Behavioural Adjustments of Lion (*Panthera leo*) in Response to Risk of Human-Caused Mortality

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ABSTRACT

Fear of predation can have a major impact on the behaviour of prey species. Despite recent codifying of the concept of the ecology of fear, there has been relatively little focus on how these ideas apply to large carnivore species which, although not prey *sensu stricto*, may experience fear as a result of threats from humans. This thesis argues that large mammalian carnivores are subject to a Landscape of Fear similar to that described for prey species, and will respond behaviourally to fear of human-caused mortality.

The idea of a "Landscape of Coexistence" is introduced to denote the perceived risk from humans and associated behavioural responses that can be overlain on spatio-temporally heterogeneous landscapes. Literature on the ecology of fear for large mammalian carnivores and, as there is a dearth of such literature, the current theory on the ecology of fear for other guilds is reviewed, and how this might inform large carnivore behaviour in a Landscape of Coexistence is explored. Behavioural effects of human-caused mortality risk are revealed for lions living in a human dominated landscape (Laikipia County, Kenya), specifically how lions adjust their movement patterns, habitat use and foraging tactics when in proximity to humans. It is argued that these behavioural adjustments represent a trade-off between maximising fitness enhancing activities and minimising the risk of human-caused mortality, thus need to be taken into consideration along with the lethal effects of humans when explaining the density, distribution and behaviour of lions throughout much of their remaining range.

Although fear is generic, 'human-caused mortality risk' represents a distinct and very important sub-set of the ecology of fear for the carnivore guild. The existence of a Landscape of Coexistence has implications for understanding their foraging ecology, and ultimately their population dynamics and role in the ecosystem, and is therefore, important for the conservation of large carnivores throughout large parts of their remaining ranges.

A young Laikipia lioness plucks up the courage to come out and feed on her kill in our presence during daylight hours, while the rest of her pride remain hidden in nearby thick bush. Photo bv: James Warwick

"It is better to be frightened now than killed hereafter"

Winston Churchill (1874-1965).

DECLARATION

The thesis presented here represents a project that I developed as a D.Phil. student of the Wildlife Conservation Research Unit, Zoology Department, University of Oxford. I designed and integrated the components relevant to lion's behavioural responses to risk of human-caused mortality as part of the wider research remit of the Living With Lions project, Kenya. I implemented all aspects of the project, analysed the results and wrote all of the material in the dissertation. While others assisted with the project at various stages, it represents a work entirely of my own doing and I assume full responsibility for the results presented here. The text, excluding figure legends, tables, references and appendices, does not exceed 50,000 words. All photographs included in the thesis are the copyright of James Warwick, Josep Oriol or Tui de Ray.

Signed:

Date: 8th October 2013.

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LIST OF COMMON AND SCIENTIFIC NAMES FOR ALL SPECIES MENTIONED IN THIS THESIS

Common name	***Scientific name***
Brown bear	*Ursus arctos*
Buffalo	*Syncerus caffer*
Cheetah	*Acinonyx jubatus*
Cougar	*Felis concolor*
Coyote	*Canis latrans*
Eland	*Taurotragus oryx*
Giraffe	*Giraffa camelopardalis*
Grant's gazelle	*Gazella grantii*
Grevy's Zebra	*Equus grevyi*
Grey wolf	*Canis lupus*
Hartebeest	*Alcelaphus buselaphus*
Iberian lynx	*Lynx pardinus*
Impala	*Aepyceros melampus*
Killer whale	*Orcinus orca*
Kudu	*Tragelaphus strepsiceros*
Leopard	*Panthera pardus*
Lion	*Panthera leo*
Oryx	*Oryx beisa*
Plains zebra	*Equus quagga*
Polar bear	*Ursus maritimus*
Spotted hyaena	*Crocuta crocuta*
Thompsons gazelle	*Gazella thomsoni*
Tiger	*Panthera tigris*
Warthog	*Phacochoerus africanus*
Waterbuck	*Kobus ellipsiprymnus*
Wild dog	*Lycaon pictus*

Chapter 1. Introduction

The ecological consequences of being downgraded from top to penultimate predator

A collared Laikipia lioness takes advantage of her relatively secure position in a rocky outcrop to watch us approach. A few seconds later she turned and disappeared. Large carnivores may employ complex avoidance strategies in order to survive in human-dominated landscapes. Photo by: James Warwick.

This chapter represents a manuscript in preparation for submission to the journal 'Oikos'. Authors: Alayne Oriol-Cotterill, Marion Valeix, Laurence Frank, Corinna Riginos and David Macdonald.

1.1. Background

Historically, the ecology of predator-prey relationships has focused on direct consumptive interactions (Rosenzweig & MacArthur 1963). More recently, ecologists have begun to consider that many effects of predators are mediated by non-lethal, fear-driven behavioural responses of prey animals to the risk of predation, referred to as the ecology of fear (Sih 1980, Lima & Dill 1990, Brown et al. 1999, Laundré et al. 2001, 2010). We define fear in this context as an emotion in response to a perceived threat to life that causes an individual to change its behaviour in order to avoid that threat. The ecology of fear, shown for diverse taxa, often manifests as costs to various fitness-enhancing activities such as foraging, and animals face a trade-off between minimising the risk of predation against optimising nutritional intake (Sih 1980, Brown & Kotler 2004). For example, prey that perceive a higher risk of predation have been shown to spend increased time in safer habitats, although such habitats are not necessarily the most nutritionally rich and spending time in them can reduce overall diet quality (Sih 1980, Hernández & Laundré 2005). As a result, the consequences of fear can extend to negatively impacting prey population dynamics (Preisser et al. 2005). The presence of predators in an ecosystem, therefore, affects prey directly through mortality and indirectly as a result of fear and the associated anti-predatory responses, which result from perceived risk of predation translated into behavioural adjustments.

Risk of predation is neither spatially uniform (e.g. habitat structure has been shown to affect the risk-aversion behaviour of a variety of prey species - Mao et al. 2005, Liley & Creel 2007), nor temporally uniform (e.g. avoidance of high risk areas varies in response to diurnal changes in predator activity - Valeix et al. 2009a). Laundré et al. (2001) first used the term “Landscape of Fear” to describe the peaks and troughs of predation risk and associated anti-predator behavioural responses that can be overlain on any heterogeneous landscape. This landscape of fear may be as or more important in influencing the distribution of prey

than any of the other 'landscapes' such as resource availability or habitat structure (Willems & Hill 2009, Laundré et al. 2010, Thaker et al. 2011).

The behavioural effects of fear have typically been considered for prey species, which are subject to the top-down effects of predators. Although fear as a potential driver of behavioural change in meso-carnivores (subject to intraguild predation and competition with larger carnivores) has received some attention, the effects of fear on apex carnivores (e.g. African lion, tiger, grey wolf, brown bear, polar bear, killer whales, shark species) have rarely been considered explicitly. Large terrestrial carnivores have been eliminated from most of the world because they often prey upon livestock (Weber & Rabinowitz 1996), and to a lesser degree threaten human life (Packer et al. 2005, 2011a). Even in protected areas, the wide ranging behaviour of large carnivores frequently brings them into contact with people and livestock along the boundaries of these areas. These edge effects impact large carnivore ecology and, in combination with stochastic processes, they make many protected areas too small to support viable populations of large carnivores in the long term (Woodroffe & Ginsberg 1998, Harcourt et al. 2001). People kill carnivores where they are perceived to be a threat to life or livelihood and given the "clear and present danger" that humans thus pose (Treves & Karanth 2003), it stands to reason that these carnivores are not only top down players in the landscape of fear experienced by herbivores and smaller carnivores, but that aspects of their own behavioural ecology may also be significantly influenced by the fear of humans. Here it is argued that large mammalian carnivores will respond behaviourally to fear of human-caused mortality, and that these behavioural effects of fear have been understudied, yet need to be taken into consideration when explaining the density, distribution and behaviour of large mammalian carnivores throughout much of their remaining range.

First the concept of a "Landscape of Coexistence" to denote the spatio-temporal variation in human-caused mortality risk to which large carnivores may respond is

introduced. The current peer-reviewed literature on the ecology of fear for large mammalian carnivores is reviewed and, as there is a dearth of literature on this subject, the current theory on the ecology of fear for large mammalian herbivores and meso-carnivores is also reviewed, and how it might inform large carnivore behaviour in a Landscape of Coexistence explored. The behavioural effects of fear in large carnivores should be broadly the same as those shown by other guilds of mammals in response to predation risk, albeit modified by some factors unique to large carnivores. The potential behavioural effects of human-caused mortality risk on large carnivores is clearly outlined, noting where there are already studies demonstrating these effects, and where further research is likely to be fruitful: the key variables characterising a Landscape of Coexistence and its consequences for large carnivore behavioural ecology are emphasised, and the need to take into account individual variability and different spatio-temporal scales is highlighted. Finally, population and ecosystem consequences of the Landscape of Coexistence for carnivores are discussed. It is argued that consideration of the behavioural effects of human induced fear is critical for understanding the full range of anthropogenic impacts on these often-threatened species, and for planning their conservation in human-dominated landscapes.

1.2. The Landscape of Coexistence

Here the term "Landscape of Coexistence" is used to denote the spatio-temporal variation in human-caused mortality risk to which large carnivores may respond. Many large carnivores experience variations in human-caused mortality risk as they move about the landscape: ranging from areas with no risk of human-caused mortality (protected areas or those too remote for significant human presence) to areas with high risk of human-caused mortality, where large carnivores are killed with relative impunity when they threaten human life or livelihood, or where they are a source of economic gain (e.g. through hunting or poaching).

Even within a given land-use type, the level of threat is not uniform: it is likely to vary spatially depending on human density and attitudes towards large carnivores (Romañach et al. 2007) and temporally with changes in environmental conditions and human activity levels. Variations in human-caused mortality risk within and between different land-use areas can result in complex peaks and troughs of human induced fear that are revealed through adjustments in carnivore behavioural ecology.

Although fear is a generic phenomenon, 'human-caused mortality risk' represents a very important sub-set of the ecology of fear that applies to large carnivores (as well as other notable mammalian species such as elephants and baboons). Human attitudes and tolerance are key to determining people's propensity to kill large carnivores (Hazzah et al. 2009, Dickman 2010). Human-caused mortality risk is likely to decline with distance from human settlements or livestock enclosures, and with human attitudes and activity levels. Key factors characterizing the Landscape of Coexistence, such as livestock husbandry practices, human settlement, grazing patterns and retaliation to livestock depredation, are directly linked to human behaviours, and therefore have the potential to be managed. The Landscape of Coexistence, its description and the processes that generate such a landscape is, therefore, extremely relevant to understanding large carnivore behavioural ecology as well as important in facilitating coexistence with humans.

1.3. The ecology of fear: from its current applications to development for large carnivore ecology

Here a brief overview of the main ways in which large mammalian herbivores and meso-carnivores respond to the fear of predation is provided, and how these might inform the understanding of large carnivore behaviour in a Landscape of Coexistence is explored.

1.3.1. Spatial avoidance

Avoidance of high risk areas is a common behavioural response to the threat of predation. Making use of the spatially heterogeneous distribution of predators by allocating more time to areas with low predator densities is a tactic used by both large herbivores (Valeix et al. 2009b, Thaker et al. 2011) and meso-carnivores (Mills & Gorman 1997, Durant 1998). Similarly, areas characterised by high levels of human activity are avoided by carnivores (for cougar see Dickson et al. 2005, for spotted hyaena see Boydston et al. 2003). However, animals may not totally avoid high risk areas. Such areas may contain valuable resources and complete avoidance would result in a substantial foraging cost. Large carnivores in Landscapes of Coexistence will likely show some large-scale spatial avoidance of human-caused mortality risk (Table 1.1.) but it is also likely that modifying behaviours such as increase in selection for specific habitat structures, temporal partitioning of activities, or increased vigilance will allow large carnivores to avoid humans on a smaller scale and at least partially utilise valuable resources in high risk areas.

1.3.2. Habitat shift

The nature of habitat can modify predator-prey encounter rates and the ultimate outcome of an encounter (Brown & Kotler 2004). Predator hunting success can be so strongly influenced by environmental factors that distinct hunting grounds and refugia are created (Kauffman et al. 2007). What might constitute a refuge habitat depends on the characteristics of both the prey and the predator, and may vary seasonally depending on changes in predator, prey and environmental factors (Mao et al. 2005). Selection for safer habitat structures is a common response to increased risk of predation among mammalian herbivores (Hernández & Laundré 2005, Creel et al. 2005, Wirsing et al. 2007). Meso-carnivores increase their use of habitat refugia in response to risk of intraspecific and intraguild predation and competition during

vulnerable activities e.g. when concealing young (Fernandez & Palomares 2000), resting (Switalski 2003), or feeding on a carcass that might attract the attention of larger carnivores (Hunter et al. 2007).

It is hunting success, not the avoidance of predation risk that is commonly considered the major driver in habitat selection for large carnivores (Hopcraft et al. 2005, Balme et al. 2007). However, any habitat structure that is little used by people, or reduces the probability of people detecting carnivores, for example rocky, steep or thick bush areas, could act as refugia in a Landscape of Coexistence. Dickson et al. (2005) demonstrated the importance of riparian woodlands to cougars moving through a landscape mosaic in California. Similarly, spotted hyaena in southern Kenya were shown to favour thicker bush when in parts of their range used more intensively by people and livestock (Boydston et al. 2003, Kolowski & Holekamp 2009), particularly during vulnerable activities such as nursing young (Pangle & Holekamp 2010a). Lions significantly increase their use of thicker bush cover when seasonal movements of people and livestock bring them into closer proximity (Schuette et al. 2013a). It is likely that certain habitat structures that provide good cover and are less permeable to people on foot or in vehicles (e.g. rocky escarpments/outcrops, thick bush) will play an important role as refugia from humans, and large carnivores in a Landscape of Coexistence will show the greatest selection for refuge habitat structures when utilising parts of their range where human-caused mortality risk is highest (Table 1.1.). This pattern of small scale spatial avoidance will likely be most extreme during activities where large carnivores are most vulnerable e.g. when resting, feeding or concealing young. A greater selection for refuge habitats could represent a significant trade-off between nutritional intake and minimising predation risk, especially for carnivores that would normally have greater hunting success or experience less intraguild competition in more open habitats.

1.3.3. Temporal avoidance

The most effective way in which animals might avoid predation but still utilise high risk areas is by showing temporal changes in activity patterns and using more risky areas at times when predators are the least active (review by Kronfeld-Schor & Dayan 2003). For instance, many large herbivore species shift the timing of their visits to waterholes to avoid the time when their predators are most likely to be hunting (Valeix et al. 2009a, Crosmary et al. 2012). The timing of foraging activities might be particularly influenced by fear since foraging is often associated with being conspicuous and vulnerable. Cheetah are believed to hunt in daylight to avoid competition from hyaenas and lions (Durant 1998, but see Cozzi et al. 2012) and forage less after hearing recordings of lion and spotted hyaena (Durant 2000). Coyotes show temporal separation of foraging activities to avoid the threat of wolves (Arjo & Pletscher 1999). Such temporal adjustments will alter an individual's chance of encountering predators without totally avoiding a particular part of the landscape or habitat type. Similarly, many carnivores in human occupied areas appear to shift the timing of foraging activities to show a greater preference for darkness (e.g. cougars (Van Dyke et al. 1986); brown bears (Knick & Kasworm 1989); tigers (Carter et al. 2012); wild dog (Rasmussen and Macdonald 2012)).

Group-living carnivore species such as lion and spotted hyaena can kill large prey and are particularly conspicuous when they hunt and feed at times when people are active. The longer a large carnivore feeds on any given kill during times when people are active, the more likely it is to be discovered by humans. It is likely that where the risk of human-caused mortality is high, large carnivores should allocate greater foraging effort to times when people are least active, abandon unfinished carcasses before dawn or move carcasses to dense cover when humans are active, and may ultimately select smaller prey species in order to decrease the time spent feeding on any carcass (Table 1.1.). Limiting foraging times to

periods when humans are least active, potentially forcing carnivores to hunt during sub-optimal times, endure greater interspecific competition, and abandon a percentage of kills early, could pose significant cost to large carnivore species living in human dominated landscapes, and potentially limit some carnivores' ability to coexist with people (see Rasmussen & Macdonald 2012).

1.3.4. Vigilance

In many studies of large herbivores and meso-carnivores, the behavioural response to risk of predation is measured is an increase in vigilance (Hunter & Skinner 1998, Hochman & Kotler 2006, Pays et al. 2012). Species, age, sex, and individual characteristics are likely to influence the effect of fear on vigilance; females with young generally show a much greater vigilance response to predation risk than males or females without young (Liley & Creel 2007). Herbivores at the periphery of a herd spend more time vigilant than do their central conspecifics (Blanchard et al. 2007), and species with smaller body size often show a more pronounced increase in vigilance than do larger ones (Hunter & Skinner 1998). Other factors such as habitat structure and forage quality also affect animal vigilance for both herbivores (Pays et al. 2012) and meso-carnivores (Hunter et al. 2007) with an increase in forage quality and visibility both reducing an animal's investment in vigilance.

The primary role of vigilance in carnivores is traditionally interpreted as maximising hunting success (Leyhausen 1979). In meso-carnivores, however, an increase in vigilance level is also a behavioural response to risk of predation by larger carnivores, and other threats such as humans. For example, Pangle and Holekamp (2010a,b) found that spotted hyaena vigilance levels were linked more to interspecific threats that have a high risk of mortality (e.g. attacks by lion or humans), than intraspecific threats or other functions such as searching for mates or prey. Hence large carnivores in a Landscape of Coexistence might be expected

to increase their vigilance in response to an increase in human-caused mortality risk. Current "Landscape of Fear" theory for herbivores and meso-carnivores leads us to predict the highest vigilance levels amongst adult females with young, in small group sizes, at times when people are most active, and when carrying out conspicuous activities such as feeding on a carcass. An increase in vigilance may allow large carnivores to avoid humans on a fine spatial scale but the trade-off between reducing predation risk through increasing vigilance versus maximising feeding efforts could represent a significant cost.

1.3.5. The ultimate foraging choice

Current foraging theory for large carnivores suggests that prey abundance (Van Orsdol et al. 1985, Palomares et al. 2001) and/or vulnerability (Hopcraft et al. 2005, Balme et al. 2007) are the key variables in determining where and what a carnivore kills. The need for livestock to spend time foraging outside of protective enclosures, and the exceptional physical abilities of large carnivore species such as lion, leopard and tiger to breach most livestock enclosures, leaves livestock potentially vulnerable to large carnivore predation even where good management and husbandry are practiced. As livestock are typically much easier to catch as well as more numerous than wild prey outside protected areas, foraging theory would predict that carnivores in human-dominated landscapes should focus on domestic livestock. The few examples of carnivore foraging decisions in Landscapes of Coexistence, however, do not support such a prediction. For example, lions in Botswana have been shown to take livestock less than would be expected based on their abundance and vulnerability (Hemson et al. 2009). Similarly, wild dogs have been found to shift their diet towards smaller wild prey species in pastoral areas in Kenya, allowing them to maintain energy requirements without killing livestock, despite reduced densities of wild prey (Woodroffe et al. 2007). These examples suggest that carnivores are making complex foraging decisions that simultaneously account

for variation in prey abundance, vulnerability, and fear of retaliation by humans for any livestock mortality. Fear of human-caused mortality may, therefore, influence large carnivores in their choice of hunting strategy where both livestock and wild prey are available. These examples support the prediction that large carnivores in Landscapes of Coexistence will kill livestock less than expected from current foraging models where wild prey are available as an alternative prey source to livestock (Table 1.1.), which although might have associated costs for the carnivore, might also give hope for their coexistence with people and livestock given minimal wild prey densities.

1.3.6. Group size

Group size in large herbivores can affect predator-prey encounter rates and outcomes. Large groups may be easier to spot but the likelihood of detecting an approaching predator is higher (the "many eyes effect" – Pulliam 1973) and the principle of dilution reduces each individual's chance of being caught (Foster & Treherne 1981). Although the relationship between group size and fear varies according to various factors (e.g. Creel & Winnie 2005); the general trend amongst large herbivores is for group size to increase in response to increases in predation risk, until limited by availability of resources.

Although inherently flexible in life history traits, the stability and integrity of a group is important to social carnivores, and even solitary carnivores are dependent on social structures for population functioning (Macdonald 1983, Creel & Creel 1995). Human-caused mortality risk could impact both group size and social stability directly when the rate of individuals killed by people is faster than replacement rate (Loveridge et al. 2007) or possibly indirectly through behavioural responses to the fear of humans. There is a paucity of information on the latter but in a Landscape of Coexistence the advantages afforded to social carnivores by forming groups may be outweighed by the greater risk of detection. Energetic

constraints on large carnivores may mean that the ability to form groups large enough for the principle of dilution (Foster & Treherne 1981) to offer a significant advantage is limited, and remaining completely undetected is key to survival for carnivores sharing the landscape with humans. Additionally, as humans are often hunting carnivores with the intention of reducing their numbers, and often have weapons that allow them to kill multiple individuals, detection may mean a large proportion of the group is lost. Contrary to general trends in large herbivore species, large social carnivores in Landscapes of Coexistence may become more solitary in parts of their range where there is an increase in the risk of human-caused mortality (Table 1.1.), and this may confer a considerable cost such as the loss of co-operative hunting advantages, and less effective defence of kills, territory, and young. In order to minimise such costs, it is further possible that social groups might exhibit fission-fusion dynamics, with core groups temporarily splitting at high risk times or in high risk areas and later regrouping when conditions are less risky.

1.4. Future research directions

1.4.1. Characterization of the Landscape of Coexistence

The Landscape of Coexistence emerges from the type and level of human disturbance and interacts with other habitat attributes, such as vegetation cover and wild prey densities, to determine the fear landscape. The shape of the Landscape of Coexistence and the resultant behavioural effects of human-caused mortality risk on large carnivores will, therefore, be dependent on a balance between the distribution of people and livestock and their behaviours, as well as overall human and livestock densities. The greatest behavioural effects of human-caused mortality risk may be expected to arise from a combination of factors such as low tolerance for carnivores, high human-caused mortality levels, widely distributed settlements, and large overlaps in human and large carnivore active periods. A better understanding of

these human determinants of a Landscape of Coexistence is needed to underpin observed changes in carnivore behaviour.

1.4.2. Measuring the effects of a Landscape of Coexistence on carnivore behaviour

Lethal effects of humans on wildlife are traditionally measured at the population level, e.g. changes in the overall population density (Loveridge et al. 2007) or general changes in territoriality and ranging behaviour (Tuyttens & Macdonald 2000, Davidson et al. 2011). Behavioural effects, however, will be best revealed by changes individuals make on a finer spatio-temporal scale as they move through a Landscape of Coexistence.

Changes in vigilance levels in large carnivores due to fear of humans may be hard to demonstrate for most species. In many Landscapes of Coexistence, large carnivores occur in low densities, are often nocturnal, and have been shown to utilise thicker habitats when under threat from humans, making them hard to observe. Even when feeding or resting, changes in vigilance are likely to be hard to measure simply because the presence of human observers is likely to bias any vigilance measures. Comparative studies using video cameras set up at carcasses in both protected areas and Landscapes of Coexistence might reveal differences in vigilance while feeding.

Spatio-temporal differences in habitat use and activity patterns in response to different levels of human-caused mortality risk may be best detected using GPS radio-collar data. Movement patterns reveal how an animal partitions its activities and can provide an understanding of an animal's perception of risk beyond that gained from analysis of simple use versus availability of different habitats in an animal's environment. A faster, straighter path may indicate a desire to pass quickly through an area or a habitat in which an animal perceives a greater degree of risk (see Douglas Hamilton 2005, Graham et al. 2009, Wall et al. 2013 for examples in African elephant). For instance, lions have been shown to speed up

when approaching guarded livestock enclosures in Botswana (Valeix et al. 2012), and cougars travel faster when moving through areas of intense human activity in California (Dickson et al. 2005). Patterns in movement, activity and habitat selection used as a proxy for perception of risk, in combination with other factors such as prey choice and characteristics of den sites and daytime rest or feeding sites, may reveal the importance of human-caused mortality risk as a determinant of behaviour, and help to identify areas and resources of special importance for large carnivores in a Landscape of Coexistence.

1.4.3. The importance of scale: spatio-temporal variations in the perception of fear

The spatio-temporal scale at which behavioural adjustments are measured is also important to consider. Spatial variation in predation risk can occur over large scales, i.e. broad differences in habitat structure and predator densities, or small scales, i.e. the middle versus the edge of a herd (Laundré et al. 2001, Blanchard et al. 2007). Scale is also important when considering temporal variations in risk (Brown & Kotler 2004). It is often hard to distinguish whether animals are utilising longer term knowledge of an area, or are being influenced by more recent experiences in other areas they have travelled through, or are responding to very recent, local signs of predators. Among herbivores, information about the current whereabouts of a predator often cause different behavioural effects than does long term knowledge of risk based on experience (Creel & Winnie 2005, Liley & Creel 2007, Valeix et al. 2009a,b). For carnivores, cheetah have been shown to respond reactively to the immediate threat of lion and spotted hyaena by avoiding them on a small scale but show very little large scale avoidance of areas preferred by these competitively dominant species (Broekhuis et al. 2013). The trade off between avoiding predation and maximising foraging success may also vary with the activity level and satiation of predators, and changes in levels of light (e.g. Packer et al. 2011a); seasonally e.g. with changes in predator and prey condition and

breeding status, vegetation growth, snow cover etc. (Liley & Creel 2007); or over years due to climatic variability (Riginos, in review). The temporal and spatial scales of risk may significantly influence the magnitude of behavioural effects, and subsequent use of the landscape (Werner & Peacor 2003). The Landscape of Coexistence thus needs to be conceived as a dynamic landscape that can be described at different spatial and temporal scales.

1.5. Implications of a Landscape of Coexistence for large carnivores

Because large carnivores share a significant percentage of their remaining range with humans and/or livestock, the Landscape of Coexistence concept is applicable to most remaining large carnivore populations. The possible population and ecosystem consequences of the ecology of fear for large carnivores are highlighted, and it is suggested that, ultimately, understanding the behavioural, as well as lethal, consequences will lead to new insights for better large carnivore management and conservation.

1.5.1. Population consequences

The lethal effects of humans on carnivore populations have received considerable attention: they can significantly affect carnivore population structure and functioning, including causing local or global extinction (Tuyttens & Macdonald 2000, Woodroffe & Frank 2005). There is growing consensus that indirect, behavioural effects of fear of predation can also exact great fitness consequences for prey populations (Werner & Peacor 2003, Preisser et al. 2005), by influencing foraging patterns and energy intake (Christianson & Creel 2010), demography (Creel et al. 2007, 2011), and ultimately the structure of herbivore communities. This raises the potential that carnivores also suffer fitness or population level consequences due to fear of human-caused mortality; see also Schuette et al. (2013a) for an example of lions being

displaced from water sources, and Rasmussen and Macdonald (2012) for an example of wild dogs being forced to hunt at times when interspecific competition is much greater by the presence of humans on the landscape. This chapter has predicted that the fear of human-caused mortality is likely to cause carnivores to exhibit several behavioural adjustments such as foraging in sub-optimal habitats or at sub-optimal times, maintaining higher levels of vigilance, abandoning kills early, or moving kills to habitat refugia when people are active. These are all likely to alter energy budgets, individual fitness and ultimately demographic parameters (e.g. losing the benefits of group living may decrease the survival of young i.e. an anthropogenic Allee effect – see Courchamp et al. 2002 for a description of the Allee effect in Wild dogs).

