p(D+O)ψ(.)	51.8	1.97	0.0102	4
		p(D)ψ(D+RW)	51.9	1.99	0.0101	5
		p(D)ψ(E+P)	51.9	1.99	0.0101	5
		p(D)ψ(E+W)	51.9	2.00	0.0101	5
Leopard	1	p(.)ψ(H+O)	54.2	0.00	0.0693	4
		p(.)ψ(C)	55.6	1.37	0.0350	3
		p(.)ψ(H+RD)	55.8	1.58	0.0315	4
		p(.)ψ(H)	55.1	1.84	0.0277	3
		p(.)ψ(.)	56.1	1.86	0.0274	2
	2-5	p(D+RD)ψ(H)	34.5	0.00	0.0270	5
		p(RD+O)ψ(H)	35.2	0.679	0.0192	5
		p(D)ψ(H)	35.2	0.734	0.0187	6
		p(H+P)ψ(D)	36.1	1.60	0.0121	5
		p(H)ψ(D)	36.2	1.71	0.0115	6
		p(H+P)ψ(W)	36.2	1.73	0.0114	5
		p(D)ψ(H+P)	36.3	1.77	0.0111	5
		p(D)ψ(W+H)	36.3	1.82	0.0109	5
		p(H)ψ(W)	36.4	1.87	0.0106	6
		p(H)ψ(RD+O)	36.4	1.87	0.0106	5
		p(H+RD+O)ψ(H)	36.4	1.94	0.0102	6

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Table C.2 – continued from previous page

Species	Round	Model	QAICc	ΔQAICc	w_i	n
	6	$p(.)\psi(.)$	9.27	0.00	0.192	2
Cheetah	1	$p(.)\psi$(D)	26.3	0.00	0.125	3
		$p(.)\psi$(E)	27.1	0.776	0.0849	3
	2-5	$p(.)\psi(.)$	13.1	0.00	0.162	2
		$p(.)\psi$(E)	14.9	1.77	0.0671	3
		$p(.)\psi$(C)	14.9	1.77	0.0669	3
		p(Eψ(E)	15.0	1.92	0.0622	3
		$p(.)\psi$(W)	15.1	1.98	0.0604	3
Wild dog	1	$p(.)\psi(.)$	35.5	0.00	0.0307	2
		$p(.)\psi$(H)	35.7	0.158	0.0284	3
		p(C)$\psi(.)$	35.7	0.176	0.0282	3
		p(H)$\psi(.)$	35.9	0.321	0.0262	3
		$p(.)\psi$(D+H)	35.9	0.395	0.0252	4
		$p(.)\psi$(H+P)	36.0	0.502	0.0239	4
		$p(.)\psi$(C)	36.4	0.899	0.0196	3
		$p(.)\psi$(W+H)	36.7	1.15	0.0173	4
		$p(.)\psi$(H+O)	36.7	1.15	0.0173	4
		$p(.)\psi$(D+O)	36.7	1.20	0.0169	4
		p(H)ψ(O)	37.1	1.53	0.0143	4
		$p(.)\psi$(H+RW)	37.3	1.78	0.0126	4
		p(C)ψ(H)	37.5	1.94	0.0116	4
	2-5	$p(.)\psi$(P)	29.9	0.00	0.0149	3
		$p(.)\psi$(E+P)	30.2	0.314	0.0127	4

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Table C.2 – continued from previous page

Species	Round	Model	QAICc	ΔQAICc	w_i	n
		p(E)ψ(P)	30.6	0.684	0.0106	4
		p(D)ψ(P)	30.8	0.878	0.00959	4
		p(P)ψ(E+P)	31.0	1.08	0.00866	5
		p(.)ψ(W)	31.0	1.13	0.00846	3
		p(E+P)ψ(D)	31.2	1.35	0.00758	5
		p(P)ψ(P)	31.4	1.46	0.00716	4
		p(.)ψ(W+O)	31.4	1.51	0.00699	4
		p(.)ψ(D+P)	31.5	1.66	0.00650	4
		p(.)ψ(RD+O)	31.8	1.93	0.00567	4
	6	p(A)ψ(RW)	10.2	0.00	0.0510	4

APPENDIX D

CHAPTER 5

D.1 SEM outputs

Standardised regression weights and associated levels of significance for all direct, indirect and total pathways from hyena and lion tolerance structural equation models.

