OPTIONS FOR ELAND: A MULTI-SCALE ASSESSMENT OF ANTIPREDATORY RESPONSES OF A VULNERABLE PREY SPECIES TO THEIR DOMINANT PREDATOR IN THE EASTERN CAPE, SOUTH AFRICA

By

Jessica Leaver

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Supervisor: Prof Graham I.H. Kerley
Co-supervisor: Dr Craig J. Tambling
DECLARATION

I, Jessica Leaver (s213426773), hereby declare that the dissertation for the degree of Master of Science is my own work and that it has not previously been submitted for assessment or completion of any postgraduate qualification to another university or for another qualification.

Jessica Leaver

Animal ethics clearance for this research was granted by the NMMU ethics committee (A12-SCI-ZOO-002).

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Abstract

Eland *Tragelaphus oryx* are the largest and slowest African antelope, falling within the preferred weight range of the prey of lions *Panthera leo*. Little is known, however, about the antipredatory strategies employed by eland. Rapid population declines in several small reserves following the reintroduction of lions suggest that the antipredatory strategies of eland may be compromised in spatially limited areas. This emphasises the need for research aimed at investigating how eland respond to lions, particularly in the spatial context, given that lions are increasingly being reintroduced into small reserves in South Africa. This study aimed to investigate lion-eland interactions at multiple scales and determine where on the landscape eland were vulnerable to predation. Adult female eland (*n = 3 per site*) in breeding herds were collared with GPS satellite collars in two study sites; the Nyathi section of Addo Elephant National Park (Nyathi) and Mountain Zebra National Park (MZNP) in the Eastern Cape, South Africa. A reintroduced population of lions, comprising two males and one female, was present in each study site, with individuals fitted with GPS satellite collars. At a broad spatiotemporal scale, eland did not avoid lions and there was considerable overlap between eland and lion home ranges in both study sites. At a finer spatiotemporal scale however, eland and lion space use was asynchronous in time, except in the case of the female lion in Nyathi where there was considerable overlap at the finest temporal scale investigated (i.e. monthly). Herd-associated eland in Nyathi were killed most frequently in areas associated with high long-term use by the female lion, showing that failure to avoid the female lion at a fine scale increased predation risk for eland. Secondly, eland in Nyathi were killed most frequently in habitat types of intermediate structural density (i.e. mixed habitats), which limited the viewshed of eland but presumably offered increased forage. This habitat type was selected for by eland, despite it being associated with a higher level of predation risk. This suggested that eland in Nyathi traded off safety for forage. In MZNP, predation of herd-associated eland was low which reflected the limited spatial overlap between eland and lion at a fine scale in this reserve. In Nyathi, but not in MZNP, eland responded to lions within 1.5 km by increasing their movement rate, with this response particularly strong at night. The findings of this study show that eland responses to lions are scale-dependent and site-specific. Furthermore, eland responses to lions were shown to be lion gender-specific. This study has increased our understanding of the antipredatory behaviours of eland and demonstrated the importance of investigating prey responses to predation risk at multiple scales.

**Key words:** eland *Tragelaphus oryx*; antipredatory response; resource selection; spatial and temporal scales; predation risk; lion *Panthera leo*; prey vulnerability.
Historically, the common eland *Tragelaphus oryx* coevolved and coexisted with its major predator, the African lion *Panthera leo* (Skead 2007), yet little is known about the antipredatory mechanisms employed by this large prey species. In the current context of wildlife populations increasingly being restricted to small, fragmented conservation areas (Hayward & Kerley 2009), particularly in South Africa, an understanding of the scales at which antipredatory mechanisms operate is essential if predator reintroductions are to restore ecological integrity to previously disturbed systems (Hayward et al. 2007). Where antipredatory mechanisms developed over an evolutionary time scale are compromised, prey may experience increased vulnerability to predation (Tambling & du Toit 2005; Louw et al. 2012), unless behaviourally-mediated responses to predation risk are able to effectively reduce predation (e.g. Tambling et al. 2012a). This thesis represents the first study aimed specifically at investigating how eland interact with lions at multiple scales, and how predation risk is behaviourally mitigated by eland in spatially limited reserves.

**1.1 Predation at the evolutionary time-scale**

Within their lifetime, animals seek to increase their individual fitness (Lima & Dill 1990). For an animal to achieve this, it needs to acquire sufficient food and water, have access to adequate mating opportunities and successfully avoid being killed (Lima & Dill 1990). On a day-to-day basis, an animal may miss a feeding opportunity, or fail to obtain a mating opportunity at this scale (Lima & Dill 1990). However, these short-term failures may have minimal effect on an animal’s lifetime fitness. On the other hand, the failure to avoid predation puts an immediate and permanent end to an animal’s life and thus precludes future fitness (Lima & Dill 1990). Predation is thus a strong selective force over evolutionary time, and has long been recognised as important in the evolution of prey adaptations (reviewed by Abrams 2000). Through coexistence and coevolution with their natural predators, prey species have thus developed multiple antipredatory strategies which are vital to a prey individual’s survival at a finer time scale, as described below.

**1.2 Predation at the ecological time scale**

Over the course of an animal’s lifetime, the risk of predation is highly variable as predators are generally mobile and landscape heterogeneity influences their lethality (Lima & Dill 1990; Gorini et al. 2011). Given that an animal needs to achieve more in its lifetime than avoid predation, antipredatory adaptations should be sensitive to current levels of predation risk (Lima & Dill 1990). At times when predation risk is perceived as low, costly antipredatory defences should be relaxed, thereby allowing the animal to maximise resource gains (Brown 1988). Conversely, when predation
risk is perceived as high, the animal should prioritise behaviours which maximise its antipredatory defences (Lima & Dill 1990). Such antipredatory flexibility is achieved when an animal integrates its evolutionary adaptations with the behavioural decision-making process (Lima & Dill 1990). This adaptive flexibility in prey behaviour in response to a dynamic risk of predation means that predators may have large impacts on ungulate communities, independent of actual predation (Sinclair 1985; Lima 1998a). This was demonstrated by Sinclair (1985) who investigated the ecological consequences of intraspecific competition and predation on an African ungulate community. The similar vegetation choices between ungulate species, the high degree of overlap in food and habitat choices with the abundant blue wildebeest Connochaetus taurinus and the close distance between multiple ungulate species’ herds and the massive wildebeest herds indicated that ungulate assemblages are not driven by interspecific competition alone (Sinclair 1985). Predation risk influenced several ungulate species to aggregate with wildebeest, a preferred prey item for lions, as this reduced their chances of being killed. Predation is thus a major shaping force in ecological communities (Sinclair 1985), affecting prey species both directly (lethal effects of predation) and indirectly (non-lethal effects of predation risk), as discussed below.

1.2.1) The direct effects of predation

The effects of predation on ungulate communities have traditionally been described in terms of the numerical abundance of prey populations as a consequence of direct consumption by predators (Peckarsky et al. 2008). The direct effects of predation are thus reflected in changes in prey population dynamics, defined as “the outcome of changing survival rates, reproductive success and movements of the animals constituting the population” (Owen-Smith et al. 2005, pp. 774). Assessing the direct effects of predation on population dynamics is challenging as teasing apart simultaneous effects of predation and other factors such as food and climate is difficult (Hebblewhite et al. 2002). Despite these challenges, predation has been shown to be a strong driver of prey population dynamics (Gasaway et al. 1992; Mills & Shenk 1992; Hebblewhite et al. 2002; Owen-Smith et al. 2005; Funston & Mills 2006). The degree to which direct predation influences prey populations is affected by several factors. The sex- and age-specific prey selection of predators (Mills & Shenk 1992), the movement ecology (sedentary or migratory) of the prey population (Fryxell et al. 1988; Funston & Mills 2006) and the abundance of predators and alternative prey species on the landscape (Owen-Smith et al. 2005) influence the effect of predation on prey population demographics. The underlying landscape characteristics (i.e. the predominant habitat type) and variation in rainfall (Ogutu & Owen-Smith 2005) are also important as they determine the susceptibility of prey species to predation. These factors indicate that prey vulnerability is spatially and temporally variable as landscape conditions, predator and prey distributions and population demographics change over time (Sunquist & Sunquist 1997).
1.2.2) The indirect effects of predation

Prey population dynamics are influenced by a multitude of variables (Owen-Smith et al. 2005), thus factors other than the removal of individuals from a population through direct predation can affect prey population dynamics. Given that prey species are able to assess the local risk of predation and incorporate this information into their decision-making, predation also affects prey populations through the costs of antipredator behavioural responses (Preisser et al. 2005; Creel & Christianson 2008). The effect of costly antipredatory behavioural responses on prey population dynamics, known as the nonlethal or indirect effects of predation, can be as large as direct effects, or larger (Schmitz et al. 1997; Nelson et al. 2004; Pangle et al. 2007; Christianson & Creel 2010). For example, in Yellowstone National Park, elk Cervus elaphus populations under high risk of predation from wolves Canis lupus had decreased levels of progesterone, which resulted in reduced calf recruitment and a decrease in population growth (Creel et al. 2009). Similarly, behavioural responses by moose Alces alces cows to the risk of predation from wolves on Isle Royale, Michigan, resulted in female moose occupying areas that provided poor quality forage (Edwards 1983). The body condition of these animals therefore decreased, resulting in a decrease in calving rate and thus a lowered population growth rate. Prey population regulation of this nature demonstrates how predation risk influences population dynamics independent of actual predation. The ‘predation-sensitive-food hypothesis’ suggests a second mechanism by which predation risk and access to food interact to affect populations (Sinclair & Arcese 1995). This hypothesis states that “predation and food jointly limit population size because as food becomes limiting animals take greater risks to obtain it and as a result, some of these are killed by predators” (Sinclair & Arcese 1995, pp. 882-883). Ultimately, the indirect effects of predation occur largely because animals exchange food and safety (Brown & Kotler 2004). Behavioural responses to predation risk, such as changes in habitat use and time allocation thus carry costs to foraging (Brown 1988; Brown & Kotler 2004) which may result in population-level declines (Christianson & Creel 2010). Behavioural responses of prey species to predation risk, and the mechanisms by which they operate, thus play a huge role in shaping predator-prey interactions and are discussed further below.

1.3 Behaviourally-mediated responses to predation risk

Predation risk is defined as the probability of being killed at some time (Lima & Dill 1990). The risk of predation is thus a function of the rate of encounter between predators and prey species, the probability of mortality given an encounter, and the time spent vulnerable to an encounter (Lima & Dill 1990). The dynamic nature of predation risk becomes evident when considering that the probability of both encountering and being killed by a predator are not uniformly distributed on the landscape and over time (Lima 1992; Lima & Bednekoff 1998; Hebblewhite et al. 2005). Predation decision-making that drives behavioural responses to predation risk is thus largely influenced by both location and time, as certain habitats and times are more risky than others (reviewed by Lima &
Behavioural responses to predation risk thus shape where, when and how animals use the landscape (Brown et al. 1999; Valeix et al. 2009; Laundré et al. 2010; Thaker et al. 2011).

Decision-making by prey species in the presence of predators may be reflected in several aspects of prey behaviour such as their sociality, mating, feeding, patch use, habitat selection, activity patterns and predator detection behaviours (Sih 1980; Edwards 1983; Brown 1988; Lima & Dill 1990; Lima 1998a, 1998b; Brown et al. 1999; Laundré et al. 2001). These behavioural responses are driven by trade-offs between the costs and benefits of resource acquisition and predation risk (Brown 1988; Lima & Dill 1990; Lima 1998a). Thus, although behavioural responses to predation may be costly and adversely affect an animals’ fitness in the long-term, they play a large role in reducing the probability of predation an animal experiences in the short-term, and potentially in the long-term (Lima 1998a, 1998b). It is thus important that prey species are able to assess the level of local predation risk and adjust their behavioural response accordingly, as over- or undercompensating will compromise the benefits of antipredatory behaviours (Berger 2007). Where an animals’ behavioural response is not strong enough, it may experience increased vulnerability to predation risk, and thus be largely affected by the direct effects of predation. Conversely, an animal that responds too strongly may experience reduced levels of fitness due to missed foraging or mating opportunities that were disproportionally traded-off for safety and thus be largely affected by the indirect effects of predation (Berger 2007). The ability of prey to assess varying levels of predation risk and relax or heighten antipredatory responses accordingly is referred to as the ‘threat-sensitive predation avoidance hypothesis’ (Helfman 1989) and allows animals to make the most efficient trade-offs between feeding and exposure to predation risk.

1.3.1) Temporal and spatial variation in predation risk

Three main theories regarding how prey species regulate their antipredatory behaviours in response to predation risk have been proposed and are based on variation in predation risk over both time and space. The ‘risky space hypothesis’ suggests that the timing of antipredatory behaviours by prey species is based on long-term background levels of predation risk experienced at a particular location (Creel et al. 2008). The ‘risky times hypothesis’ stipulates that prey species will engage in antipredatory behaviours only when predators are present, regardless of previous presence or absence of predation risk in the area (Creel et al. 2008). The ‘risk allocation hypothesis’ is based strongly on the temporal variation in predation risk, and is thus an extension of the risky time hypothesis, and suggests that prey species allocate efforts to both feeding and antipredatory behaviours in an environment of ever-changing predation risk (Lima & Bednekoff 1999). Assuming that antipredatory responses are traded-off for forage, the risk allocation hypothesis predicts that antipredatory responses should be highest during a pulse of risk within a background of safety, because there is a high probability that safer feeding conditions will soon return. Antipredatory responses should then be lowest during a pulse of safety within a background of risk because there
is a high probability that risky feeding conditions will soon return. (Lima & Bednekoff 1999; Creel et al. 2008). Thus, predictions of the risky space hypothesis are directly contrary to those of the risk allocation hypothesis (Creel et al. 2008).

Empirical support has been found for the risk allocation hypothesis by assessing the vigilance levels of elk in response to temporal variation in predation risk from wolves in Yellowstone National Park (Creel et al. 2008). Elk that experienced lower levels of predation risk were more vigilant than elk exposed to higher levels of risk. This finding implies that the indirect effects of predation are not necessarily highest in places with the most frequent exposure to risk, contrary to what has been previously assumed. Studies have also, however, found support for the risky space hypothesis, for example, ungulate species in Hwange National Park, Zimbabwe and Karongwe Private Nature Reserve, South Africa, avoided areas associated with high background levels of predation risk (Valeix et al. 2009; Thaker et al. 2011). In support of the risky times hypothesis, ungulates in Hwange exhibited behaviourally-mediated shifts in habitat use when lions were present in the immediate vicinity i.e. within 2 km (Valeix et al. 2009). Studies investigating the behavioural responses of prey to predation risk thus illustrate the diversity of behavioural adjustments prey make as they seek to reduce the risk of predation over space and time (Creel et al. 2008; Valeix et al. 2009; Thaker et al. 2011).

1.3.2) The landscape of fear

The landscape of fear provides a visual model that aids in explaining the influence of predation risk on the spatial distribution of prey animals (Laundré et al. 2010). Under the landscape of fear model, the area used by prey consists of high- to low-risk microhabitat patches, as determined by the lethality and presence of predators in those patches (Shrader et al. 2008; van der Merwe & Brown 2008). The landscape of fear thus represents the variable risk of mortality that is associated with a heterogeneous landscape, based on the ecology of the primary predator (Laundré et al. 2010). The concept of the landscape of fear (Laundré et al. 2001) stems from a fairly recent approach referred to as the ecology of fear in which fear is considered a major driver of ecological interactions across the landscape (Brown et al. 1999). Based on this approach, use of the landscape by prey is fear-driven such that spatial patterns observed in prey populations are considered a direct result of behavioural response to predation risk (Brown et al 1999; Laundré et al. 2001). The escape tactics of prey species are also considered an important component of the landscape of fear (Lima 1992; Wirsing et al. 2010), as the mechanisms by which prey species are able to reduce predation risk play a large role in determining where they chose to occur on the landscape (Heithaus et al. 2009).

Fundamental to the landscape of fear theory is the assumption that prey species are capable of learning to recognise areas where mortality risk is heightened by habitat-mediated factors and respond with the aim to reduce this risk (Laundré et al. 2010). Prey species are thought to do this
through previously experienced unsuccessful attack events (Laundré et al. 2010) and through social learning (Kavaliers & Choleris 2001). The landscape of fear model may thus be extended to help explain other landscape-scale ecological concepts of animal space use, including the concept of the home range (Laundré et al. 2010). By confining their activity to a single area, animals may learn where predation risk is high and where they may find refuge from predation, and this has survival advantages to prey (Clark et al. 1993). Thus a known home range provides predator avoidance benefits (Laundré et al. 2010). An animal is thus able to integrate its knowledge of the spatial distribution of resources and predation risk within its home range to make its daily foraging decisions (Brown et al. 1994; Brown & Kotler 2004).