1.5.1.1. Individual variability

Behavioural adjustments to the fear of humans are likely to affect individuals differently. For example, females with young are likely to be most sensitive to risk and, therefore, show the greatest behavioural changes to a Landscape of Coexistence. Further, dispersing individuals are characterized by very large home ranges and are often forced to use sub-optimal areas, sometimes bringing them into recurrent contact with humans (Stander 1990). They are more likely, therefore, to suffer greater exposure to the risk of human-caused mortality. Hunger may also affect how an individual will use a "risk-prone" versus a "risk-averse" foraging strategy (Gilby & Wrangham 2007). Nutritionally stressed animals such as females with young (Wydeven et al. 2004), dispersing juveniles, or old and decrepit animals (Rabinowitz 1986) may change their perception of risk and utilize riskier habitats or even engage in high risk activities such as killing livestock. The magnitude of the behavioural effects versus lethal effects of humans on large carnivores will likely vary with sex, age, breeding and social

status, nutritional state and health condition of an individual. This would result in different segments of a carnivore population being affected by risk in varying ways and degrees.

1.5.1.2. Species variability

Carnivores display flexible behaviour and life history traits that confer a level of resilience to environmental disturbance (e.g. plasticity in foraging behaviours and habitat requirements), demographic compensation in response to exploitation, and dispersal patterns that provide connectivity among fragmented populations (Macdonald 1983). Ability to adjust group size or hunting behaviour in human-dominated areas may confer greater resilience for flexible species than more obligatorily social ones, such as wild dogs which are subject to an Allee effect (Courchamp et al. 2002). Ambush predators such as lions, tigers and leopards may be predicted to suffer little foraging trade-off from spending more time in densely vegetated refugia, whereas coursing predators, such as cheetah, wild dog and wolves, despite flexibility in habitat selection, may still experience greater foraging costs when excluded from open habitats in response to human pressures. Likewise, predominantly nocturnal carnivores would be expected to experience less cost linked to partitioning their activities with those of humans than crepuscular species. For instance, wolves experience a trade-off between minimising predation risk by humans and increased hunting success during twilight hours and show less temporal partitioning with people when hunting wild prey than they do when hunting livestock (Theuerkauf 2009). Different species of carnivore are, therefore, likely to show different suits of behavioural adjustments to risk of human-caused mortality depending on the trade-offs they face, and will suffer these trade-offs to different levels.

1.5.2. Ecosystem implications

Top down impacts of large predators are increasingly recognized as having major effects on structuring ecosystems through both direct (density-mediated) and indirect (behaviourally-mediated) impacts on herbivores (Werner & Peacor 2003, Ripple & Beschta 2004, 2007, Schmitz et al. 2004, Riginos & Grace 2008). There is growing evidence that behaviourally mediated trophic cascades may affect ecosystem processes as diverse as the dynamics of fire, carbon sequestration, disease transmission, spread of invasive species, stability of riverine systems, and biogeochemical cycling (Estes et al. 2011).

In their 2004 synthesis, Schmitz et al. suggested that in freshwater systems 'where penultimate predators mediate interactions between top predators and herbivores, the penultimate predators should display behaviours similar to herbivores'. In Landscapes of Coexistence, similar cascades may be mediated by carnivores' fear of people, with large carnivores being the penultimate, not the top predator. By changing aspects of their behavioural ecology where there is risk from humans, large carnivores may indirectly affect the behaviour of herbivores (Muhly et al. 2011), which may in turn impact the vegetation and other ecosystem processes. The prevalence and magnitude of such multi-trophic cascading effects, however, are poorly understood and merit further investigation.

Table 1.1 Summary of predictions for the behavioural effects of human-caused mortality risk on large carnivores in Landscapes of Coexistence.

	Risk of human-caused mortality	
	High	**Low**
Spatio-temporal use of the landscape	Explained primarily by human factors; densities, distribution and activities.	Explained primarily by the distribution of resources and competition with other carnivores.
Vigilance	Increased during times and places where people are active, particularly when feeding and/or accompanied by young.	Linked primarily to foraging activities, or competition with other carnivores.
Habitat selection	Primarily driven by the need to find refuge from people e.g. habitat structures with low visibility, and low permeability to people and livestock.	Primarily driven by hunting success, or physical comfort NB exceptions include females with tiny young.
Movement patterns	Primarily influenced by human presence and activities.	Primarily influenced by the distribution of resources and competition with other carnivores.
Foraging patterns	Temporal shifts in foraging activities to overlap less with human active periods.	Temporal foraging patterns maximise hunting success and/or energetics.
Prey selection	Not explained by normal foraging models. Livestock may be selected as prey in smaller proportions than expected from their abundance and/or vulnerability. NB Only where enough wild prey is available as an alternative prey source to livestock.	Prey species selected in proportion to abundance and/or vulnerability.
Feeding behaviour	Prey carcasses more likely to be abandoned or moved to refuge habitats	Prey carcasses only abandoned in response to competition with larger or more dominant carnivores.
Group size (social carnivores)	Smaller than explained by resource abundance. Potential fission-fusion dynamics	Primarily limited by resource abundance.

1.6. Research aims

Large carnivores must navigate the peaks and troughs of a Landscape of Coexistence and make trade-offs in order to optimise reduction of human-caused mortality risk and associated costs. Although the behaviourally mediated effects of the risk of predation have been demonstrated to be more important than the lethal effects of predation in large mammalian herbivores (Schmitz et al. 1997, Laundré et al. 2001, Preisser et al. 2005) the effects of humans on lions has so far only been measured in terms of direct mortality. It stands to reason that, should lions adjust aspects of their behavioural ecology in response to risk of human-caused mortality, these behavioural effects may also be crucial when predicting the full impact of humans on the demography of lion populations overlapping with people and livestock. The main aim of this research is to use lion as a model to investigate adjustments in their behavioural ecology in response to risk of human-caused mortality, hence describe an example of a Landscape of Coexistence. Potential behaviourally mediated effects of a Landscape of Coexistence on African lion demography, and the potential for coexistence with people are also explored.

1.7. Thesis structure

In addition to this introduction chapter, there are 5 other chapters outlined below.

Chapter 2 - Study site, background and general methods

The African lion (*Panthera leo*) is particularly vulnerable to direct persecution by people and is often the first large carnivore species to be eradicated when living alongside people and livestock (Woodroffe 2001). Lions are, therefore, a revealing model for testing whether behavioural adjustments occur as a result of human-caused mortality risk. Behavioural adjustments are particularly expected amongst breeding female groups (prides), as breeding

females exhibit the strongest behavioural responses to fear of predation in other species. In this chapter the study area (Laikipia County, Kenya) is described, explaining why this area is an ideal location to study the behavioural effects of human-caused mortality risk on lions. A background to previous research in the study area is given, and methodology that is common to all chapters is outlined here.

Chapter 3 - When lions use Landscapes of Coexistence: insights into their behavioural plasticity in response to fear of human-caused mortality.

The spatio-temporal scales at which lions respond to people may determine the extent and cost of behavioural adjustments. In this chapter, movement data derived from GPS radio-collar data is used to compare the spatio-temporal behaviour of lions at two scales in Laikipia County, Kenya: a landscape-scale response to land-use, and a local-scale response to actual locations of people and livestock. In particular, it is predicted that lions should avoid areas where human-caused mortality risk is high, or use these high-risk areas at times when the risk of detection by people is lowest. Movement parameters are also analysed at the two scales to test the prediction that lions would move faster and straighter in high-risk areas. Finally, it is predicted that lion behavioural adjustments in response to people and livestock should be influenced by environmental conditions that affect their hunting success of wild prey and detection by people. Thus this chapter explores the influence of rainfall and moonlight levels on spatio-temporal variations in the behaviour of lions in a Landscape of Coexistence.

Chapter 4 - Food or fear: determinants of habitat selection for lion (*Panthera leo*) living in a Landscape of Coexistence.

In this chapter GPS collar data from lions is used to study habitat selection (using resource selection functions) at two scales a) within lion home ranges, and b) at specific sites such as

kill and primary daytime rest sites. It is predicted that lions living in Landscapes of Coexistence should select habitats to optimise the trade-off between maximising foraging success and minimising detection by humans. To illustrate this, this chapter investigates the applicability of the following resource versus human based hypotheses to explain habitat selection by lions at different human activity levels: 1) Prey searching drives lion habitat selection during the night, 2) Avoidance of detection by humans drives lion habitat selection during the day. Finally how habitat structures that offer refuge from humans may mediate lions' spatial avoidance of humans, thus potentially reducing costs associated with behavioural changes to reduce contact with humans, is considered.

Chapter 5 - Human-carnivore coexistence: lion movements inform livestock protection techniques.

This chapter uses data on livestock depredation (using ground investigation at the scene of lion attacks on livestock) and lion movements (using GPS collars) to examine husbandry and environmental predictors of (1) lion's proximity to bomas, (2) the probability of attack, and (3) the probability that an attack results in the death or injury of livestock once it occurs. It is predicted that lions distinguish between well protected livestock (held within strong bomas and/or accompanied by people, thus representing greater human-caused mortality risk), and poorly protected/unprotected livestock. The prediction that environmental factors, which affect lions' success when hunting wild prey, will also affect their tendency to hunt livestock is also explored.

Chapter 6 – General discussion and conclusions

In this chapter the behavioural adaptations shown by study lions in response to a Landscape of Coexistence are summarised, along with the potential costs that may be associated with

such behavioural effects of fear, and factors that mediate their extent. This knowledge is then applied to landscape conservation planning for the species.

Chapter 2.

Study site, background and general methods

One of Laikipia's collared lion prides enjoys some early morning sun on the edge of a thick patch of bush, into which they later disappeared. Laikipia is home to a healthy population of lions, as well as people and livestock. Sufficient wild prey densities, habitats that provide good cover, and good livestock husbandry practices may all contribute to this continued coexistence. Photo by: Josep Oriol.

2.1. Laikipia County

Laikipia County (36°10'-37°3' E and 0°17'S-0°45'N) comprises 9700km^2 of wooded savannah and open grassland located in north-central Kenya at an elevation of 1700–2000m a.s.l., north-west of Mt. Kenya, north-east of the Aberdare highlands, west of the Rift Valley and south of Samburu County. Rainfall in Laikipia is bimodal, mostly falling in two seasons, the 'long rains', between April and June, and the 'short rains', between October and December, although rain is unpredictable and may fall at any time of year (Graham 2009). Out of season rainfall is most likely between July – September making the clearest dry season from mid December to late March (Georgiadis et al. 2007). Mt. Kenya (5199m) and the Aberdare Highlands (3999m) influence the annual rainfall leading to a North-South gradient from a relatively arid 300mm in the lower lying north of the county to 750mm in the foothills of Mount Kenya to the south (Gichuki, Hanspeter & Schwilch 1998).

The region hosts the second highest densities of wildlife in Kenya after the Maasai Mara, including a complete suite of large carnivores (Georgiadis et al. 2007), and this resource has lead to a growing nature based tourism industry in the region (Graham 2009). Surprisingly, considering the presence of such high wildlife densities and important resident populations of highly endangered species such as wild dog and Grevy's zebra, none of Laikipia has IUCN protected area status (I-IV). Despite Laikipia's lack of formal protection and the presence of people and livestock throughout the region, the county supports a relatively healthy population of lion, at an average density of 0.04/km^2 where they occur (unpublished Living With Lions data) compared to: 0.03-0.10/km^2 in the Kruger NP (Mills 1995) and 0.08-0.13/ km^2 in the Selous game reserve (Creel and Creel, 1997). An absence of lion proof fencing means that lion are able to move freely throughout the area, limited only by low prey numbers and persecution in some of the region.

2.2. Study area

Laikipia is comprised of a complex mosaic of different land uses and forms of land tenure, including commercial ranch land, traditional communally owned pastoral areas, and small farms in the south. The two largest and most important land-use types for wildlife are commercial ranch land and traditional transhumant pastoralism. The total area of Laikipia is 9700km^2; 3288km^2 of which is classed as pro-wildlife i.e. large scale commercial ranches where wildlife is tolerated or encouraged (mean biomass of 1700kg/km^2 wildlife and 2700kg/km^2 livestock - Georgiadis et al. 2007). Wildlife also coexists with livestock and people, be it in lower densities, in traditional pastoralist and some woodland areas (Georgiadis et al. 2007).

2.2.1. Core study area

The ***core study area*** (Fig 2.1.) comprises an area of commercial ranch land (699km^2) and pastoral land (1030km^2) in northern Laikipia, which was chosen for the following reasons: 1) it was the only significantly sized area in Laikipia where commercial ranch land and pastoral land occurred side by side without any boundary demarcated by potential barriers that may influence lion or wild prey movements, e.g. without wildlife fences, rivers, main roads or major settlements, 2) The habitat was very similar in the two land-use types within the study site, showing little of the characteristic denudation of vegetation in the pastoral land in many other areas, 3) Wild prey densities were similar on both land-use types based on long term aerial census data (Georgiadis et al. 2007), and 4) lions were known to occur throughout the area. The two land-use types within the core study area were, therefore, considered similar during the study period in all respects except the density and socio-economic status of the people inhabiting them, the densities of livestock, and the associated implications for human-caused mortality risk.

2.2.2. Wider study area

Data on overall depredation losses (chapter 5) were collected over a ***wider study area*** consisting of 12 pro-wildlife commercial ranches covering a total of 1544 km^2 (Fig. 2.1.). The wider study area was characterised by the presence of lions, livestock, and a level of co-operation from land managers and owners such that lion-livestock depredation incidences were always reported.

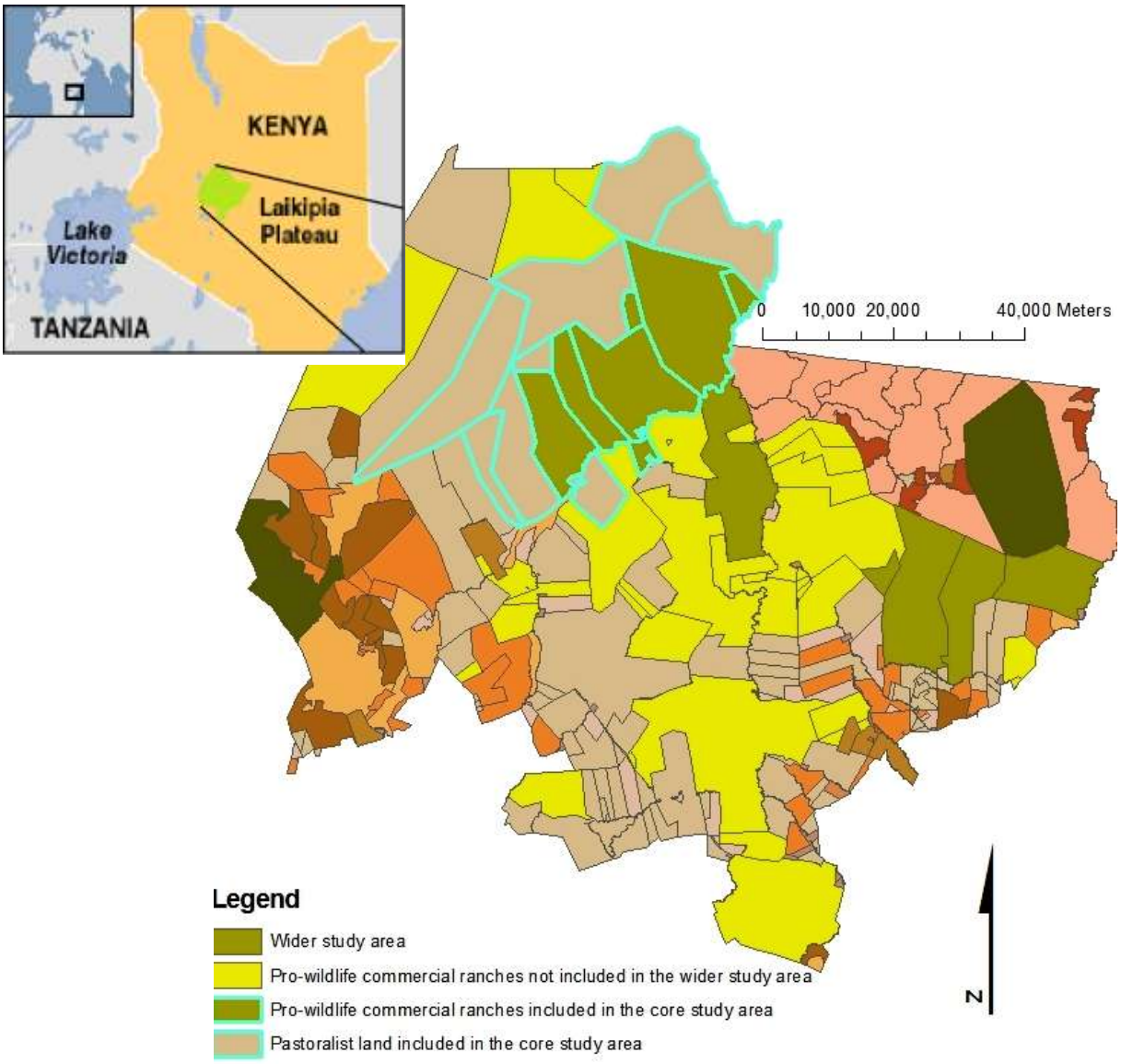

Figure 2.1. Map of Laikipia County, Kenya, showing its location, and the core (highlighted in blue) and wider study areas.

2.3. Livestock husbandry and lion depredation in Laikipia

The main income for land owners throughout the wider study area was livestock ranching, and traditional livestock husbandry was still practiced on both land-use types (Frank 1998, 2011, Ogada et al. 2003, Woodroffe et al. 2005): livestock were kept in livestock enclosures (known as 'bomas' hereafter) at night to protect them from thieves and large carnivores, and herded out to graze by day, accompanied by herders. Boma designs varied (see table 2.1. and Fig 2.2.) but the general principle was the same; boma walls were designed to keep livestock inside and predators out. Livestock were always secured inside bomas well before sunset (1830h) and herded out to graze after sunrise (0630h) so that all people and livestock were in bomas at night when lion, leopard, and spotted hyaena were active. Individual animals occasionally became separated from the herd during the day and if not found, remained out of the boma overnight. Herds were moved to different boma locations at intervals of 2–24 weeks, depending on the quality of the grazing, and in this way utilised all parts of the landscape over time. Night guards and herders were generally from local pastoralist tribes.

Lions regularly attack livestock, and are killed by people in response, on both land-use types in the study area (Frank 1998, Ogada et al. 2003, Woodroffe and Frank 2005). As a result 20 collared lions were known to be killed by people during the study period, whilst only one collared lion died of natural causes (Frank and Oriol-Cotterill unpublished data). Woodroffe and Frank (2005) documented a 19.4% mortality rate for collared lions in Laikipia between 1998-2004, with 17 of 18 deaths of collared lions due to retaliatory killing by humans after depredation on livestock. People, therefore, represent the main mortality risk to adult lions in the study area. Risk of human-caused mortality was taken to vary on two scales, 1) with land-use type (pastoral land had higher densities of livestock and people than commercial ranch land, therefore, more probability of encountering them - Georgiadis et al.

2007, Mpala Research Centre Department of Resource Surveys and Remote Sensing unpublished data), and 2) with proximity to actual human locations.

Table 2.1. Boma designs in the study area during the study period

Boma Design	Description	Comments
Thorn bomas	The oldest traditional method; walls made of tightly packed cut thorn trees and bushes. Gate usually made of a cut thorn tree that can be pulled across the opening at night.	All the materials are locally sourced and can be very effective at keeping livestock in and predators out if built very strongly. Walls and thorn gates can be penetrable to predators and livestock if not built well. Dependent on the availability of plentiful thorn trees.
Post and rail bomas	Large timber post and rail wall usually reinforced with a thin layer of cut thorn trees/bushes to deter predators from walking in. Gate normally consists of removable rails on one section and thorn trees that can be pulled across.	Strong walls that require less cutting of thorn trees than traditional thorn bomas. Generally good at keeping livestock inside but often penetrable by carnivores unless thorn wall and gate is also well maintained. Otherwise relies on good herders to react quickly and chase away carnivore before they enter the boma.
Chainlink bomas	Traditional thorn bomas reinforced with wire mesh.	Thin thorn walls can be made more impenetrable to carnivores by a layer of wire mesh. Cheaper than mobile bomas but only good if maintained well. Can be very effective but often badly maintained and therefore weak.
Stone bomas	Walls built using dry stone walling methods, gates can be made of steel or wood. Usually requires a layer of thorn or cactus on the top of the wall to stop predators climbing in.	Strong, durable and impenetrable walls (almost impossible for livestock to break out and carnivores to jump or force their way in) that require less cutting of thorn trees than traditional thorn bomas. Only as strong as its weakest point, i.e. the gate. Depends on a local source of suitable stone.
Mobile bomas	Boma wall made of steel (round bar) and mesh gates held together with large metal stakes driven into the ground. Gates can be separated and stacked on a tractor trailer to be transported to other areas, or simply carried and reformed close by in a process known as 'creeping'.	No use of thorn trees. Very affective at keeping predators out and livestock in. Can be easily moved to help with grazing management. Durable, requires little maintenance but requires significant initial investment.
Mixed	Boma walls made up of more than one of the above designs	Tend to be only as good as the weakest design used. Are normally a sign of poor husbandry practices.

Fig 2.2. Photographs of boma wall construction in the study area a) mobile boma, b) thorn boma, c) stone boma (temporarily reinforced with chainlink until cactus planted on the top grows), and d) chainlink reinforcing weak thorn walls.

2.4. Background to research in the study area

Research into the drivers and mitigation of conflict between lion and people in unprotected areas has been carried out since 1997 by Living With Lions (Frank 1998, 211, Frank and Woodroffe 2001, Ogada et al. 2003, Frank et al. 2005, Woodroffe and Frank 2005). During this period lion have been extensively monitored using VHF collars and work has been done with commercial ranchers and pastoral people to improve livestock husbandry practices and reduce the number of livestock killed by large carnivores in the area. A great deal has been learned about the movements of the lion in the area, and techniques have been developed to

help reduce lion-human conflict (e.g. Ogada et al 2003, Frank & Woodroffe 2005). However, the use of VHF collars and the fact that the lion in this area are persecuted, meant that past movement data unbiased by the presence of observers could only be collected from the air (tracking flights), and was thus limited to daylight hours. Conversely, most lion movements and livestock depredation events occur at night (Frank 1998, 2011, Ogada et al 2003, Frank & Woodroffe 2005). Movement in a predominantly nocturnal species cannot be conferred from locations taken only in the daylight hours (Dickson et al. 2005). In the past VHF collars were the only reliable way of tracking lion movements, however, recent improvements in Global Positioning Systems (GPS) telemetry has meant the use of GPS collars is now considered reliable enough to be a feasible way of monitoring lion movements. The research for this thesis, therefore, uses GPS technology to build on past research in the area by revealing fine-scale lion movements in proximity to humans during lion's most active period; at night.

2.5. Justification for study animals

Lion are the first large predator to be eliminated in pastoral areas in Africa (Woodroffe 2001) indicating that they are the most difficult of the large predators for pastoral people to coexist with, or that they are the most vulnerable species to persecution. It is thus likely that lion will be the carnivore species most influenced by risk of human-caused mortality, and most likely to illustrate the effects of different levels of human-caused mortality risk on aspects of their behavioural ecology. In so far as lion are social carnivores that form supportive groups (prides) consisting of related adult females and their offspring (Schaller 1972, Packer et al. 1990), it follows that adult pride females are likely to reflect the movements of the largest segment of the population. Mammalian females with young have consistently been shown to have the greatest behavioural response to risk (Laundré et al. 2001, Childress & Lung 2003,

Liley & Creel 2007). Similar behaviours in mammalian males can often be attributed to intraspecific competition rather than a fear of predation. This is probably due to the fact lifetime breeding success for males of most species depends on maintaining a level of fitness to defend breeding rights, whereas for females avoiding predation of her offspring is the best way of ensuring lifetime breeding success (Lung & Childress 2006). It is therefore predicted that the pride females will be the segment of the Laikipia lion population whose actions will be most closely tied to avoiding mortality for herself and her young, and whose behavioural changes will most reflect changes in level of risk of human-caused mortality, and demonstrate the presence of a Landscape of Coexistence for carnivores. Movements of male lions may be more linked to the defence of territory from other lions than minimising risk of human-caused mortality.

2.6. General methods

2.6.1. Lion movement data

Lion movement data was collected using remote satellite telemetry methods based on global positioning system (GPS) technology. GPS technology substantially increases potential research capabilities by allowing the researcher to obtain fine grain movement data regardless of the terrain and time, and without affecting lion behaviour. GPS collars can be programmed to record the location of the animal at regular intervals chosen by the researcher, allowing the collection of a robust data set. Recent advances in GPS technologies have provided huge quantities of data on the temporal and spatial partitioning of an animal's activities (e.g. Jonsen et al. 2003, Frair et al. 2005, Graham 2009). Quantitative analysis of movement data collected using remote sensing technologies to give information about an animal's relationship with aspects of its environment is particularly useful when direct observations are not possible (Bailey & Thompson 2006), which is often the case for a large nocturnal

carnivore like a lion, travelling through rugged terrain. Lion in Laikipia have survived despite persecution by people, and so remote sensing methods are not only logistically more feasible but methodologically crucial when trying to answer questions about behavioural responses to the risk of human-caused mortality.

All the lion prides having territories along the unfenced boundary between commercial ranch land and pastoral land in the core study area were identified from long term VHF radio tracking data (Living With Lions). Five prides were identified as potentially using both land-use types and one mature adult female in each pride fitted with a GPS collar (Vectronics Aerospace GmbH). GPS collars represented a high cost and pseudo replication was avoided by limiting the number of GPS collars to one female per pride. A VHF collar was placed on at least one other of the adult females in the same pride to help locate any malfunctioning GPS collars.

GPS collars used were manufactured by Vectronics Aerospace GmbH especially for use on lion, and fell within the ethically accepted weight limit of less than 3% of the animal's body weight. Collars were programmed to take 15 GPS fixes a day; hourly from 18:00-07:00, and one fix at midday. This schedule was chosen to cover the lion's active period whilst saving battery power by collecting the minimum data during the daylight hours when lion were found to move very little. GPS data were downloaded by UHF link at regular (monthly) intervals between 2009 and 2012; mean data collection period per female was 26 months, range 4.5-50 months.