Hyena Tolerance Structural Equation Model Outputs

Standardized Regression Weights

Parameter			Estimate	Lower	Upper	P
Population trend	<---	RCP engagements	.333	.192	.449	.002
Population trend	<---	Direct experience	.301	.173	.408	.001
Population trend	<---	Social trust	-.125	-.267	.011	.073
Population trend	<---	Personal control	.111	-.030	.242	.123
Population trend	<---	Indirect experience	.075	-.062	.205	.298
Positive beliefs	<---	RCP engagements	-.204	-.356	-.035	.017
Cognitive risk	<---	Population trend	.734	.631	.807	.002
Village benefits	<---	Indirect experience	-.161	-.285	-.042	.008
Village benefits	<---	RCP engagements	.125	-.027	.282	.099
Positive beliefs	<---	Social trust	.242	.072	.414	.003
Village benefits	<---	Social trust	.126	-.009	.244	.070
Affective risk	<---	RCP engagements	-.273	-.401	-.132	.002
Acceptance capacity	<---	Cognitive risk	-.212	-.354	-.074	.006
Tourism benefits	<---	Positive beliefs	.559	.422	.682	.001
Deserve protection	<---	Positive beliefs	.854	.758	.930	.001
Are beautiful	<---	Positive beliefs	.920	.835	.989	.001
Acceptance capacity	<---	Positive beliefs	.195	.018	.358	.033
Acceptance capacity	<---	Village benefits	.325	.184	.458	.001
Affective risk	<---	Personal control	.420	.277	.553	.001
Affective risk	<---	Positive beliefs	.119	-.014	.259	.072

Standardized Total Effects

	Personal control	Social trust	Direct experience	Indirect experience	RCP engagements	Population trend	Village benefits	Positive beliefs	Cognitive risk
Population trend	.111	-.125	.301	.075	.333	.000	.000	.000	.000
Village benefits	.000	.126	.000	-.161	.125	.000	.000	.000	.000
Positive beliefs	.000	.242	.000	.000	-.204	.000	.000	.000	.000
Cognitive risk	.081	-.092	.221	.055	.244	.734	.000	.000	.000
Are beautiful	.000	.223	.000	.000	-.188	.000	.000	.920	.000
Deserve protection	.000	.207	.000	.000	-.174	.000	.000	.854	.000
Tourism benefits	.000	.135	.000	.000	-.114	.000	.000	.559	.000
Affective risk	.420	.029	.000	.000	-.297	.000	.000	.119	.000
Acceptance capacity	-.017	.108	-.047	-.064	-.051	-.156	.325	.195	-.212

Standardized Total Effects - Two Tailed Significance (BC)

	Personal control	Social trust	Direct experience	Indirect experience	RCP engagements	Population trend	Village benefits	Positive beliefs	Cognitive risk
Population trend	.123	.073	.001	.298	.002	...	...	...	...
Village benefits	...	.070	...	.008	.099	...	...	...	...
Positive beliefs	...	.003	...	...	.017	...	...	...	...
Cognitive risk	.128	.078	.001	.299	.002	.002	...	...	...
Are beautiful	...	.004	...	...	.018	...	...	.001	...
Deserve protection	...	.004	...	...	.016	...	...	.001	...
Tourism benefits	...	.003	...	...	.013	...	...	.001	...
Affective risk	.001	.053	...	...	.002	...	...	.072	...
Acceptance capacity	.070	.005	.005	.004	.262	.005	.001	.033	.006

Standardized Indirect Effects

	Personal control	Social trust	Direct experience	Indirect experience	RCP engagements	Population trend
Population trend	.000	.000	.000	.000	.000	.000
Village benefits	.000	.000	.000	.000	.000	.000
Positive beliefs	.000	.000	.000	.000	.000	.000
Cognitive risk	.081	-.092	.221	.055	.244	.000
Are beautiful	.000	.223	.000	.000	-.188	.000
Deserve protection	.000	.207	.000	.000	-.174	.000
Tourism benefits	.000	.135	.000	.000	-.114	.000
Affective risk	.000	.029	.000	.000	-.024	.000
Acceptance capacity	-.017	.108	-.047	-.064	-.051	-.156

Standardized Indirect Effects - Two Tailed Significance (BC)

	Personal control	Social trust	Direct experience	Indirect experience	RCP engagements	Population trend
Population trend	...	...	...	...	...	...
Village benefits	...	...	...	...	...	...
Positive beliefs	...	...	...	...	...	...
Cognitive risk	.128	.078	.001	.299	.002	...
Are beautiful	...	.004	...	...	.018	...
Deserve protection	...	.004	...	...	.016	...
Tourism benefits	...	.003	...	...	.013	...
Affective risk	...	.053	...	...	.048	...
Acceptance capacity	.070	.005	.005	.004	.262	.005