More recently, the landscape of fear model has been applied to investigate the mechanisms of prey population regulation, where the proportion of risky to safe microhabitat patches is thought to influence whether bottom-up or top-down factors regulate populations (Laundré et al. 2014). Prey populations occurring on landscapes dominated by risky habitats are more likely to be regulated by predation, whilst populations occurring on landscapes of predominantly safe habitats may be regulated more strongly by bottom-up forces.

1.4 Predator avoidance and escape strategies
A variety of antipredatory mechanisms are employed by prey species to reduce predation risk ranging from rapid escape speeds, concealment through cryptic colouration, active defence aided by morphological or chemical weaponry, being scarce or highly abundant on the landscape or avoiding predators (Caro 2005). Spatial and temporal avoidance of predators is a fundamental antipredatory strategy (Caro 2005). Prey animals that are able to effectively avoid predators at a broad scale reduce the probability of encountering predators, and thus of being attacked. Large-scale avoidance effectively reduces both the direct and indirect effects of predation as animals are able to minimise costly antipredator behaviours such as vigilance and behaviourally-mediated habitat shifts that are a foraging cost (Hebblewhite & Merrill 2009). The predation risk avoidance hypothesis suggests that large-scale movements such as migration and nomadism occur to reduce predation risk (Bergerud et al. 1984; Fryxell et al. 1988). Alternatively, the predation refuge hypothesis suggests that prey may avoid predators at a finer scale by avoiding areas that are associated with an increased probability of death given an encounter or by exploiting fine scale spatiotemporal variation in predation risk (Hebblewhite & Merrill 2007;2009). Avoidance behaviours may thus operate at multiple scales (Lima & Zollner 1996).

Large-scale spatial avoidance may be achieved through migratory or nomadic behaviour that see prey species move extensively across the landscape and beyond the home ranges of territorial predators for large portions of the year (Bergerud et al. 1984; Fryxell et al. 1988). Migratory prey populations are under less predation pressure compared to that experienced by resident
populations in African ecosystems such as Kruger National Park (Mills & Shenk 1992; Funston & Mills 2006), the Kalahari desert (Mills 1990) and the Serengeti in East Africa (Fryxell et al. 1988; Schaller 1972). Similarly, Hebblewhite and Merrill (2007) found that migrant elk in Banff National Park, Canada reduced the risk of wolf predation by 70% relative to resident populations. In a study documenting lion predation in Nairobi National Park, Kenya, the nomadic behaviour of eland allowed them to avoid predation by resident lions in the reserve for six months of the year through large-scale movements beyond the park boundaries (Rudnai 1974). Migratory and nomadic behaviours may therefore represent an anti-predatory adaptation which developed over evolutionary time under the constant predation pressure from coexistent predators, so that other defensive adaptations may not have been under strong selective pressure (Louw et al. 2012).

At a finer scale, behaviourally-mediated avoidance operates through shifts in space use and time allocation in response to spatiotemporal variation in predation risk (Anderson et al. 2005; Fortin et al. 2005; Creel et al. 2008; Halofsky & Ripple 2008). Fine scale avoidance may effectively reduce predation given that the areas where prey are most likely to encounter a predator may not necessarily be where they are most likely to be killed (Hebblewhite et al. 2005). Thus, even where predator and prey space use overlaps at a broad spatial scale, fine scale habitat selection for areas that reduce the hunting efficiency of predators and increase the effectiveness of prey escape tactics may reduce predation pressure on prey animals (Heithaus et al. 2009). Prey species may avoid predators at a fine scale, particularly in the case of territorial predators (Thomson et al. 2006), by avoiding areas of high predator use within their home ranges (Anderson et al. 2005) or occupying areas between predator territories (Lewis & Murray 1993).

1.5 Problem statement

Antipredatory responses to predation, although costly, play an important role in reducing the rate of direct predation experienced by a prey species (Lima 1998a; 1998b). Antipredatory strategies thus contribute to prey population persistence under predation pressure (Ives & Dobson 1987). However, when prey are unable to effectively employ antipredatory strategies they may experience increased predation pressure which may result in population declines or crashes (Tambling & du Toit 2005; Louw et al. 2012). With increased human pressure on the environment, wildlife populations are increasingly restricted to small, fragmented conservation areas (Hayward & Kerley 2009), where large-scale movement is restricted (Ben-Shahar 1992). The effects of predation on wide-ranging species are likely to be heightened (Louw et al. 2012) and the regulation of prey populations may shift from being dominated by bottom-up processes to top-down processes (Hopcraft et al. 2010; Grange et al. 2012). An important question is; how do wide-ranging prey species which avoid predators at a broad scale in natural, open systems, adapt to predation pressure in smaller reserves that restrict their movement?
In South Africa, the reintroduction of apex predators into protected wildlife areas, both private and state-owned, has increased (Hayward et al. 2007; Hayward & Somers 2009), with at least 37 lion reintroductions occurring in the past two decades (Slowtow & Hunter 2009). Although much has been learnt from studies of North American predator reintroductions and subsequent prey responses (Laundré et al. 2001; White & Garrot 2005; Berger 2007; Ripple et al. 2010; Ripple & Beschta 2012), there are vast gaps in research on prey responses to predation risk, largely because few other systems have received much attention (Tambling et al. 2012a). Of particular concern is that there are “few insights regarding the conditions allowing both prey and predator populations to be sustained in enclosed areas of limited extent…” (Grange et al. 2012, pp. 17).

Rapid declines in eland numbers have been observed in several small reserves following lion reintroductions (Tambling & du Toit 2005; Louw et al. 2012; SANParks, unpublished data), indicating a possible break-down in eland antipredatory strategies. Despite the occurrence of population crashes following lion reintroductions, little information is available on the behavioural response of eland, and indeed most African bovids, to predation risk presented by lions, particularly in the context of small, fenced reserves (but see Tambling et al. 2012a). In 2003, lions were reintroduced into the Main Camp Section of Addo Elephant National Park (AENP) after over 100 years of absence (Hayward & Hayward 2006). Following predator reintroduction, the eland population in the 13 400 ha reserve was reduced from 188 in 2003 to ten individuals in 2010 (SANParks, unpublished data). Investigating how such seemingly vulnerable prey respond to predation risk is thus vital in contributing to our understanding of the mechanisms that drive these destabilizing predator-prey interactions.

Following the lion reintroduction in AENP, behavioural adjustments by Cape buffalo Syncerus caffer, namely an increase in group size and preference for open habitats particularly during times of increased lion activity, reduced the rate of juvenile mortalities from lion predation such that the population did not suffer any major, long-term declines (Tambling et al. 2012a). Buffalo and eland are similar in size and weight, and together constitute the largest extant bovids (Hillman 1988). The apparent disparity in the ability of these two species to effectively mitigate predation in small to medium sized reserves, despite their similar body size, indicates that behavioural antipredatory responses of prey, and their ability to effective employ them, play a large role in determining how vulnerable a prey species is to predation in small reserves.

Eland are the largest and slowest antelope in Africa and are generally non-aggressive (Estes 1991) making them a highly desirable prey item. Historically, eland were common across South Africa, thus they coexisted with lions across their natural distribution (Skead 2007). Aspects of eland ecology are thus likely to reflect antipredatory adaptations that allowed them to coexist with their major predator, lions (Estes 1991; see below). Of the few studies on eland, most have investigated diet and
habitat selection in small, closed reserves free of predators (Underwood 1975; Fabricius & Mentis 1999; Watson & Owen-Smith 2000; Wallington 2007). A study of eland in a large, open system in Kenya reported bottom-up processes as the drivers of eland distribution, with little mention of predator effects (Hillman 1988). This is likely because where eland are free to range widely, predation is not a major regulating factor (Skogland 1991; Schaller 1972).

In a meta-analysis on lion prey selection, lion were found to prefer prey species between 190 and 550 kg (Hayward & Kerley 2005). The body mass of eland (calculated as 3/4 x mean adult female body weight to account for sub-adults and calves eaten) is estimated as 345 kg (Hayward & Kerley 2005). Eland therefore fall within the preferred weight range of lion prey (Hayward & Kerley 2005). Despite this, the meta-analysis found that eland were not significantly preferred by lions but were preyed upon in accordance with their abundance. This was attributed to antipredatory behaviours of eland that effectively reduce predation risk, namely, their active defence of young against lions (Hillman 1988), their large herd sizes (Hamilton 1971) and their weaponry used against lions (Estes 1991). At a broader scale, eland may effectively avoid predation by being highly mobile and covering vast areas over the annual cycle, as reflected by their nomadic behaviour (e.g. Rudnai 1974). It has also been suggested that eland reduce predation by persisting at low densities thereby reducing the selection of morphological or behavioural traits that would allow lions to hunt eland specifically (Hayward 2011). In small reserves however, ungulate assemblages are often the product of managerial decisions such that eland may be stocked at higher densities than would occur in open systems, thereby increasing their vulnerability to predation (Louw et al. 2012).

Eland are nomadic, and have the largest home ranges of all African antelope (Hillman 1988). Several aspects of eland biology allow for their wide-ranging behaviour, such as their non-territoriality (Underwood 1975; Hillman 1988), their adaptability to a wide range of habitats (Estes 1991) and food types (Hoffman & Stewart 1972; Fabricius & Mentis 1990) and their water-independence (King et al. 1975). Eland are thus well adapted to large-scale movements which may represent an important antipredatory strategy allowing them to avoid predators at a broad scale. Behaviours such as nomadism eliminate or greatly reduce the risk of attack and thus increase survival without the need to employ behaviours that reduce the probability of capture following an attack (Sansom et al. 2009). Once an individual is exposed to attack however, escape enhancing behaviours become important for survival (Sansom et al. 2009). Predator avoidance mechanisms and escape behaviours are therefore under different selective pressures and the evolution of one type of survival mechanism reduces selection on the other (Brodie & Formanowicz 1991).

1.6 Aims and hypotheses

With little investment in other antipredatory defences, eland may face increased vulnerability to predation in small reserves, unless they are able to effectively reduce predation levels through fine
scale behaviourally-mediated responses. The current study thus aims to investigate how eland respond to predation risk in small to medium sized reserves. By investigating eland space use and movement relative to that of lions, this study aims to assess the spatial and temporal responses of eland to predation risk at multiple scales. Furthermore, the assessment of eland kill sites aims to provide insight into the conditions under which antipredatory mechanisms of eland fail. This study therefore sets out to test the following hypotheses;

1) Eland are broad scale predator avoiders and therefore eland and lion home ranges do not overlap.
2) Eland responses to predation risk vary at different spatial scales, with variation similarly present at different temporal scales.
3) Predation risk and vulnerability are not uniformly distributed on the landscape and are a function of lion distribution and habitat features.
4) Eland respond to lions at a fine spatiotemporal scale to reduce the risk of encountering lions at close proximity.

Chapter two of this thesis assesses eland habitat selection under predation risk at the landscape and home range scale. Results of this chapter shed light on the biotic and abiotic factors that influence where eland establish home ranges within an area available to them, and the factors that drive resource selection within their home range. This chapter includes a description of the two study sites.

Chapter three deals with eland and lion interactions at a fine scale and aims to investigate whether eland habitat selection at the landscape and home range scale, shown in chapter two, facilitate eland in avoiding areas where they are more vulnerable to predation. Eland kill sites were investigated and compared to sites where eland were known to be alive, thereby identifying landscape characteristics that represent risky areas for eland. Furthermore, the pattern of spatial overlap between eland and lions was investigated at multiple temporal scales, thereby providing further insight into the fine scale spatial dynamics between eland and lions in small reserves.

Chapter four integrates the findings of chapters two and three into a concluding discussion. This chapter aims to synthesise and contextualise the findings of this study, relate key findings to the objectives of the study, critically examine the strengths and weakness of the research approach, discuss the practical implications of the key findings and provide direction for future research.
Chapter 2

Scale-dependent habitat selection by eland under predation risk

2.1 Introduction

In predator-prey systems, habitat selection by prey species may require trade-offs between the acquisition of resources (forage, mates and shelter) and avoidance of predators (Werner & Anholt 1993). Habitat use by prey species therefore represents the outcome of these trade-offs between the costs and benefits associated with the different habitats (Kittle et al. 2008). Disproportionate use of habitat types should therefore reflect habitat selection that maximises an animal’s fitness (Rosenzweig 1981; Morris 2003). The factors that drive habitat selection differ in their magnitude of effect (Preisser et al. 2005), especially since the spatial distribution of resources can be relatively stable at an ecological time-scale, whereas predation risk is dynamic as mobile predators move through the landscape (Sih et al. 2000). Furthermore, factors that drive habitat selection are scale-dependent (Wiens 1989) such that animals may pursue different goals at broad and fine spatial scales because resource distribution, foraging costs, physiological and reproductive demands and predation risk vary with scale (Senft et al. 1987; Bailey et al. 1996; Boyce et al. 2003).

Insight into the factors that drive resource selection decisions at varying spatial scales is essential to understanding an animal’s ecology (Boyce & McDonald 1999). Habitat selection must therefore be viewed as a hierarchical process (Johnson 1980), as biotic and abiotic impacts on the spatial distribution of animals depends on the scale at which they are investigated (Bowyer & Kie 2006). To recognise the hierarchical nature of habitat selection, Johnson (1980) proposed a four-tiered definition of selection. At the broadest scale, first order selection is defined as the selection of the physical or geographical range of a species (Johnson 1980). Within that range, second order selection determines the home range of an animal, referred to as landscape scale selection (Dussault et al. 2005), whilst third order selection pertains to the usage of various habitat components within the home range (Johnson 1980), referred to as home range scale selection (Dussault et al. 2005). Assessing habitat selection at too fine a scale runs the risk of under-evaluating important habitats whilst the assessment of habitat selection at too coarse a scale may mask the importance of fine scale habitat features critical to an animal’s survival (Bowyer & Kie 2006). Multi-scale assessment of habitat selection thus provides a comprehensive understanding of the factors influencing the spatial distribution of animals.

The pattern of habitat selection across spatial scales should reflect the hierarchy of the factors that potentially limit individual fitness (Rettie & Messier 2000). Decisions at the large scale are thought to be made less frequently but are more likely to have a greater influence on fitness than those at fine scales (Senft et al. 1987). Given that predation precludes future fitness (Lima & Dill 1990), predation
risk is considered a primary limiting factor of individual fitness for prey species in predator-prey systems (Sinclair 1985). Predation risk is defined as the probability of being killed during some time period (Lima & Dill 1990), and can be broken down into two components; the probability that a prey species encounters a predator and the probability that the prey is killed as a result of the encounter (Lima 1992). Prey species can reduce predation risk by directly avoiding areas where the chance of encountering a predator is high (Rettie & Messier 2000; Valeix et al. 2009) or by selecting habitats where the risk of being killed by a predator is reduced (McLoughlin et al. 2005; Thaker et al. 2011; Tambling et al. 2012a; Burkepile et al. 2013).

The spatial distribution of prey species is thus largely influenced by spatial variation in predation risk caused by a mobile predators’ presence in a spatially heterogeneous landscape (Brown et al. 1999; Laundré et al. 2001). For prey species that are able to perceive changes in the level of threat, the spatiotemporal variation in predation risk creates a structured and dynamic ‘landscape of fear’ (Laundré et al. 2001) in which they can minimise the risk of predation through behaviourally-mediated antipredatory mechanisms at varying scales (Tolon et al. 2009).

Habitat shifts by prey species in response to predation risk illustrate how variation in both predator ecology (Preisser et al. 2007; Thaker et al. 2011) and prey escape tactics (Lima 1992; Wirsing et al. 2010) affect habitat selection by prey species under predation risk. For example, wolves Canis lupus, as coursing predators, have increased hunting success in open habitats, such that prey species move into structurally complex habitats when wolves are present (Creel & Winnie 2005; Fortin et al. 2005; Atwood et al. 2007). Conversely, lions Panthera leo are ambush hunters such that their hunting mode relies on sufficient cover from which to stalk prey (Funston et al. 2001; Hopcraft et al. 2005). Prey species thus tend to use open habitats preferentially in response to predation risk from lions (Valeix et al. 2009; Thaker et al. 2011; Tambling et al. 2012a). Furthermore, the territory and space use of ambush predators is relatively stable and therefore more predictable than the variable space use patterns of coursing predators (Preisser et al. 2007). Cues from ambush predators therefore provide more information about local predation risk (Lima & Bednekoff 1999) resulting in antipredatory responses that are stronger in response to ambush predators than coursing predators (Preisser et al. 2007; Thaker et al. 2011).