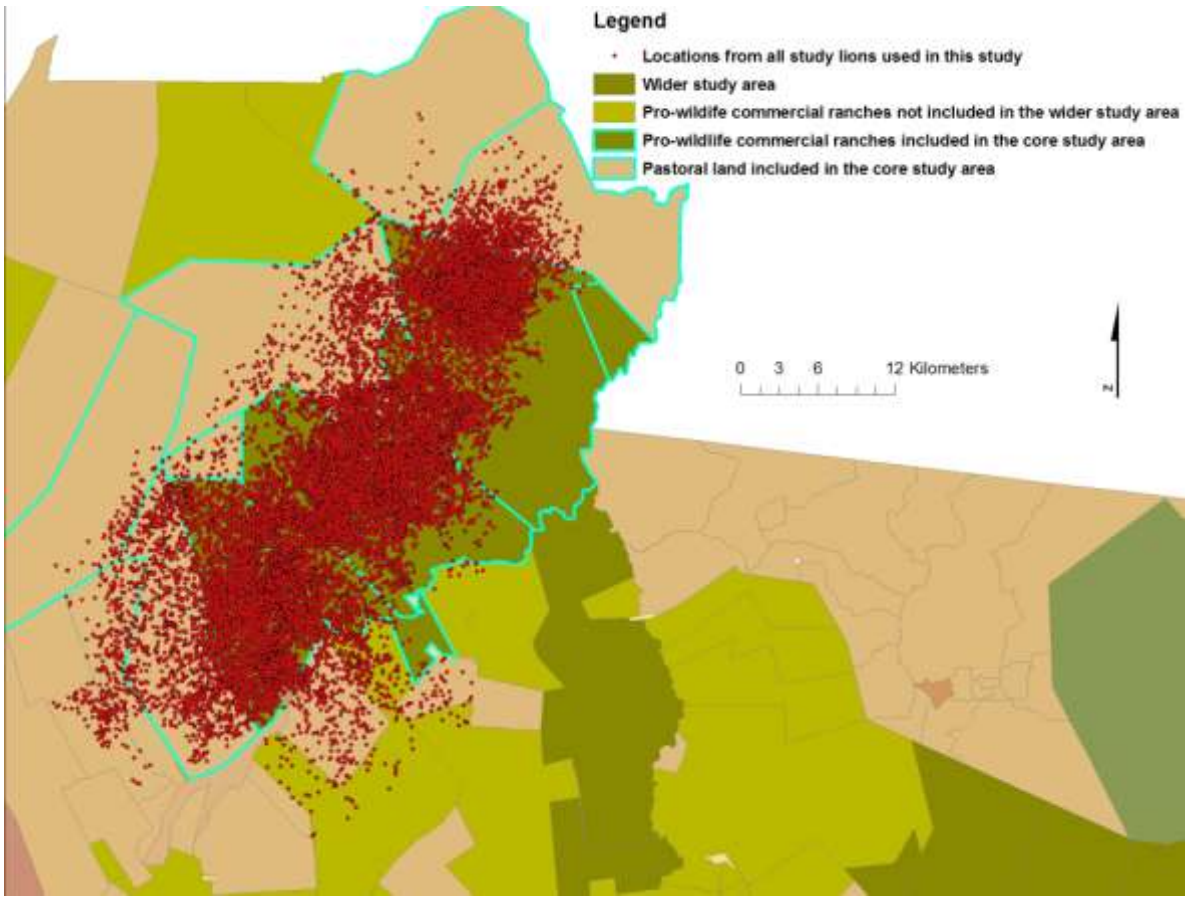

Fig 2.3. Map of the core study area showing all the GPS lion locations used in this study. N.B. There were no hard boundaries (e.g. fences, busy roads or rivers) between any of the properties in the core study area during the study period.

2.6.2. Lion immobilisation

Approval for capture and collaring was received from the appropriate agencies (Kenya Wildlife Service) and all capture and animal care followed University of California Animal Care and Use Protocol R191 using methodology described by Frank et al. (2003). All lions captured for this study were mature adult females, who were members of an established pride. A Dan-inject CO_2 rifle system (Dan-inject RSA, Skukuza, South Africa) was used to dart lions from a car parked at a distance of 10-30m with a 2ml dart containing the drug combination outlined in Table 2.2. Once the study lion was immobilised, other members of the pride were driven away from the immediate area by getting out of the car and showing the human form, or if this failed, banging the sides of the car and shouting. Blood, tissue and hair samples, and extensive body measurements were taken from the immobilised animal to ensure that all possible scientific benefit from the immobilisation was gained. Data not used in this study was shared with other relevant projects. The main purpose for any immobilisation carried out for this study was to fit the GPS or VHF collar. The lion was then reversed and observed until able to walk without difficulty and rejoined with other pride members. The drug combinations used in this study meant the lion was immobilised for approximately 1 hour.

Table 2.2. Dosage and drug combination used for immobilising adult female lions for this study.

Drug name	Action	Dose for adult female lion
Ketamine	NMDA receptor antagonist	30mg (0.2 mg/kg)
Medetomidine	Alpha 2 adrenergic agonist	5mg (0.03 mg/kg)
Atipamezole	Alpha 2 adrenergic antagonist	50mg (0.33 mg/kg)

2.6.3. Livestock movement data

All livestock and people were usually confined to bomas during the dark hours, when lions are most active (see section 2.3) so night time livestock movements were tracked by recording all boma positions on commercial ranches in the core study area over the study period (2009-2012); date, new position, boma design and livestock details were recorded each time a boma position moved. This data collection was restricted to commercial ranch land because of the unreliability of all efforts to record the same measures on the pastoral land. This was primarily due to extensive and frequent movements made by pastoral people in the area, the frequent use of temporary bomas away from the main homesteads exacerbated by tribal insecurity in the area. All analysis involving lion behavioural adjustments with proximity to actual livestock (hence human) locations was, therefore, only done using data on commercial ranch land within the core study area. This was considered to be valuable because human and livestock densities (hence risk of human-caused mortality for lion) was greater in pastoral areas (Georgiadis et al. 2007, Mpala Research Centre Department of Resource Surveys and Remote Sensing unpublished data) thus, any behavioural responses shown by lions towards human locations on the lower risk commercial ranch land was likely to be accentuated on the higher risk pastoral land. All conclusions drawn from this data are, therefore, believed to be conservative.

2.6.4. GPS data handling and storage

All GPS data was collected monthly by manually downloading with a handheld UHF receiver. Collars were removed by recapture at the end of the data collection period. Data was cleaned before storage in preparation for analysis; spurious GPS fixes were identified and removed from the data set. This was done by initially mapping the hourly locations and deleting any that fall outside of the region. A second level of filtering errors was achieved by

attributing a speed value to each location based on the time and distance between fixes, and setting parameters for a biologically reasonable maximum travel speed for a lion/livestock. Any locations with a speed value above that threshold were assumed to be error readings and discarded. For this analysis the threshold speed value was taken as 10km/hr.

2.6.5. GIS mapping data

All spatial data were imported into ArcMap (ESRI 2004) and projected to the Universal Transverse Mercator (UTM) WGS-84 reference system (Zone 37^0 N). The following GIS layers were used in global information systems (GIS) analysis:

Habitat – A 30m resolution vegetation map raster layer of Laikipia, derived from a supervised classification of two 2002 Landsat ETM scenes, was created by Centre for Training and Integrated Research in ASAL Development (CETRAD). Classifications given by CETRAD were then adapted to reflect the habitat structures important to lion as part of this study.

Rivers and roads – Line layers showing the main roads and rivers in the study area were obtained from Mpala Research Centre (MRC). Other important water sources and human habitations in the study area were also located and marked using a handheld GPS in order to create point layers for the locations of permanent water as part of this study.

Land-use – A polygon layer showing the land-use of every property in the study area was obtained from MRC and simplified into the two land-use types used in this research; commercial ranch land and pastoral land.

DEM – A 50m demographic raster layer was obtained from MRC showing the landform beneath the vegetation. Values for slope and altitude could be obtained from this layer.

Annual wildlife and livestock counts – The Department of Resource Surveys and Remote Sensing (DRSRS; Ministry of Environment and Natural Resources, Government of

Kenya) using systematic aerial sample survey methods (Norton-Griffiths, 1978) have monitored the abundance of 10 wild herbivore species, domestic cattle and 'shoats' (sheep and goats), human habitation and cultivation over the entire Laikipia county since 1985. Elephants were omitted from this analysis because they are highly mobile, and tend to unduly skew biomass densities where they are encountered during surveys. Since 1997 surveys have been designed and analyzed in collaboration with the MRC (Georgiadis et al. 2007) using transect a 5km grid prior to 1997 and a high resolution 2.5km grid from 1997 to date. Results from this census were used in the selection of the core study area for this study (see section 2.2).

2.6.6. Moonlight and rainfall

Daily rainfall was available from Mpala Research Centre (MRC) meteorological station on the southern border of the study area (Mpala Research Centre unpublished data). Rainfall was very localised and patchy over the study area and daily rainfall recorded at MRC was not taken to be representative of the whole study area. Daily rainfall was averaged over a one month period throughout the study period (2009-2012) in order to reduce the effect of spatial 'patchiness' in daily rainfall, and this mean daily rainfall value was assumed to be representative of the study area as a whole, and thus allocated to each lion location. Due to a lack of clear seasons during the study period, the 11 driest months (mean daily rainfall range: 0 – 0.65mm) and the 11 wettest months (mean daily rainfall range: 2.4 – 7.3mm) were contrasted for any analysis comparing wet and dry periods.

A moonlight index was calculated for each lion location using the moon phase and moon rise and set times available at the NASA website http://aa.usno.navy.mil/data/docs/MoonFraction.php. A moonlight index corresponding to the daily moon phase (e.g. full moon: 1; new moon: 0) was given to each lion GPS data collected

between moonrise and moonset. A moonlight index of '0' was assigned to any lion GPS data collected at night between sunset and moonrise or moonset and sunrise, thus accounting for dark periods on otherwise moonlit nights. Dark periods were defined as the nights between new moon and first quarter waxing and last quarter waning and new moon, and hours when the moon is below the horizon on other nights. Light periods were defined as the night between first quarter waxing and last quarter waning moon. Only data from months with a mean daily rainfall of <1mm (the 11 driest months) were used for any analyses involving the variable moonlight index to ensure that results were not significantly affected by cloud cover.

Chapter 3.

When lions use Landscapes of Coexistence; insights into their behavioural plasticity in response to risk of human-caused mortality

A collared Laikipia lioness is disturbed from a daytime rest site by the approach of a grazing livestock herd accompanied by herders. Study lions did not significantly spatially avoid people on commercial ranches, but they did change movement parameters in close proximity to people and livestock in ways that may reduce the probability of detection. Photo by: Tui de Roy.

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Abstract

The African lion is threatened throughout much of its remaining range by human-caused mortality in response to livestock depredation. Lions' ability to adjust their behaviour to reduce direct contact with people may affect their survival in human-dominated landscapes. This study carried out in Laikipia County, Kenya, uses fine-scale GPS data on lion movements to measure their reactions to people at two scales: a landscape-scale response to land-use type (commercial ranches versus pastoral lands), and a local-scale response to locations occupied by people within commercial ranch land, represented by the presence of livestock enclosures ('bomas'). Study lions on commercial ranches responded reactively to the location and activity levels of people on the local-scale; showing no overall spatial avoidance but fine-scale temporal partitioning in their use of areas in close proximity to bomas, approaching most frequently at times when people were least likely to be active (i.e. between 2300h and 0400h). This spatio-temporal avoidance allowed study lions to utilise areas close to bomas at times when they were least likely to be detected. At the land-use scale, however, study lions showed significant spatial avoidance of pastoral land, despite similar prey densities and habitat structure on both land-use types, indicating that lions' ability to utilise pastoral land was limited (although not precluded) by pastoral people. No significant temporal partitioning of time spent on the different land-use types was found. Spatio-temporal avoidance patterns were, therefore, best revealed at the local-scale. Study lions moved significantly faster and straighter, and remained stationary for shorter periods of time, in pastoral lands and when close to bomas, indicating that lions adjust 'how', as well as 'where', they move in response to human-caused mortality risk. Study lions were found closer to bomas with increasing rainfall and moonlight levels, two environmental factors likely to reduce lions' ability to hunt wild prey successfully. Overall, study lion movements suggested an ability to spatio-temporally partition their activities with those of humans such

that risk of human-caused mortality was minimised whilst use of a human-dominated landscape was maximised.

3.1. Introduction

Persecution by humans as a result of livestock depredation is a major cause of mortality among large carnivores and may threaten the viability of many populations (Woodroffe 2000, Macdonald & Willis 2013). Variations in human densities, distribution, land-use, and attitudes towards conservation in general, and carnivores in particular, create spatial variation in the likelihood of human-caused mortality. This 'Landscape of Coexistence' may ultimately result in a variety of heterogeneously distributed behavioural responses of large carnivores to the threat posed by people (Chapter 1). Carnivores may thus trade-off activities that enhance their fitness, such as foraging near humans, against risk of human-caused mortality.

In this context, studies have predominantly focused on spatial avoidance of people by large carnivores (Olson & Gilbert 1994, Kolowski & Holekamp 2009, Schuette et al. 2013a,b). A carnivore's response to people, however, may not be as simple as straightforward avoidance of human-occupied areas. Such areas may contain valuable resources (e.g. livestock), or access to a limited resource (e.g. dry season water sources - Schuette et al. 2013) such that complete avoidance would result in substantial foraging costs. Hence, large carnivores in Landscapes of Coexistence may use such human-occupied areas and behave adaptively by following strategies that optimise resource acquisition while minimizing contact with people, hence risk of human-caused mortality (Macdonald et al. 2010).

Behavioural responses to fear shown by herbivores and meso-carnivores suggest temporal partitioning of habitats and resources can be a strategy to reduce predation risk (Durant 1998, Linnell & Strand 2000, Kronfeld-Schor & Dayan 2003, Harrington et al. 2009, Valeix et al. 2009a,b). Large carnivores can become more nocturnal in human-occupied areas (e.g. all carnivores - Frank & Woodroffe 2001; spotted hyaena - Boydston et al. 2003, Holekamp & Dloniak 2010; wild dog - Rasmussen & Macdonald 2012; and tiger - Carter et al. 2012). Responding to human activity levels rather than just their physical location through

spatio-temporal avoidance, may 'fine-tune' a large carnivore's avoidance of people to allow use of human-occupied areas at times when risk of detection is lowest.

Additionally, the spatio-temporal partitioning of activities across Landscapes of Coexistence may allow carnivores to utilise areas in closer proximity to people in ways that reduce their risk of detection. Foraging, for example, may be associated with a higher risk of detection by people than moving quickly through an area (see Douglas Hamilton 2005, Graham et al. 2009, Wall et al. 2013 for examples in African elephant). Carnivores may, therefore, be expected to take straighter, faster movement paths in human-occupied areas of a Landscape of Coexistence. The characteristics of an animal's movement path can reveal where, for how long, and also 'how' an animal spends its time (Valeix et al 2010). Movement parameters may thus allow measurement of changes in an animal's behaviour in response to people and livestock (e.g. Valeix et al. 2012). Finally, environmental variables that affect success at hunting wild prey e.g. vegetation cover, prey densities and vigour, and light levels (Van Orsdol 1984, Funston et al. 2001, Cozzi et al. 2012, Rasmussen & Macdonald 2012, Packer et al. 2011a) may affect the trade-off between costs and benefits of killing livestock for large carnivores, thus limit their spatio-temporal avoidance of people and livestock (see Theuerkauf 2009).

The African lion is particularly vulnerable to direct persecution by people and is often the first large carnivore species to be eradicated when living alongside people and livestock (Woodroffe 2001). Lions are, therefore, a revealing model for testing whether behavioural adjustments occur as a result of human-caused mortality risk. We expect behavioural adjustment particularly amongst breeding female groups (prides), as they exhibit the strongest behavioural responses to fear of predation in other species (e.g. Caro 1987; Childress & Lung 2003; Liley & Creel 2007; Pangle & Holekamp 2010a,b). The spatio-temporal scales at which lions respond to the presence of people may determine the extent and cost of

behavioural adjustments. In this study, we used movement data derived from GPS radio-collar data to compare the spatio-temporal behaviour of lions at two scales in Laikipia County, Kenya: a landscape-scale response to land-use, and a local-scale response to actual locations of people and livestock. In particular, we predicted that lions should avoid areas with high risk of human-caused mortality when risk of detection by people is high but utilise these areas during periods when risk of detection is low. Movement parameters were also analysed at the two scales to test the prediction that lions would move faster and straighter in areas where the risk of human-caused mortality is high. Finally, we predicted that lion behavioural adjustments in response to people and livestock should be influenced by environmental conditions that affect their hunting success of wild prey and detection by people. We thus explored the influence of rainfall and moonlight levels on spatio-temporal variations in the behaviour of lions in a Landscape of Coexistence.

3.2. Methods

3.2.1. Study Site

Laikipia County, in the central highlands of Kenya ($36^{o}10'$-$37^{o}3'$ E and $0^{o}17'$S-$0^{o}45'$N) is a place where people, livestock, wild ungulates and all the local large carnivore species share the landscape (Woodroffe and Frank 2005; Georgiadis et al. 2007). The county comprises a mosaic of different land-use types. We selected a 2800km² area in the north of the county which included two land-use types, livestock being the main source of income for both 1) commercial ranches, and 2) pastoral land. We selected pastoral areas which were characterised by population densities of wild prey, and habitat structure, that were similar to those on the privately-owned commercial ranches with which we made comparisons, based on long term aerial census data (Georgiadis et al. 2007).

Lions regularly attack livestock, and are killed by people in response, on both land-use types (Ogada et al. 2003; Frank 2011). As a result 17 collared lions were known to be killed by people during the study period, whilst 2 collared lions died of other causes (Frank and Oriol-Cotterill unpublished data). Woodroffe and Frank (2005) documented a 19.4% mortality rate for collared lions in Laikipia between 1998-2004, with 17 of 18 deaths of collared lions due to retaliatory killing by humans after depredation on livestock. People, therefore, represent the main mortality risk to adult lions in the study area. Both commercial ranchers and pastoralists used traditional livestock husbandry techniques (Ogada et al 2003; Woodroffe et al. 2006; Frank 2011): livestock was herded into bomas at night for protection against thieves and large carnivores, and moved out to graze by day, guarded by herders.

3.2.2. Data Collection

3.2.2.1. Lion movements

Five female lions from different prides using both land use-types in the core study area (Fig. 3.1.) were equipped with a GPS Plus radio-collar (Vectronics Aerospace GmbH). Approval for capture and collaring was received from the appropriate agencies (Kenya Wildlife Services) and all capture and animal care followed University of California Animal Care and Use Protocol R191 using methodology described by Frank et al. (2003). One lioness per social group was collared at any given time to minimise data duplication insofar as lions form cohesive groups, which often move together (Schaller 1972). GPS data were downloaded by UHF link at monthly intervals between 2009 and 2012; mean data collection period per female was 26 months, range 4.5-50 months. GPS collars recorded hourly fixes between 18:00 and 07:00 plus one midday fix. All spatial data were imported into ArcMap (ESRI 2004) and projected to the Universal Transverse Mercator (UTM) WGS-84 reference system (Zone 37^0 N). Hawth's tools for ESRI ArcMap 9.2 (Beyer 2004) were used to extract travel

speed and turn-angle for each lion location. Lion locations logged at times when, or in areas where, boma movements were not accurately recorded were excluded from the analyses including the variable 'distance to nearest boma'.

'Clusters' in the lion GPS data, i.e. two or more consecutive locations falling within a 50m radius of each other, were located using an algorithm adapted from the Warren-Cougar-algorithm (Knopff et al. 2009). Clusters might represent sites where the lions either rested or made a kill, and are referred to collectively as 'stop sites'. The time spent at a stop site is referred to as the 'stop-duration'.

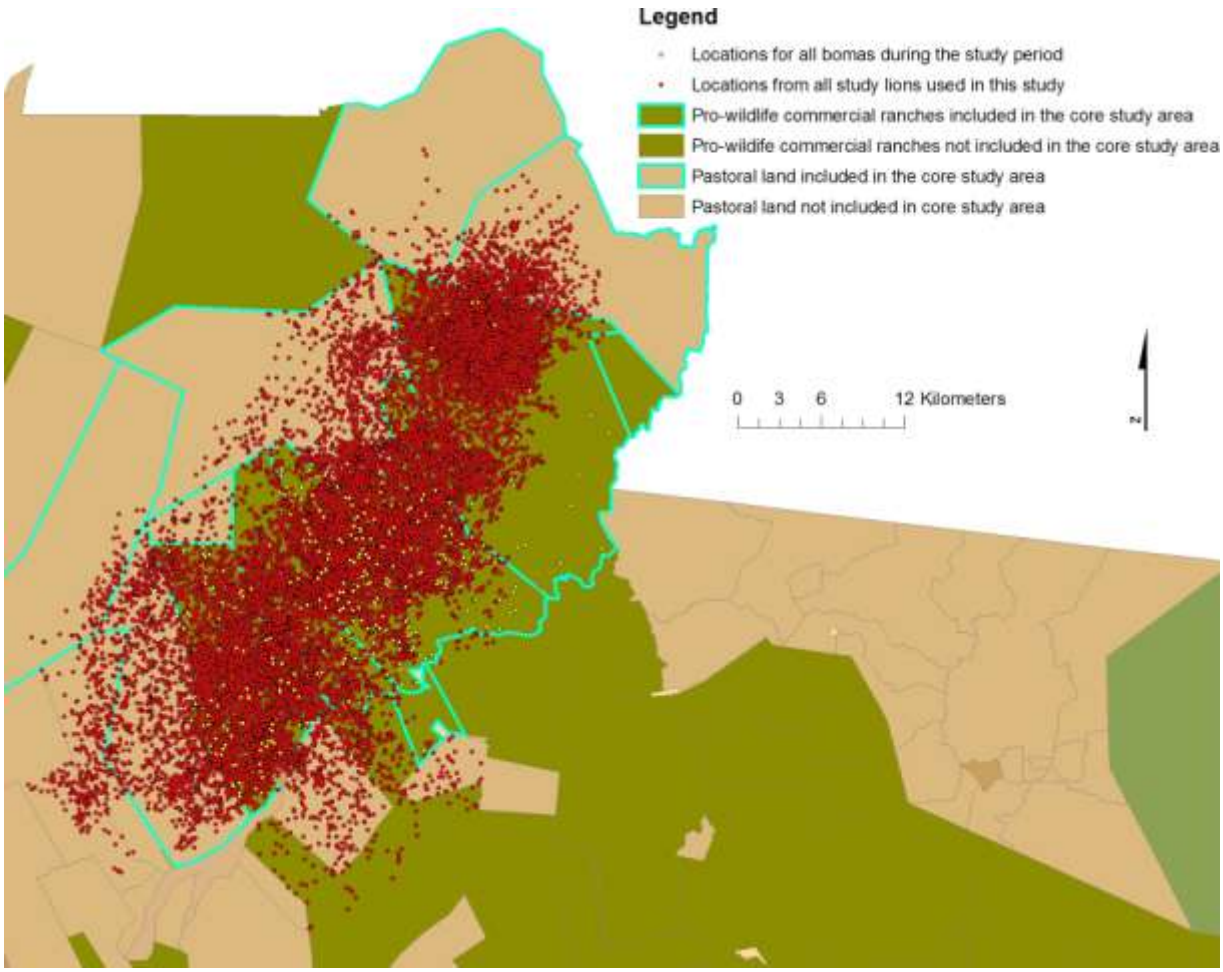

Figure 3.1. Map showing the two land-use types making up the core study area (highlighted in blue) and all lion and boma locations collected during the study period. Lion locations represent the movements of 5 different pride females, each female being a member of a different pride and using both land-use types. Boma movements were only collected on commercial ranches within the core study area and so all analyses using the variable 'distance to nearest boma' excluded all lion locations falling on pastoral land or on commercial ranch land outside of the core study area. N.B. There were no hard boundaries (e.g. fences, busy roads or rivers) between any of the properties in the core study area during the study period.

3.2.2.2. Human distribution and activities

The two different land-use types were assessed based on a GIS layer (Centre for Training and Integrated Research in ASAL Development, modified by Mpala Research Centre, Kenya). Human locations on both land-use types were closely associated with livestock movements; people stay within bomas between sunset (1830h) and sunrise (0630h) but leave the bomas to herd cattle during the day (Frank 1998, Patterson 2004). Boma locations were, therefore, a good proxy for human locations at night, and by day the probability of encountering humans was assumed to decline as distance to the nearest boma increased. Due to poor reporting of lions killed by pastoral people, the relative risk of human-caused mortality on one land-use type-compared to the other was not measured but it was assumed to be higher on pastoral land where people are less tolerant of loss of livestock to predators (Romañache et al. 2007). For the purpose of this study, pastoral land and areas in close proximity to bomas on commercial ranch land, were classed as having high human-caused mortality risk and are termed 'high-risk areas'.

Frequent movements made by pastoral people, and the use of temporary bomas exacerbated by tribal insecurity in the pastoral areas meant that boma data collection was restricted to commercial ranch land. Analyses investigating lion responses to human and livestock locations (bomas) were, therefore, carried out on this one land-use type. Bomas on the commercial ranches were moved to maximise grazing at intervals of 2-12 weeks, and their locations were recorded over the study period. We calculated the distance from each lion location to the nearest active boma using R (R Development Core Team 2012).

Lion movement data was assigned a human activity category 1) High activity (0700-1800hrs), when people are awake and moving about on the landscape, 2) Medium activity (1900-2200hrs, and 0600hrs), when people are inside bomas but likely to be awake, and 3) Low activity (2300-0500hrs) when people are inside bomas and likely to be asleep.

3.2.2.3. Environmental data

Daily rainfall was available from Mpala Research Centre meteorological station on the southern border of the study area, which was assumed to be representative of the area (Mpala Research Centre unpublished data). Daily rainfall was averaged over monthly periods to give a mean daily rainfall value used for each month. Due to a lack of clear seasons during the study period, we contrasted the 11 driest months (mean daily rainfall range: 0 – 0.65mm) and the 11 wettest months (mean daily rainfall range: 2.4 – 7.3mm).

A moonlight index was calculated for each lion location using the moon phase and moon rise and set times available at the NASA website http://aa.usno.navy.mil/data/docs/MoonFraction.php. A moonlight index corresponding to the daily moon phase (e.g. full moon: 1; new moon: 0) was given to each lion GPS data collected between moonrise and moonset. A moonlight index of '0' was assigned to any lion GPS data collected at night between sunset and moonrise or moonset and sunrise, thus accounting for dark periods on otherwise moonlit nights. Dark periods were defined as the nights between new moon and first quarter, waxing and last quarter waning and new moon, and hours when the moon is below the horizon on other nights. Light periods were defined as the night between first quarter waxing and last quarter waning moon. Only data from months with a mean daily rainfall of <1mm (the 11 driest months) were used for any analyses involving the variable moonlight index to ensure that results were not significantly affected by cloud cover.