Lion Tolerance Structural Equation Model Outputs

Standardized Regression Weights

Parameter			Estimate	Lower	Upper	P
Positive beliefs	<---	Personal control	-.162	-.309	-.009	.037
Population trend	<---	RCP engagements	.327	.190	.447	.001
Benefits	<---	RCP engagements	.581	.417	.716	.001
Population trend	<---	Positive beliefs	-.269	-.408	-.133	.001
Cognitive risk	<---	Positive beliefs	-.149	-.301	.000	.050
Cognitive risk	<---	Benefits	.119	-.042	.288	.140
Cognitive risk	<---	Population trend	.646	.534	.730	.002
Cognitive risk	<---	Personal control	-.072	-.180	.037	.210
Affective risk	<---	RCP engagements	-.233	-.388	-.090	.002
Acceptance capacity	<---	Cognitive risk	-.190	-.397	.050	.140
Tourism benefits	<---	Positive beliefs	.477	.306	.628	.001
Deserve protection	<---	Positive beliefs	.851	.741	.934	.001
Are beautiful	<---	Positive beliefs	.894	.787	.984	.002
Affective risk	<---	Positive beliefs	.239	.092	.381	.001
Acceptance capacity	<---	Positive beliefs	.282	.098	.469	.006
Household benefits	<---	Benefits	.742	.602	.848	.001
Village benefits	<---	Benefits	.814	.687	.925	.002
Acceptance capacity	<---	Benefits	.332	.151	.490	.002
Acceptance capacity	<---	Population trend	.170	-.044	.374	.109
Affective risk	<---	Personal control	.188	.023	.345	.028

Standardized Total Effects

	Personal control	Positive beliefs	RCP engagements	Benefits	Population trend	Cognitive risk
Positive beliefs	-.162	.000	.000	.000	.000	.000
Benefits	.000	.000	.581	.000	.000	.000
Population trend	.044	-.269	.327	.000	.000	.000
Cognitive risk	-.020	-.323	.281	.119	.646	.000
Village benefits	.000	.000	.472	.814	.000	.000
Household benefits	.000	.000	.431	.742	.000	.000
Are beautiful	-.144	.894	.000	.000	.000	.000
Deserve protection	-.137	.851	.000	.000	.000	.000
Tourism benefits	-.077	.477	.000	.000	.000	.000
Affective risk	.149	.239	-.233	.000	.000	.000
Acceptance capacity	-.034	.298	.195	.309	.047	-.190

Standardized Total Effects - Two Tailed Significance (BC)

	Personal control	Positive beliefs	RCP engagements	Benefits	Population trend	Cognitive risk
Positive beliefs	.037	...	...	...	...	...
Benefits	...	...	.001	...	...	...
Population trend	.023	.001	.001	...	...	...
Cognitive risk	.740	.001	.001	.140	.002	...
Village benefits	...	...	.001	.002	...	...
Household benefits	...	...	.001	.001	...	...
Are beautiful	.039	.002	...	...	...	...
Deserve protection	.035	.001	...	...	...	...
Tourism benefits	.032	.001	...	...	...	...
Affective risk	.078	.001	.002	...	...	...
Acceptance capacity	.228	.001	.001	.001	.531	.140

Standardized Indirect Effects

	Personal control	Positive beliefs	RCP engagements	Benefits	Population trend	Cognitive risk
Positive beliefs	.000	.000	.000	.000	.000	.000
Benefits	.000	.000	.000	.000	.000	.000
Population trend	.044	.000	.000	.000	.000	.000
Cognitive risk	.052	-.174	.281	.000	.000	.000
Village benefits	.000	.000	.472	.000	.000	.000
Household benefits	.000	.000	.431	.000	.000	.000
Are beautiful	-.144	.000	.000	.000	.000	.000
Deserve protection	-.137	.000	.000	.000	.000	.000
Tourism benefits	-.077	.000	.000	.000	.000	.000
Affective risk	-.039	.000	.000	.000	.000	.000
Acceptance capacity	-.034	.016	.195	-.023	-.123	.000

Indirect Effects - Two Tailed Significance (BC)

	Personal control	Positive beliefs	RCP engagements	Benefits	Population trend	Cognitive risk
Positive beliefs	...	...	...	...	...	...
Benefits	...	...	...	...	...	...
Population trend	.023	...	...	...	...	...
Cognitive risk	.021	.001	.001	...	...	...
Village benefits	...	...	.001	...	...	...
Household benefits	...	...	.001	...	...	...
Are beautiful	.036	...	...	...	...	...
Deserve protection	.031	...	...	...	...	...
Tourism benefits	.031	...	...	...	...	...
Affective risk	.021	...	...	...	...	...
Acceptance capacity	.231	.518	.001	.152	.138	...

APPENDIX E

SOFTWARE USED

The majority of data manipulation, analysis and visualising was conducted in R (R Core Team, 2017) using the following packages:
Data Manipulation and Graphing: Tidyverse (Wickham, 2017). Spatial analysis: Raster (Hijmans and Etten, 2014), rgdal (Bivand et al., 2017), sp (Pebesma and Bivand, 2005), maps (Richard A. Becker et al., 2018), Grid2Polygons (Fisher, 2017), Maptools (Bivand and Lewin-Koh, 2018). Statistical Analysis and Modelling: Unmarked (Fiske and Chandler, 2011), rms (Harrell Jr, 2018), MuMIn (Barto, 2018), DeSolve (Soetaert et al., 2010). Miscellaneous: Beepr (Bååth, 2015).

QGIS (Team, 2017) was used for visualising spatial data, planning field work and drawing maps.

Google Earth Engine (Gorelick et al., 2017) was used to access, visualise and process remote sensed spatial data.