These studies illustrate that predators drive shifts in habitat selection by prey species, thereby reducing the risk of predation they experience (Tambling et al. 2012a). Therefore, the reintroduction of lions provides the opportunity to investigate the behavioural responses of a large, yet understudied prey species, the common eland Tragelaphus oryx, to predation risk. Following the reintroduction of lions into several reserves in South Africa, eland populations suffered rapid declines (Tambling & du Toit 2005; Louw et al. 2012; SANParks, unpublished data), indicating a potential break-down in their antipredatory strategies. A need thus exists for a better understanding of the antipredatory mechanisms employed by eland, and the conditions required for them to
effectively avoid predation within fenced reserves, thereby allowing for stable predator-prey

dynamics (Ives & Dobson 1987). Given that lions are territorial, and thus spatially predictable, large-
scale movement by eland that effectively avoid lion home ranges should act to reduce the

probability of encountering lions. This should reduce the chances of having to attempt escape at a

fine scale, to which eland are poorly adapted, being the largest and slowest African antelope (Estes

1991). Eland are nomadic and thus well adapted to large scale movements (Hillman 1988; Augustine

2010). Based on these ideas, it was hypothesised that eland space use at a broad scale i.e. at the

landscape scale, would reflect predator avoidance behaviours.

The objective of this chapter was to examine space use patterns and habitat selection by eland

exposed to predation risk at both the landscape (2nd order) and home range (3rd order) scale. By

assessing habitat selection of eland at multiple scales, this chapter aims to gain insight into predator

avoidance behaviours of eland and the scale at which they operate. Given the hypothesis that eland

avoid lions at a broad scale, it was predicted that eland home ranges would not overlap with lion

home ranges, consistent with the predation risk avoidance hypothesis (Hebblewhite & Merrill 2007).

Furthermore, it was hypothesised that eland habitat selection would reflect avoidance of areas

associated with a higher probability of mortality, given an encounter with a lion. It was therefore

predicted that eland would avoid dense habitats which increase lion hunting success (Funston et al.

2001; Hopcraft et al. 2005; Burkepile et al. 2013; Loarie et al. 2013), consistent with the predation

refuge hypothesis (Hebblewhite & Merrill 2007). Thus, it was expected that predation risk would be

a major factor driving the spatial distribution and habitat selection of eland at both the landscape

and home range scale.

2.2 Methods

2.2.1) Study sites

This study was conducted at two study sites, Nyathi Section of Addo Elephant National Park (Nyathi)

and Mountain Zebra National Park (MZNP), which are described below.

2.2.1.1) Nyathi Section, Addo Elephant National Park (AENP)

2.2.1.1a) Site description, Topography and Geology

The study was conducted in the Nyathi section of the Greater Addo Elephant National Park (GAENP)

(henceforth referred to as Nyathi). The GAENP (33°30’S, 25°45’E) is 80 km north-east of Port

Elizabeth on the south east coast of South Africa (Fig. 2.1). Nyathi (33°39’S, 25°83’E) constitutes one

of the fenced terrestrial sections of the GAENP and at the time of the study was 14 000 ha in size.

The topography of Nyathi is characterised by a series of steep valleys, and with ridges of the

Zuurberg Mountains in the north of the section. The southern part of Nyathi is less rugged and

characterised by gently undulating hills and flat plains, as well as the Coerney River Valley (De Klerk

2009). Soils in the Zuurberg Mountains are sandy and nutrient-poor, derived from the Bokkeveld and
Witteberg Groups (Cape Supergroup, Mucina & Rutherford 2006). Several natural, ephemeral waterholes are present across Nyathi, as well as permanent artificial water holes.

Fig. 2.1 a) South Africa’s location within Africa, b) Nyathi’s location within South Africa and c) the Nyathi section (AENP) with the reserve boundary in black.

2.2.1.1b) Vegetation

Nyathi is dominated by Sundays Thicket vegetation, which is comprised of dense stands of various tree, shrub and succulent species, many of which are spinescent (Mucina & Rutherford 2006). Kowie Thicket is present in the north-east of the reserve, where it occurs on the steep slopes of the mountainous landscape (Mucina & Rutherford 2006). This vegetation is taller and is largely dominated by tree euphorbias, tall shrubs and woody lianas with numerous succulents forming a dense understorey. On moister, south-facing slopes, the Kowie Thicket vegetation is comprised of evergreen tree species (*Cussonia, Pappea* and *Schotia*) and shrubs (*Azima, Carissa, Euclea, Gymnosporia, Hippobromus* and *Putterlicka*), with fewer succulent species present. Zuurberg Quartzite Fynbos and Zuurberg Shale Fynbos occur on the mountain plateau in the northern section of the reserve (Mucina & Rutherford 2006). This vegetation type is characterised by a grassy understorey with localised patches of proteoid and ericaceous fynbos (Mucina & Rutherford 2006). A small patch of Southern Mistbelt Forest is found in the north of the reserve (Mucina & Rutherford 2006). Along the southern boundary, where the terrain is much flatter, Albany Alluvial Vegetation dominates (Mucina & Rutherford 2006). Several large open plains exist in areas where vegetation was historically cleared for agricultural purposes, primarily pastoralism (G.I.H. Kerley, personal communication). These large open plains are generally devoid of trees or shrubs and are dominated by grass species (*Eragrostis obtusa, Cynodon dactylon, Panicum maximum* and *P. deustum*). Large
stands of *Acacia karroo* are present along drainage lines and have established in previously cleared areas.

### 2.2.1.1c) Habitat types

#### i) Defining habitat types and availability

Vegetation density maps of each reserve were developed from aerial images (Google Earth) by classifying predominant vegetation cover into three categories based on vegetation structure; i) dense, ii) mixed or iii) open. These habitat categories represent the cover provided by vegetation, which influences lion predation risk (Loarie *et al.* 2013), as well as a broad measure of forage type associated with each habitat type. Dense habitat types were characterised by areas where bush density is so high that no ground or ground-cover vegetation (such as grasses) is exposed. Areas defined as mixed are characterised by an intermediate level of bush density i.e. ground space is easily visible amongst bush clumps and/or individual trees/shrubs. Open areas are defined as areas where no large vegetation structures occur so that only ground or ground-cover vegetation (such as grass) is visible. Habitat type classifications were aimed at representing the amount of cover, (defined as a habitat feature which may conceal, shelter or protect) that the vegetation offers. The amount of cover influences both habitat selection and predation risk of herbivores (Mysterud & Østbye 1999). Aerial images were digitized in ArcGIS 10.1 by combining polygons outlining each habitat type. Using the “Feature to raster” tool in ArcGIS 10.1, a habitat raster image was developed from the digitized aerial images of each reserve. The proportional availability of open, mixed and dense habitat types in each reserve was assessed in ArcGIS 10.1 by summing the area of all polygons representing each habitat type respectively and dividing that by the overall size of the reserve.

#### ii) Proportional representation of habitat types in Nyathi

Nyathi is dominated by dense habitats (69%, Fig. 2.2). These habitats are dominated by thicket vegetation and therefore represent habitats with a high biomass of browse but a low level of visibility (measure of the ability of an eland to observe an approaching lion). Fourteen percent of the reserve is characterised by open habitats. These open areas occur primarily along the southern boundary, as well as on the mountain plateaus in the north of the section. Open habitats are dominated by grasses and low-growing vegetation with few trees, thus providing ground-level forage for grazing. These habitats offer a high level of visibility. Mixed habitats, characterised by spatially dispersed vegetation structures such as bush clumps and trees, such as stands of *Acacia karroo*, comprise 17% of Nyathi. Consequently, Nyathi is characterised by a stark dichotomy between the dominant dense thicket vegetation and the limited open habitats. Open habitats, particularly along the southern boundary, are bordered by stands of *Acacia karroo* (i.e. mixed habitats) or dense thicket such that clearly defined edges existed between habitat types.
2.2.1.1d) Climate

Nyathi falls in the semi-arid zone of South Africa (Landman et al. 2008). Rainfall records from Addo Main Camp (less than 1 km south of Nyathi) between 1959 and 2013 show that the region receives an estimated 401 ± 16 mm of rainfall per annum, with high inter-annual fluctuation (SANParks, unpublished data). Although rainfall is largely non-seasonal, slight peaks occur in March and October/November (Fig. 2.3). Average monthly day temperatures in summer (December - February) range from 11.8 ± 0.1°C to 32.4 ± 0.1°C and from 3.4 ± 0.09°C to 25.7 ± 0.1°C in winter (June – August) (South African Weather Services, unpublished data, 1959-2013).

The occurrence of distinct seasons was established such that data analyses for this study could be conducted at an ecologically relevant temporal scale. Rainfall data from 1959 to 2013 was assessed to determine where changes in average monthly rainfall were significantly different between successive months, based on a moving window analysis (Tambling et al. 2012a). The difference in the average monthly rainfall of two consecutive months was tested using Student’s t-tests (i.e. January’s average rainfall was compared to February’s and so forth). Where a significant difference ($p < 0.05$) in average monthly rainfall occurred, it was used as a measure of an ecologically relevant change in rainfall patterns and marked as the beginning of a new season. Analyses of rainfall data from Addo resulted in the delineation of two distinct seasons, namely a wet season (October – April, average 38.38 ± 2 mm of rainfall per month) and a dry season (May – September, average 26.71 ± 2 of rainfall mm per month).
2.2.1.1 Medium to large mammal community

Nyathi, at its current size, was established in 2002, merging several farms into a single fenced unit of protected land. Initially, the medium to large mammal community consisted of several antelope species including greater kudu *Tragelaphus strepsiceros*, bushbuck *Tragelaphus scriptus* and common duiker *Sylvicapra grimmia*, and small carnivores and omnivore species, including caracal *Felis caracal*, genet *Genetta species*, black-backed jackal *Canis mesomelas* and porcupine *Hystricomorph Hystricidae*. The exotic warthog *Phacochoerus africanus* species was, and remains prevalent in the reserve. Megaherbivores and apex predators, namely lion *Panthera leo* and spotted hyena *Crocuta crocuta*, had been previously extirpated from the area (Skead 2007).

Following the establishment of Nyathi as a section of the GAENP, several species reintroductions occurred. Antelope species reintroduced included common eland and red hartebeest *Alcelaphus buselaphu*. Sixty-three elephant *Loxodonta africana* were reintroduced in 2003, taken from the expanding elephant population in the Main Camp section (SANParks, unpublished data). Seventy-one Cape buffalo *Syncerus caffer* were reintroduced in 2003 (Tambling et al. 2012a). Black rhino *Diceros bicornis* were also reintroduced following the establishment of Nyathi. The existing eland population was supplemented by an additional 38 individuals in 2003 (SANParks, unpublished data).
In September 2011, three lion were reintroduced into Nyathi, following an absence of about 100 years (Hayward & Hayward 2006). Currently, Nyathi supports breeding populations of African elephant, common eland, Cape buffalo, plains zebra *Equus quagga*, greater kudu, red hartebeest, bushbuck and the exotic warthog species, as well as several small antelope species. The carnivore guild is represented by mesocarnivore species such as black-backed jackal and caracal, the three reintroduced lion as well as the presence of at least one resident leopard *Panthera pardus* and brown hyena *Hyaena brunnea* (C.J. Tambling, personal communication.). Following their reintroduction in 2011, lion in Nyathi consumed predominantly ostrich *Struthio camelus*, warthog, eland and hartebeest (Craig Tambling, unpublished data).

### 2.2.1.2) Mountain Zebra National Park (MZNP)

#### 2.2.1.2a) Site description, Topography and Geology

The second site for this study is the Mountain Zebra National Park (MZNP). MZNP (32.18° S, 25.62° E) is situated 24 km west of the town of Cradock in the Eastern Cape, South Africa (Fig. 2.4). MZNP consists of three sections, this study conducted in the eastern-most section, which was 28 000 ha at the time of the study. Topographically, the park is characterised by mountainous terrain, with distinct plateaus at elevated altitudes, steep valleys and slopes (Penzhorn 1979). The Wilgeboom River runs through the length of the park in north-north-easterly direction (Penzhorn 1979). A series of dams have been built in the river, ensuring permanent water in the river except during severe drought (Penzhorn 1979). Additionally, perennial surface water is available in the form of numerous artificial waterholes across the reserve, whilst several natural pans hold water for a limited time following periods of good rainfall. The reserve falls in the Karoo Basin with a substrate dominated by mudstones, siltstones and sandstones of the Beaufort Group (Karoo Supergroup), as well as post-Karoo dolerite intrusions (Toerien 1972) which form ridges (Mucina & Rutherford 2006). Soils in this region are typically shallow (Mucina & Rutherford 2006).

#### 2.2.1.2b) Vegetation

Three of South Africa’s biomes are represented in MZNP; Nama-Karoo, Grassland and Thicket (Mucina & Rutherford 2006). The reserve is dominated by Karoo Escarpment Grassland vegetation whilst Eastern Upper Karoo and Eastern Cape Escarpment Thicket cover 37% and 10% of the reserve, respectively (Mucina & Rutherford 2006). Karoo Escarpment Grassland is characterized by a dominance of the grass species *Merxmuellera disticha* as well as an important low shrub component, with a high occurrence of shrub species *Euryops annuus* and *Dicerorhthenus rhinocerotis* (Mucina & Rutherford 2006). Eastern Upper Karoo vegetation is dominated by dwarf microphyllous shrubs such as *Pentzia incana* and *Eriocephalus ericoides* however, grass species of the genera *Aristida* and *Eragrostis* as well as *Themeda triandra* become prominent following summer rainfall (Mucina & Rutherford 2006). Along the water-courses running through valleys, dense stands of *Acacia Karroo*
have developed (Penzhorn 1979). The distribution of various vegetation communities in MZNP is strongly influenced by both topography and rainfall, creating distinct habitat types across the reserve (van der Walt 1980).

![Fig. 2.4](image)

**Fig. 2.4** a) South Africa’s location within Africa, b) Mountain Zebra National Park’s (MZNP) location within South Africa and c) the MZNP with the reserve boundary in black.

### 2.2.1.2c Proportional representation of habitat types in MZNP

MZNP is dominated by open habitats (58%) which occur on the elevated plateaus across the reserve (Fig. 2.5). These areas are predominantly treeless and are dominated by grass species and low-growing forbs and dwarf shrubs (Penzhorn 1979). This habitat provides an important grazing area for many herbivores in the reserve, particularly during the wet season when grasses are growing (Novellie *et al.* 1988). Visibility in these areas is high given the lack of structural complexity. Mixed habitats represent 40% of the landscape in MZNP. These habitats are largely present on slopes and along drainage lines and are characterised by shrubland communities i.e. a diversity of tall-growing and dwarf shrub species, tall stands of *Acacia karroo*, and an understory of grass. Due to the rich diversity of woody species, this habitat type represents an important browse component across the landscape. Structural complexity is higher in these areas, resulting in reduced visibility. Only 2% of MZNP is defined as dense habitat based on vegetation structure. This habitat type is restricted to the riparian zone along the Wilgeboom River where tall, riverine vegetation, dominated by tall *Acacia* and shrubs, occurs. Visibility in this habitat type is low given the density of the vegetation. Vegetation structure in MZNP is less distinct than in Nyathi, with the landscape dominated by open to semi-open habitats separated by soft edges.
2.2.1.2d) Climate

The mean annual rainfall received at MZNP is 403 ± 17 mm (South African Weather Services, unpublished data, 1962 - 2013). Rainfall is not evenly distributed across the reserve, with the southern and western regions receiving more rainfall than the eastern regions (van der Walt 1980). Rainfall peaks in January and March with the lowest amount of rainfall received in June and July (Fig. 2.6). Frost occurs in winter when temperatures drop below 0°C and snow may occur on mountain tops (Mucina & Rutherford 2006). Monthly average day temperatures in summer (December - February) range from 12 ± 0.2°C to 35.2 ± 0.2°C and in winter (June – August) range from 0.5 ± 0.2°C to 23.5 ± 0.3°C (Data from the Cradock weather station from 1985 – 2013, provided by South African Weather Services).