3.2.3. Data Analysis

3.2.3.1. Spatio-temporal Avoidance

Habitat availability was represented by an equal number of random points as actual lion locations generated within each lions home range using the ''Generate Random Points'' option of Hawth's tools for ESRI ArcGIS 9.2 (Beyer 2007). This achieved a 1:1 ratio of use

versus available sites for all lion locations. Actual points were buffered (50m) when generating random points so no random points used overlapped with actual locations. Lion home range was calculated as a minimum convex polygon (MCP), using the extension Hawth's tools in ArcGIS 9.3. Although MCP's often overestimate space use (Macdonald et al. 1980, Douglas-Hamilton et al. 2005), they are a better estimate of the total area potentially available to lion when measuring avoidance of certain areas than home range methods that exclude areas that are unused such as Kernel Density Estimates (Graham 2009). 'Distance to nearest boma' and 'land-use type' were extracted for both actual and randomly generated locations ("Intersect point", Hawths Tools, in ArcGIS 9.3). 'Distance to nearest boma' and 'land-use' were then compared between actual and randomly sampled locations within the home range of the respective individuals using logistic regression. To avoid temporal serial autocorrelation, one lion location in each 24 hour period for each human activity category was randomly selected and all other lion locations discarded for this analysis.

To reveal any patterns in lions' use of high-risk areas in response to diel variations in human activity, and monthly or seasonal variations in environmental conditions, we repeated logistic regressions on subsections of the data a) the 11 wettest months, b) the 11 driest months (monthly rainfall being a proxy for seasonal changes in vegetation cover and prey body condition), c) high human activity periods, d) medium human activity periods, e) low human activity periods (representing diel changes in human activity levels on the landscape), f) moonlight index >= 0.75, and g) moonlight index < = 0.25 (Moonlight index being a proxy for hourly changes in visibility (e.g. Rasmussen and Macdonald 2012)). Lion identity was included as a fixed variable in all models. The effect of moonlight index and mean daily rainfall on diel patterns of habitat use were also demonstrated visually by plotting mean

distance to nearest boma for each hour of the night during dark periods versus light periods, and wet months versus dry months.

3.2.3.2. Movement parameters

To assess whether lions adjusted their movements to people and livestock, we performed covariance analyses on a) speed, b) tortuosity (measured as the turn-angle between each consecutive location), and c) stop-duration, with 'land-use type' and 'distance to nearest boma', as explanatory variables, 'lion identity' as a fixed variable, and 'night identity' as a random effect. Speed and stop-duration were both log transformed to meet normality requirements. As temporal serial autocorrelation affects independence of data recorded during the same night, it was accounted for using a first-order autoregressive covariance structure (Zuur et al. 2009), allowing us to use all lion locations. In order to investigate any variation in movement parameters with direction of lion movement, we performed the same covariance analysis on two sub-sets of 'speed' and 'turn-angle' data; lion direction of movement 1) away from a boma, and 2) towards a boma. To measure how lions' movements changed in response to moonlight or rainfall, we performed the same covariance analyses including 'mean daily rainfall' and 'moonlight index' as explanatory variables.

All analyses were done using R 2.14.2 software (R Development Core Team, 2012). Logistic regressions (spatio-temporal avoidance) were performed using the function 'glm' in the package 'MASS' (Vanables & Ripley 2002). Covariance analyses (movement parameters) were performed using the function 'lme' in the package 'nlme' (R Development Core Team, 2012).

3.3. Results

3.3.1. Spatio-temporal Avoidance

We recorded 403 different boma locations over a total of 34,340 boma nights (nights * number of bomas). Throughout the study area, there was an average of 28 boma locations on any one night. Once cleaned and processed, 33,486 usable lion locations from 5 individuals were analysed. Study lions did show a significant avoidance of pastoral land when all data were included, and this avoidance remained consistent for all subsections of the data analyses (Table 3.1.). No significant avoidance of boma locations was shown overall, or for the subsections of the data analysed, with the exception of periods of high rainfall (mean monthly rainfall>2.5), bright moonlight (moonlight index >= 0.75) and low human activity (between 2300-0500hrs), when lions were found significantly closer to bomas than expected from random (Table 3.1.). The relationship between rainfall, moonlight and human activity levels is further illustrated in Fig 3.2. Although the overall diel pattern of boma avoidance remained consistent, the mean distance to nearest boma for every hour (i.e. the extent of the diel pattern of avoidance) was consistently lower in wet months (Fig. 3.2.a.) and during light periods (Fig. 3.2.b.).

Table 3.1. Summary statistics for logistic regression models comparing actual lion locations and randomly generated locations, with 'Lion ID' as a fixed variable and 'Land-use' and 'Distance to nearest boma' as explanatory variables. Data were analysed as a whole, and after being split into different subsections according to levels of moonlight index, rainfall and human activity.

		Model results			
	Description of data	**Estimate**	**SE**	**Z value**	**P**
Land-use	***All data***	***-1.868***	***0.045***	***-41.878***	***<0.0001***
	Moonlight index >=0.75	***-1.515***	***0.181***	***-8.390***	***<0.0001***
	Moonlight index <=0.25	***-1.973***	***0.118***	***-16.663***	***<0.0001***
	Rainfall >2.5mm	***-1.942***	***0.079***	***-24.568***	***<0.0001***
	Rainfall > 0,7mm	***-1.463***	***0.068***	***-25.980***	***<0.0001***
	Low human activity	***-1.630***	***0.072***	***-22.530***	***<0.0001***
	Medium human activity	***-1.920***	***0.072***	***-26.759***	***<0.0001***
	High human activity	***-2.053***	***0.080***	***-25.752***	***<0.0001***
Distance to nearest boma	All data	-8.66E-06	9.95E-06	-0.870	0.384
	Moonlight index >=0.75	***-1.16E-04***	***4.46E-05***	***-2.590***	***0.009***
	Moonlight index <=0.25	-1.49E-05	2.56E-05	-0.583	0.560
	Rainfall >2.5mm	***-4.05E-05***	***1.94E-05***	***-2.09***	***0.0366***
	Rainfall <0.7mm	-1.54E-05	1.63E-05	-0.948	0.343
	Low human activity	***-4.51E-05***	***1.79E-05***	***-2.523***	***0.012***
	Medium human activity	9.83E-07	1.66E-05	0.059	0.953
	High human activity	1.40E-05	1.78E+00	0.798	0.425

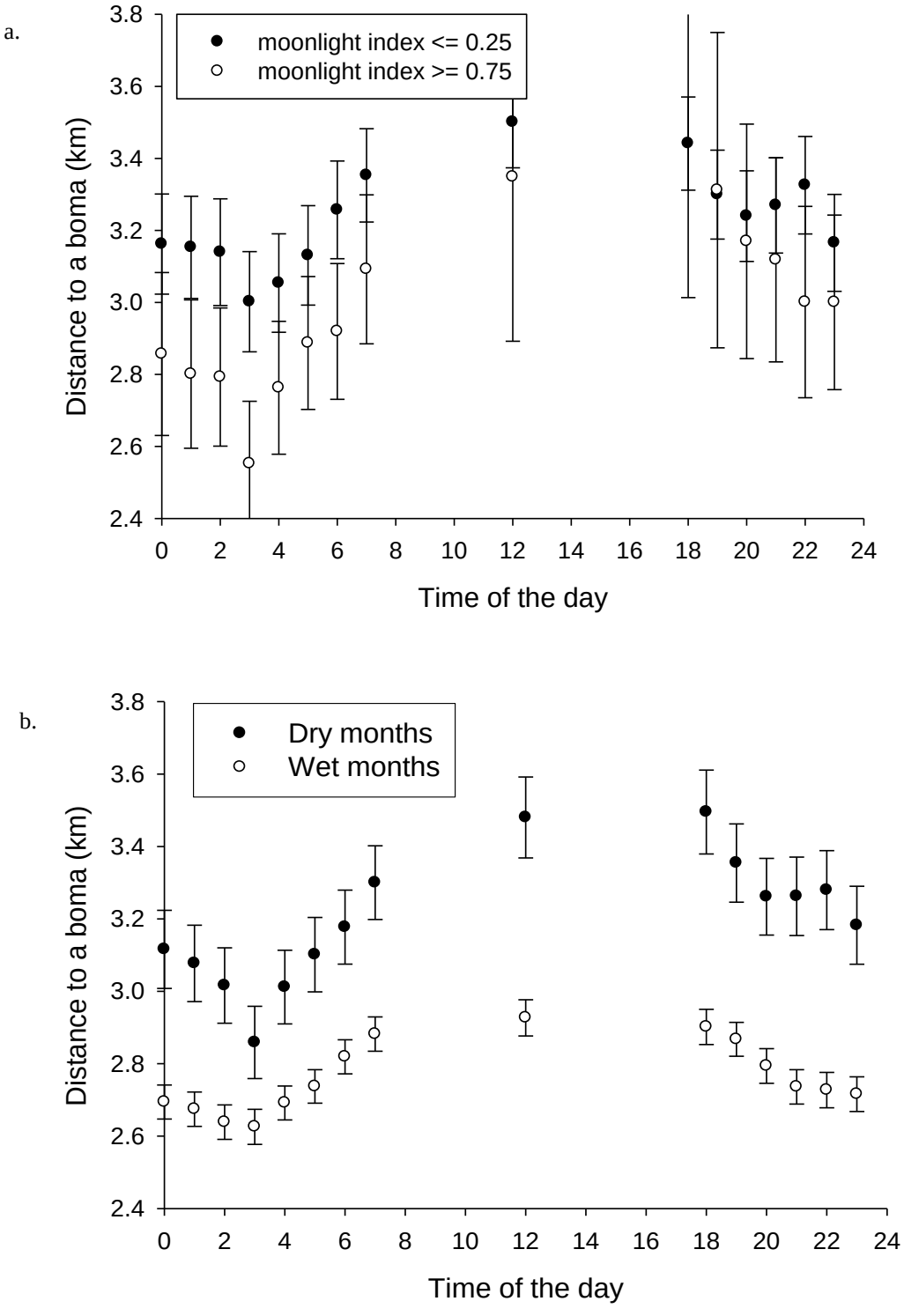

Figure 3.2. Distance to a boma (mean +/- SE) for lionesses in Laikipia County, Kenya, for each hour of the day with the effect of a) rainfall, where wet months (mean daily rainfall >2.5mm) are contrasted to dry months (mean daily rainfall <0.7mm), and b) moonlight, where dark hours (moonlight index ≤0.25) are contrasted to bright moonlit hours (moonlight index ≥0.75)

3.3.2. Movement parameters

Lion speed was significantly higher (estimate ± SE = 0.24 ± 0.02; $F_{1,\ 40435}$ = 106.5, p=<0.0001), and turn-angle and stop-duration were significantly lower (estimate ± SE = -5.02 ± 1.09; $F_{1,\ 34471}$ = 21.2, p=<0.0001 and estimate ± SE = -0.04 ± 0.016; $F_{1,\ 1432}$, 6.5, p=0.0108 respectively) when moving through pastoral land compared to commercial ranch land. Likewise lion speed significantly decreased (estimate ± SE = -5.17E-05 ± 5.59E-06; $F_{1,\ 30992}$, 85.4, p=<0.0001), and turn-angle and stop-duration significantly increased (estimate ± SE = 0.001 ± 2.56E-04; $F_{1,\ 25853}$, 28.6, p=<0.0001 and estimate ± SE = 8.9E-06 ± 3.31E-06; $F_{1,\ 1052}$, 7.2, p=0.0074 respectively) with distance to nearest boma (Fig. 3.3.).

Results showed a difference in the relationship between lion speed and distance to nearest boma, when lionesses moved towards versus away from a boma. When direction of movement was towards a boma, lion speed significantly decreased (estimate ± SE = -0.096 ± 0.004; $F_{1,\ 16294}$, -25.721, p<0.0001) with distance to nearest boma. When the direction of movement was away from a boma, however, speed significantly increased (estimate ± SE = 0.021 ± 0.004; $F_{1,\ 15247}$, 5.125, p<0.0001) with distance to boma. The relationship between distance to boma and turn-angle remained the same regardless of the direction of movement of the lion. From figure 3.3.b. three zones of boma influence on lion movements could be differentiated for the movement parameter ‘speed’. At distances within approximately 1.5km of a boma, the relationship between lion speed and distance to nearest boma diverged for lions moving away from bomas versus lions moving towards bomas. At distances between 1.5 and 4.5km, the relationship between speed and distance to nearest boma was similar regardless of the direction of movement. At distances above 4.5km away from bomas, there started to be much more variation in the data for all movement parameters (Fig. 3.3.).

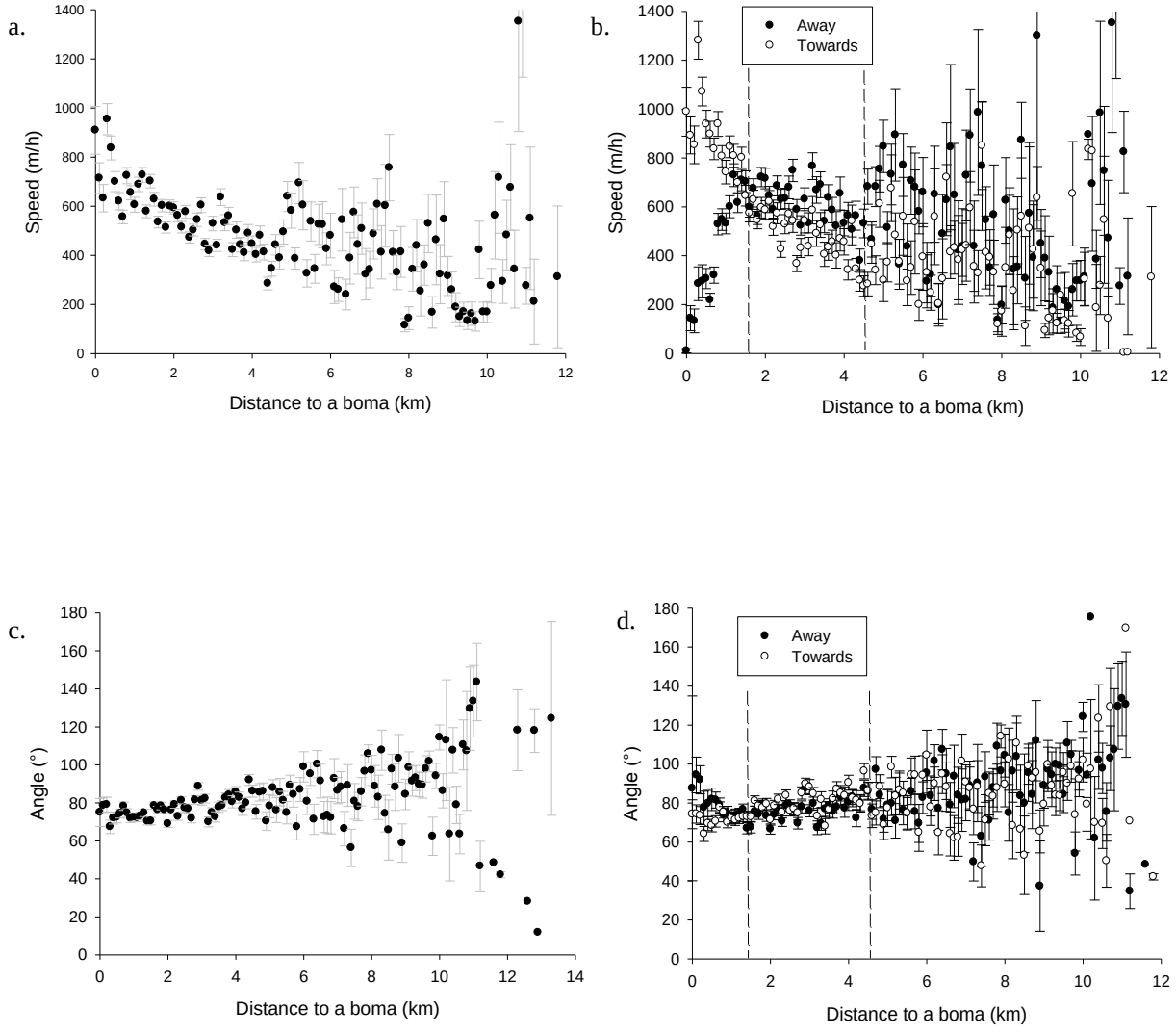

Figure 3.3. Mean (± SE) value of movement parameter against distance to the nearest boma for a) Speed (all data combined), b) Speed (data separated for direction of travel), c) Turn-angle (all data combined), d) Turn-angle (data separated for direction of travel), and e) Stop-duration (all data combined).

Although lion movement patterns changed on a diel basis, lions consistently had a greater mean speed and a lower mean turn-angle for all hours spent active on pastoral land (Fig. 3.4.). As stop-durations extended over two or more hours, an hourly comparison was not possible for this movement parameter on the different land-use types.

Lions moved significantly slower (estimate ± SE = -0.02 ± 0.006; $F_{1, 30905}$= 10.5, p=0.0012), had higher turn-angles (estimate ± SE = 1.11 ± 0.25; $F_{1, 25786}$= 4.4, p=<0.0001) and stopped for longer periods of time (estimate ± SE = 0.008 ± 0.003; $F_{1, 2111}$= 8.0, p=0.0048) during wetter months. Speed and turn-angle were not significantly influenced by moonlight index (speed - estimate ± SE = 27.95 ± 24.42; $F_{1, 8900}$= 1.21, p=0.27; turn-angle - estimate ± SE = 3.29 ± 1.95; $F_{1, 7483}$ = 2.85, p=0.09). Stop-duration could not be compared to moonlight index as the value for moonlight index changed hourly.

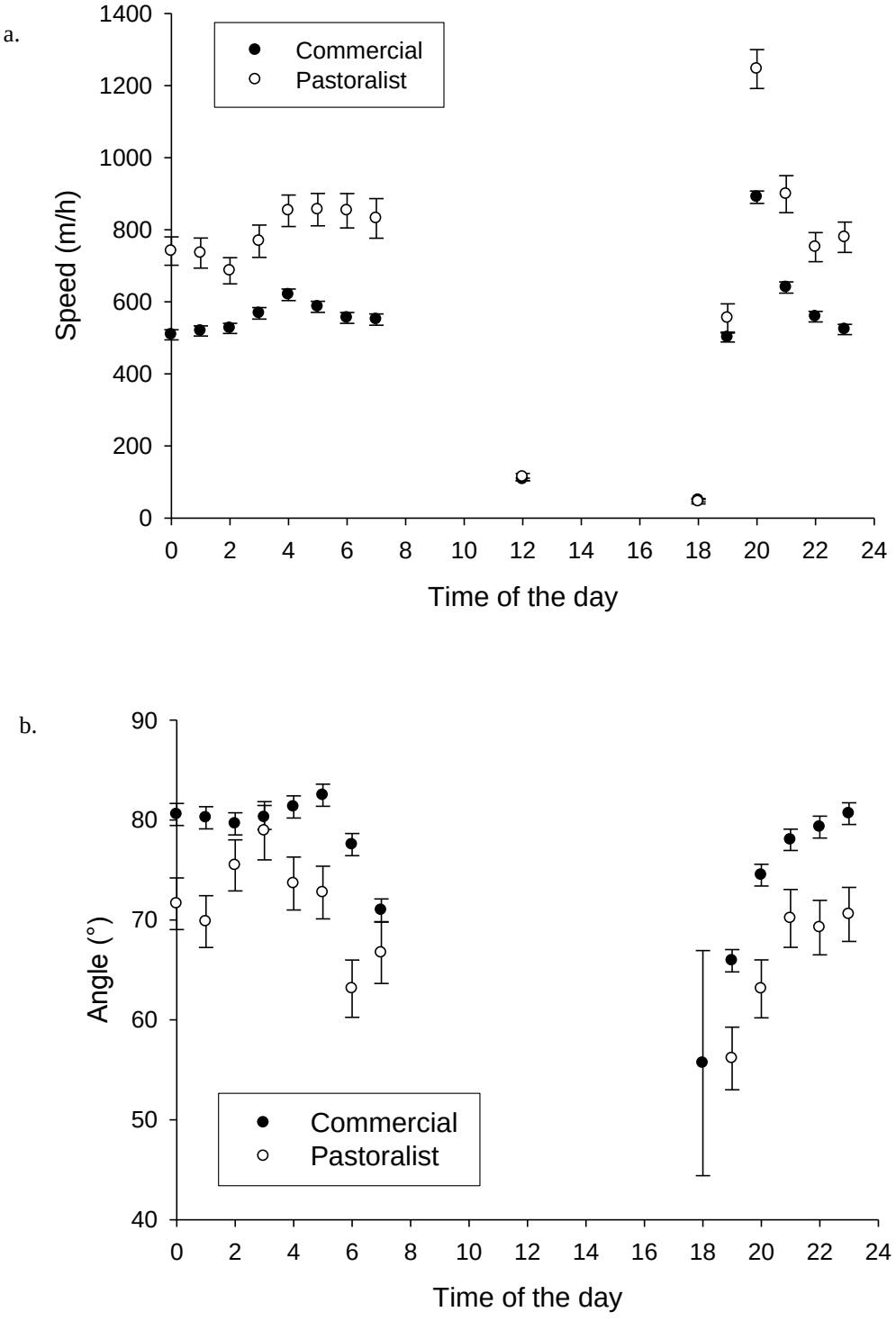

Figure 3.4. Distribution of mean (± SE) a) speed, and b) turn-angle for all collared lionesses on pastoral versus commercial ranch land over the 24hr period. Only hours where fixes were recorded by the GPS collars are represented.

3.4. Discussion

3.4.1. Spatial avoidance: scale matters

Several studies have demonstrated carnivore avoidance of areas characterised by intense human activity (Van Dyke et al. 1986, Gese et al. 1989, Mattson 1990, Reinhart & Mattson 1990, Olson & Gilbert 1994). Here, we show that a study lions' response to people is not as simple as total spatial avoidance. Study lions showed significant spatial avoidance of high-risk areas at the land-use scale (avoiding pastoral lands) but no significant spatial avoidance of bomas on commercial ranch land. In this study lions made other behavioural adjustments when using high-risk areas depending on the scale, adopting different strategies in the vicinity of a boma than on pastoral land. Use of high-risk areas was positively influenced at the local-scale by a lower likelihood of human activity, higher rainfall and higher levels of moonlight. At the broader landscape-scale, study lions showed significant avoidance of pastoral land under all the conditions measured. We conclude that behavioural adjustments to people other than total spatial avoidance, may be better revealed at the local-scale, i.e. by a carnivore's response to actual locations of people and livestock. This reflects findings in other studies where scale has been shown to be important when measuring behavioural adjustments to risk, e.g. cheetah respond reactively to the immediate threat of lion and spotted hyaena by avoiding them on a local-scale but show very little large-scale avoidance of areas preferred by these competitively dominant species (Broekhuis et al. 2013).

3.4.2. Temporal adjustments to utilise high-risk areas undetected by people

Lions are generally crepuscular and nocturnal (Schaller 1972, Prins & Iason 1989, Hayward & Slotow 2009, Cozzi et al. 2012). Livestock in Laikipia is kept in bomas between 1830h and 0630h. However, although also confined to boma sites during the dark hours, people remained active in situ during the pre-dawn and post-sunset periods (pers. comm. with

Laikipia's herders and ranchers), which have been shown to be important active periods for lions (Cozzi et al. 2012). Limiting all activities to periods when people are least active, therefore, would constrain lions to be more nocturnal than they would be in safer areas and could potentially result in significant foraging costs. Study lion mean hourly speeds (Fig. 3.4.a.) indicate that there is some overlap in active periods between lions and people pre-dawn and post-sunset. Study lion speed in combination with location, however, demonstrate that heterogeneity in the distribution of people and livestock across the study area allowed study lions to use a combination of temporal and spatial partitioning to utilise high-risk areas when people were least active, but remain more active further from people and livestock during times when people were also active.

The importance of scale when measuring avoidance was again highlighted, as study lions avoided pastoral land in all human activity levels, and yet did utilise areas closer to bomas during periods when people were least likely to be active (2300-0500hrs). These results accord with Carter et al.'s (2012) and Rasmussen and Macdonald's (2012) observations that temporal avoidance may facilitate the use of Landscapes of Coexistence by tigers in Nepal and Wild dogs in Zimbabwe respectively. Broad-scale avoidance of pastoral land in this study, during which wild prey densities and habitat conditions were similar on both land-use types, indicates that lions' use of high-risk areas on the larger scale is limited by the presence of pastoral people. A threshold human density for lion-human coexistence of around 25 people per km^2 has been given in other studies (Woodroffe 2000, Riggio et al. 2012). Study lion movements indicated that this threshold may vary with the level of human-caused mortality risk that the human population represents, such that lions avoid people to a greater extent where they are less tolerated.

3.4.3. Movement adjustments to minimise use of high-risk areas

GPS collar data revealed that study lions moved significantly faster and straighter when on pastoral land and in close proximity to bomas. Since prey densities were similar, such movement patterns were unlikely to be a response to low resource availability (see Fauchauld 1999, Valeix et al. 2010). A faster straighter path might instead indicate a tendency to pass quickly through an area or a habitat which represents a greater risk to an animal (Douglas Hamilton 2005, Graham 2009, Wall et al. 2013). While this may be the case on a landscape-scale i.e. when travelling through one land-use versus another, study lion movements on a local-scale i.e. in response to actual locations of people (represented by bomas in this study) may be more complex than simply hurrying past higher risk areas. Lions do kill livestock at bomas in the study area (Frank & Woodroffe 2005, Chapter 5), thus bomas represent a secondary source of prey as well as a focus for human threat (see also Valeix et al. 2012). While risk of detection by people may be reduced by temporal partitioning of activities, lion movement patterns once in the vicinity of bomas may be indicative of a foraging pattern at a known source of potential prey that does not respond to expected patch-disturbance rules i.e. livestock confined to a boma cannot move away in response to the proximity of a predator (Valeix et al. 2011). Study lions sped up and straighten their path as they approached within 1.5km of a boma, indicating a need to access resources at a known boma location quickly. Study lions departed a boma more slowly, however, possible due to the fact that livestock constrained within a robust boma are difficult to access but continue to represent a foraging opportunity until lions make a kill, give up or are chased away. Study lion movements away from bomas after they have killed compared to when they have not been successful, or when they are chased away by people versus simply give up, may further reveal the determinants of observed movement patterns. Relationships between speed or path tortuosity, and distance to nearest boma, were found to decline at distances greater than 4.5km suggesting that the

presence of people and livestock does not influence study lion movements beyond that distance.

Additionally, periods spent stationary by study lions are significantly shorter on pastoral land and when in close proximity to bomas. Lion activity at stop sites cannot accurately be determined from GPS data, so we do not know if shorter stops were due to study lions resting or feeding for shorter periods (or both) in high-risk areas; either could impose an energetic cost.