Seasonal delineation based on monthly average rainfall was assessed in the same way as for Nyathi. Significant differences in average rainfall between months were not the same as in Nyathi. However, two distinct rainfall seasons were still applicable, supported by the highly significant difference ($p < 0.001$) in average rainfall between October – April (wet season receiving an average 48 ± 9 mm of rainfall per month) and May – September (dry season receiving an average 14 ± 2 mm of rainfall per month, South African Weather Services, unpublished data 1962 – 2013).
2.2.1.2e) Medium to large mammal community

MZNP was proclaimed in 1937 when 1712 ha of land were set aside for the protection of the last Cape mountain zebra *Equus zebra zebra* in the area. In addition to the Cape mountain zebra, additional mammals present in MZNP at the time of its establishment were mountain reedbuck *Redunca fulvorufula*, common duiker, steenbok *Raphicerus campestris*, and klipspringer *Oreatragus oreataurus*. No large carnivores were present in the area (Penzhorn 1979).

Species have been reintroduced through the park’s history (Penzhorn 1979). Initially, common eland, black wildebeest *Connochaetes gnou*, red hartebeest, blesbok *Damaliscus pygargus phillipsi*, springbok *Antidorcas marsupialis*, and gemsbok *Oryx gazelle* were reintroduced (Penzhorn 1979). Eland have adapted well since their reintroduction into MZNP, resulting in various translocation to reduce their numbers (Penzhorn 1979). In 1973 the eland population was estimated to be 106 individuals (Penzhorn 1979). Currently, the population estimate is ca 200 individuals (personal observation). Over the years, the park has expanded to its current size of 28 000 ha, allowing for further reintroductions of large herbivore species such as Cape buffalo *Syncerus caffer* and black rhino, as well as the reintroduction of predator species. Predator reintroductions began in 2007 when cheetah *Acinonyx jubatus* where reintroduced into the reserve, followed by brown hyena in

![Graph showing mean monthly rainfall and temperature](image-url)

**Fig. 2.6** Mean monthly rainfall in mm ±SE and mean daily temperatures measured from 1985 to 2013 for Mountain Zebra National Park (South African Weather Services, unpublished data, 1962 - 2013).
2008 and most recently, three lion in 2013. At the time of the study, five cheetah, an unknown number of brown hyena and three lion were present in the reserve. Following their reintroduction, preferred prey species of lions were Cape buffalo, common eland and Cape mountain zebra (D.B. van de Vyver, Rhodes University, personal communication).

2.2.2) Data collection

2.2.2.1) Selection of eland individuals for collaring

Eland social systems are known to be fluid with marked seasonal flexibility in herd size (Hillman 1987). This fission-fusion social system results in the occasional movement of individuals between herds. However, the strong association between mothers and young calves (Underwood 1975; Hillman 1987) results in stable breeding herds that remain fairly constant, thus breeding herds composed of adult females and associated young were identified for collaring in each reserve. Hence, the small sample of collared female individuals was assumed to be representative of the breeding population in each study site and considered adequate to investigate eland responses at both the individual female and breeding population scale.

Three breeding herds were identified in Nyathi at the time of the study, along with numerous independent bachelor groups (D. Zimmerman, SANParks, personal communication). Four collars were deployed across the herds so that two herds were represented by a single collared individual and the third and largest herd was represented by two collared individuals. Collared female eland are referred to as NF1, NF2, NF3 and NF4. Similarly, three breeding herds were identified in MZNP at the time of the study (C. Williams, SANParks, personal communication). A single female from each of the three herds was collared, namely MF1, MF2 and MF3. Initially, these three herds were independent of one another but over the study period, herds associated with MF1 and MF2 fused for extended periods.

2.2.2.2) Collaring procedure

Adult female eland were fitted with GPS/Satellite collars (African Wildlife Tracking, Pretoria, South Africa, http://www.awt.co.za) in Nyathi (n = 4) and MZNP (n = 3). Collaring took place in Nyathi on 15 March 2013 and in MZNP on 16 May 2013. Capture operations and collaring were conducted by the South African National Parks (SANParks) game capture unit and a SANParks veterinarian. Eland were located and immobilised from a helicopter. Collaring was performed under conditions that met the ethical criteria stipulated by the Nelson Mandela Metropolitan University (Research Ethics Committee: Animal Ref. no: A12-SCI-ZOO-002). The minimum age of collared females was 2.5 years as this is the age at which female eland are sexually mature (Underwood 1975).

2.2.2.3) Eland GPS data collection

To maximise eland collar longevity, collars were cycled through two fixed schedules that rotated on a five week cycle. For one week, collars logged a GPS point on the hour, then for four weeks collars
logged a GPS point every six hours, at 06h00, 12h00, 18h00 and 00h00. The two collar schedules yielded data used to assess broad scale eland movement patterns, utilization distributions and habitat selection, as well as fine scale movement patterns. Two datasets were used for data analyses; i) broad-scale GPS data (eland locations at 6 hour intervals, including comparable data from both schedules such that this dataset spanned the full duration of the study), and ii) fine scale GPS data (eland locations every hour for a total of 9 weeks recorded periodically during the study period). Data from all collars were downloaded weekly from an Internet-based portal and screened for duplicate fixes and incorrect fix locations beyond the reserve boundary.

2.2.2.4) Lion GPS data collection

The lion population in both reserves consisted of two males and one female during the study. Lions were reintroduced in Nyathi in September 2011 (C. J. Tambling, personal communication) and in MZNP in April 2013 (C. Williams, personal communication). All lions in both reserves were monitored by park management with GPS-satellite collars upon their release. Lion GPS data was obtained from SANParks (Project contract reference number; TAMCJ 1123 - Eland-lion interactions in Addo Elephant National Park). In both reserves, male lions formed a coalition so that movement data from both male collars was correlated (SANParks, unpublished data). Male lion location data was therefore collected from one male collar, representing the movement of both male lions in each reserve. The female lion in both reserves spent considerable time alone (SANParks, unpublished data), resulting in female movement that differed from males, and hence was included in analyses independently. For the analyses in this chapter, lion GPS data were collected from the day that eland collars were deployed in each reserve.

The collar schedule of the SANParks lion collars in Nyathi varied, with GPS fixes for the male and female received every four and two hours, respectively. GPS locations of the female lion were selected so that there was a four hour interval between each location. The temporal resolution of location data of the male and female lion was thus the same in Nyathi i.e. a fix every four hours for each lion. SANParks lion collars in MZNP were set to receive a GPS fix every 6 hours at 06h00, 12h00, 18h00 and 00h00.

2.2.2.5) Field observations

Visual observations of collared eland were conducted monthly in Nyathi between March 2013 and June 2014. Field trips to MZNP were less frequent with field observations of collared eland in MZNP conducted in June, July and October in 2013 and in January and June in 2014. During each field trip, collared eland were located and filmed with a video recorder so that the herd size and demographics (sex and age structures) could be obtained. The social structure of the herds with which collared animals were associated was thus monitored throughout the study period. Demographic records obtained from field observations thus allowed for coarse monitoring of population dynamics, such as
the proportion of juveniles in breeding herds throughout the year, as well as social behaviours, such as rutting.

2.2.3) Data analysis

Eland habitat selection was investigated at the second and third order (Johnson 1980). Second order habitat selection refers to the selected home range of an animal within the total area available to it (Johnson 1980) i.e. habitat selection at the landscape scale. Resource selection at the third order refers to the use of various habitat components within a home range (Johnson 1980) i.e. patch selection at the home range scale.

2.2.3.1) Landscape scale analyses

i) Estimating home ranges

Home ranges are defined as areas where individual animals perform normal activities and spend the majority of their time (Burt 1943). Home ranges were estimated for all collared eland in each reserve to investigate; i) habitat selection at the landscape level and, ii) seasonal variation in home range size and location. Home range analyses were conducted at two temporal scales, 1) over the full study duration and, 2) at the scale of the defined seasons (as defined in section 2.2.1.1c). To investigate eland home ranges in Nyathi and MZNP, utilization distributions (UDs) of all collared eland were generated with the adaptive local convex hull (α-LoCoH) non-parametric kernel method (Getz et al. 2007) using the ‘T-LoCoH package’ (Lyons et al. 2014). The α-LoCoH method constructs isopleths by identifying nearest neighbours of each point by summing their cumulative distance from the parent point, and stopping when the value of α has been reached (Getz et al. 2007). This method effectively identifies hard boundaries, i.e. fences (Getz et al. 2007), making it applicable for the current study. Furthermore, the α-LoCoH method is designed so that the number of locations used in constructing isopleths increases with increasing density of data, thereby constructing clearly defined isopleths in areas where animal occurrence is highest (Getz et al. 2007). Given that isopleths are defined based on point density, the 50% UD represents the area used frequently by the animal, therefore called the core area, whilst the 95% UD represents the broader range of the animals’ movement and is defined as the home range (Getz et al. 2007).

Broad scale GPS data from all collared eland, collected in decimal degrees, were re-projected to Universal Transverse Mercator (UTM) [WGS84, zone 35S] in ArcGIS 10.1. Using this re-projected location data, the ‘auto.a’ function was used to calculate the value of α that results in 98% of the points having 15 or more nearest neighbours (Lyons et al. 2014). These settings were selected as they effectively accounted for the spatial variation in the density of GPS data, determined by examining isopleth area and edge:area curves as suggested by Lyons et al. (2014). Second order habitat selection was assessed using the 95% isopleth (considered to represent the full extent of the
ii) Habitat selection at the landscape scale (2nd order selection)

Habitat selection at the landscape scale was investigated by comparing habitat use in individual eland home ranges to the availability of habitat types across each reserve. Proportional use of each habitat type was assessed using the broad scale GPS data (6 hour GPS collar schedule) from each collared eland in their respective home ranges. The proportional use of a habitat type was calculated as the number of GPS locations in each habitat type, divided by the total number of GPS locations in the home range. The proportional representation of each habitat type in eland home ranges in both reserves was calculated across seasons and over the full study period. Chi-square tests were conducted (per eland) to test the hypothesis that eland use habitat types in proportion to their availability across the reserve (Neu et al. 1974). Chi-square tests require that no more than 20% of all observations are less than five (Dixon & Massey 1969). Given that this restriction was not adhered to in MZNP due to the very low proportion of dense habitat available in the reserve, log likelihood Ratio tests (G tests) were used to test whether eland habitat use was proportional to availability in the reserve (Zar 1984). These tests however do not indicate which habitats are used more or less than the relative availability.

The degree of selection, or lack thereof, for each habitat type was assessed by calculating 95% confidence intervals surrounding the proportion of use for each habitat type (Neu et al. 1974) and comparing this range to habitat availability in each individual eland home range. The degree of overlap, or lack thereof, can be considered as a test for the significance of the selection or avoidance. Where there is no overlap between the availability and the 95% confidence intervals the habitat type is considered to be significantly selected or avoided (Landman et al. 2008).

2.2.7.2) Home range scale analyses (3rd order selection)

i) Covariates of third order habitat selection

Eland habitat selection at the third order was explored in relation to landscape, habitat and predator covariates. Covariates were selected based on previous studies that investigated, i) habitat selection of ungulates (White et al. 2009; Baigas et al. 2011) and, ii) lion ecology and hunting success (Funston et al. 2001; Hopcroft et al. 2005; Hayward & Hayward 2006). The covariates included in the models encompassed variation in landscape features and variation in predation risk across the landscape that may influence eland habitat selection. Time of day is known to influence habitat selection given that predators may be more active at night than during the day (Mills & Biggs 1993). All GPS location points were categorised as being recorded during the night or day based on ecological sunset and sunrise times over the duration of the study period (Nouvellet et al. 2011). Ecological sunset is defined as the time at which the sun has sunk sufficiently below the horizon and it is functionally
dark. Similarly, ecological sunrise is the time at which the sun has risen sufficiently, yet not necessarily above the horizon, to effectively illuminate the environment (Nouvellet et al. 2011). GPS points recorded during the day and night, respectively, were used to estimate time-specific (i.e. day and night) home ranges for each eland in each reserve using the alpha-LoCoH method (as described in section 2.2.3.1i). Thus for this analysis, covariate values were extracted from GPS locations within day and night home ranges (i.e. 95% isopleths) of each eland separately.

**a) Habitat and topographic covariates**

Altitude, slope, ruggedness, distance to tourist roads and habitat type were included in *a priori* models to investigate third order selection of eland. A 25 m digital elevation model (DEM, Eastern Cape Parks and Tourism) for each reserve was used to extract topographical features (altitude, slope and ruggedness) across both reserves. Roads may provide a disturbance through the presence of traffic that create noise, light and chemical disturbances (Jaeger et al. 2005). Roads were classified as either tourist roads (open access with high-density of use) or management roads (restricted access with low density of use) as the intensity of use is known to affect the level of disturbance, and thus the behavioural responses a road evokes in animals (Leblond et al. 2012). Management roads were not included in the analyses as the potential disturbance provided by these low density roads was considered to be negligible. For each reserve, the Euclidean distance from tourist roads to each GPS location was calculated in ArcGIS 10.1 using the “near” spatial analyst tool. The habitat type at each point was extracted from the habitat structure maps (described in section 2.2.3.1ii). Distance to water is commonly included in resource selection function models, particularly in an African context where it has been found to influence the level of predation risk and therefore prey distribution and behaviour (Valeix et al. 2009; de Boer et al. 2010; Davidson et al. 2012). In this study however, the availability of surface water across the landscape could not be accurately quantified. In Nyathi and MZNP, rivers are subject to seasonal changes such that at times of the year they may be flowing, whilst in drier months, isolated pools of water may occur along the rivers’ course (personal observation). The spatial and temporal variation in the presence of water in these rivers, as well as in natural ephemeral water holes observed in both reserves, was such that water availability throughout the study period could not be accurately measured. Distance to water was thus not included in the analysis of third order habitat selection. Furthermore, eland are water-independent (King et al. 1975), so that water is not expected to be a defining factor driving eland habitat selection.

**b) Long-term predation risk**

The risk of predation influences prey habitat selection (Brown 1999; Dussault et al. 2005; Valeix et al. 2009; Thaker et al. 2011; Tambling et al. 2012a). Lion movement across the landscape results in predation risk that is spatially variable. To incorporate predation risk into eland resource selection models, long-term predation risk was estimated from lion GPS data collected over the duration of
the study. The long-term predation risk index is proportional to the probability of a lion being present at a location (following Valeix *et al.* 2009). Predation risk for male and female lions was assessed separately because male and female lions were shown to move independently on the landscape. Furthermore, male and female lions have different hunting behaviours (Funston *et al.* 2001; Loarie *et al.* 2013). Given that prey responses to predation risk are affected by the hunting mode of the predator (Preisser *et al.* 2007), differences in hunting behaviour between male and female lion may result in gender-specific responses to lion predation risk. Consecutive 10% kernel isopleths were developed using the a-LoCoH methods (as described in section 2.2.3.1i). The probability of lion presence was thereafter calculated as $0.10 / (A_i - A_{i-1})$; where $A_i$ is the area covered by isopleth $i$ with 0.10 representing 10% bands of locations between consecutive isopleths (Valeix *et al.* 2009). The relative probability of lion presence in each isopleth band was calculated by dividing the value indicating lion probability of presence in each isopleth band by the summed total of lion probability of presence across all isopleth bands. Isopleths of male and female lions from each reserve were then converted to a raster layer using ArcGIS 10.1 with each ten percent isopleth associated with a relative probability of lion presence. The spatial variation in predation risk was thus quantified and ranked from 1, representing the 100% isopleth band and lowest probability of lion presence, to 10, representing the 10% isopleth band and the highest probability of lion presence.

c) **Temporal autocorrelation and collinearity of location data**

The collection of fine scale GPS data may result in temporally autocorrelated covariates where attributes at an eland’s current location are not independent of its location at the previous GPS point (Zuur *et al.* 2009). To check the data for temporal autocorrelation, GPS data in each reserve were sorted by date and time (oldest to newest) for each eland individual. The data was then offset such that values for each predictor variable at time $t$ could be correlated to values at time $t + 1$. The value of each covariate at each GPS location was thus regressed against the corresponding covariate value at its nearest neighbour (Winnie *et al.* 2008).

Explanatory variables were checked for collinearity in each reserve separately, with data from eland in each reserve pooled. Pairwise correlations between explanatory variables in each reserve were conducted using Spearman rank correlation tests. Pairs of variables were considered collinear if the correlation coefficient was greater than 0.7 or smaller than -0.7 (Girard *et al.* 2013). In order to deal with highly collinear explanatory variables, one variable was removed such that remaining explanatory variables were not subject to collinearity (Booth *et al.* 1994). The variable retained was selected based on its ecological relevance as shown by previous studies investigating ungulate habitat selection (Zuur *et al.* 2009).
ii) Resource selection functions at the third-order

Resource selection functions (RSFs) quantify how animals select areas of the landscape (Manly et al. 2002). A type III study design (Manly et al. 2002) was used where selection of used vs. available resources was investigated in each reserve. Resource use, estimated from eland GPS locations, was compared to resource availability in eland home ranges using logistic regression models to develop RSFs (Boyce & McDonald 1999; Manly et al. 2002) at the home range scale.

Because time of day was included as a covariate, use and availability were characterised independently for day and night home ranges of each individual eland (as described in section 2.2.7.2i). Eland GPS locations in the bounds of the 95% isopleths for day and night respectively (i.e. day and night home range extent) were used to represent resource use. Similarly, availability was represented by randomly generated points using the ‘create random point’ data management tool in ArcGIS 10.1, equal to the number of eland GPS locations in each home range, for each eland. Corresponding habitat, topographic and predation risk data were then extracted for eland GPS locations and randomly generated points in each eland day and night home range in ArcGIS 10.1.

Generalised linear mixed models (GLMMs) with a binomial distribution and logit link were fitted to identify the most influential drivers of resource use by eland across both reserves (combined data from all collared eland; n = 7), and in each reserve independently. For the RSFs of all eland (n = 7) from both reserves (n = 2), eland individual and reserve were set as random effects, whilst at the reserve-level, eland individual (Nyathi: n = 4; MZNP: n = 3) was included as a random effect. A binary response variable ‘State’, consisting of used (eland GPS points; state = 1) and available (randomly generated points; state = 0) locations, was assessed in relation to a candidate suite of a priori models (Burnham & Anderson 2002), consisting of a total of 46 models (Appendix 1). The list of ecologically relevant models that could have been compiled was extensive, however, candidate models fitted were restricted to those explained by hypotheses developed through field observation, and those that were justified and supported based on previous habitat selection studies. Mixed effects RSF models had the form;

\[ w(X) = \exp (\beta_1 x_1 + \ldots + \beta_n x_n + Y_j + Y_k) \]

where \( w(X) \) is the relative probability of use by eland, \( \beta_n \) is the estimated selection coefficient for covariate \( x_n \), \( Y_j \) is the random intercept for eland \( j \) and \( Y_k \) is the random intercept for reserve \( k \). When \( \beta_n > 0 \), eland selection occurred, i.e. use was more than would be expected if used in proportion to availability, whilst when \( \beta_n < 0 \), eland avoided a covariate given the availability of the resource (Zuur et al. 2009). Before running the candidate set of models, variance inflation factors (VIFs) were examined to assess the extent of any remaining collinearity between the explanatory variables. VIFs were examined by fitting a generalised linear model with binomial response and logit link function to the used/available response variable ‘State’, i.e. a logistic regression model,
containing all explanatory variables (Zuur et al. 2009). VIFs were then calculated for each variable from the resulting model with VIF values of <2 indicating that collinearity between explanatory variables is negligible (Neter et al. 1990).

iii) Model selection

Model strength was assessed using Akaike’s Information Criterion (AIC), where alternative candidate models were compared and the most parsimonious model identified (Burnham & Anderson 2002). Model strength was estimated using:

$$\text{AIC} = -2L + 2K,$$

where $L$ is the log-likelihood of the model and $K$ is the number of parameters in the models (Akaike 1973). Candidate models were fitted to the data and then ranked based on their AIC scores, with lower AIC scores indicating a higher degree of parsimony i.e. stronger support for the model. The relative probability of each model being the best model was calculated using Akaike weights ($w_i$) which is the relative likelihood of model $i$ divided by the sum of likelihoods of each of the $a$ priori models. Akaike weight for model $i$ is thus defined as;

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{j=1}^{R} \exp\left(-\frac{1}{2}\Delta_j\right)}.$$  

where $\Delta_i$ is the difference between the AIC for model $i$ and the model with the lowest AIC value and the sum is over all the candidate models in the set $j = 1, \ldots, R$ (Zuur et al. 2009). Where the $w_i$ of the top ranked model was different from 1.0, model uncertainty (wherein no single model was shown to be more likely to be the best model among competing models), was acknowledged (Burnham & Anderson 2002). Each set of analyses for this study (i.e. for the combined data and each reserve independently) exhibited model uncertainty. In such cases, it is recommended that ecological interpretations from model outcomes are based on the top set of models, selected based on $w_i$, rather than the top-ranked model alone (Burnham & Anderson 2002). A 95% confidence set of models was thus constructed by adding consecutive $w_i$ starting with the model with the highest $w_i$ until the cumulative Akaike weight exceeded 0.95 (Burnham & Anderson 2002). Clear interpretation of a number of top competing models is challenging (Galipaud et al. 2014), thus a single consensus model was built, averaging the predictor variables present in the 95% confidence set of models and their effect size (Burnham & Anderson 2002). Model averaging allows coefficients to be estimated and model predictions to be made that consider the inherent uncertainty in the models and the parameters (Zuur et al. 2009). Model averaged coefficients were assessed where model uncertainty occurred. Akaike weights were also used to calculate the relative importance of individual parameters i.e. the probability that a given parameter appears in the best model, by summing Akaike weights of models that included that parameter (Burnham & Anderson 2002).
For each candidate model fitted to the data, the AIC value, Akaike weight and model rank were computed, and a 95 percent confidence set of models identified. Model selection and model averaging were conducted using the ‘AICcmodavg’ package (Mazerolle 2013). Model averaged coefficients with shrinkage were used as this accounts for potential inflation of less important variables that may occur through the model averaging process (Mazerolle 2013). From model averaged coefficient estimates, the probability of eland presence was predicted relative to the range of each significant explanatory variable while holding all others at their mean, using the ‘predict’ function in the ‘AICcmodavg’ package (Mazerolle 2013). Probability of presence graphs created in this way aided in determining which statistically significant variables were ecologically relevant. All statistical analyses were conducted in R version 3.0.1 (R Development Core Team 2014).

iv) Adding raw data to modelled predictions of eland presence plots

Raw data were plotted to accompany the modelled probability of eland presence in relation to variables found to significantly influence the model. Raw data were binned into categories, defined by the range of the explanatory variable. The proportion of used points (i.e. eland GPS locations) relative to the total number of points (used sites plus available sites) in each binned category was plotted, with binomial confidence limits. This assisted in evaluating the biological significance of the modelled variables.

2.3. Results

2.3.1) Eland telemetry data

A total of 4718 and 4359 telemetry locations were acquired from collared adult female eland in Nyathi (n = 4) and MZNP (n = 3) on a six hour interval schedule, respectively, with a pooled total of 9077 locations acquired in both reserves. Collars recorded an average of 1180 fixes (range: 290 – 1481 locations) in Nyathi (n = 4) and 1453 (range: 1428 – 1470 locations) in MZNP (n = 3). Fix success of the collars in Nyathi was 91% and 95% in MZNP. All collars were operational for the full study period except for NF4 which collected data for only 4 months, as the eland carrying the collar was killed by lions in October 2013 (Table 2.1).
Table 2.1 Durations of operation of GPS collars used for the second and third order habitat selection analyses and details of social groups that each collared animal represents.

<table>
<thead>
<tr>
<th>Reserve</th>
<th>GPS collar (name)</th>
<th>Demographics/ herd size</th>
<th>Period spanned</th>
<th>Duration (months)</th>
<th>Number of GPS fixes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nyathi</td>
<td>Sat549 (NF1)</td>
<td>Mixed adult, 16-30</td>
<td>15/03/2013-06/05/2014</td>
<td>15</td>
<td>1467</td>
</tr>
<tr>
<td></td>
<td>Sat552 (NF2)</td>
<td>Breeding, ~56</td>
<td>15/03/2013-06/05/2014</td>
<td>15</td>
<td>1481</td>
</tr>
<tr>
<td></td>
<td>Sat553 (NF3)</td>
<td>Breeding, ~50</td>
<td>15/03/2013-06/05/2014</td>
<td>15</td>
<td>1480</td>
</tr>
<tr>
<td></td>
<td>Sat878 (NF4)</td>
<td>Breeding, ~20</td>
<td>12/07/2013-01/10/2013</td>
<td>4</td>
<td>290*</td>
</tr>
<tr>
<td>MZNP</td>
<td>Sat786 (MF1)</td>
<td>Breeding, ~90</td>
<td>16/05/2013-06/05/2014</td>
<td>13</td>
<td>1470</td>
</tr>
<tr>
<td></td>
<td>Sat787 (MF2)</td>
<td>Breeding, ~45</td>
<td>16/05/2013-06/05/2014</td>
<td>13</td>
<td>1461</td>
</tr>
<tr>
<td></td>
<td>Sat788 (MF3)</td>
<td>Mixed adult/ Breeding, ~10</td>
<td>16/05/2014-28/04/2014</td>
<td>12</td>
<td>1428</td>
</tr>
</tbody>
</table>

TOTAL: 9077

* Killed by lions in October 2013 (4 months after collaring)

2.3.2) Landscape scale habitat selection

2.3.2.1. Home range selection in Nyathi and MZNP

The average home range size of the four collared eland in Nyathi was $12 \pm 1.9 \text{ km}^2$ (Table 2.2). Relative to the reserve size ($140 \text{ km}^2$), average eland home ranges covered 6 – 11% of the reserve. Average core areas were $3 \pm 0.4 \text{ km}^2$ (Table 2.2). Three of the herds associated with collared individuals (NF1, NF2 and NF3) occupied adjacent and largely overlapping home ranges in the southwestern part of the reserve. Due to the close association between NF2 and NF3, where the two collared individuals were frequently observed in a single herd, home range and core use areas for these two groups overlapped considerably (Fig. 2.7). The herd with which NF1 was associated occupied a home range largely overlapping that of NF2 and NF3, however the core use areas were to the south of core use areas of NF2 and NF3. The fourth herd represented by a collared individual (NF4) occupied a home range to the east of the other monitored herds (Fig. 2.7). The home range size for this individual was smaller ($6 \text{ km}^2$) than that of the other three collared eland (mean home range of NF1, NF2 and NF3 = $14 \text{ km}^2$). This is likely due to a shorter sampling period (4 months of data collection for NF4 compared to 15 months for NF1, NF2 and NF3).

Season did not influence the position of eland home ranges in Nyathi (Appendix 2). Home range sizes also remained similar between the wet and the dry season ($14 \pm 0.3 \text{ km}^2$ vs. $12 \pm 0.5 \text{ km}^2$, Table 2.2) with a slight increase in home range size in the wet season. The sample size ($n = 3$ for each season) was however inadequate to statistically analyse variation in home range size between seasons.
The average home range size of the three collared eland in MZNP was $74 \pm 5.8 \text{ km}^2$ with core areas occupying an average size of $17 \pm 2.8 \text{ km}^2$ (Table 2.2). Average home ranges of eland in MZNP covered 23 – 30% of the reserve (280 km$^2$). Herds with which collared eland were associated in MZNP occupied significantly larger areas than in Nyathi at both the home range ($12 \text{ km}^2$ vs. $74 \text{ km}^2$, $t = 10.12$, df = 2, $p < 0.01$) and core level ($3 \text{ km}^2$ vs. $17 \text{ km}^2$, $t = 4.94$, df = 2, $p < 0.05$). Home ranges of collared eland in MZNP extended across the northern portion of the reserve and overlapped considerably (Fig. 2.8). Core areas of MF1 and MF2 were similar due to these individuals associating closely and often being found in a single large herd (Personal observation). The smaller herd associated with MF3 occupied a core use area in the central part of the reserve, as opposed to the core areas of MF1 and MF2 which occurred in the north-western and eastern parts of the reserve (Fig. 2.8). None of the eland herds with which a collared individual was associated in MZNP utilised the southern portion of the reserve.

**Fig. 2.7** Home range and core areas of the four collared eland in Nyathi based on the duration and number of GPS fixes shown in Table 2.1.
Among individual eland, wet season home ranges occurred predominantly in the north-western portion of the reserve whereas dry season home ranges occurred in the eastern and central parts of the reserve (Appendix 3). As such, seasonal variation appeared to influence the position of home ranges in MZNP. The average size of eland home ranges was larger than average home range size in the dry season (65 ± 6 km$^2$ vs. 35 ± 3 km$^2$, Table 2.2), however the sample size was insufficient to analyse this variation statistically.

Fig. 2.8 Home range and core areas of the three collared eland in Mountain Zebra National Park (MZNP) based on the duration and number of GPS fixes shown in Table 2.1.
Table 2.2 Individual and mean (± SE) home range (95% UD) and core area extents (50% UD) of collared eland in Nyathi (km²) and Mountain Zebra National Park (km²) estimated using a LoCoH over the full study period and per season.

<table>
<thead>
<tr>
<th>Reserve</th>
<th>Eland ID</th>
<th>95% isopleth</th>
<th>50% isopleth</th>
<th>95% isopleth</th>
<th>95% isopleth</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td><strong>Full study period</strong></td>
<td><strong>Wet season</strong></td>
<td><strong>Dry season</strong></td>
<td></td>
</tr>
<tr>
<td>Nyathi</td>
<td>NF1</td>
<td>13</td>
<td>4</td>
<td>14</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td>NF2</td>
<td>14</td>
<td>3</td>
<td>15</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td>NF3</td>
<td>14</td>
<td>3</td>
<td>14</td>
<td>13</td>
</tr>
<tr>
<td></td>
<td>NF4</td>
<td>6</td>
<td>2</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>Mean (± SE)</td>
<td>12 (± 1.9)</td>
<td>3 (± 0.4)</td>
<td>14 (± 0.3)*</td>
<td>12 (± 0.5)*</td>
<td></td>
</tr>
<tr>
<td>MZNP</td>
<td>MF1</td>
<td>85</td>
<td>21</td>
<td>73</td>
<td>29</td>
</tr>
<tr>
<td></td>
<td>MF2</td>
<td>66</td>
<td>18</td>
<td>52</td>
<td>39</td>
</tr>
<tr>
<td></td>
<td>MF3</td>
<td>71</td>
<td>11</td>
<td>60</td>
<td>38</td>
</tr>
<tr>
<td>Mean (± SE)</td>
<td>74 (± 5.8)</td>
<td>17 (± 2.8)</td>
<td>62 (± 5.9)</td>
<td>35 (± 3.2)</td>
<td></td>
</tr>
</tbody>
</table>

*Mean seasonal home ranges calculated from NF1, NF2 and NF3 as NF4 was killed by lions after a single season

2.3.2.2) Habitat use and availability at the landscape scale

Eland habitat use in their home ranges in Nyathi differed significantly from habitat availability across the reserve ($\chi^2 = 69.11$, df = 2, $p < 0.01$). Use of habitat types by eland in Nyathi at the second order (landscape scale) was dominated by open habitat types, with dense areas representing the smallest proportion of used habitat types (Table 2.3). Open habitats were used more than three times as much as expected from availability, and dense habitats were utilized up to three times less than expected from availability. Mixed habitat types were significantly preferred by all eland except NF4 (Fig. 2.9d), which avoided mixed habitats. Habitat use was not influenced by season in Nyathi, with the relative proportion of habitat types within the wet and dry season home range remaining consistent (Table 2.3).

Table 2.3 Proportion of habitat type availability in Nyathi and Mountain Zebra National Park (MZNP) and mean proportion of use in eland home range over the full study period, the wet season and the dry season.