3.4.4. Trade-off between foraging opportunities and the risk of mortality: insights from rainfall and moonlight

Study lions were more likely to utilise areas closer to bomas during periods of brighter moonlight and more rain, both of which are potential periods of reduced hunting success of wild prey (Schaller 1972, Van Orsdol 1984, Funston et al. 2001, Patterson et al. 2004, Woodroffe & Frank 2005, Packer et al. 2011a). Packer et al. (2011a) showed that dark periods overlapping with times when people are still active represent the highest probability of lion attacks on people in southern Tanzania. In Kenya, by contrast, man-eating is extremely rare and lions' may use areas near bomas (thus people) during periods of bright moonlight and wetter weather in order to access livestock when hunting wild prey is more difficult.

Increased rainfall was also associated with resting closer to bomas by day. This may be a response to reduced risk of detection due to increased vegetation thickness (Chapter 4), and/or increased availability of grass and water reducing the distance livestock and their herders move from bomas. Habitat structure and daytime grazing practices are candidate factors in determining lions' ability to partition their activities with livestock and people in a Landscape of Coexistence.

Our data did not rule out the possibility that study lions were responding to changes in other variables at different moonlight or rainfall levels. Although unlikely, an alternate hypothesis that lions are attracted closer to bomas by an increase in wild prey abundance and/or vulnerability around bomas during periods of brighter moonlight or higher rainfall should be investigated.

Chapter 4.

Food or fear: determinants of habitat selection for lion living in a Landscape of Coexistence

A collared male lion in Laikipia watches a passing tourist vehicle from a 'high refuge' habitat, which could provide good concealment from people when needed thus reducing the need for spatial avoidance. Photo by: James Warwick.

This chapter represents a manuscript in preparation for submission to a journal (undecided). Authors: Alayne Oriol-Cotterill, Marion Valeix, Laurence Frank, Zeke Davidson, Jake Wall Lyman MacDonald, Steve Ekwanga and David Macdonald.

Abstract

Most habitat selection studies involving large carnivores have been carried out in protected areas, whereas a significant portion of their remaining range is in human-dominated landscapes. In protected areas the proximate drivers of habitat selection by large carnivores have been identified as prey abundance and/or functional features on the landscape that increase prey vulnerability. In human dominated landscapes, however, we expect behavioural changes that minimise risk of being killed by humans whilst maximising fitness. Hence, in places or at times where humans are a threat to lions, the need to avoid humans may become the proximate driver of habitat selection. We developed resource selection functions to study habitat selection by lions on commercial ranches in Laikipia County, Kenya, a) for three different periods in the 24 hr cycle representing different levels of human activity, and b) at two different scales: within the animal's home range, and at specific sites i.e. kill sites and primary daytime rest sites. Habitat selection for large carnivores in human dominated landscapes may not be adequately explained by resource based hypotheses such as prey abundance and/or vulnerability. While prey abundance was an important determinant of study lion habitat selection at night when humans were least and lions were most active, our results suggest that avoiding detection by humans when in their proximity (through the use of habitat refugia) becomes paramount during the day. Study lions did not show any spatial avoidance of human locations (bomas) during the day when humans were active on the landscape, rather a clear shift in habitat structure use was shown such that open habitats were increasingly avoided in close proximity to bomas. This suggests that the presence of habitat refugia may be important in mediating the spatio-temporal avoidance of humans by large carnivores in a Landscape of Coexistence. This study reveals the importance of temporal as well as spatial scale when assessing resource requirements of large carnivores in human-dominated landscapes.

4.1. Introduction

Optimal use of heterogeneous landscapes arises from a trade-off between maximising foraging efficiency where resources are plentiful or 'bottom up' drivers of habitat selection, and avoiding predation or 'top down' drivers of habitat selection (Houston et al. 1993, Brown & Kotler 2004). Humans pose a "clear and present danger" to many large carnivores (Treves & Karanth 2003). Because large carnivores are wide ranging species that are particularly vulnerable to habitat fragmentation, reduced wild prey numbers, and being killed by humans in response to livestock depredation (Woodroffe 2000, Gittleman et al. 2001, Macdonald and Sillero-Zubiri, 2004), even populations within protected areas may be vulnerable to human activities (Woodroffe & Ginsburg 1998, Harcourt et al. 2001). Spatio-temporal heterogeneity in the level of threat posed by humans has been referred to as the 'Landscape of Coexistence' and may result in behavioural changes to minimise the threat of human-caused mortality while optimising hunting success (Chapter 1). Where carnivores overlap with humans, they may attempt to find 'refuges' from humans. Such refuges may include areas of low human abundance or low levels of human activity (Carter et al 2012, Chapter 3) but may also include selection for habitat structures that offer physical refuge by reducing risk of detection by humans (Boydston et al. 2003, Apps et al. 2004, Dickson et al. 2005; Kolowski & Holekamp 2009, Schuette et al. 2013a).

We studied habitat selection in the African lion in response to habitat structure, prey abundance and human influences. As an apex predator, the lion suffers minimal interspecific competition, but it does suffer severely from human impacts such as high rates of retaliatory killing over the depredation of livestock (Frank1998, Woodroffe & Frank 2005, Hazzah et al. 2009); reduced wild prey due to overgrazing by livestock (Ogutu & Dublin 2002, Ogutu et al. 2005), poaching (Becker et al. 2013), habitat fragmentation (Riggio et al. 2012); and unsustainable trophy hunting off-takes in some areas (Loveridge et al. 2007, Packer et al.

2011b, Becker et al. 2012). Lions are often the first large carnivores to be eradicated in parts of their range shared with pastoral people (Woodroffe 2001).

Most habitat selection studies on lions have been carried out in protected areas (but see Schuette et al. 2013a), whereas over 48% of the African lion's remaining range consists of non-protected rangelands shared with humans, and the remaining 52% consists of hunting areas, reserves or National Parks (Chardonnet 2002), none of which are entirely free from human activities. There is thus a clear gap in our knowledge of lion habitat selection in human-dominated landscapes. Current hypotheses on lion habitat selection have focused on prey abundance (Van Orsdol et al. 1985, Spong 2002, Ogutu & Dublin 2004, Hayward et al. 2007, De Boer et al. 2010), prey vulnerability (Hopcraft et al. 2005), and interactions between the two (Davidson et al. 2012). These predict that lions will select habitats that offer the highest densities of prey or habitat structures such as thicker vegetation that provide ambush opportunities. Water sources may affect both factors; attracting prey (Van Orsdol 1984, Valeix et al. 2009b) and increasing its vulnerability due to riparian vegetation (Hopcraft et al. 2005). Certain habitat structures may also provide a refuge for females with young (Schaller 1972, Packer et al. 2001). Lions increase their use of thicker habitat structures and select for habitats further from water in response to seasonal increases in humans and livestock (Schuette et al. 2013a), but little is known about the trade-offs between resource requirements and human influences on lion habitat selection in a Landscape of Coexistence.

Pastoralists and lions normally show opposite circadian activity patterns (Frank 1998, 2011, Maclennan et al. 2009), as humans and livestock are active by day but are usually within settlements and bomas at night when large carnivores such as lion and spotted hyaena are most active. Lions living in Landscapes of Coexistence may, therefore, show a corresponding temporal shift in the proximate factors affecting habitat selection. When

human activity on the landscape is lowest, lions might select habitats according to bottom up principles of prey abundance or vulnerability. When humans are active, however, lion may spatially avoid them, or select habitats to avoid detection by them. We used GPS collar data from lions living amongst humans and livestock in Laikipia County, Kenya, to study lion habitat selection (by developing resource selection functions) at two scales a) within lion home ranges, and b) at specific sites i.e. kill and primary daytime rest sites. We predicted that lions living in a Landscape of Coexistence would select habitats to optimise the trade-off between maximising foraging success and minimising detection by humans. To illustrate this, we investigated the applicability of the following resource versus human based hypotheses to explain habitat selection by lions at different human activity levels: 1) Prey searching drives lion habitat selection during the night, 2) Avoidance of detection by humans drives lion habitat selection during the day. Finally we consider how habitat structures that offer refuge from humans may mediate lions' spatial avoidance of humans (Schuette et al. 2013a, Chapter 3), thus potentially reducing costs associated with behavioural changes to reduce contact with humans.

4.2. Methods

4.2.1. Study area

Laikipia County, in the central highlands of Kenya ($36^{o}10'$-$37^{o}3'$ E and $0^{o}17'$S-$0^{o}45'$N) encompasses a plateau of rolling low hills, open grassland and bush savannah at an elevation of 1700-2000m above sea level. Humans, livestock, wild ungulates and all the large carnivore species share the landscape (Woodroffe and Frank 2005, Georgiadis et al. 2007). The county comprises a mosaic of different land-use types including pastoralism and small scale farming, but the highest lion and wildlife densities occur on commercial ranches which raise livestock using traditional husbandry techniques (Ogada et al. 2003, Woodroffe et al. 2006).

Retaliatory killing of lions in response to livestock depredation is the main mortality risk to adult lions in the study area (Frank 1998, Ogada et al. 2003, Woodroffe and Frank 2005, Chapter 5). We considered a 677km² area of commercial ranch land in the north of the county, where movements of both lion and livestock night time enclosures (bomas) could be accurately recorded.

4.2.2. Lion data

Five female lions from different prides were fitted with GPS Plus collars (Vectronics Aerospace GmbH) programmed to record hourly fixes between 18:00 and 07:00, plus one midday fix. Lions were captured and collared under permit from the Kenya Wildlife Service and followed University of California Animal Care and Use Protocol R191 using methodology described by Frank et al. (2003). One individual per social group was collared at any given time to avoid data duplication. GPS data were downloaded by UHF link at regular intervals between 2009 and 2012; mean data collection period per female was 26 months, range 4.5-50 months. Lion locations falling outside of the study period (2009-2012) or outside of the commercial ranch land areas of the core study area were excluded from analyses. Distance to nearest boma was calculated for each lion location using R (R Development Core Team 2012). Figure 4.1. shows lion locations and boma locations recorded for this study.

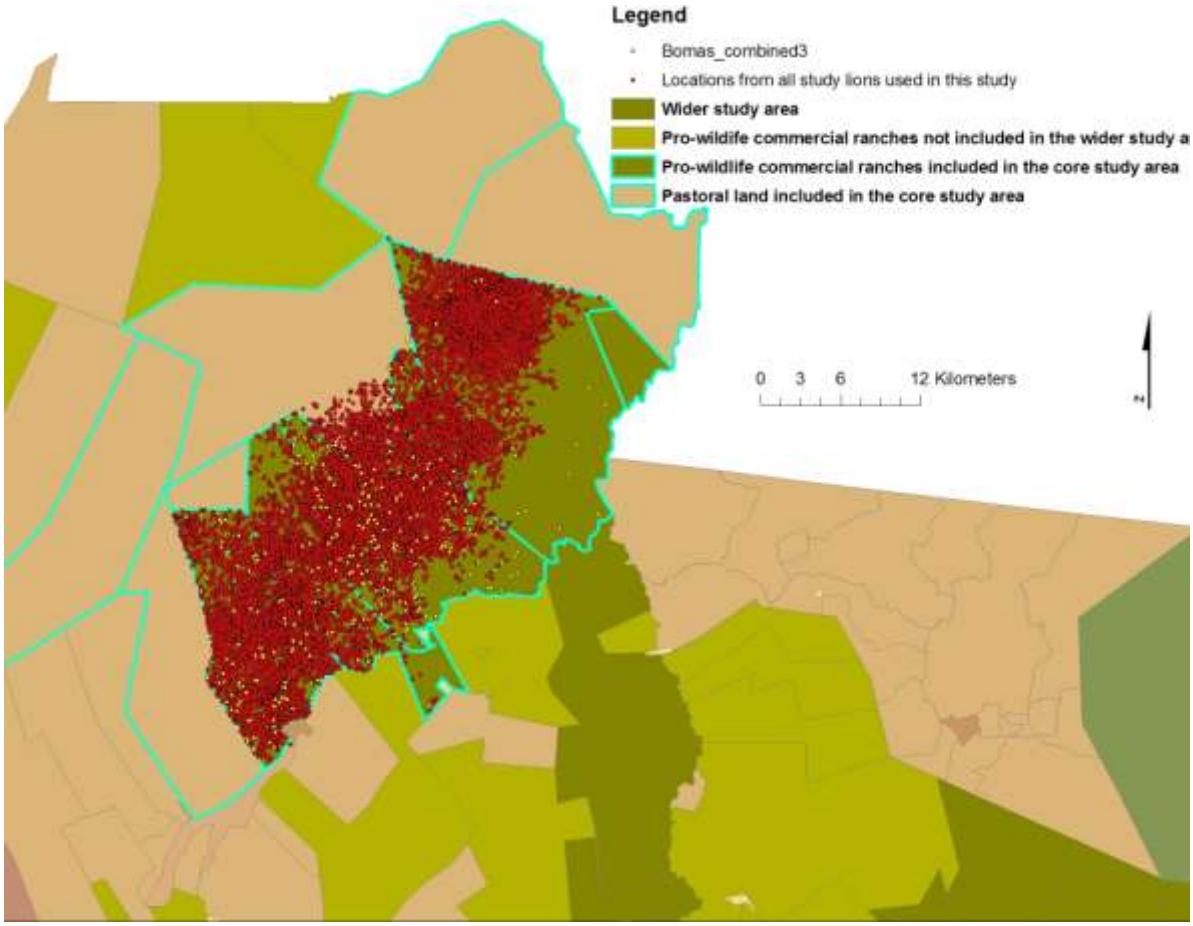

Figure 4.1. Map showing the lion and boma locations used for analyses in this chapter. Lion locations represent the movements of 5 different pride females, each female being a member of a different pride. Only lion locations falling within the area where boma movements were recorded were used in this chapter.

4.2.3. Kill and primary daytime rest sites

Potential kill sites were identified from an algorithm adapted from the Warren-Cougar-algorithm (Knopff et al 2009), which identified clusters of 4 or more consecutive GPS locations within a 200m radius, representing a location where lions had spent more than 3 hours in one location. These clusters were investigated on the ground on a monthly basis and classified as a kill site if remains of a carcass or gut contents were found. Which predator made the kill was determined wherever possible by using supporting indicators such as the type and location of the remains, the pattern of consumption, tracks (lion and prey leading up to the kill site as well as at the kill site), hairs, and other signs left on any remaining carcass such as teeth and claw marks. If a site was conclusively determined to be a lion kill site, a suite of habitat structure variables were recorded (Table 4.1.).

Primary daytime rest sites (referred to as "primary rest sites" hereafter) were identified using time density analysis i.e. distribution of time spent per unit landscape (Wall et al. 2013) on midday fixes only. The landscape units (30x30m) representing the top 1% of usage for each lion at midday were classified as primary rest sites and investigated on the ground. The same suite of habitat structure variables as used for kill sites were recorded at each primary rest site (Table 4.1.). Table 4.2. shows the distribution of kill and primary rest sites between the collared lions investigated during the study.

Table 4.1. Habitat variables collected or calculated for all models.

Variable Name	Description	Variable type and code
Distance to nearest boma[a]	Distance between each lion location and the nearest boma. Calculated using Hawths tools in ArcGIS and R.	Continuous data
Distance to nearest water[a]	Distance between each lion location and the nearest permanent water source. Calculated using Hawths tools in ArcGIS.	Continuous data
Habitat structure[a]	The cover value offered by the habitat. Taken from a habitat structure GIS layer (see habitat data collection and classification).	Discrete ordinal data. Three categories: high, medium and low refuge.
Visibility[b]	The mean value of distance to nearest obstruction (branches, leaves, thick grass). Readings were taken using a range finder every 15^{o} of the compass at average shoulder height for Laikipia lions (965cm, estimated from capture records). Variable was log transformed in order to fit the assumptions of normality.	Continuous data
Rock index[b]	The presence of rocks big enough to conceal a lion	Discrete ordinal data. Two categories: rocks, no rocks.

[a] variables calculated using GIS layers.
[b] variables measured by trained scouts at lion kill, daytime rest, and random sites.

Table 4.2. Distribution of kill and rest sites at which habitat data was collected between the different study lions.

Lion ID	Number of primary rest sites	Number of kill sites
LF153	31	18
LF161	30	23
LF176	32	26
LF177	30	7
LF185	32	31

4.2.4. Habitat data

Habitat classes were adapted from a habitat GIS layer showing 8 classes of habitat structure: 'bare earth or rock', 'open grassland', 'agriculture', 'grass with rock', 'grass with some trees and bush', 'tree and bush', 'trees and bush with some grass', and 'trees and bush with some rocks' (Centre for Training and Integrated Research in ASAL Development). These classes were then collapsed to reflect the potential refuge from detection by humans a habitat structure offered, using a combination of vegetation cover and the presence of rocks big enough to conceal a lion. Open habitat structures ('bare earth or rock', 'open grassland', and 'agriculture') were classed as 'low refuge', the class 'grass with some tree and bush' was classed as 'medium refuge', and any habitat structure classes that were predominantly trees and bush, or any other category plus rocks ('tree and bush', 'tree and bush with some grass', 'tree and bush with rocks', 'grass and rocks') were classed as 'high refuge'. These habitat structures constituted 26%, 40% and 34% of the area respectively. Permanent water sources were plotted on a GIS layer created using ArcGIS 9.3 (ESRI [UK] Ltd. Millennium House).

4.2.5. Human distribution and activities

Human locations on the commercial ranch land were closely associated with livestock movements; humans stay within bomas between sunset (1830h) and sunrise (0630h) but leave the bomas to herd cattle during the day (Frank 1998, 2011, Patterson 2004). Boma locations were, therefore, a good proxy for human locations at night, and by day the probability of encountering humans could be assumed to decline as distance to the nearest boma increased. Bomas on the commercial ranches were moved to maximise grazing at intervals of 2-12 weeks, and their locations were recorded over the study period (Fig. 4.1.).

4.2.6. Prey abundance and distribution

Road count surveys following the distance sampling method (Buckland et al. 2001) were carried out during one wet period (October) and one dry period (January-February) for each year between 2009 and 2011. Twelve 20km routes were chosen across the study area to give equal coverage of the two land-use types (pastoral and commercial ranch land) and the three habitat structures (low, medium and high refuge). During each survey, one route was driven each morning (0700-1000hrs) and each evening (1530-1830hrs). Each route was divided into seven 2 km transects, separated by 1km with no data collection. On the 2km transects, all animals sighted were recorded (species and number) along with a bearing describing the direction of the animals sighted, and a second bearing describing the direction of the route driven. A range finder was used to record the distance from the observer that the animals were first sighted. As distinct wet and dry seasons did not occur during the study period, due to frequent unseasonable rain, all count data were combined for analysis. In total 168km of road transects were driven in each survey using two observers and one driver/scribe. Surveys included common prey species: buffalo, plains zebra, Grevy's zebra, oryx, eland, giraffe, kudu, Hartebeest, Grant's gazelle, Thompsons gazelle, impala, warthog, and waterbuck. First, we calculated the kilometric abundance index for each species sighted during road transect counts (Maillard et al. 2001; Vincent et al. 1991). This index represented an encounter (sighting) rate per kilometre of road driven and was taken as a proxy for the rate at which lions encountered individuals of each species of prey. We then converted the abundance index into biomass by multiplying the average mass of individuals (Georgiadis et al. 2007, Cumming & Cumming 2003) by their abundance. The wild prey kilometric biomass for each of the three habitat structure classes was then calculated, and an ANOVA was performed on the results in order to determine if wild prey kilometric biomass significantly differed between the different habitat structure classes.

4.2.7. Habitat selection analyses

Habitat availability was represented by an equal number of random points as actual locations generated within each lions home range using the ‘‘Generate Random Points’’ option of Hawth’s tools for ESRI ArcGIS 9.2 (Beyer 2007). This achieved a 1:1 ratio of use vs. available sites for 1) all lion locations, 2) kill sites, 3) primary rest sites. To maximise the likelihood of random points being true zeros i.e. never having been visited by lions, a 50m buffer was added around each actual location within which no random points were generated. Lion home range was calculated as a minimum convex polygon (MCP), again using the extension Hawth's tools in ArcGIS 9.3. Although MCP’s often overestimate space use (Macdonald et al. 1980, Douglas-Hamilton et al. 2005), they are a better estimate of the total area potentially available to lion when measuring avoidance of certain areas than home range methods that exclude areas that are unused such as Kernel Density Estimates (Graham 2009). Habitat structure class, distance to nearest water, and distance to nearest boma were extracted for both actual and randomly generated locations (“Intersect point”, and “Distance between points”, Hawths Tools, in ArcGIS 9.3). Fine-scale habitat data were also collected on the ground for kill sites, primary rest sites, and random locations generated as a comparison (Table 4.1). We compared lion locations in three periods of the 24 hr cycle which contrasted in terms of human activity: 1) Daytime (0700h-1800h) when humans are active and moving about the landscape, 2) Evening (1900h-2200h and 0600h) when humans are at bomas but still active, and c) Dead of night (2300h-0500h) when humans are within bomas and inactive.

4.2.7.1. Habitat selection within an animal’s home range

Selection for habitats within lions’ home ranges was investigated for data sets from the three human activity periods, in order to test whether resource or human based hypotheses best described the data. Habitat use, estimated from lion GPS locations, was compared to habitat

availability, estimated from randomly sampled locations within the home range of the respective individuals, using mixed effects logistic regression models to develop resource selection functions (Boyce & McDonald 1999, Johnson et al 2006, Manly et al. 2002). Explanatory variables included 'distance to nearest boma', 'distance to nearest water', and 'habitat structure'. 'Lion identity' was entered into the models as a fixed effect. Interactions corresponding to plausible hypotheses about lions' selection of habitat were included; these were 'Habitat structure*Distance to nearest boma' and 'Habitat structure*Distance to nearest water'. To avoid collinearity between variables, we computed Pearson's correlation coefficients for all pairs of variables and excluded one of the variables if the correlation coefficient was ≤ 0.5. To minimise serial temporal autocorrelation in the data, we randomly selected one location per 24hr cycle for each human activity period (Swihart and Slade, 1985a,b). Rarefying the data in this way has proven to be highly conservative, albeit resulting in the loss of a large amount of data (McNay et al., 1994).

4.2.7.2. Habitat selection at specific sites

We investigated selection for habitat at kill sites and primary rest sites. Resource selection functions at these sites were developed by comparing habitat variables at random points to those at actual lion locations using logistic regression, in the same way as for habitat selection within animal's home ranges. Explanatory variables looked in more detail at aspects of the habitat structure and included: 'rock index', 'visibility', and 'distance to nearest water' (Table 4.1.). 'Distance to nearest boma' could not be included in any model predicting the use of primary rest sites as boma locations moved regularly but primary rest sites were chosen on the basis of cumulative time lions spent in these sites over the whole study period. Distance to nearest boma was therefore, excluded from this analysis. 'Lion identity' was again included in all models as a fixed effect to account for behavioural variability. To avoid

collinearity between variables, we computed Pearson's correlation coefficients for all pairs of variables and excluded one of the pair from model selection if the coefficient was ≤ 0.05.

Logistic regressions were performed with R 2.14.2 software (R Development Core Team, 2012) using the function 'glm' in the package 'MASS' (Venables & Ripley 2002). Model selection was performed using Akaike Information Criteria (AIC - Burnham & Anderson 2002). Relative strength of evidence of each model was assessed using Akaike weights (denoted *w*) and the best-fit models were taken to be those where $w \leq 2$. We then used the function 'CVbinomial' in the package' DAAG' (Maindonald & Braun 2011) to carry out K-fold cross validation of the models identified as having the best-fit, following a 10 – fold application (Harrell, 1998). This approach improved our interpretation of the predictive ability of our best-fit models, and therefore the reliability of these models as resource management tools (Boyce et al. 2002).

4.3. Results

4.3.1. Habitat selection within an animal's home range

None of the variables were found to have a correlation value >0.5 and were all, therefore, included in model selection. Lions showed habitat selection within their home range during all three human activity periods (Table 4.3.). An interaction between 'distance to nearest water' and 'habitat structure' was present throughout the 24hr cycle (Fig 4.2.a.i and 4.2.a.ii). Both high and low refuge habitats were increasingly selected when within approximately 2km of water during all periods but particularly during the day.

The use of habitats in proximity to bomas was different for all three human activity periods. Distance to nearest boma was included in one of the best-fit models for all time

periods (Table 4.3). During the dead of night, lions were closer to bomas than expected at random (estimate ± SE = -3.334e-05 ± 1.821e-05), however, during the evening lions were further from bomas than expected from random (estimate ± SE = 1.522e-05e-05 ± 1.694e-05). During the day, there was an interaction between 'distance to nearest boma' and 'habitat structure' (Fig 4.2.b.iii) such that the probability of selecting low refuge habitat decreased with distance to the nearest boma. Within 4.5km of a boma, low refuge habitat, and to a lesser degree medium refuge habitat, were increasingly avoided. Although Akaikes weights were in favour of the most parsimonious best-fit model during the evening, K-fold cross validation results indicated that the model 'Lion ID + distance to water * habitat structure + distance to boma' had better predictive powers than the same model excluding the variable distance to boma. All best-fit models for other time periods performed equally well and had little to chose between them in terms of their ability to predict lion locations; the difference between internal estimates of accuracy and cross validation estimates of accuracy were similarly low (Table 4.4.).

Table 4.3. Summary statistics for models explaining habitat selection for lions in Laikipia, Kenya; a) during dead of night, b) during the evening, and c) during the daytime. Lion identity was included in every model as a fixed effect. The models in boldface italic type are the models where $w \leq 2$.

	Model	AIC	ΔAIC	Akaikes weights (*w*)
a	Null	5949.20	30.10	0.00
	Lion ID + Distance to water	5932.20	13.10	0.00
	Lion ID + Distance to boma	5941.30	22.20	0.00
	Lion ID + Habitat structure	5938.80	19.70	0.00
	Lion ID + Distance to water + Distance to boma	5930.70	11.60	0.00
	Lion ID + Distance to boma + Habitat structure	5934.60	15.50	0.00
	Lion ID + Habitat structure + Distance to water	5926.60	7.50	0.01
	Lion ID + Distance to water + Distance to boma + Habitat structure	5925.10	6.00	0.03
	Lion ID + Distance to water * Habitat structure	***5920.50***	***1.40***	***0.28***
	Lion ID + Distance to Boma * Habitat structure	5937.70	18.60	0.00
	Lion ID + Distance to water * Habitat structure + Distance to Boma	***5919.10***	***0.00***	***0.57***
	Lion ID + Distance to Boma * Habitat structure + Distance to water	5928.40	9.30	0.01
	Lion ID + Distance to water * Habitat structure + Distance to Boma * Habitat structure	5922.60	3.50	0.10
b	Null	6467.70	12.60	0.00
	Lion ID + Distance to water	6461.00	5.90	0.03
	Lion ID + Distance to boma	6477.60	22.50	0.00
	Lion ID + Habitat structure	6475.40	20.30	0.00
	Lion ID + Distance to water + Distance to boma	6462.60	7.50	0.01
	Lion ID + Distance to boma + Habitat structure	6477.40	22.30	0.00
	Lion ID + Habitat structure + Distance to water	6461.60	6.50	0.02
	Lion ID + Distance to water + Distance to boma + Habitat structure	6463.00	7.90	0.01
	Lion ID + Distance to water * Habitat structure	***6455.10***	***0.00***	***0.55***
	Lion ID + Distance to Boma * Habitat structure	6481.30	26.20	0.00
	Lion ID + Distance to water * Habitat structure + Distance to Boma	***6456.30***	***1.20***	***0.30***
	Lion ID + Distance to Boma * Habitat structure + Distance to water	6466.70	11.60	0.00
	Lion ID + Distance to water * Habitat structure + Distance to Boma * Habitat structure	6459.00	3.90	0.08
c	Null	5635.90	72.10	0.00
	Lion ID + Distance to water	5613.60	49.80	0.00
	Lion ID + Distance to boma	5645.30	81.50	0.00
	Lion ID + Habitat structure	5607.00	43.20	0.00
	Lion ID + Distance to water + Distance to boma	5612.90	49.10	0.00
	Lion ID + Distance to boma + Habitat structure	5607.20	43.40	0.00
	Lion ID + Habitat structure + Distance to water	5581.40	17.60	0.00
	Lion ID + Distance to water + Distance to boma + Habitat structure	5579.10	15.30	0.00
	Lion ID + Distance to water * Habitat structure	5573.10	9.30	0.01
	Lion ID + Distance to Boma * Habitat structure	5602.50	38.70	0.00
	Lion ID + Distance to water * Habitat structure + Distance to Boma	5570.20	6.40	0.04
	Lion ID + Distance to Boma * Habitat structure + Distance to water	5572.90	9.10	0.01
	Lion ID + Distance to water * Habitat structure + Distance to Boma * Habitat structure	***5563.80***	***0.00***	***0.94***

Table 4.4. Results of K-fold cross validation on the best-fit models (listed in Table 4.3.) explaining habitat selection for lions in Laikipia, Kenya; a) during dead of night, b) during the evening, and c) during the daytime.

	Model	*Internal estimate of accuracy*	*Cross-validation estimate of accuracy*	*Difference*
a.	Lion ID + Distance to water * Habitat structure	0.534	0.522	0.012
	Lion ID + Distance to water * Habitat structure + Distance to Boma	0.548	0.534	0.014
b.	Lion ID + Distance to water * Habitat structure	0.511	0.488	0.023
	Lion ID + Distance to water * Habitat structure + Distance to Boma	0.506	0.493	0.013
c.	Lion ID + Distance to water * Habitat structure + Distance to Boma * Habitat structure	0.552	0.543	0.009

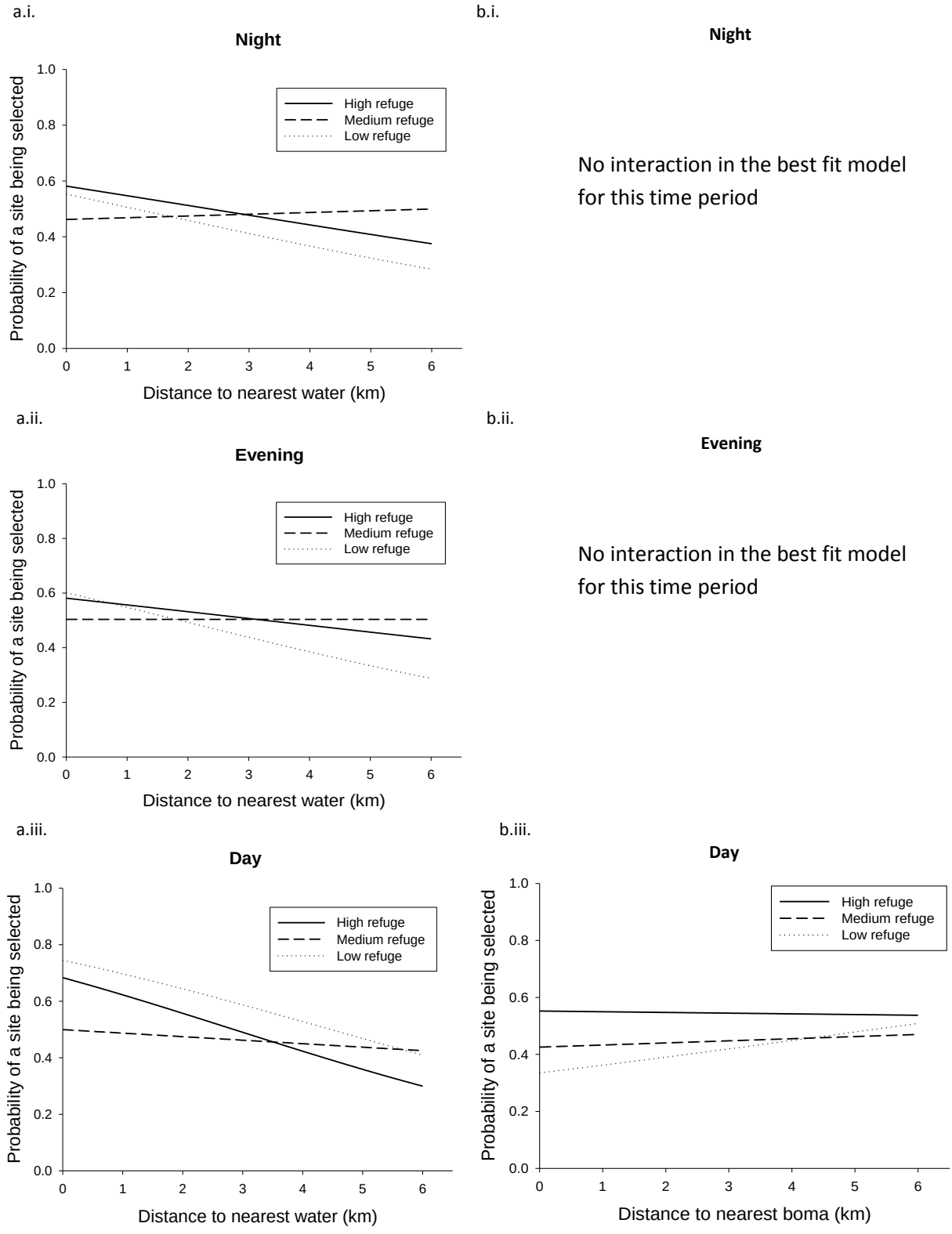

Figure 4.2. Interaction between the three refuge habitat structures and a) distance to water, and b) distance to nearest boma during i. dead of night, ii. evening, and iii. day time. NB. Gaps mean that there was no interaction in the best fit model for that time period. Other variables in the models were held constant at their mean value for the data set.

4.3.2. Habitat selection at kill sites

Lion kill sites (Table 4.5.) were closer to water (averaged estimate ± SE = -0.001± 0.0001) and less likely to be where there were rocks (averaged estimate ± SE = -1.86 ± 0.43) than expected from random in both best-fit models. In one best-fit model probability of a location being a kill site increased with visibility (estimate ± SE = 0.58 ± 0.34). After K-fold cross validation, both best-fit models showed internal estimates of accuracy that were not much higher than the cross validation estimates of accuracy, therefore showed good predictive powers (Table 4.6.). The most parsimonious model, 'Lion ID + distance to water + rock index' performed particularly well in terms of its ability to predict lion locations.

4.3.3. Habitat selection at primary rest sites

The probability of a site being a primary rest site increased as visibility decreased (averaged estimate ± SE = -3.61 ± 0.42) in all three best-fit models (Table 4.5.). The most parsimonious best-fit model included only 'Lion ID + Visibility'. In the second best-fit model, distance to nearest water was also included such that the probability of a site being a primary rest site decreased as distance to water increased (estimate ± SE = -0.00008 ± 0.00007). A third best-fit model included the variable rock index; lions had a lower probability of selecting a site as a primary rest site if there were rocks (estimate ± SE = -0.13 ± 0.32). Again, all three best-fit models showed internal estimates of accuracy that were not much higher than the cross validation estimates of accuracy, therefore showed similarly good predictive powers (Table 4.6.).

Table 4.5. Summary statistics for models explaining habitat selection for lions in Laikipia, Kenya; a) at kill sites, and b) at primary rest sites. Lion identity was included in every model as a fixed effect. The models in boldface italic type are the models providing the best fit ($w \leq 2$).

	Model	AIC	ΔAIC	Akaikes weights (w)
a.	Null	291.73	74.18	0.00
	Lion ID	294.93	77.38	0.00
	Lion ID + Distance to water	238.01	20.46	0.00
	Lion ID + Rock index	277.72	60.17	0.00
	Lion ID + Visibility	295.69	78.14	0.00
	Lion ID + Distance to water + Rock index	***218.51***	***0.96***	***0.38***
	Lion ID + Distance to water + Visibility	236.60	19.05	0.00
	Lion ID + Rock index + Visibility	278.23	60.68	0.00
	Lion ID + Rock index + Visibility + Distance to water	***217.55***	***0.00***	***0.62***
b.	Null	428.98	159.90	0.00
	Lion ID	436.98	167.90	0.00
	Lion ID + Distance to water	412.87	143.79	0.00
	Lion ID + Rock index	438.10	169.02	0.00
	Lion ID + Visibility	***269.08***	***0.00***	***0.44***
	Lion ID + Distance to water + Rock index	414.02	144.94	0.00
	Lion ID + Distance to water + Visibility	***269.98***	***0.90***	***0.28***
	Lion ID + Rock index + Visibility	***270.92***	***1.84***	***0.17***
	Lion ID + Rock index + Visibility + Distance to water	271.80	2.72	0.11

Table 4.6. Results of K-fold cross validation on the best-fit models (listed in Table 4.5.) explaining habitat selection for lions in Laikipia, Kenya; a) at kill sites, and b) at primary rest sites.

	Model	*Internal estimate of accuracy*	*Cross-validation estimate of accuracy*	*Difference*
a.	Lion ID + Distance to water + Rock index	0.737	0.737	0.000
	Lion ID + Rock index + Visibility + Distance to water	0.732	0.713	0.019
b.	Lion ID + Visibility	0.782	0.766	0.016
	Lion ID + Distance to water + Visibility	0.779	0.766	0.013
	Lion ID + Rock index + Visibility	0.782	0.769	0.013

4.3.4. Distribution of prey between habitat structure classes

Prey kilometric biomass in high refuge habitat was 2709kg/km^2, medium refuge habitat was 3035kg/km^2, and low refuge habitat was 2450kg/km^2. Prey kilometric biomass was not significantly different between habitat structure classes (ANOVA: F = 0.03, p = 0.97) (Fig 4.3.).

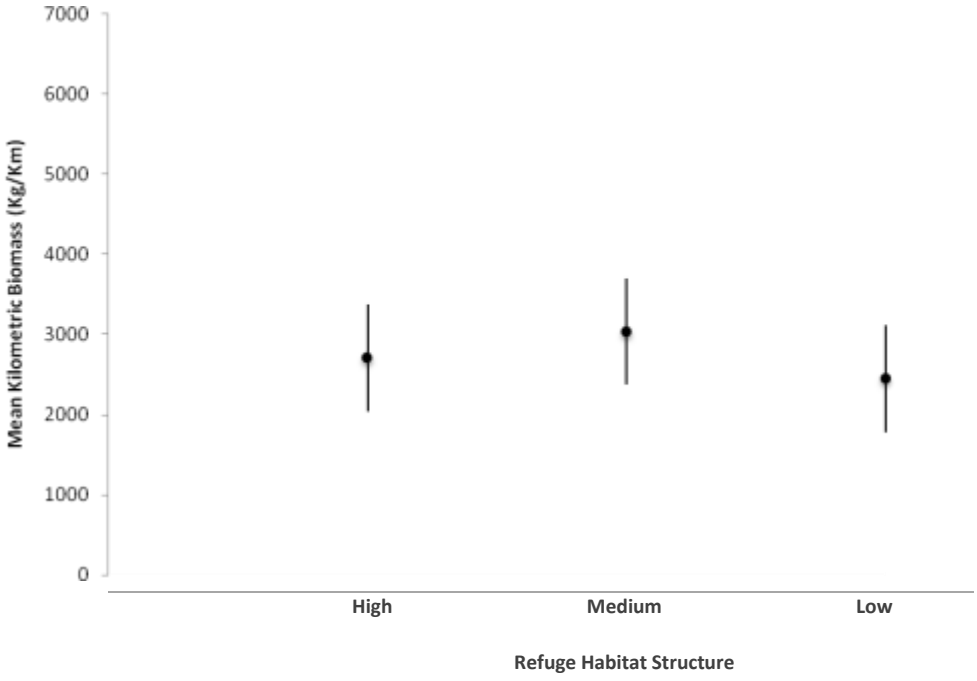

Figure 4.3. Wild prey kilometric biomass ± SD (kg/kms^2) for each refuge habitat structure in the study area.

4.4. Discussion

Results support our prediction that habitat selection by lions in a Landscape of Coexistence represents a trade-off between maximising hunting success and minimising detection by humans. A habitat structure may be chosen for the resources it offers lions (e.g. prey densities, water, and/or cover for ambush opportunities), or for the refuge it offers lions from humans. The hierarchical importance of resource versus human factors affecting habitat selection appears to vary on a fine temporal scale with human activity levels.

4.4.1. Prey searching drives lion habitat selection during the night

The dark hours are when lions are most likely to be foraging (Van Orsdol 1984, Prins and Iason 1989, Cozzi et al. 2012). Night time habitat selection at both scales (within home range and at specific kill sites) indicates that prey vulnerability as well as abundance may be important determinants, and support the suggestion that water sources form 'passive traps' for prey that significantly influence lion foraging (Valeix et al. 2010, Davidson et al. 2012, 2013). Habitat selection within the home range and at kill sites were more likely to be closer to water than expected, probably due to increased prey abundance (Valeix et al. 2009b, Mosser et al 2009, Davidson et al. 2012, 2013). Where lions in protected areas have been shown to spend most of their time in more open habitats with higher prey abundance (Selous Game Reserve, Tanzania - Spong 2002, Hwange NP, Zimbabwe - Davidson et al 2012), habitat selection on the home range scale showed study lions increasingly selecting both low and high refuge habitat in proximity to water. An increase in the selection of open (low refuge) habitats closer to water by Laikipia lion may be explained by many water points being surrounded by a ring of more open habitat, or piosphere (Thrash & Derry 1999), whereas selection for high refuge habitats may increase prey vulnerability (Hopcraft et al. 2005). Findings from Davidson et al. (2012) showed habitat selection by lions in Hwange NP

was driven by a combination of prey abundance within an animal's home range, and prey vulnerability at specific sites. Kill sites in this study, however, were associated with increased levels of visibility (more open habitat) and a lack of rocks. Although game counts in this study were too course to pick up changes in prey densities on the basis of those variables, open habitat was associated with higher prey densities in another Laikipia study (Riginos & Grace 2008) and in several other studies (e.g. Davidson et al. 2012, Hopcraft et al. 2005). Although high refuge habitats offering cover are possibly important for increasing ambush opportunities, kill site selection by study lions supported the fact prey abundance was the most important factor in determining foraging success. Laikipia is characterised by very patchy distribution of different habitat structures however, and, unlike studies done in the Serengetti and Hwange (Hopcraft et al. 2005, Davidson et al. 2012) where there are large areas of very open habitat, some cover is offered in almost all areas, possibly limiting our ability to pick up on the role of habitat structure in increasing prey vulnerability.

De Boer et al. (2010) separated the importance of proximity to water from thicker habitat structures and found that distance to water was the most important variable in determining lion hunting success in a protected private reserve. Although Loarie et al (2013) linked hunting success of male lions to thicker habitat, other studies in protected areas (Van Orsdol 1984, Prins & Iason 1989, Funston et al. 2001) have shown only marginal influence of habitat density. The observed selection for high refuge habitat structures by study lions in a human dominated landscape may, therefore, not be made solely on the basis of optimising hunting success.

4.4.2. Avoidance of detection by humans drives lion habitat selection during the day

Habitat structures with dense vegetation and/or rough terrain may provide refuge from humans, particularly at times or in places where humans are more likely to be active. The

observed increase in selection for high refuge habitat when within 4.5km of water during the day (Fig 4.2.a.iii) may reflect a need to avoid detection at times when humans and livestock use water points (Frank 1998, 2011, Coppolillo 2000). Selection for different habitat structures also varied at different distances to bomas during the day but not during either night time period. Although bomas have a human presence at all times in the 24 hour cycle, we documented no overall spatial avoidance of them. During daytime, when humans were active on the landscape, a clear switch in habitat structure preference for study lions within 4.5km of a boma was observed, such that low, and to a lesser extent medium, refuge habitat were avoided (Fig. 4.2.b.iii). The hypothesis that avoiding detection by humans drives daytime habitat selection by study lions is further supported by habitat structure at primary rest sites. These were selected on the basis of low visibility, the measure taken as a proxy for how visible a lion might be to humans. Study lions may select denser habitat structures by day in order to find shade, but shade is also freely available in patchy habitats or under tall trees, suggesting that concealment rather than shade may determine site selection by day. Hopcraft et al. (2005) showed that although cover was important in habitat selection for lions, selecting vantage points with good view sheds increased the chance of spotting scavenging opportunities. Although cover is undoubtedly important for a sit and wait predator, cover that reduces visibility too much may not be a tactic that optimises foraging success. The theory that areas of low visibility were not selected to optimise hunting success is further supported by the fact kill sites were associated with areas of higher visibility.

At night, when people were confined to bomas, risk of detection by humans was unlikely to be a major factor influencing study lion movements except when very close to bomas. Predictably there was no interaction between habitat structure and distance to nearest boma during either evening or dead of night. However, human activity levels did still influence study lion habitat selection at night; study lions avoided bomas during the evening

hours when humans were active, but during the dead of night when humans are least active, study lions moved closer to bomas than expected, possibly allowing them to hunt in the vicinity of bomas at times when the risk of detection by humans was lowest. Lions may also investigate bomas as a potential source of livestock prey (Valeix et al. 2012, Chapter 5). Risk of detection by humans may also influence lion hunting behaviour at night; to avoid detection by humans when feeding in proximity to bomas, lions would need to either; kill and consume their prey before daylight, abandon the carcass as humans become active, or kill in or near habitats that offer refuge. Further research into the effect of habitat structure on prey selection and consumption in the vicinity of humans may reveal more behavioural effects of human-caused mortality risks not investigated here.

Seasonal variations in habitat use were not investigated in this study due to unseasonal rainfall during normally dry periods resulting in a lack of distinct wet and dry seasons. Where distinct seasons do occur, however, cover availability, thus risk of detection by humans, is likely to vary in response to rainfall (e.g. grass length and tree/bush leaf density). Increased rainfall may also reduce the distances livestock and humans move from bomas in search of good grazing and water. Although seasonal changes in habitat selection were not found to be significant in one protected area study (Davidson et al.2012), a seasonal variation in habitat selection with proximity to humans may be expected in Landscapes of Coexistence, particularly during periods when humans are active.

Chapter 5.

Human-carnivore coexistence: lion movements inform livestock protection techniques

A collared lioness in Laikipia, makes a daytime livestock kill. Given the abundance and vulnerability of livestock when grazing on the landscape, it is surprising how rarely it is chosen as prey. Photos by: Tui de Roy.

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Abstract

The drivers of human-carnivore coexistence include the behaviour of both humans and carnivores, yet studies on how best to facilitate this coexistence have primarily focused on understanding and improving human practices and attitudes. Carnivores' behavioural adjustments in response are largely unknown. This study combines data on lion-livestock interactions (incidents where lions were observed in proximity to livestock) and on lion movements (from GPS collared lions) in Laikipia County, Kenya, to investigate which factors are most important in determining the propensity of study lions to approach bomas, as well as the likelihood that they will attack livestock and that the attack will be successful. Boma design was the strongest predictor of both study lion proximity to bomas and the likelihood of a successful attack, with study lions maintaining a higher mean distance from boma designs at which probability of success was low. Rather than identify boma design from a distance and react to it, study lions appeared to visit livestock more in areas where they had had previous success. Avoidance of livestock in areas where the husbandry had been improved thus appeared to be learnt over time. Human activity levels, habitat surrounding bomas, moonlight and mean daily rainfall also influenced the distance to which study lions approach bomas; lions being found significantly closer to bomas during the dead of night when people were least likely to be active., wetter periods and times of brighter moonlight (conditions associated with lower wild prey hunting success in other studies). Study lions were also more likely to be found closer to bomas, situated in habitat that provided some cover. Keys to successful coexistence between lions and humans include consistently strong boma designs throughout a geographic area, careful day time herding, and adequate densities of wild prey. Studying carnivore behaviour in response to husbandry practices brings new insight to facilitating human-carnivore coexistence.

5.1. Introduction

Retaliatory killing of large carnivores by people in response to livestock depredation is one of the primary reasons for the collapse of large carnivore populations through much of their remaining range (Weber & Rabinowitz 1996, Woodroffe & Ginsberg 1999, Sillero-Zubiri & Laurenson, 2001, Macdonald & Sillero-Zubiri, 2004). Even in protected areas, the wide ranging nature of large carnivores means they often encounter human-caused mortality risk in the surrounding non-protected areas, and this edge effect can impact the survival of a population (Woodroffe & Ginsberg 1998, Harcourt et al. 2001). The drivers of human-carnivore coexistence are complex (Treves & Karanth 2003, Hazzah et al 2009, Zimmerman et al 2005) and the propensity for people to kill carnivores may not be related directly to the amount of livestock lost (Marker et al. 2003, Dickman 2010, Marchini & Macdonald 2012). However, living with carnivores can be costly for pastoral people and commercial ranchers alike (Frank 1998, 2011, Patterson et al. 2004, Maclennan et al. 2009) and finding ways to minimise those costs is key to human-carnivore coexistence (Bagchi & Mishra 2006, Macdonald et al. 2010, Karanth et al. 2012).

Many carnivore attacks on livestock are preventable through careful management and most studies on human-carnivore coexistence have focused on husbandry practises (Ogada et al. 2003, Woodroffe et al. 2007). Husbandry decisions are largely economic, depending on local costs and relative benefits (Ogada et al. 2003), and simple, traditional, low cost methods, such as protecting livestock in bomas made of local materials (e.g. thorn trees) at night, work when built well (Ogada et al. 2003, Treves & Karanth 2003, Frank et al 2005, Woodroffe et al. 2006). Even relatively small changes to livestock husbandry practices, for example the use of dogs or solid gates on thornbush bomas can substantially reduce depredation losses (Marker 2005, Woodroffe et al. 2006, Marker et al. 2010).

Facilitating human-carnivore coexistence, however, also depends on understanding and the behaviours of carnivores themselves. Variation in the risk of human-caused mortality across a heterogeneous landscape creates a 'Landscape of Coexistence' for large carnivores (Chapter 1). In a Landscape of Coexistence, carnivores may adjust their behaviour to reduce the risk of human-caused mortality, e.g. the avoidance of livestock as a prey species where an alternative wild prey base allows (Mattioli et al. 1995, 2004, Capitani et al. 2004, Woodroffe et al. 2005). In many unprotected rangelands, however, livestock make up the larger proportion of ungulate biomass and avoiding it may appear counter-adaptive. Livestock husbandry in much of East Africa is still based on traditional pastoral practices: bomas and daytime herding (Frank, 2011). Livestock is thus distinguishable from wild prey predominantly by their circumstance i.e. the presence of humans and their location within bomas during the night. Our ability to reduce livestock losses, and the consequent retaliation against carnivores, depends not only upon practices that help people defend livestock from predators, but also upon understanding the factors which allow carnivores to avoid livestock, particularly the criteria by which they discriminate livestock from wild prey.

Livestock depredation by lions (*Panthera leo*) is more expensive and difficult to prevent than depredation by any other large African carnivore (Singh & Kamboj 1996, Bauer & de Iongh 2005) predominantly due to their tendency to kill the largest and most valuable livestock (e.g. cattle - Butler 2000, O'Connell-Rodwell et al. 2000; and camels – data from this study). Yet, many livestock husbandry practices that effectively reduce attacks by lions are effective against other large carnivores as well; thus, reducing livestock lost to lions also facilitates coexistence with other carnivore species.

This study uses data on livestock depredation (using ground investigation at the scene of lion attacks on livestock) and movements (using GPS collars) to examine husbandry and environmental predictors of (1) lion's proximity to bomas, (2) the probability of attack, and

(3) the probability that an attack results in the death or injury of livestock once it occurs. We predict that lions will distinguish between well protected livestock (held within strong bomas and/or accompanied by people, thus representing greater human-caused mortality risk), and poorly protected/unprotected livestock. We also predict that environmental factors which affect lions' success when hunting wild prey will also affect their tendency to hunt livestock.

5.2. Methods

5.2.1. Study Site

Laikipia County, in the central highlands of Kenya ($36^{o}10'$-$37^{o}3'$ E and $0^{o}17'$S-$0^{o}45'$N), is at an elevation of 1700-2000m above sea level and comprises wooded savannah and open grassland northwest of Mount Kenya. None of Laikipia has IUCN protected area status (I-IV) but is unusual in that a low density human population and livestock coexist with a relatively high density of wildlife, including all the region's large carnivores, (mean biomass of 1700kg/km^2 wildlife and 2700kg/km^2 livestock on pro-wildlife ranches - Georgiadis et al. 2007). Annual rainfall is highest in the south of the county, closest to Mount Kenya (~750mm) and gradually declines to the north of the county (~300mm). Although some rain falls all year, most is concentrated in the long rains - between April and June, and the short rains - between October and December, (Berger 1989, Gichuki et al. 1998).

Laikipia is comprised of a complex mosaic of different land uses and forms of land-tenure, including commercial ranch land, traditional communally owned pastoralist areas, and small farms in the south. Total area of Laikipia is 9666km^2, 3288km^2 of which is classed as pro-wildlife i.e. large scale commercial ranches where wildlife is tolerated or encouraged (Georgiadis et al. 2007). For this study, we collected data on lion and livestock boma movements on contiguous pro-wildlife commercial ranches totalling 677 km^2, referred to as

the core study area. Data on overall depredation losses were collected over a wider study area consisting of 12 pro-wildlife commercial ranches covering a total of 1544 km^2 (Fig. 5.1).