<table>
<thead>
<tr>
<th>Reserve</th>
<th>Habitat</th>
<th>Availability Across reserve</th>
<th>Use Overall</th>
<th>Wet</th>
<th>Dry</th>
</tr>
</thead>
<tbody>
<tr>
<td>NYATHI</td>
<td>Open</td>
<td>0.14</td>
<td>0.60</td>
<td>0.62 (± 0.04)</td>
<td>0.61 (± 0.05)</td>
</tr>
<tr>
<td></td>
<td>Mixed</td>
<td>0.17</td>
<td>0.26</td>
<td>0.28 (± 0.02)</td>
<td>0.27 (± 0.06)</td>
</tr>
<tr>
<td></td>
<td>Dense</td>
<td>0.69</td>
<td>0.13</td>
<td>0.10 (± 0.01)</td>
<td>0.12 (± 0.01)</td>
</tr>
<tr>
<td>MZNP</td>
<td>Open</td>
<td>0.58</td>
<td>0.54</td>
<td>0.53 (± 0.07)</td>
<td>0.54 (± 0.06)</td>
</tr>
<tr>
<td></td>
<td>Mixed</td>
<td>0.40</td>
<td>0.45</td>
<td>0.46 (± 0.08)</td>
<td>0.45 (± 0.07)</td>
</tr>
<tr>
<td></td>
<td>Dense</td>
<td>0.02</td>
<td>0.01</td>
<td>0.01 (± 0.01)</td>
<td>0.01 (± 0.01)</td>
</tr>
</tbody>
</table>
Fig. 2.9 Standardized (proportion occurrence - proportion habitat available) pattern of habitat use by a) NF1, b) NF2, c) NF3 and d) NF4 indicating habitat significantly preferred (*p) or significantly avoided (*a). Error bars represent 95% confidence intervals.

Use of the different habitat types in eland home ranges in MZNP did not differ significantly from available habitat types across the reserve (G = 0.984, df = 2, p = 0.611). Despite the observed change in home range size and shift in location between the wet and dry season in MZNP, the representation of habitat types within eland home ranges did not change between seasons (Table 2.3).

2.3.3) Home range scale habitat selection

2.3.3.1. Long-term predation risk in Nyathi and MZNP

Lion activity in Nyathi was concentrated along the southern boundary of the reserve with considerable overlap between female and male lion space use in this area (Fig. 2.10). Male lions, and not the female lion, used the eastern part of Nyathi (Fig. 2.10). The probability of encountering a lion generally increased as the isopleth level decreased (i.e. areas of higher use), however, where a step-wise decrease in probability is not observed, this is due to isopleths not necessarily decreasing incrementally in size at each consecutive isopleth (Table 2.4). In the 10% isopleth (referenced by an index score of 10) of the male lion home range i.e. the area associated with the highest risk...
(indicated in red), the probability of encountering a male lion was measured as 0.48, whereas for the female lion in Nyathi, the highest risk areas were associated with a 0.36 probability of encounter (Table 2.4). High risk areas of encountering male lions were localised to a small area along the southern boundary of the reserve (Fig. 2.10a), whereas high risk areas of the female lion were found in four discreet areas in the south western corner of the reserve (Fig. 2.10b).

![Map showing the landscape of long-term predation risk of a) the male lions and b) the female lion in Nyathi. The ten levels represent 10% isopleth bands. Warm colours indicate high probability of lion presence.](image)

**Fig. 2.10** Map showing the landscape of long-term predation risk of a) the male lions and b) the female lion in Nyathi. The ten levels represent 10% isopleth bands. Warm colours indicate high probability of lion presence.
Table 2.4 Probability of lion presence represented by 10% isopleths of male and female lion in Nyathi graphically depicted in Fig. 2.4.

<table>
<thead>
<tr>
<th>Risk level</th>
<th>Isopleth level (%)</th>
<th>Male probability of presence</th>
<th>Female probability of presence</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>100</td>
<td>0.004</td>
<td>0.004</td>
</tr>
<tr>
<td>2</td>
<td>90</td>
<td>0.013</td>
<td>0.013</td>
</tr>
<tr>
<td>3</td>
<td>80</td>
<td>0.025</td>
<td>0.019</td>
</tr>
<tr>
<td>4</td>
<td>70</td>
<td>0.033</td>
<td>0.024</td>
</tr>
<tr>
<td>5</td>
<td>60</td>
<td>0.030</td>
<td>0.037</td>
</tr>
<tr>
<td>6</td>
<td>50</td>
<td>0.048</td>
<td>0.050</td>
</tr>
<tr>
<td>7</td>
<td>40</td>
<td>0.059</td>
<td>0.054</td>
</tr>
<tr>
<td>8</td>
<td>30</td>
<td>0.100</td>
<td>0.153</td>
</tr>
<tr>
<td>9</td>
<td>20</td>
<td>0.199</td>
<td>0.291</td>
</tr>
<tr>
<td>10</td>
<td>10</td>
<td>0.488</td>
<td>0.356</td>
</tr>
</tbody>
</table>

In MZNP, probabilities of eland encountering a lion on the landscape were lower than in Nyathi (Table 2.5). High risk areas of encountering male lions were located along a narrow strip in the central region of the reserve (Fig. 2.11a). In these areas, probability of encountering male lions was estimated to be 0.295 (Table 2.5). Male lions did not use the northern-most part of the reserve, or the area along the south eastern boundary. The highest probability of encountering the female lion was estimated at 0.345, with discreet patches of high risk areas distributed across the central and north-eastern portions of the reserve (Fig. 2.11b).

Fig. 2.11 Map showing the landscape of long-term predation risk of a) male and b) female lion in Mountain Zebra National Park (MZNP). The ten levels represent 10% isopleths. Warm colours indicate high probability of lion presence.
Table 2.5 Probability of lion presence represented by 10% isopleths of male and female lion in Mountain Zebra National Park.

<table>
<thead>
<tr>
<th>Risk level</th>
<th>Isopleth level (%)</th>
<th>Male probability of presence</th>
<th>Female probability of presence</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>100</td>
<td>0.005</td>
<td>0.009</td>
</tr>
<tr>
<td>2</td>
<td>90</td>
<td>0.012</td>
<td>0.027</td>
</tr>
<tr>
<td>3</td>
<td>80</td>
<td>0.024</td>
<td>0.049</td>
</tr>
<tr>
<td>4</td>
<td>70</td>
<td>0.039</td>
<td>0.041</td>
</tr>
<tr>
<td>5</td>
<td>60</td>
<td>0.050</td>
<td>0.060</td>
</tr>
<tr>
<td>6</td>
<td>50</td>
<td>0.113</td>
<td>0.106</td>
</tr>
<tr>
<td>7</td>
<td>40</td>
<td>0.085</td>
<td>0.081</td>
</tr>
<tr>
<td>8</td>
<td>30</td>
<td>0.103</td>
<td>0.140</td>
</tr>
<tr>
<td>9</td>
<td>20</td>
<td>0.274</td>
<td>0.142</td>
</tr>
<tr>
<td>10</td>
<td>10</td>
<td>0.295</td>
<td>0.345</td>
</tr>
</tbody>
</table>

2.3.3.2. Resource selection functions models

i) Temporal autocorrelation of GPS data and covariate collinearity

Eland GPS data were not temporally autocorrelated for all of the tested covariates (r < 0.4 for all variables at a single lagged time-step). Therefore, the 6 hour interval between locations was sufficient to ensure independence between successive locations. In Nyathi, distance to the single tourist road in the reserve was temporally autocorrelated (r > 0.9) for eland NF4. Distance to the tourist road for each location was measured as the straight-line distance (in meters) to the single (high activity) tourist road that exists in the reserve. NF4 remained far from this road, whereas locations for NF1, NF2 and NF3 were in an area surrounding the road. Given the low level of temporal autocorrelation associated with this parameter for NF1, NF2 and NF3 (Appendix 4), as well as field based observations indicting that the tourist road would not be a strong disturbance factor affecting eland habitat selection, the correlation associated with NF4 was not assumed to affect model results.

All pair-wise correlations of explanatory variables resulted in Spearman rank correlation coefficients indicating low magnitudes of collinearity except for the correlation between ruggedness and slope which produced a correlation coefficient of <0.7. For these analyses, ruggedness was retained as it has been shown to influence habitat selection of prey species (Sappington et al. 2007).
Table 2.6 Generalised linear mixed effects models for the probability of eland presence assessed using data from Nyathi and MZNP with eland individual (n=7) and reserve (n=2) set as random effects. The top 95% confidence set of models are shown with the number of parameters (K), Akaike’s Information Criterion (AICc), change in Akaike’s Information Criterion (ΔAICc), and model weight (ωi). Cumulative ωi of top models equals 0.99. The estimated coefficients are given, with standard errors (SE). Values in bold indicate a p-value < 0.05. Model averaged coefficients (with shrinkage) (±SE) and relative variable importance calculated from the 95% confidence set of models are shown.

<table>
<thead>
<tr>
<th>Model</th>
<th>k</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>ωi</th>
<th>Male risk (SE)</th>
<th>Female risk (SE)</th>
<th>Dense (SE)</th>
<th>Open (SE)</th>
<th>Ruggedness (SE)</th>
<th>Time (Night) (SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male risk + Female risk + Open + Dense</td>
<td>7</td>
<td>23624.36</td>
<td>0</td>
<td>0.41</td>
<td><strong>-0.106</strong> (0.010)</td>
<td><strong>0.025</strong> (0.007)</td>
<td><strong>-0.859</strong> (0.060)</td>
<td><strong>0.224</strong> (0.033)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male risk + Female risk + Open + Dense + Ruggedness</td>
<td>8</td>
<td>23624.93</td>
<td>0.57</td>
<td>0.29</td>
<td><strong>-0.107</strong> (0.010)</td>
<td><strong>0.025</strong> (0.007)</td>
<td><strong>-0.858</strong> (0.060)</td>
<td><strong>0.216</strong> (0.034)</td>
<td>-0.001 (0.001)</td>
<td></td>
</tr>
<tr>
<td>Male risk + Female risk + Open + Dense + Time</td>
<td>8</td>
<td>23626.69</td>
<td>1.72</td>
<td>0.17</td>
<td><strong>-0.106</strong> (0.010)</td>
<td><strong>0.025</strong> (0.007)</td>
<td><strong>-0.860</strong> (0.060)</td>
<td><strong>0.225</strong> (0.033)</td>
<td>-0.018 (0.033)</td>
<td></td>
</tr>
<tr>
<td>Male risk + Female risk + Open + Dense + Ruggedness + Time</td>
<td>9</td>
<td>23626.69</td>
<td>2.33</td>
<td>0.12</td>
<td><strong>-0.107</strong> (0.010)</td>
<td><strong>0.024</strong> (0.007)</td>
<td><strong>-0.859</strong> (0.060)</td>
<td><strong>0.217</strong> (0.034)</td>
<td>-0.001 (0.001)</td>
<td>-0.017 (0.034)</td>
</tr>
<tr>
<td>Model averaged coefficients (with shrinkage)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td><strong>-0.106</strong> (0.010)</td>
<td><strong>0.025</strong> (0.007)</td>
<td><strong>-0.859</strong> (0.060)</td>
<td><strong>0.221</strong> (0.034)</td>
<td>-0.001 (0.001)</td>
<td>-0.005 (0.607)</td>
</tr>
<tr>
<td>Relative variable importance</td>
<td></td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0.43</td>
<td>0.3</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 2.7 Generalised linear mixed effects models for the probability of eland presence in Nyathi with eland individual (n=4) set as random effect. The top 95% confidence set of models are shown with the number of parameters ($K$), Akaike’s Information Criterion ($AIC_c$), change in Akaike’s Information Criterion ($\Delta AIC_c$), and model weight ($\omega_i$). Cumulative $\omega_i$ of top models equals 1.0. The estimated coefficients are given with standard errors (SE). Values in bold indicate a p-value < 0.05. Model averaged coefficients (with shrinkage) (±SE) and relative variable importance calculated from the 95% confidence set of models are shown.

<table>
<thead>
<tr>
<th>Model</th>
<th>$k$</th>
<th>$AIC_c$</th>
<th>$\Delta AIC$</th>
<th>$\omega_i$</th>
<th>Male risk</th>
<th>Female risk</th>
<th>Dense</th>
<th>Open</th>
<th>Ruggedness</th>
<th>Time (Night)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male risk + Dense + Open + Time</td>
<td>6</td>
<td>11957.85</td>
<td>0</td>
<td>0.22</td>
<td>-0.128</td>
<td>-0.652</td>
<td>0.737</td>
<td>-0.081</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(0.013)</td>
<td>(0.064)</td>
<td>(0.050)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male risk + Dense + Open + Ruggedness + Time</td>
<td>7</td>
<td>11977.92</td>
<td>0.42</td>
<td>0.18</td>
<td>-0.123</td>
<td>-0.671</td>
<td>0.752</td>
<td>-0.004</td>
<td>-0.082</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(0.014)</td>
<td>(0.066)</td>
<td>(0.051)</td>
<td>(0.003)</td>
<td>(0.046)</td>
<td></td>
</tr>
<tr>
<td>Male risk + Dense + Open</td>
<td>5</td>
<td>11978.58</td>
<td>1.09</td>
<td>0.13</td>
<td>-0.127</td>
<td>-0.649</td>
<td>0.732</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(0.013)</td>
<td>(0.064)</td>
<td>(0.05)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male risk + Female risk + Dense + Open + Time</td>
<td>7</td>
<td>11978.61</td>
<td>1.12</td>
<td>0.12</td>
<td>-0.133</td>
<td>0.009</td>
<td>-0.643</td>
<td>0.743</td>
<td>-0.079</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(0.014)</td>
<td>(0.009)</td>
<td>(0.065)</td>
<td>(0.050)</td>
<td>(0.046)</td>
<td></td>
</tr>
<tr>
<td>Male risk + Female risk + Dense + Open + Ruggedness + Time</td>
<td>8</td>
<td>11978.82</td>
<td>1.33</td>
<td>0.11</td>
<td>-0.128</td>
<td>0.010</td>
<td>-0.662</td>
<td>0.760</td>
<td>0.005</td>
<td>-0.080</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(0.014)</td>
<td>(0.009)</td>
<td>(0.066)</td>
<td>(0.052)</td>
<td>(0.003)</td>
<td>(0.046)</td>
</tr>
<tr>
<td>Male risk + Dense + Open + Ruggedness</td>
<td>6</td>
<td>11979.11</td>
<td>1.62</td>
<td>0.1</td>
<td>-0.122</td>
<td>-0.667</td>
<td>0.747</td>
<td>0.004</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(0.014)</td>
<td>(0.065)</td>
<td>(0.051)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male risk + Female risk + Open + Dense</td>
<td>6</td>
<td>11979.53</td>
<td>2.03</td>
<td>0.08</td>
<td>-0.132</td>
<td>0.009</td>
<td>-0.640</td>
<td>0.739</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(0.014)</td>
<td>(0.009)</td>
<td>(0.065)</td>
<td>(0.050)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male risk + Female risk + Dense + Open + Ruggedness</td>
<td>7</td>
<td>11979.84</td>
<td>2.34</td>
<td>0.07</td>
<td>-0.128</td>
<td>0.010</td>
<td>-0.658</td>
<td>0.756</td>
<td>0.004</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(0.014)</td>
<td>(0.009)</td>
<td>(0.066)</td>
<td>(0.052)</td>
<td>(0.003)</td>
<td></td>
</tr>
</tbody>
</table>

Model averaged coefficients (with shrinkage)

|                           | 1   | 0.38   | 1 | 1   | 0.45 | 0.63 |

Relative variable importance
Table 2.8 Generalised linear mixed effects models for the probability of eland presence in Mountain Zebra National Park (MZNP) with eland individual (n=3) set as random effect. The top 95% confidence set of models are shown with the number of parameters (K), Akaike’s Information Criterion (AICc), change in Akaike’s Information Criterion (ΔAICc), and model weight (ω). Cumulative ω of top models equals 0.98. The estimated coefficients are given with standard errors (SE). Values in bold indicate p-value < 0.05. Model averaged coefficients (with shrinkage) (±SE) and relative variable importance calculated from the 95% confidence set of models are shown.