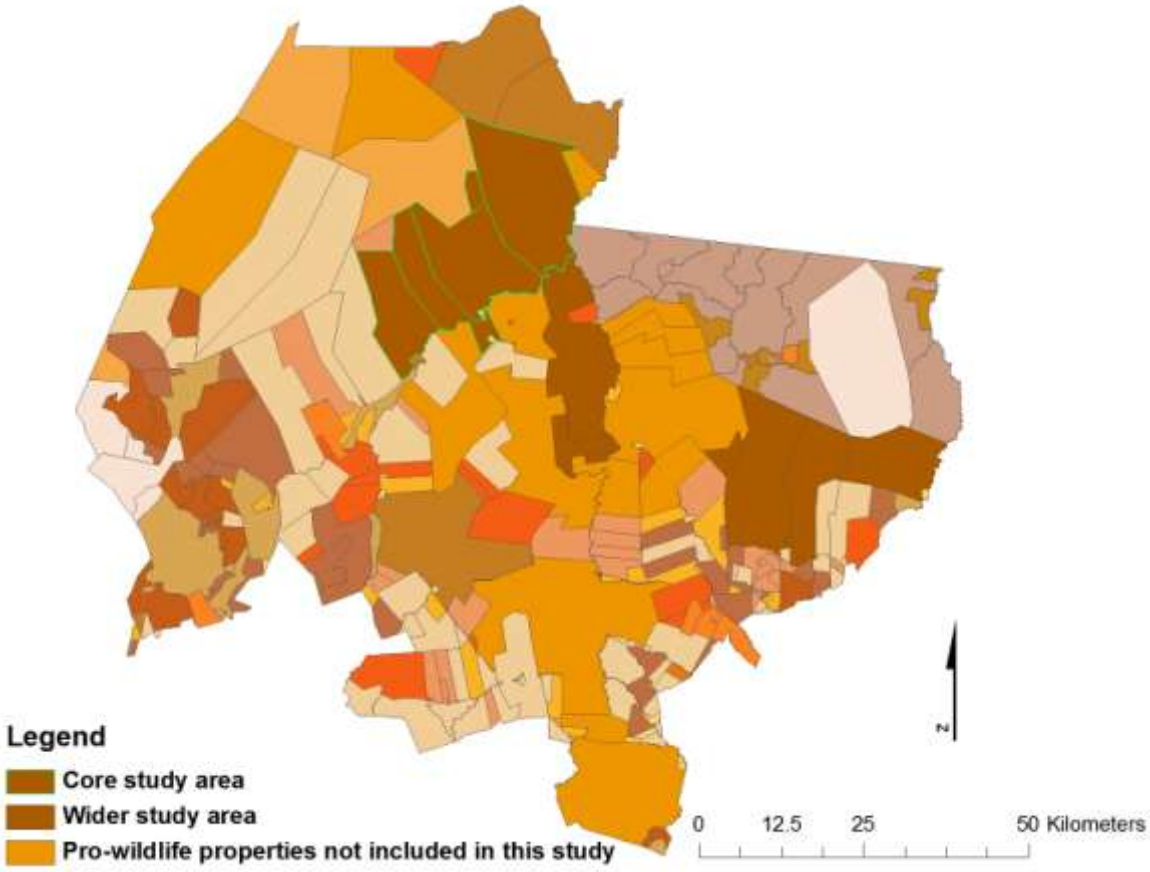

Figure 5.1: Map of Laikipia County, Kenya, showing the core and wider study area.

5.2.1.1. Livestock husbandry and depredation in Laikipia

The main income for land owners throughout the wider study area was livestock ranching, and traditional livestock husbandry was still practiced (Frank 2011, Ogada et al 2003, Woodroffe et al. 2005): livestock were kept in bomas at night to protect from thieves and large carnivores, and herded out to graze by day, accompanied by herders. Livestock were always secured inside bomas well before sunset (1830h) and herded out to graze after sunrise (0630h) so that all people and livestock were in bomas at night when lion, leopard, and spotted hyaena were active. Individual animals occasionally became separated from the herd during the day, and if not found, remained out of the boma overnight. Herds were moved to different boma locations at intervals of 2–24 weeks, depending on the quality of the grazing, and in this way utilised all parts of the landscape over time. Night guards and herders were generally from local pastoralist tribes. Until recently, commercial ranches used the traditional African thornbush bomas but most have recently adopted moveable steel frame and wire mesh designs (mobile bomas) which reduce depredation losses and improve grazing management (http://www.olpejetaconservancy.org/sites/default/files/Predator%20Proof%20Boma%20Design%20Specs.pdf). Boma designs in use over the study period, and the proportion of bomas represented by each design, are summarized in Table 5.1.

All large carnivore species in Laikipia take livestock (Frank 2011, Ogada et al. 2003, Woodroffe et al. 2005). However, in recent years improved standards of livestock husbandry on commercial ranches have reduced depredation by all species. Most ranches tolerate some loss to lions but when an individual kills livestock repetitively the problem individual is verified and shot, with permission from the Kenya Wildlife Service (Frank et al. 2005). Between 1998 and 2003, adult lions suffered 19.4% shooting mortality annually on the

commercial ranches in response to livestock depredation (Woodroffe and Frank 2005), and this remained similar over the study period (Frank and Oriol-Cotterill unpublished data).

5.2.2. Lion proximity to boma data

Five female lions from different prides in the core study area were fitted with GPS Plus collars (Vectronics Aerospace GmbH) that were programmed to record hourly fixes between 18:00 and 07:00, plus one midday fix. Lions were captured and collared under permit from the Kenya Wildlife Service and followed University of California Animal Care and Use Protocol R191 using methodology described by Frank et al. 2003. One individual per social group was collared at any given time to avoid data duplication. Lion locations falling outside of the study period (2009-2012), or the core study area, were excluded from analyses. Fixes were imported into ArcGIS 9.2 and projected to the Universal Transverse Mercator (UTM) WGS-84 reference system (Zone 37 N). Ninety five percent kernel density estimates of home range were calculated using ‘‘Fixed kernel density estimator’’ option of Hawth’s tools for ESRI ArcGIS 9.2 (Beyer 2004). Bomas on the commercial ranches were moved to maximise grazing at intervals of 2-12 weeks, and their locations were recorded over the study period. Distance to nearest boma was calculated for each lion location using R (R Development Core Team 2012).

A ‘boma visit’ made by lions was defined as lion locations falling within 200m of a boma. Two hundred meters was chosen to represent the distance at which lions may be detected by eye shine using a torch beam from a boma sited in open habitat. Bomas have been shown to most influence lion movements at a distance of 1500m (Chapter 3). The percentage of lion nights on which a lion came within the zone of influence (<1500m) of a boma and went on to visit the boma (<200m) was measured for different boma designs.

Table 5.1. Boma designs in the study area during the study period.

Boma Design	Description	Comments	Representation in the core study area
Thorn bomas	The oldest traditional method; walls made of tightly packed cut thorn trees and bushes. Gate usually made of a cut thorn tree that can be pulled across the opening at night.	All the materials are locally sourced and can be very effective at keeping livestock in and predators out if built very strongly. Walls and thorn gates can be penetrable to predators and livestock if not built well. Dependent on the availability of plentiful thorn trees.	36%
Post and rail bomas	Large timber post and rail wall usually reinforced with a thin layer of cut thorn trees/bushes to deter predators from walking in. Gate normally consists of removable rails on one section and thorn trees that can be pulled across.	Strong walls that require less cutting of thorn trees than traditional thorn bomas. Generally good at keeping livestock inside but often penetrable by carnivores unless thorn wall and gate is also well maintained. Otherwise relies on good herders to react quickly and chase away carnivore before they enter the boma.	3%
Chainlink bomas	Traditional thorn bomas reinforced with wire mesh.	Thin thorn walls can be made more impenetrable to carnivores by a layer of wire mesh. Effective and cheaper than mobile bomas but only good if maintained well. Often badly maintained and therefore weak.	8%
Stone bomas	Walls built using dry stone walling methods, gates can be made of steel or wood. Usually requires a layer of thorn or cactus on the top of the wall to stop predators climbing in.	Strong, durable and impenetrable walls (almost impossible for livestock to break out and carnivores to jump or force their way in) that require less cutting of thorn trees than traditional thorn bomas. Only as strong as its weakest point, i.e. the gate. Dependent on a local supply of suitable stone.	13%
Mobile bomas	Boma wall made of steel (round bar) and mesh gates held together with large metal stakes driven into the ground. Gates can be separated and stacked on a tractor trailer to be transported to other areas, or simply carried and reformed close by in a process known as 'creeping'.	No use of thorn trees. Very affective at keeping predators out and livestock in. Can be easily moved to help with grazing management. Durable, requires little maintenance but requires significant initial investment.	32%
Mixed	Boma walls made up of more than one of the above designs	Tend to be only as good as the weakest design used. Are normally a sign of poor husbandry practices.	8%

5.2.3. Livestock depredation data

Lion attacks on livestock were recorded throughout the wider study area for a 3 year period (2009-2012). A lion attack was defined as an incident where a lion was seen to attempt to hunt (stalk or chase) livestock, and was recorded as successful if the lions killed or mauled livestock. An attack was recorded as unsuccessful if the lions stalked or chased livestock but

were chased away by herders before making contact. 'Lost' livestock were defined as unaccompanied by people (i.e. separated from the herd during the day, and/or left outside a boma overnight).

Data were collected by trained scouts who responded to reports of attacks by interviewing the herder or night guard as soon as possible, in order to minimize the influence of perception and memory. They recorded predator, livestock, husbandry, and environmental variables through a combination of systematic investigation of the scene and interviews with the primary witnesses. Scouts visited each ranch weekly, so the maximum time between incident and data collection was seven days. Reports made more than seven days after the incident were excluded. When witnesses were uncertain or there were discrepancies between reports and physical evidence, reports were omitted from analyses. Control data were also collected for the closest boma/grazing livestock herd (≤ 5km) that was not attacked at the time of the incident.

5.2.4. Human distribution and activity levels

Human locations on the commercial ranch land were closely associated with livestock movements; humans stay within bomas between sunset (1830h) and sunrise (0630h) but leave the bomas to herd cattle during the day (Frank 1998, 2011, Patterson 2004). Boma locations were, therefore, a good proxy for human locations at night, and by day the probability of encountering humans was assumed to decline as distance to the nearest boma increased.

Lion movement data was assigned a human activity category 1) High activity (0700-1800hrs), when people are awake and moving about on the landscape, 2)Medium activity (1900-2200hrs, and 0600hrs), when all people are inside bomas but likely to be awake, and 3) Low activity (2300-0500hrs) when people are inside bomas and likely to be asleep.

5.2.5. Environmental data

Boma location (GPS) and design were recorded for all bomas throughout the commercial ranch land in the core study area from 2009-2012. The "Point intercept" option of Hawth's tools for ESRI ArcMap 9.3 (Beyer 2004) was then used to assign 'habitat structure' values to all bomas from a habitat structure layer (Centre for Training and Integrated Research in ASAL Development, Kenya). Habitat values were collapsed to three categories to reflect the cover available for lions in the vicinity of bomas; open (bare rock, open grassland, agriculture), mixed (predominantly grass with some bush or trees), and dense (predominantly bush and trees with some grass or rocks).

Daily rainfall data were taken from the Mpala Research Centre meteorological station on the southern border of the study area and assumed to be representative of the study area as a whole. Daily rainfall was averaged over a one month period to give the value 'mean daily rainfall' in order to reduce the effect of spatial 'patchiness'. Moon fraction, and moon rise and set data, for the study area was taken from the NASA website http://aa.usno.navy.mil/data/docs/MoonFraction.php. A moonlight index corresponding to the daily moon phase (e.g. full moon: 1; new moon: 0) was given to each lion's GPS data collected between moonrise and moonset. A moon-index of 0 was assigned to any lion's GPS data collected at night when there was no moon, accounting for dark periods on otherwise moonlit nights.

To avoid collinearity between variables, we computed Pearson's' correlation coefficients for all pairs of variables. For variables with high correlation (>0.5), only one variable was included on further analyses (all variables included in the final analyses are listed in Table 5.2.).

Table 5.2. Lion-livestock depredation variables included in the model selection that were recorded by trained scouts at the site where lion attacks were initiated, or the closest grazing herd or boma that was not attacked in the case of control data.

Variable Name	Description	Variable type and code
Boma design	The type of boma design	Discrete nominal data. Three categories: Mobile and stone bomas=1, Thorn/cactus bomas=2, all other boma designs=3
Boma wall height	Boma wall height	Discrete ordinal data. Three categories: <1m=1, 1m-1.5m=2, >1.5m=3
Boma wall penetrability	The presence of any holes in the boma wall through which a large carnivore could potentially squeeze itself meant the wall was classed as penetrable.	Discrete ordinal data. Two categories: penetrable =1, impenetrable=2
Gate design	The design of the boma gate	Discrete ordinal data. Two categories: penetrable =1, solid =2
No of night guards	The number of night guards awake and actively guarding livestock at the time of an incident, at bomas only.	Discrete ordinal data. Three categories: No night guards=0, one night guard=1, two or more night guards=2
Grass length	The grass length where the incident occurred	Discrete ordinal data. Two categories: <=50cm=1, >50cm=2
Bush Cover	The percentage bush cover where the incident occurred.	Discrete ordinal data. Two categories: <=50%=1, >50%=2
Livestock controlled or stampeded	Were livestock kept together in a herd, or kept inside the boma during an attack, or did they stampede (run away).	Discrete nominal data. Two categories: Controlled=1, Stampeded=0.
Torches used	Were torches (flashlights) used during the incident?	Discrete nominal data. Two categories: True=1, False=0
No. Of herders	The number of people actively herding the livestock at the time of the incident, whilst out grazing during the day only.	Discrete ordinal data. Three categories: No herders=0, one herder=1, two or more herders=2

5.2.6. Statistical analyses

5.2.6.1. Lion proximity to bomas

To test for a relationship between lion distance to nearest boma, husbandry and environmental variables, we performed a covariance analysis on distance to nearest boma with a) boma design, b) mean daily rainfall, c) moonlight index, d) boma habitat class, and e) human activity level, as explanatory variables, 'lion identity' as a fixed effect, and 'night

identity' as a random effect. As temporal serial autocorrelation may affect the data from the same night, we accounted for it using a first-order autoregressive covariance structure.

5.2.6.2. Lion attacks on livestock at bomas

We used logistic regression on the dependent variable 'Attack' (lion attack vs. control data) to model the probability of a boma being attacked by lions as a function of: 'boma design', 'boma wall height', 'boma wall penetrability', 'gate design', and 'number of guards present' (Table 5.2.). NB, whether livestock was controlled and whether torches were used as a deterrent, were not included in this analysis because controlling livestock and using deterrents was only done in the case of an attack, therefore never for control data. Rainfall and moonlight variables could not be used due to the way the control data was collected i.e. moonlight and rainfall was always exactly the same for both the boma that was attacked and the control (the nearest boma that was not attacked).

We then used logistic regressions on the dependent variable 'Attack success' (successful attacks vs. unsuccessful attacks) to model attack success as a function of the same variables plus, whether livestock stampeded or was controlled, whether torches were used as a deterrent, mean daily rainfall, and moonlight index. For these analyses, boma design categories were collapsed from the 6 categories used in the lion proximity to boma analysis to 3 categories; 'Penetrable walls' (mixed designs, chainlink and post and rail – similar in that they all have walls that tend to be weaker and penetrable by carnivores), 'Thorn walls' (thorn and cactus bomas), and 'Solid walls' (stone wall and mobile bomas - similar in that they have very strong walls, which are impenetrable to a carnivore). This was due to the small number of lion attacks recorded at stone wall, chainlink and post and rail bomas in part because of the low number of these boma types in use (Table 5.1.).

5.2.6.3. Lion attacks on livestock while grazing

Logistic regression was again used to model the probability of a) a lion attack away from a boma, and b) the probability of this attack being successful as a function of the variables: 'number of herders', 'whether deterrents were used' (attack success only), 'grass length' and 'bush cover' at attack locations. Again rainfall and moonlight variables could not be used to explain the dependant variable 'attack' due to the way the control data was collected.

Linear mixed effect models and logistic regressions were performed with R 2.14.2 software (R Development Core Team, 2012) using the function 'lme' in the package 'nlme' (R Development Core Team, 2012), and the function 'glm' in the package 'MASS' (Vanables & Ripley 2002) respectively. Model selection was performed using Akaike information criteria (AIC - Burnham and Anderson 2002). Relative strength of evidence of each model was assessed using Akaike weights (*w).* If one model was clearly dominant ($w > 0.9$) this was used, otherwise model averaging was performed to estimate the best fit model (Burnham & Anderson 2002).

5.3. Results

5.3.1. Lion proximity to bomas

Boma movements resulted in 403 different night time livestock locations recorded over a total of 34,340 boma nights (nights * number of bomas), with an average of 28 bomas located in the core study area on any one night. Once cleaned and processed, 33,486 usable lion locations were used in analysis. GPS collared lions had a mean 95% KDE home range of 314km^2 (range 112-441km^2) and utilised on average 9.6 ranches (range 7-12 ranches).

Distance to nearest boma was best described by a model including 'Boma design + Habitat + Moonlight index + Monthly rainfall + Human activity level'; this model dominated

all comparisons (the closest relative weight was 0.04 and all others were 0; Table 5.2.). Boma design was the strongest explanatory variable, with lions maintaining greatest distance from stone bomas and mobile bomas, and closest to mixed boma designs (bomas incorporating more than one of the other boma designs) (Fig. 5.2.a). Lions also had a greater tendency to be closer to bomas that were in mixed bush/grass rather than open grassland (estimate ± SE = -306.30± 50.83). Lions were closer to bomas during months with higher rainfall (estimate ± SE = -49.46 ± 17.76), and bright moonlit periods (estimate ± SE = -300.50 ± 89.96). Human activity level also influenced lion distance to nearest boma, such that lions were closest to bomas during the dead of night (2300-0500hrs) (estimate ± SE = -224.43 ± 18.73), Fig. 5.3. further illustrates the influence of human activity on lion proximity to bomas by showing the mean distance to nearest boma for each hour for which data was collected. Only 210 of 33,486 collared lion locations were within 200m of a boma during the study period, and boma 'visits' were, therefore, rare events. Boma type influenced the number of boma visits made by collared lions (Fig 5.2.b).

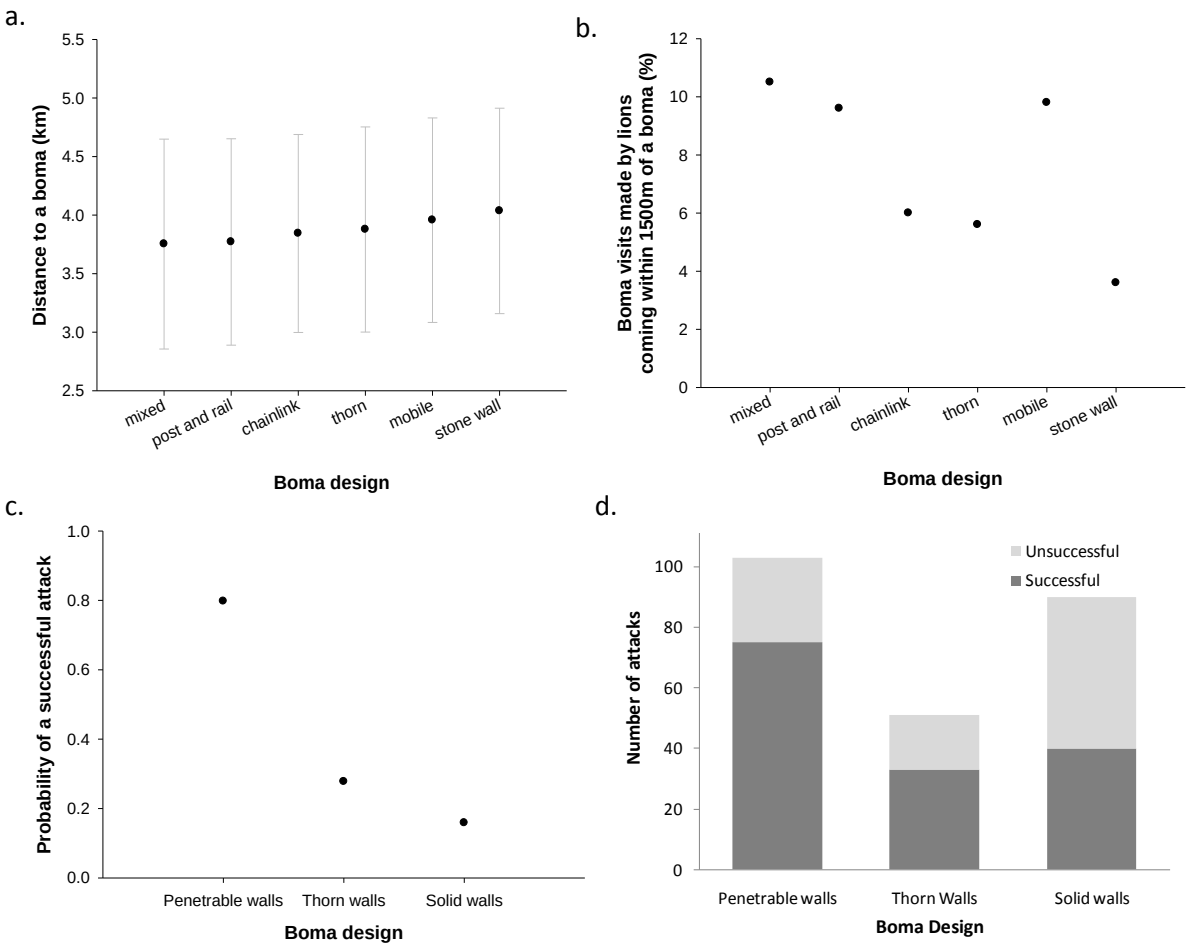

Figure 5.2. The effect of boma design on a) mean distance (km) to nearest boma (+/- SE), b) boma visits made by lions as a percentage of nights when lions come within 1500m of a boma, c) the probability of a successful lion attack on livestock, and d) the distribution of successful and unsuccessful attacks, for collared lions in Laikipia District, Kenya.

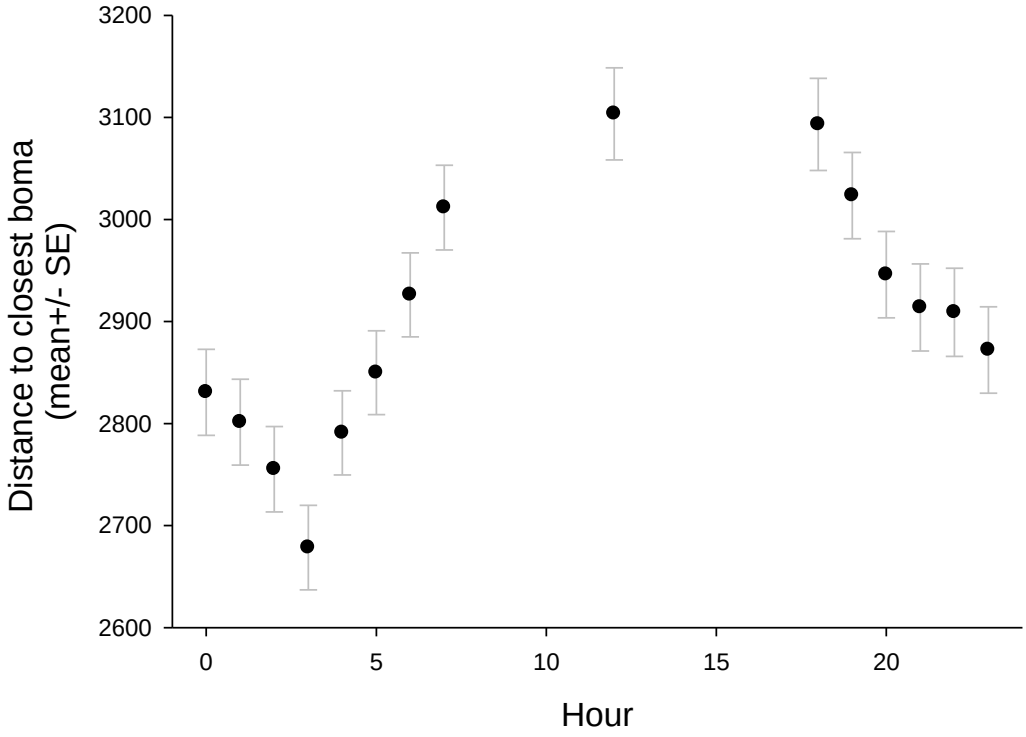

Figure 5.3. Distance from nearest boma (mean +/- SE) using all GPS data for all lionesses for each hour in a 24hr period.

Table 5.3. Summary statistics for models explaining mean distance to nearest boma for lionesses in Laikipia, Kenya. Lion identity and path identity were included in every model as random effects. The model in boldface italic type is the model providing the best fit.

Model	*AIC*	*ΔAIC*	*Akaikes weights (w)*
Null	595567.00	21760.20	0.00
Lion ID	577350.20	3543.40	0.00
Lion ID + Boma design	575564.30	1757.50	0.00
Lion ID + Moonlight index	577335.40	3528.60	0.00
Lion ID + Rainfall	577336.60	3529.80	0.00
Lion ID + Habitat	576006.40	2199.60	0.00
Lion ID + Human activity	577201.30	3394.50	0.00
Lion ID + Boma design + Moonlight index	575550.60	1743.80	0.00
Lion ID + Boma design + Rainfall	575549.90	1743.10	0.00
Lion ID + Boma design + Habitat	573994.40	187.60	0.00
Lion ID + Boma design + Human activity	575420.80	1614.00	0.00
Lion ID + Moonlight index + Rainfall	577321.80	3515.00	0.00
Lion ID + Moonlight index + Habitat	575989.50	2182.70	0.00
Lion ID + Moonlight index + Human activity	577194.80	3388.00	0.00
Lion ID + Rainfall + Habitat	575994.30	2187.50	0.00
Lion ID + Rainfall + Human activity	577187.80	3381.00	0.00
Lion ID + Habitat + Human activity	575819.00	2012.20	0.00
Lion ID + Boma design + Moonlight index + Rainfall	575536.20	1729.40	0.00
Lion ID + Boma design + Moonlight index + Habitat	573979.60	172.80	0.00
Lion ID + Boma design + Moonlight index + Human activity	575414.30	1607.50	0.00
Lion ID + Rainfall + Habitat + Human activity	575807.10	2000.30	0.00
Lion ID + Rainfall + Habitat + Moonlight index	575977.50	2170.70	0.00
Lion ID + Habitat + Human activity + Boma design	573826.60	19.80	0.00
Lion ID + Habitat + Human activity + Moonlight index	575812.60	2005.80	0.00
Lion ID + Human activity + Boma design + Moonlight index	575414.30	1607.50	0.00
Lion ID + Human activity + Boma design + Rainfall	575406.50	1599.70	0.00
Lion ID + Boma design + Moonlight index + Rainfall + Habitat	573966.10	159.30	0.00
Lion ID + Moonlight index + Rainfall + Habitat + Human activity	575800.60	1993.80	0.00
Lion ID + Rainfall + Habitat + Human activity + Boma design	573813.30	6.50	0.04
Lion ID + Habitat + Human activity + Boma design + Moonlight index	573820.10	13.30	0.00
Lion ID + Human activity + Boma design + Moonlight index + Rainfall	575400.00	1593.20	0.00
Lion ID + Boma design + Moonlight index + Rainfall + Habitat + Human activity	***573806.80***	***0.00***	***0.96***

5.3.2. Livestock depredation

A total of 308 lion-livestock incidents, and 236 control datasets were recorded over the 3 year study period. After removing all observations where data were missing and/or where inconsistencies were found in primary witness reports, 173 lion-livestock incidents and 164 control datasets were included in logistic regression. Livestock killed or mauled by all carnivore species in the study area represented 0.52% of all cattle, 0.66% of all goats and sheep, and 2.83% of all camels. Camel depredation was mainly from one property that had large herds of camels and poor husbandry practices. For similar sized ranches in the core study area, where effort collecting livestock depredation data was known to be consistent over the study period, the annual number of successful lion attacks per ranch ranged from 1 to 30 (mean 10). Lions were responsible for 90% (n=308) of all livestock depredation incidents over the 3 year data collection period, with leopard responsible for 5% (n=18), spotted hyaena 4% (n=13), wild dog 0.3% (n=1) and cheetah 0.3% (n=1).

5.3.2.1. Lion attacks on livestock at bomas

Sixty-one percent of lion attacks occurred at bomas (and 39% on livestock in the field, see below), and all occurred during the hours of darkness (1900h-0630h). Seventy four percent of lion attacks at bomas were successful but unsuccessful attacks may have been underreported.

None of the models predicting lion attack (lion-livestock incident data) vs. non attack (control data) performed significantly better than the null model during the AIC selection process (Table 5.4). The three best fit models predicting the success of a lion attack on livestock at a boma contained 4 independent variables: boma design, whether livestock stampeded, whether torches were shone at the lions, and whether the boma wall was classed as penetrable i.e. contained any holes big enough for a large carnivore to enter (Table 5.5.). After model averaging, boma design was the strongest predictor. The likelihood of a lion

attack being successful was significantly reduced when the boma had 'solid walls' (estimate ± SE = -1.67 ± 0.62) (Fig. 5.2.c). Lion attacks had a greater probability of being successful when they were able to stampede cattle out of a boma (after model averaging estimate ± SE = 1.48 ± 0.63). Additionally, attack success was lower when torches were used to scare away lions (estimate ± SE = -0.81 ± 0.72) and higher when boma walls were penetrable (estimate ± SE = 0.49 ± 0.60).

Table 5.4. Summary statistics for variables collected to explain lion attack versus non attack (control data) at a boma for lionesses in Laikipia, Kenya.

Model	***AIC***
Null	273.96
Boma design	276.50
Boma wall height	277.12
Boma wall penetrability	277.16
Boma gate design	273.52
Number of fires	274.65
Number of askaris	273.80

Table 5.5. Summary statistics for models explaining success of lion attacks at a boma in Laikipia, Kenya. The models in boldface italic type are the models providing the best fit (w≤2).

Model	*AIC*	*ΔAIC*	*Akaikes weights (w)*
Boma design	127.05	5.32	0.02
Boma wall height	129.77	8.04	0.01
Boma wall permeability	129.46	7.73	0.01
Boma gate design	131.75	10.02	0.00
Livestock stampeded	127.35	5.62	0.02
Torches used	129.49	7.76	0.01
Boma design+Boma wall penetrability	127.42	5.69	0.02
Boma design+Torches used	126.07	4.34	0.03
Boma design + wall height	128.56	6.83	0.01
Boma design + Boma gate design	129.01	7.28	0.01
Boma design + livestock stampeded	***121.73***	***0.00***	***0.30***
Boma design + livestock stampeded + torches used	***122.37***	***0.64***	***0.22***
Boma design + livestock stampeded + boma wall height	124.35	2.62	0.08
Boma design + livestock stampeded + boma wall penetrability	***123.05***	***1.32***	***0.16***
Boma design + livestock stampeded + boma gate design	123.73	2.00	0.11

5.3.2.2. Lion attacks on livestock in the field

Incidents in the field accounted for 39% of all attacks by lions; 49% of these attacks in the field were on livestock grazing accompanied by a herder during the day (0630-1900h). A further 51% of attacks in the field were carried out on livestock lost and left out at night unaccompanied. Lion attacks outside bomas were successful 96% of the time. As with attacks at bomas, unsuccessful attacks may be underreported. None of the models predicting attack (livestock depredation data) vs. non attack (control data) away from the boma performed significantly better than the null model during the AIC selection process i.e. did not explain the variability in the data (Table 5.6.). Logistic regression could not be used to compare

successful attacks to unsuccessful attacks because too few attacks away from bomas were unsuccessful (n=5).

Table 5.6. Summary statistics for variables collected to explain lion attack versus non attack (control data) away from the boma for lionesses in Laikipia, Kenya.

Model	*AIC*
Null	195.05
Number of herders	196.15
Bush cover	194.75
Grass length	197.02

5.4. Discussion

In a context where increasing human and livestock populations are putting pressure on habitat available to lions (Riggio et al. 2012), minimising livestock lost to lions is likely to be key to continued coexistence. By combining information on livestock depredation events and lion GPS data, this study provides novel insights into the influence of human behaviours (livestock husbandry) on lion behaviours (spatial ecology and propensity to approach, attack and successfully kill livestock).

5.4.1. Importance of boma design

Lion movement data revealed that study lions were less likely to visit some boma designs (solid wall bomas and thorn bomas, but see discussion below about mobile bomas) over others (penetrable wall bomas). Study lions were also found at a significantly greater mean distance from solid wall boma designs than penetrable designs. The average distance to which study lions approach different boma designs may not appear biologically meaningful at first glance but boma visits by lions are rare events in Laikipia, and a small change in the measure 'mean distance to boma' can indicate a meaningful increase in the number of boma visits by lions in lion-human coexistence terms.

Boma design largely influenced the outcome of the attack, with stone wall and mobile bomas (solid wall bomas) being the most efficient in preventing an attack from being successful. The relevance of 'boma design', 'preventing livestock from stampeding out of a boma', and 'the presence of holes in the boma wall that could permit access to a large carnivore' (wall penetrability) in reducing attack success, indicates that bomas should be designed to fulfil two purposes: preventing lions from breaking in, and preventing livestock from breaking out: 36% of successful attacks were made after livestock stampeded out of the boma.

Our results support earlier studies that found well designed and constructed bomas to be effective in deterring attacks by large carnivores (Ogada et al. 2003, Treves & Karanth, 2003; Woodroffe et al., 2006, 2007) but also demonstrate that study lions are less likely to even approach better boma designs. Bomas begin to influence lion movement patterns at a distance of 4500m but had the strongest effect within 1500m (Chapter 3), even though lions could presumably not discern details of the boma from that distance. Different ranches use different types of boma, so it is likely that study lions simply knew which ranches had poor livestock protection and preferentially visited those bomas. Where weaker boma designs had been recently replaced by the new mobile bomas, at which study lions had a low probability of success, these bomas were still visited frequently (Fig 5.2.b) indicating that a period of learning is required before lion behavior adjusts. We predict that low attack success rate on mobile bomas will reduce lions' tendency to visit them.

Although other studies have shown that human activity around livestock reduces attacks by lions (Ogada et al 2003, Woodroffe et al. 2006), we did not find that number of night guards at bomas influenced the outcome of an attack. Lion movement data, however, revealed that human activity levels did influence study lions' proximity to bomas. If lions are more likely to approach bomas during the dead of night, when human activity levels are lowest then it stands to reason that maintaining a level of human activity around bomas, or at least the appearance of human activity (e.g. flashing lights), will deter lions from approaching. The efficacy of deterrents, specifically bright lights shone at lions, suggests that people were important in reducing the severity of an attack once an attack occurs, likewise they were likely to be important in controlling panicked livestock, although strong bomas should stop livestock breaking out in any circumstance.

5.4.2. Lion attacks while grazing

Lions are less likely to draw a distinction between livestock outside of bomas and the wild prey with which they mix, and attacks on these livestock are harder to deter for herders. The low number of unsuccessful daytime attacks (only five of 78) may account for the lack of significant predictors of lion attack success away from bomas, likely exacerbated by underreporting of attacks where no livestock was mauled or killed. Environmental factors such as distance to nearest water and habitat structure were found to influence study lion locations during the day (Chapter 4) but these data were not collected consistently by scouts at sites where lions attacked livestock. Results from Chapter 4 show an increasing probability of encountering lions closer to water sources, and it might be expected that, as study lions were also found to kill wild prey more often closer to water, the probability of an attack on livestock would also increase with proximity to water. Further more, results from Chapter 4 and Woodroffe et al 2006 show that, during daylight hours, lions in Laikipia select for habitat that reduces the risk of being detected by people (e.g. habitat structures that provide a large amount of cover) when close to human activity. Herders should avoid moving cattle into these habitats, particularly when close to water, or be extra vigilant and make noise to scare away lion when they do. Thicker habitats are often associated with water and shade, however, and avoiding them completely may incur a cost for livestock. Providing water points in more open habitats and seeking shade under larger trees with open understory could reduce the probability of encountering lions.

Although we only had data for lost livestock that were actually attacked by carnivores, Laikipia ranchers (pers. comm.) said most livestock left unattended in the bush were attacked. Good herding practices on the Laikipia commercial ranches meant a relatively small number of livestock were lost; 26% of all incidents in Laikipia involved livestock unaccompanied by herders, as opposed to 55% of incidents among pastoralists on Mbirikani

Group Ranch in southern Kenya (Maclennan et al. 2009) and almost all livestock killed by lion in Makgadikgadi Pans National Park in Botswana (Hemson et al. 2009). However, 38.5% of all attacks on lost livestock occurred on one ranch, indicating that improvements in herding practices on this ranch could significantly reduce overall losses to lions. Lion behavioural ecology is such that they are less active during daylight hours (Schaller 1972, Prins & Iason 1989, Hayward & Slotow 2009, Cozzi et al. 2012), and therefore less likely to kill livestock, however it will be interesting to see whether recent improvements in boma design, making livestock less accessible during the night, will lead to an increase in daytime attacks.

5.4.3. Environmental predictors of lion attacks

Habitat surrounding a boma influenced study lions' proximity to that boma. Ranchers avoid siting bomas in thick bush, but even patchy cover near bomas may enable lions to approach them. Study lions were also found closer to bomas with increasing moonlight and mean daily rainfall. Wet periods were associated with higher depredation in other studies (Woodroffe & Frank 2005, Patterson 2004). Bright moonlight and higher rainfall have been shown to reduce lion's success hunting wild prey (Van Orsdol 1984, Funston et al. 2001, Patterson et al. 2004, Packer et al. 2011a, Woodroffe & Frank, 2005). The importance of moon index (a measure of moonlight variations on the same night) rather than moon phase demonstrates that lions respond to variations in hunting conditions on a fine temporal scale (see also Packer 2011, Rasmussen & Macdonald 2012, Broekhuis et al. 2013), suggesting that livestock held in bomas are secondary prey during periods when wild prey are harder to catch (Valeix et al. 2012, Chapter 3).

5.4.4. Livestock: a secondary prey associated with a cost

Carnivore home range size is normally inversely related to prey biomass (Loveridge et al. 2009). The home ranges of Laikipia study lions are larger than those in protected areas (e.g. range: 112-441km^2 KDE compared to 22-226km^2- Van Orsdol, Hanby & Bygott 1985), and larger than expected based on the overall herbivore biomass when livestock are included (prey density = 4400 kg/km^2 – Georgiadis et al. 2007). Coupled with the low depredation rates in the study area, this suggests livestock are distinguished from wild prey and largely avoided.

Avoiding livestock in favour of wild prey has been shown in other carnivore species living in human dominated landscapes e.g. grey wolf (Mattioli et al. 1995, 2004, Capitani et al. 2004) and African wild dogs (Woodroffe et al. 2005). Livestock outnumber wild ungulates in Laikipia (mean of 1700 kg/km2 wild prey, and 2700 kg/km2 of livestock on commercial ranches - Georgiadis et al. 2007). Avoiding livestock as prey, therefore, may represent a trade-off for Laikipia's lions in terms of optimising foraging and minimising human-caused mortality risk.

Chapter 6.

General discussion and conclusions

A collared Laikipia lioness feeds on the remains of a kill at first light. Having to seek refuge from humans during daylight hours may have associated costs such as abandoning unfinished kills made in low refuge habitats. Photo by: Josep Oriol.

6.1. Behavioural adaptations in response to a Landscape of Coexistence revealed

The ecology of fear theory, originally developed to explain the behavioural ecology, distribution and density of prey and meso-carnivores (Sih 1980, Durant 1998, Laundré et al. 2001), has here been applied to lions under risk of predation by humans. A combination of behavioural strategies observed in study lions may allow them to reduce the risk of detection by people and yet utilise resources in human-dominated landscapes.

Complete spatial avoidance of human-occupied areas by study lions was not observed, either at the scale of land-use type or actual human locations, although a significant preference for commercial ranch land was observed. Temporal avoidance patterns were revealed at the finer spatial scale; study lions responded to human activity levels on a 24 hour cycle, spending time further from human locations during the daylight hours, when people were more likely to be active, and coming closest to human locations (bomas) during the dead of night (2300hrs-0400hrs). Study lions combined this temporal avoidance with changes in their movement parameters, prey and habitat selection such that study lions used areas in close proximity to human locations, not only at times but also in ways that potentially minimised the risk of detection by people.

A carnivore's use of a Landscape of Coexistence may not be adequately explained by 'bottom up' resource based hypotheses such as prey abundance and/or vulnerability, which have been shown to drive carnivore habitat selection in protected areas (Van Orsdol et al. 1985, Palomares et al. 2001, Hopcraft et al. 2005, Balme et al. 2007). While the distribution of resources (prey abundance and vulnerability) was found to be an important determinant of study lion habitat selection at night, when humans were least, and lions were most active, results suggest that avoiding detection by humans became paramount during the day. Resource selection is a nested hierarchical process and the proximal factors affecting selection may vary at different spatial and temporal scales (Boyce 2006; Ciarnello et al.

2007). Other studies have shown changes in carnivore habitat selection patterns in response to human densities and distribution, specifically an increasing use of habitat structures that offer refuge from humans (cougar – Dickson et al. 2005; Eurasian lynx – Schadt et al. 2002; grizzly bears - Apps et al. 2004; spotted hyenas – Kolowski & Holekamp 2009; lions - Schuette et al 2013a; Wild dog - Rasmussen & Macdonald 2012). This study reveals the importance of temporal as well as spatial scale when assessing resource requirements of large carnivores in human dominated landscapes.

6.2. Costs associated with the behavioural effects of human-caused mortality

6.2.1. The importance of scale

The spatial and temporal scales at which avoidance of human activities becomes significant for large carnivores will determine the cost of the behavioural effects of fear. Pre-emptive avoidance at larger spatial scales would limit the ability of large carnivores to utilise Landscapes of Coexistence, particularly where the density and distributions of people and livestock is such that complete avoidance is difficult. Study lions showed a preference for commercial ranch land over pastoral land, thus showing some spatial avoidance of humans at the land-use scale where they have the choice; all study lions were pride females who had territories that covered both commercial and pastoral land, therefore did have choice. Avoidance of pastoral land in this study was not complete and lions did utilise it. However, pastoral land in the study area had similar wild-prey densities and habitat to commercial ranch land, thus any spatial avoidance of that land-use type represented a cost. Other studies suggest a threshold value of human density for successful human-lion coexistence; Woodroffe 2000 and Riggio et al. 2012 suggest approximately 25people/km^2. While Riggio et al. (2012) suggest that above this threshold value of human density ceases to be suitable for lion due to land transformation, there was no land transformation, nor reduction in resources

(prey and cover), on pastoral land in this study area. Our results suggest that, in areas where people regularly kill lions to protect livestock, the presence of people alone may limit lions' use of the landscape. Although lions' use of pastoral land was limited, study lions did utilise high-risk areas on commercial ranch land, by reactively responding to actual locations and activity levels of humans on a local-scale. Reactive avoidance on smaller spatio-temporal scales has been shown by meso-carnivores at risk of predation by larger carnivores (Broekhuis et al. 2013). When coupled with other behavioural adjustments that may further reduce risk of detection by people (specifically, partitioning of activities such that vulnerable activities are minimised, and use of refuge habitats is increased, while in close proximity to active humans) is probably the most efficient way in which large carnivores can optimise the trade-off between maximising use of resources in a Landscape of Coexistence and minimising the risk of human-caused mortality.

6.2.2. Mediating factors

Factors that determine the extent, and ultimately the cost, of behavioural responses to humans were revealed. Habitat structures that potentially reduce the risk of humans detecting the presence of lions (referred to as high refuge habitats in this thesis) appear to allow them to reduce their spatio-temporal avoidance of human locations during periods of human activity. Lack of cover within a lion's home range, however, may increase the need for spatial avoidance of humans and livestock during periods when people are active, and potential associated costs e.g. abandoning kills early and having to move longer distances between night time foraging sites and day time rest sites. Thus, although lions have a wide habitat tolerance (Chardonnet 2002, Riggio et al. 2012), a lack of cover may limit their ability to coexist with humans.

Likewise, a lion's ability to avoid livestock as prey will be determined by the presence of wild herbivore species. The influence of a lion's ability to hunt wild prey on their propensity to approach livestock as a secondary prey source was demonstrated; use of areas in close proximity to bomas was increased by environmental factors that have been shown in other studies to reduce lion's success when hunting wild prey i.e. bright moonlight and higher rainfall (Schaller 1972, Van Orsdol 1984, Funston et al. 2001, Patterson et al. 2004, Woodroffe & Frank 2005, Packer et al. 2011a). Woodroffe et al. (2007) found that wild dogs in the same Landscape of Coexistence shifted their diet to smaller wild prey species where densities of larger wild prey species were reduced, rather than risk killing livestock. For a large carnivore such as lion, however, this may not be as energetically feasible (Carbone et al. 2007) and a sufficient density of medium to large wild herbivores is likely to be needed to reduce attacks on livestock. The importance of sufficient wild prey densities in facilitating human-carnivore coexistence has been commonly highlighted in other studies (Meriggi & Lovari 1996, Mech et al. 1998, Rasmussen, 1999, Sillero-Zubiri & Laurenson 2001, Patterson 2004, Woodroffe et al. 2005, Frank et al. 2006, Bauer et al. 2008, Hemson et al. 2009 but see Treves et al. 2002). This study (Chapter 3), however, reveals how study lion's propensity to move closer to a boma changes with fluctuations in environmental conditions month to month (rainfall) and even from hour to hour (moonlight levels). This study also revealed (Chapter 5) how lions visited bomas more where livestock husbandry was weak and their success killing livestock was high. Thus, study lions' propensity to approach bomas appears to adjust on a fine temporal scale according to the relative ease of killing wild prey (wild prey densities and environmental conditions) vs. livestock (livestock husbandry standards). Sufficient wild prey densities in combination with good livestock husbandry would, therefore, help ensure livestock depredation is minimised.

Overall, the observed fine scale shifts in foraging strategies shown by study lions in response to environmental variables are perhaps indicative of the opportunistic nature of the lions as a species, and an inherent flexibility important to their survival in a Landscape of Coexistence. Fine scale behavioural adjustments that allow human occupied areas to be utilised could be particularly important as human occupied parts of the Landscape of Coexistence can represent a disproportionately high percentage of available resources. For example, bomas are often placed in the more open areas, which also have the highest densities of game in Laikipia (Riginos & Grace 2008) as well as containing livestock (a known prey in the area), or close to dry season water sources (Schuette et al. 2013a).

Aspects of lion behavioural ecology, and the presence of mediating factors such as refuge habitats and sufficient wild prey in the study area, meant that the observed behavioural adjustments shown by study lions in response to people may have minimal associated costs. Lions are naturally nocturnal (Schaller 1972, Stander 1991, Cozzi et al. 2012), and people in Laikipia restrict their activities on the landscape to daylight hours. Thus, costs associated with partitioning lion's active periods with people may not be significant compared to those faced by other carnivore species (e.g. grey wolves - Theuerkauf 2009; and wild dogs - Rasmussen and Macdonald 2012). Lions are ambush predators that use thicker habitats as cover when hunting (Schaller 1972, Funston et al. 1998, 2001), thus the trade-off between avoiding detection by humans and maximising hunting success may also be less than for cursorial predators. Wild prey densities in the study area meant that avoiding livestock as prey may not have represented a severe foraging cost. The presence of plentiful refuge habitat (34% of the study area was classed as high refuge habitat and a further 40% was classed as medium refuge) meant that study lion's spatial avoidance of bomas during the daylight hours was minimised, as was the probability of other associated costs such as kills made being

discovered by people. In other guilds, however, the behavioural effects of predation have been shown to represent a significant trade-off between minimising the risk of predation against optimising nutritional intake (Sih 1980, Brown & Kotler 2004). The behavioural effects of predation may be more important in determining the distribution and density of a prey species on the landscape than the lethal effects (Schmitz et al 1997, Laundré et al. 2001). Although this is unlikely to be the case for lions in this study area, avoiding detection by humans, and only utilising livestock as a secondary prey source, could still reduce overall foraging intake for Laikipia's lions. Such trade-offs may have population level consequences (see Werner & Peacor 2003, Preisser et al. 2005 for other guilds) that need to be better measured and considered when assessing the full impact of human-caused mortality on the densities and distribution of large carnivores. Factors such as human and wild prey densities and distribution, habitat structures, and livestock husbandry are likely to pose limitations on lion's ability to share a Landscape of Coexistence with people.

6.3. Conclusions - implications of a Landscape of Coexistence for the conservation of large carnivores

Thresholds for human – carnivore coexistence will vary due to the human, carnivore and habitat characteristics of the Landscape of Coexistence itself. Understanding the processes that generate a Landscape of Coexistence is, therefore, key to determining the critical factors influencing the thresholds of coexistence, and balancing the needs of people and large carnivores. Landscape of Coexistence characteristics such as carnivore life history traits, weather and light levels cannot be managed directly, but understanding the behavioural as well as the lethal effects generated by changes in these factors can facilitate the design and implementation of mitigation techniques. Other characteristics of the Landscape of Coexistence such as wild prey densities, key habitat structures, and the distribution and

behaviours of people and livestock on the landscape can potentially be managed, given suitable incentives.

Informed management of Landscape of Coexistence characteristics should strive to meet two goals: a) help minimise human-caused mortality risk for carnivores, and b) help people to minimise the costs of sharing the landscape with carnivores. These goals may not be mutually exclusive. For example, results from Chapter 4 indicate that the creation of a network of 'refuge' areas within land-use classes that do not have any official protection status may mediate the lethal and behavioural effects of humans (see also Schuette et al. 2013a,b), even if these refuge areas are small. Key characteristics of refuge areas should be a) use by humans and livestock is limited, and b) carnivore refugia characteristics are included. In Laikipia, habitat refugia for lions are comprised of dense bush and/or rocks that limit visibility, characteristics that would also offer refuge from people to other large carnivore species and can be found in most savannah ecosystems. Such a network of small scale refuges may also help to recover wild prey populations, thus reduce the predation pressure on livestock in human dominated rangelands, as well as double as grazing 'banks' for livestock during extreme climatic events. The importance of including habitat refugia in the creation of core security areas (where breeding populations of carnivores can be supported) and linkage areas (allowing the movement of large carnivores between core security areas) in human dominated landscapes has been applied to strategic planning for other species that suffer from human-caused mortality e.g. Grizzly bears (Mattson 1990, McLellan & Hovey 2001) cougar (Beier et al. 2005, Dickson et al. 2005) and Iberian lynx (Schadt et al. 2002, Fernandez et al. 2006) but has so far not been an important consideration in landscape planning for lions.

Chapter 5 reveals that good livestock husbandry (specifically: strong bomas that stop livestock breaking out, and carnivores breaking in; and good herders/night guards in the possession of bright torches) can reduce the probability of a successful attack by lions,

increase the mean distance lions spend from livestock, and reduce the number of boma visits made by lions, thus creating a virtuous cycle. Despite the low proportion of livestock lost to lions on the large scale commercial ranches in the study area, the difference in number of livestock depredation incidents between these ranches indicates that losses can still be important to some farmers (see also Treves et al. 2004, Woodroffe et al. 2005, and Gazzola et al. 2007 for patchy distributions in livestock depredation levels). As the number of large carnivores killed by farmers is correlated with depredation losses in the study area (Ogada et al. 2003), livestock depredation hotspots can represent carnivore 'sinks' that lower the viability of the overall population. In a land-use mosaic such as Laikipia, coexistence may only be as good as its weakest link. Thus, incentives to ensure uniformly high livestock husbandry standards, particularly boma design, could reduce both regional livestock losses and retaliatory carnivore killing.

Results from Chapter 3 and 4 suggest that human locations most strongly influence study lion movements and habitat selection within a 1.5 kms radius, but have some influence within a 4.5kms radius. Within this zone of influence study lions moved increasingly faster, straighter, and rested less at all times in the 24 hour cycle, but were also more likely to avoid open habitat structures during the daylight hours. This zone of influence may vary according to characteristics of the Landscape of Coexistence (such as: wild prey density and distribution, human attitudes, livestock husbandry standards, and characteristics of the carnivore species of concern) but provides an indication of how human distribution on the landscape may also be an important factor to consider. Further zoning to cluster human habitation and night time livestock enclosures could allow large carnivores more space to avoid people and livestock whilst at the same time allowing people to communally and more effectively protect their livestock. Results suggest that zonation could be done on a relatively small scale i.e. at a property level rather than on an ecosystem level, and still be effective.

It may also be important to understand better how lions learn to fear people and reinforce this behavioural trait. A carnivore without fear, who focused on killing livestock in a human-dominated landscape would not be expected to survive long. Understanding whether there is an evolutionary selection for individuals with greater preparedness towards fearing humans, and to what extent fear of human-caused mortality is learnt, may allow us to manage for 'scaredy cats'.

The scale at which managers approach the conservation of large carnivores may be influenced by a better understanding of their behaviour in a Landscape of Coexistence. The conservation of large carnivores is traditionally viewed from the perspective of protecting areas big enough to support viable populations (Lande 1988), and it is accepted that smaller protected areas are much more vulnerable to the lethal effects of humans on carnivores and other stochastic processes (Woodroffe & Ginsberg 1998). Although the protection of large areas supporting viable populations of carnivores is without doubt the most crucial step to the survival of these species, the examples given above show how there may be some merit in also focusing at smaller scales to make sub-optimal habitats more viable for large carnivores. This could be a valuable conservation approach in buffer zones surrounding protected carnivore populations, or corridors linking them, thus making them more viable in the long term. Contrary to arguments given by Packer et al. (2013) that suggest fencing remaining lion populations might be the most appropriate conservation approach with increasing habitat conversion to land uses that are not suitable for large carnivores (see Riggio et al. 2012, for an in-depth look at this problem for the African lion), the findings in this thesis indicate that the identification and better management of key buffer zones and corridors shared with people and livestock will likely be an important part of landscape level conservation planning.

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