<table>
<thead>
<tr>
<th>Model</th>
<th>k</th>
<th>AICc</th>
<th>ΔAIC</th>
<th>ω</th>
<th>Male risk</th>
<th>Female risk</th>
<th>Dense</th>
<th>Open</th>
<th>Mixed</th>
<th>Ruggedness</th>
<th>Time (Night)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male risk + Female risk + Dense + Open + Ruggedness</td>
<td>7</td>
<td>11414.97</td>
<td>0</td>
<td>0.48</td>
<td>-0.132 (0.014)</td>
<td>0.049 (0.014)</td>
<td>-0.411 (0.235)</td>
<td>-0.223 (0.048)</td>
<td>-0.003 (0.001)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male risk + Female risk + Dense + Open + Ruggedness + Time day</td>
<td>8</td>
<td>11416.84</td>
<td>1.87</td>
<td>0.19</td>
<td>-0.132 (0.014)</td>
<td>0.049 (0.014)</td>
<td>-0.409 (0.235)</td>
<td>-0.223 (0.048)</td>
<td>-0.003 (0.001)</td>
<td>0.018 (0.050)</td>
<td></td>
</tr>
<tr>
<td>Male risk + Female risk + Mixed</td>
<td>5</td>
<td>11417.54</td>
<td>2.57</td>
<td>0.13</td>
<td>-0.131 (0.014)</td>
<td>0.045 (0.013)</td>
<td>0.204 (0.046)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male risk + Female risk + Dense + Open</td>
<td>6</td>
<td>11419.13</td>
<td>4.17</td>
<td>0.06</td>
<td>-0.130 (0.014)</td>
<td>0.047 (0.014)</td>
<td>-0.350 (0.234)</td>
<td>-0.199 (0.047)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male risk + Female risk + Open</td>
<td>5</td>
<td>11419.41</td>
<td>4.45</td>
<td>0.05</td>
<td>-0.132 (0.014)</td>
<td>0.044 (0.013)</td>
<td>-0.197 (0.046)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male risk + Female risk + Time + Mixed</td>
<td>6</td>
<td>11419.47</td>
<td>4.5</td>
<td>0.05</td>
<td>-0.131 (0.014)</td>
<td>0.045 (0.013)</td>
<td>0.204 (0.046)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male risk + Female risk + Dense + Open + Time</td>
<td>7</td>
<td>11421.07</td>
<td>6.1</td>
<td>0.02</td>
<td>-0.130 (0.014)</td>
<td>0.047 (0.014)</td>
<td>-0.346 (0.234)</td>
<td>-0.199 (0.047)</td>
<td>0.013 (0.050)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Model averaged coefficients (with shrinkage)

-0.132 (0.014) | 0.048 (0.014) | -0.307 (0.236) | -0.178 (0.048) | 0.038 (0.046) | -0.002 (0.001) | 0.004 (0.050)

Relative variable importance

1 | 1 | 0.76 | 0.81 | 0.19 | 0.68 | 0.27
ii) Eland resource selection models across Nyathi and MZNP

At the broad scale (i.e. including both reserves), eland habitat selection was best predicted by the presence of open and dense habitat types and long-term predation risk by male and female lions (Table 2.6). Eland selected open habitats ($\beta = 0.221, p < 0.001$) and avoided dense habitats ($\beta = -0.859, p < 0.01$) resulting in the probability of eland presence being highest in open habitats ($p = 0.55 \pm 0.02$) and lowest in dense habitats ($p = 0.29 \pm 0.02$, Fig. 2.12). Although included in the final model, time (Appendix 5) and ruggedness (Appendix 6) did not drive eland habitat selection. Eland probability of presence was negatively related to the long-term predation risk of male lions ($\beta = -0.106, p < 0.01$, Fig. 2.13a) and positively related to the long-term predation risk of the female lion ($\beta = 0.025, p < 0.01$, Fig. 2.13b).

Fig. 2.12 The modelled average probability of eland presence ($n = 7$) at the three defined habitat types in Nyathi and Mountain Zebra National Park (MZNP) with all other modelled variables held at their mean, determined using generalised linear mixed effects models. Error bars represent standard error.
Fig. 2.13 The relationship between long-term risk of predation from a) male and b) female lions (proportional to the likelihood of male and female lion presence) and the modelled probability of eland presence (n = 7) in open and dense habitat types in Nyathi and Mountain Zebra National Park (MZNP) determined using generalised linear mixed effects models. Red lines represent 95% confidence intervals. Data points show the binned proportion of presence (with binomial confidence limits) from the raw data in each habitat type (■ = open, ▲ = dense). Data is binned into predation risk categories from 0 – 2, 2.01 – 4, 4.01 – 6 and 6.01 – 8. Modelled probabilities and the proportion of presence data are from day points only as time of day was not shown to significantly influence the model.
iii) Eland resource selection models in Nyathi

In Nyathi, the presence of open and dense habitat types and long-term predation risk of male lions significantly influenced the probability of eland presence (Table 2.7). Regardless of the level of predation risk, the probability of eland presence in Nyathi was highest in open habitats ($p = 0.62 \pm 0.01$) and lowest in dense habitats ($p = 0.29 \pm 0.01$, Fig. 2.14). The probability of eland presence was negatively related to the long-term predation risk of male lions ($\beta = -0.127$, $p < 0.01$, Fig. 2.15). The average probability of eland presence was lowest when the chance of encountering a male lion was high and the habitat type was dense, and highest when the chance of encountering a male lion was low and the habitat type was open (Fig 2.15). The long-term predation risk of the female lion ($\beta = -0.004$, $p = 0.31$, Appendix 7), ruggedness ($\beta = -0.02$, $p = 0.20$, Appendix 8) and time (i.e. night locations compared to day locations; $\beta = -0.051$, $p = 0.08$; Appendix 9) were included in the final model but had a negligible impact on eland habitat selection in Nyathi.

Fig. 2.14 The modelled average probability of eland presence ($n = 4$) at the three defined habitat types in Nyathi with all other modelled variables held at their mean, determined using generalised linear mixed effects models. Error bars represent standard error.
iv) Eland resource selection models in MZNP

In MZNP, the presence of open and mixed habitat types, long-term predation risk of male and the female lions and the ruggedness significantly influenced the probability of eland presence (Table 2.8). Eland avoided open habitat types ($\beta = -0.178$, $p < 0.001$) and selected mixed habitats ($\beta = 0.038$, $p < 0.01$). As seen in Nyathi, there was a negative relationship between the probability of eland presence and dense habitats, however in MZNP the relationship was not significant ($\beta = -0.307$, $p = 0.09$). Regardless of the level of predation risk, the average probability of eland presence in MZNP was highest in mixed habitats ($p = 0.53 \pm 0.01$, Fig. 2.16) and lowest in dense habitats ($p = 0.44 \pm 0.06$, Fig. 2.16). The probability of eland presence was negatively related to the long-term predation risk of male lions ($\beta = -0.132$, $p < 0.01$, Fig. 2.17a) and positively related to long-term predation risk of the female lion ($\beta = 0.048$, $p < 0.01$, Fig. 2.17b). The probability of eland presence was negatively associated with ruggedness ($\beta = -0.02$, $p < 0.01$, Fig. 2.18). The plotted predicted probability of eland presence as a function of ruggedness indicates, however, that ruggedness has a negligible effect on eland resource selection (Fig. 2.18). Time of day also had no significant effect on eland resource.
selection at the home range scale ($\beta = 0.004, p = 0.76$, Appendix 10). The plotted predictions of probability of eland presence relative to long-term predation risk of male and female lions (Fig. 2.17) and ruggedness (Fig. 2.18) are for data points associated with open habitat types (representing the largest sample size) as 95% confidence intervals of predicted probabilities in all habitat types overlapped.

![Graph](image-url)

**Fig. 2.16** The modelled probability of eland presence ($n = 3$) at the three defined habitat types in Mountain Zebra National Park (MZNP) with all other modelled variables held at their mean, determined using generalised linear mixed effects models. Error bars represent standard error.
Fig. 2.17 The relationship between long-term risk of predation from a) male and b) female lions (proportional to the likelihood of male and female lion presence) and the modelled probability of eland presence (n = 3) in open habitats in Mountain Zebra National Park, determined using generalised linear mixed effects models. Red lines represent 95% confidence intervals. Data points show the binned proportion of presence (with binomial confidence limits) from the raw data in each habitat type (■ = open). Data is binned into predation risk categories from 0 - 2, 2.01 - 4, 4.01 - 6 and 6.01 - 8. Modelled probabilities and the proportion of presence data are from day points only as time of day was not shown to significantly influence the model.
Fig. 2.18 The relationship between ruggedness and the modelled probability of eland presence (n = 3) in open habitat types in Mountain Zebra National Park (MZNP), determined using generalised linear mixed effects models. Red lines represent 95% confidence intervals. Data points show the binned proportion of presence (with binomial confidence limits) from the raw data in each habitat type ([square] = open). Data is binned into ruggedness categories from 0 - 20, 20.01 - 40, 40.01 - 60, 60.01 - 80 and 80.01 - 100. Modelled probabilities and the proportion of presence data are from day points only as time of day was not shown to significantly influence the model.

2.4 Discussion

2.4.1) Landscape level assessment (2nd order selection)

The results of the study did not support the hypothesis that eland avoid areas used by lions at the landscape scale. Contrary to this hypothesis, eland home ranges in both Nyathi and MZNP occurred in areas overlapped by lion territories. Furthermore, characteristics of eland home ranges between the reserves indicated that eland populations in these two reserves were influenced by different ecological processes at the landscape level (McLoughlin & Ferguson 2000). There was a vast disparity in eland home range sizes between the two reserves. Eland home ranges in the two reserves also differed in terms of the effect of seasonal variation in rainfall and the proportional representation of habitat types within home ranges.

Home ranges link the movement of animals to the distribution of the resources necessary for survival and reproduction (Börger et al. 2008). Home ranges must therefore be large enough to include sufficient resources but also small enough to allow for familiarity, which allows for knowledge of areas frequented by predators or the location of particular feeding stations (McLoughlin & Ferguson 2000; Laundré et al. 2010). The breeding eland population in both Nyathi...
and MZNP did not decline over the study period, with healthy proportions of juvenile observed in herds’ (average of 41% and 31% of the herd less than two years old in Nyathi and MZNP, respectively). Home ranges of eland herds in Nyathi and MZNP therefore appeared to provide sufficient resources for survival and reproduction. At the population level, climate and its effect on primary productivity, seasonality and food availability, are considered the primary limiting factor driving home range size (McLoughlin & Ferguson 2000). Predation may also influence home range size by initiating predator-avoidance behaviours in prey animals (Tufto et al. 1996; McLoughlin & Ferguson 2000).

A limited number of studies have investigated the spatial extent of eland home ranges. Furthermore, there is a vast disparity in the size of the systems in which the studies were conducted. For example, in Nairobi National Park and the adjacent Athi Kapiti plains, Kenya, an unfenced area comprising more than 1 700 km², Hillman (1988) estimated a mean home range size of 222 km² for adult females, with the largest home range measured (422 km²) assumed to be more representative of adult female home ranges (Hillman 1988). Eland in the vast Kgalagadi Transfrontier Park were similarly found to occupy extensive home ranges (M. Knight, personal communication). These vast home range sizes were largely driven by extensive seasonal movement by eland in these systems. Conversely, in a study conducted in the Loskop Nature Reserve, South Africa, an enclosed area of 120 km², home range sizes were not investigated as the area was deemed too small to allow for accurate home range estimation (Underwood 1975). The current study thus represents an important contribution of knowledge regarding eland space use in fenced reserves and the drivers thereof.

2.4.1.1) Home range size and seasonal variation in Nyathi

In Nyathi, the mean home range size of female eland and the herds with which they were associated was 12 ± 2 km². Home range size increased slightly during the wet season (dry season = 12 ± 0.5 km², wet season = 14 ± 0.5 km²) however, the location of eland home ranges in Nyathi remained constant throughout the study period. The small, localised home ranges of eland in Nyathi thus differ from previous studies reporting extensive home ranges, large-scale movements and seasonal variation in vegetation type preferences (Skinstad 1972; Underwood 1975; Hillman 1988; Fabricius & Mentis 1990; Mwangi & Western 1998; Watson & Owen-Smith 2000). These differences could be the result of highly localised availability of required resources (McLoughlin & Ferguson 2000) such that eland do not need to range widely. These small home ranges could also be largely restricted by the limited availability of open habitats and therefore reflect a response to predation risk (e.g. Tufto et al. 1996). Given that seasonal variation in rainfall did not have a large influence on eland home ranges, and that seasonal difference in rainfall is limited, it is suggested that the spatial distribution of eland in Nyathi is influenced more strongly by top-down than bottom-up processes (McLoughlin &
Furthermore, given that Nyathi is dominated by dense habitats that increase the hunting success of lions (Funston et al. 2001; Hopcraft et al. 2005; Burkepile et al. 2013; Loarie et al. 2013), the majority of the landscape represents risky areas for eland. This supports the suggestion that top-down forces are likely to be more important than bottom-up forces in Nyathi (Laundré et al. 2014).

2.4.1.2) Habitat selection at the landscape level in Nyathi

Across spatial scales, habitat selection should reflect factors limiting individual fitness in a hierarchal fashion (Rettie and Messier 2000). Habitat selection at large spatial scales i.e. at the landscape level, should therefore allow for avoidance of the most important limiting factor (Dussault et al. 2005). Consequently, the spatial heterogeneity in vegetation structure influences prey distribution due to the amount of cover provided by different vegetation structures (Valeix et al. 2009; Thaker et al. 2011; Hopcraft et al. 2010). Cover is a habitat feature which may affect important aspects of ungulate biology (Mysterud and Østbye 1999), with predation risk key amongst these (Loarie et al. 2013). Habitat selection at the landscape level in Nyathi indicated that eland did not use habitat types relative to their availability, but rather selected open habitats and avoided dense habitats. This selection for open areas was evident, with eland home ranges, regardless of season, centred on the open plains. Furthermore, eland and lion home ranges overlapped considerably in Nyathi such that eland faced a constant risk of encountering lions. The selection of open habitats may be driven by a behavioural response to predation risk, with open habitats providing early predator detection (Jarman 1974) and reduced lion hunting efficiency (Hopcraft et al. 2005). Cover can provide a spatial refuge from predation as it reduces capture success (Sih 1984). For example, in a study conducted on roe deer Capreolus capreolus, home range size was directly related to visibility in the home range such that the smallest home ranges were those that contained the most hiding cover, an important landscape variable to reduce predation (Tufto et al. 1996). Thus, at the landscape level, eland in Nyathi did not avoid lions, but selected open habitats and avoided dense habitats to reduce the probability of being killed by a lion given an encounter (Funston et al. 2001; Hopcraft et al. 2005; Loarie et al. 2013; Burkepile et al. 2013). Open plains may thus offer an important refuge from predation for eland. Similarly, Thaker et al. (2011) found that selection of safe habitats by ungulates in Karongwe Game Reserve, Limpopo Province, South Africa, and avoidance of risky areas was stronger than the avoidance of areas associated with predator activity.

Eland are predominantly browsers (Hoffman 1973; Watson & Owen-Smith 2000; Schlebusch 2002; Wallington et al. 2007) therefore open habitats potentially do not provide sufficient woody forage for their high daily food requirements (Watson & Owen-Smith 2000). The selection of open habitats by eland in Nyathi, presumably due to increased safety from predation, may thus come at a high cost.
to foraging (Brown & Kotler 2004). Mixed habitat types were preferred by eland in Nyathi, potentially due to the increased abundance of woody plants on which to browse offered by this habitat type. Eland appeared to accept an increased level of predation risk in order to meet their energy demands (Brown 1988; Brown & Kotler 2004). The patterns of habitat selection by eland in Nyathi may thus represent a trade-off between access to sufficient forage and safety from predation risk (e.g. Burklepil et al. 2013). This exemplifies the large effect that the nonlethal effects of predation may have on prey species distribution at a broad scale (e.g. Thaker et al. 2011).

2.4.1.3) Home range size and seasonal variation in MZNP

In MZNP, the average home range size over the full study period was $74 \pm 6 \text{ km}^2$. Seasonal variation in rainfall during the study period was greater in MZNP than in Nyathi, driven largely by low rainfall recorded in the dry season (SANParks, unpublished data, Appendix 11). The seasonal increase in average home range size was greater in MZNP than in Nyathi, with the average home range size in the dry season ($35 \pm 3 \text{ km}^2$) almost half that of the average wet season home range ($62 \pm 6 \text{ km}^2$). Eland in MZNP also occupied different, although not mutually exclusive, regions of the park depending on the season (Appendix 3). Seasonal variation in space use therefore contributed to the larger cumulative home ranges in MZNP compared to in Nyathi. The shift in eland home ranges westward during the wet season may be because the western regions of the reserve receive more rainfall than the eastern areas (van der Walt 1980), and therefore presumably provide a high abundance of palatable young grasses and shoots during the wet season (Watson & Owen-Smith 2000; 2002).

The variation in eland home range size and location in response to increased rainfall in MZNP indicate that eland home ranges are largely influenced by bottom-up processes (McLoughlin & Ferguson 2000). This is supported by observations of the diet of eland in MZNP which changes with seasonal variation in rainfall due to the changes in shoot phenology between seasons (Wataon & Owen-Smith 2002). Consequently, eland have a wider diet breadth during the wet season than during the dry season (Watson & Owen-Smith 2002). Home range size of eland in MZNP was thus positively related to food availability (e.g. Ebersole 1980), indicating that food may be a limiting factor for eland in MZNP. During the dry season, when food availability is low, eland in MZNP occupy smaller, more localised home ranges as the energy costs associated with occupying a larger home range in which to forage may not be compensated by energy gains (e.g. Massei et al. 1997). Eland home ranges are therefore larger in the wet season as eland seek to take advantage of dispersed patches offering a high abundance of preferred food items. Larger home ranges during wet season were similarly recorded for breeding herds of eland in Kenya (Hillman 1988). Home range sizes of moose in Norway were also found to increase in summer as browse density increased (van Beest et
al. 2011). Furthermore, given that MZNP is dominated by largely open to semi-open habitats, which reduce the hunting success of lions (Funston et al. 2001; Hopcraft et al. 2005) bottom-up forces are likely to be more important than top-down forces, as suggested by the landscape of fear model (Laundré et al. 2014).

2.4.1.4) Habitat selection at the landscape level in MZNP

Eland used habitat types in proportion to their availability in MZNP. However, habitat selection was not assessed in terms of vegetation composition and associated forage quality and quantity as habitat types were delineated based only on vegetation structure for this study. The habitat types defined based on vegetation structure (open, mixed and dense) were thus probably at too coarse a scale to show habitat selection driven by bottom-up processes. Habitat selection by eland at the landscape level in MZNP appeared to be driven by the spatial distribution of food resources, with seasonal differences in forage quality and quantity driving changes in home range size and location (Watson & Owen-Smith 2000). Given that MZNP is characterised by largely open and semi-open habitats, with a small proportion of dense habitats, predation may have a reduced impact on eland, as lions require sufficient cover for their ambush hunting strategy (Funston et al. 2001; Hopcraft et al. 2005). This may explain why male lions in MZNP spent most of their time along the Wilgeboom River, characterised by dense vegetation, and a source of water for herbivores. Eland in MZNP are predominantly browsers, feeding mainly on woody shrub species that occur in the shrubland communities across the reserve (Watson & Owen-Smith 2000; 2002). Eland are also largely water independent (King et al. 1975). Eland herds in MZNP therefore probably had little need to use dense, riparian areas that are associated with high levels of predation risk and may thus experience low predation pressure.

2.4.2) Home range level assessment  (3rd order selection)

2.4.2.1) Resource selection at the home range scale

The spatial distribution of eland at the home range scale, across both reserves was influenced by the risk of predation. Furthermore, eland responses to lion predation risk were lion gender-specific, where areas associated with a high probability of encountering a male lion were avoided whilst those associated with a high probability of encountering a female lion were not. Therefore, results partially supported the prediction that eland spatially avoid lions however this was shown at a finer-scale than expected (home range scale as opposed to landscape scale) and was sensitive to lion gender, which was not expected.

Lions exhibit strong sexual dimorphism, both physically and behaviourally (Schaller 1972), thus their hunting strategies differ (Funston et al. 2001; Loarie et al. 2013). A recent study in Kruger National
Park, South Africa, found that male lions rely strongly on dense vegetation that provides ambush opportunities to hunt successfully, whilst females were found to hunt in more open habitats (Loarie et al. 2013). Conversely, in Addo, of which Nyathi is one site, male and female lions rely equally on dense habitats to hunt, with kills made by both lion sexes found in similarly dense habitats (A. Davies, unpublished data). The difference in eland responses to lion predation risk in Nyathi were thus not driven by a difference in male and female lion hunting mode.

The position of areas associated with high levels of long-term predation risk of male and female lions in Nyathi were spatially isolated, except for a small area along the southern boundary where male and female high risk areas overlapped. This area represented the only patch of highest male risk, whilst for the female lion it was one of four discreet areas of high risk in the western part of the reserve. When male lions were present in the western part of the reserve, they focused their activity in this small area and were presumably joined by the female lion (indicated by the high level of overlap of male and female high risk areas). Hence, the single area representing the highest long-term predation risk of male lions also represented an area associated with high female lion predation risk. This area was strongly avoided by eland. The strong avoidance of areas associated with high levels of male lion predation risk may thus, in part, be driven by a strong avoidance of areas that are associated with high levels of predation risk from both male and female lions. In these areas, male and female lions may hunt co-operatively, thus representing an area of intensified predation risk. Furthermore, male lions rest and select territories in largely open areas relative to the areas in which they hunt (Davidson et al. 2012; Loarie et al. 2013). Eland are possibly able to detect male lions more frequently from a safe distance when their home ranges occur in the same area. In this way, eland may be able to more efficiently establish and update the space use patterns of male lions such that their spatial distribution may be based on well-informed background levels of male lion presence. The areas associated with high levels of predation risk of the female lion were located within eland home ranges but occurred partially in mixed and dense habitats. Eland may thus detect the female lion less frequently and are therefore less effective at avoiding areas of high female predation risk.

In Nyathi, the spatial distribution of eland was strongly influenced by the location of open plains at both the landscape and home range scale. Such open areas are limited, and are spatially isolated in a matrix of dense thicket vegetation, which eland avoid. Given that male and female lion territories in Nyathi overlapped these open plains independently, eland may be unable to avoid both male and female lion territories effectively at a large scale. Eland in Nyathi therefore appear to prioritise avoidance of areas associated with highest lion density (i.e. areas where male and female lions spend considerable time together) by avoiding these areas at the landscape level. At the home range
scale, eland appear to reduce predation risk by avoiding habitats that increase the hunting success of lions and areas associated with a high probability of male lion presence.

Results from Nyathi thus supported the prediction that eland would avoid dense habitats associated with increased probability of mortality, and select open habitats that minimise the risk of predation from ambush hunters (Funston et al. 2001; Hopcraft et al. 2005; Loarie et al. 2013; Burkepile et al. 2013). Furthermore, eland adjusted the level of avoidance-response in relation to the long-term probability of a male lion being present. For example, dense habitats were more likely to be used if the level of long-term male lion predation risk there was low, whilst areas of dense habitat associated with high levels of male lion activity were avoided. This illustrates threat-sensitive predator avoidance where antipredatory responses of eland were matched to the degree of threat based on long-term cues of male lion presence (e.g. Thaker et al. 2010).

Given that eland and lion in both reserves occupy overlapping home ranges, eland are exposed to predation risk at all times. Consequently, predation risk may force eland to trade-off food acquisition for safety, with this most evident in Nyathi. In the neighbouring Main Camp section of the GAENP eland diet was dominated by browse species whilst the prominent grass species that occur on open plains such as those occupied by eland in Nyathi, contributed minimally to eland diet (Schlebusch 2002). Schlebusch’s (2002) study was however conducted prior to the reintroduction of lions into Main Camp, so that, as with the diet study done for eland in MZNP by Watson & Owen-Smith (2000), it reflects resource use by eland free of predation risk. To my knowledge, no study has been done on the feeding ecology of eland under predation risk in small reserves. Eland in Nyathi occupy open areas where browse opportunities may be reduced but where safety is increased. By adjusting their level of antipredatory response based on the probability of encountering male lions, eland presumably moved into mixed habitats to browse in areas associated with a lower probability of a male lion being present, allowing them to acquire food resources whilst reducing predation risk. Given that rainfall occurs throughout the year in Nyathi, and that frost days are limited, grasses on the plains on which eland occur may remain palatable for long periods and eland may be able to exploit grass as a food source throughout the year, thereby limiting their need to move into more risky areas to browse. Confirmation of this could be obtained through the assessment of eland diet in areas where habitat shifts may reflect a behavioural response to predation risk.

In MZNP, although predation risk influenced resource selection at the home range scale, where areas with a high probability of male lion presence were avoided, the selection of habitat types appeared to be more strongly driven by food acquisition. This was indicated by the avoidance of open areas and the selection for mixed habitats. The edge of these habitats is soft however which
could have led to the misclassification of habitat types. Areas of high long-term predation risk of male and female lions in MZNP occurred in mixed and dense habitats, indicating that predation risk, in terms of both the chance of encountering a lion and the probability of death given an encounter, was lowest in open habitats. However, open areas in MZNP may offer limited forage, particularly in the dry season when grasses are mature and largely unpalatable (Watson & Owen-Smith 2000). Eland therefore preferred mixed habitats that offer a diversity of woody species from which to browse selectively (Watson & Owen-Smith 2000; 2002).

This study was conducted within the first year of lion reintroduction into MZNP, thus the spatial distribution of lions in the reserve may represent much exploratory space use (D.B. van de Vyver, personal communication). This may be why space use by lions in MZNP covered the majority of the reserve (average home range size = 108 km²), reflecting wide ranging movement across the landscape. Conversely, lions in Nyathi have established stable territories (average home range size = 25 km²) since their reintroduction in 2011, with space use patterns largely concentrated along the western part and southern boundary of the reserve. The risk of encountering a lion in MZNP is therefore lower than in Nyathi given that lion density is lower (~0.03 lions/km² in MZNP vs.~ 0.12 lions/km² in Nyathi). Eland in Nyathi therefore experienced higher levels of predation risk than eland in MZNP and this is likely to play a large role in the antipredator responses of eland observed between the two reserves.

Overall, results from this study indicate that predation risk is an important factor driving the spatial distribution of eland at multiple scales. However, there are differences between the two study sites in how top-down and bottom-up effects impact habitat selection (Thaker et al. 2011; Burkepile et al. 2013). Top-down forces may be an important determinant of eland habitat selection in areas dominates by risky habitats (Laundré et al. 2014), such as Nyathi, where the predominant dense habitats increase the hunting success of lions (Funston et al. 2001; Hopcraft et al. 2005; Burkepile et al. 2013; Loarie et al. 2013). Conversely, MZNP is dominated by open to semi-open habitats which are safer as they reduce the hunting success of lions (Funston et al. 2001) such that predation risk may be less important than bottom-up forces in MZNP (Laundré et al. 2014). Results of this study show that eland may attempt to reduce predation risk through avoidance of risky habitats and high risk areas of male lions at the home range scale, with their ability to do so strongly reliant on sufficient access to open habitats, which may act as a spatial refuge from predation. Lion density within reserves is also an important factor which may influence the degree to which eland are able to effectively reduce predation risk.
Chapter 3

Fine-scale responses of eland to lion and characteristics of eland mortality sites

3.1 Introduction

For prey animals to reduce both the direct and indirect effects of predation, they should seek to avoid predators at a broad scale (Rettie & Messier 2000), thereby reducing the probability of encountering, or being attacked by predators. However, complete avoidance of predation is uncommon (Hebblewhite & Merrill 2009). In natural systems where predators and prey are mobile, the presence of one evokes a behavioural response from the other, resulting in predators and prey often occurring in the same area (Sih 1984; Formanowics & Bobka 1989). Thus, at a broad spatial scale, the behavioural interactions between predators and prey may result in high overlap in space use (Sih 1984; Heithaus & Dill 2006; Torres et al. 2006). At a fine scale, however, the areas where prey are most likely to encounter a predator may not necessarily be where they are most likely to be killed (Hebblewhite et al. 2005). Fine scale behavioural responses of prey to predation risk thus constitute an important aspect of predator-prey interactions.

The relationship between the predator-prey encounter rate and the number of resultant kills is determined by the prey animals’ vulnerability to predation (Schaller 1972; Mills & Shenk 1992). How vulnerable a prey species is to predation is influenced by features of both the predator and prey in question (Hayward & Kerley 2005), as well as by environmental features (Bergman et al. 2006; Laundré et al. 2010). Features of prey species that affect its vulnerability to predation are its abundance, size, spatial and temporal distribution, defences and antipredatory tactics (Sunquist & Sunquist 1997). At the individual level, a prey animal’s vulnerability is determined by its age, sex, body condition and reproductive status (Childress & Lung 2003), as well as the presence or absence of conspecifics (Hamilton 1971; Estes 1976; Childress & Lung 2003).

Although vulnerability is typically defined by intrinsic features of the prey animal, such as its age or health, it is determined to a large degree by the surrounding landscape (Bergman et al. 2006; Kauffman et al. 2007; Laundré et al. 2010). The location at which a predator successfully kills a prey animal represents a location on the landscape where conditions favour the hunting strategy of the predator and are potentially, yet not necessarily, unfavourable to the escape tactic of the prey (see review in Gorini et al. 2012). These locations on the landscape increase the vulnerability of prey to predation, with much of this increased risk attributed to habitat-mediated increases in predator success (Van Orsdol 1984; Laundré & Hernandéz 2003; Hopcraft et al. 2005; Laorie et al. 2013). Given that habitat heterogeneity is common (Longland & Price 1991), the probability of being killed...
is not uniformly distributed across the landscape and is driven by spatial changes in habitat type (Brown & Kotler 2004; Laundré et al. 2010). Predators may thus select to hunt in habitats that offer increased prey catchability over areas of high prey abundance (Hebblewhite et al. 2005; Hopcraft et al. 2005; Balme et al. 2007). Spatial refugia from areas that increase catchability are therefore important for prey species persistence under predation pressure (Bergman et al. 2006; Berryman & Hawkins 2006).

Behavioural responses of prey that reduce predation risk range from broad scale activities which act through avoidance of risk, such as habitat choice and activity patterns, to very specific, fine scale behaviours which reduce risk of capture when attacked, such as flight responses or active defence (Lima & Dill 1990; Caro 2005). Effective antipredator behaviours at both the broad and fine scale should therefore increase survival (Lind & Cresswell 2005). Habitat selection by a prey animal may thus be related to its individual fitness as avoidance of risky habitats (i.e. areas of high predation risk), and selection for refugia (i.e. areas of low predation risk), reduce the risk of mortality (McLoughlin et al. 2005). Ungulates in Hwange National Park moved into open habitats when lions were detected within 2 km thereby reducing their vulnerability to predation (Valeix et al. 2009). Similarly, elk Cervus elaphus in Yellowstone moved into the protective cover of more wooded areas when wolves were present (Creel et al. 2005). Habitat-specific predation risk may be assessed by analysing kill sites in order to determine the landscape conditions under which prey animals are most vulnerable to predation (Bergman et al. 2006). Essentially, these areas represent dangerous habitats which should be avoided by prey animals if behaviourally-mediated habitat selection is to have fitness benefits. Prey may thus reduce predation risk through spatial avoidance of high risk areas (Johnson et al. 2002; Anderson et al. 2005; Moa et al. 2005; Tambling et al. 2012a).

Temporal avoidance of high risk areas may also allow prey to effectively avoid encountering predators (Creel et al. 2005). Predation risk varies temporally as predators move through the landscape and respond to environmental variation over multiple temporal scales (Lima & Bednekoff 1999). At a broad temporal scale, predation risk may vary with season (Lucas et al. 1996), as variation in rainfall changes vegetation conditions thereby altering prey vulnerability (Ogutu & Owen-Smith 2005). Predation risk also varies over the lunar cycle (Kotler et al. 1994), with variation in light level influencing the hunting success of nocturnal predators (Funston et al. 2001; Schaller 1972). At a fine scale, predation risk varies with the diel activity patterns of predators (Fenn & Macdonald 1995) whilst at the finest temporal scale predation risk varies on a minute-to-minute basis during an encounter with predators (Sih 1992). Such temporal variation in risk means that prey species may reduce their exposure to predators through space use that is asynchronous with that of predators at multiple temporal scales. Given that the dynamic nature of predator-prey interactions
may result in space use overlap between predators and prey at a broad temporal scale, spatial asynchrony in time may be achieved through prey exploiting fine scale temporal variation in the space use of predators. For example, plains zebras (*Equus quagga*) in Ol Pejeta Conservancy, Kenya avoided areas where lions had been present in the previous 24 hours thereby reducing predation risk by altering their spatial distribution in response to fine scale temporal variation in lion space use (Fischhoff *et al.* 2007).

Complete spatial or temporal avoidance of risky areas is often not compatible with other essential activities such as foraging (Dussault *et al.* 2005). Prey species may therefore have to occasionally accept a high risk of predation in order to achieve their forage requirements (Brown 1988; Brown & Kotler 2004). In such situations, where prey animals are more frequently exposed to attack, fine scale responses that reduce risk of capture are important for survival (Sansom *et al.* 2009). Behaviourally-mediated adjustments in movement patterns may reduce predation risk both before and after encountering a predator (Sih 1984). Before a predator is detected, decreased movement rates by prey are associated with reduced predation risk as this allows for increased vigilance (McAdam & Kramer 1998), reduces the ability of predators to detect prey (Roche *et al.* 1999) and increases preys’ ability to detect predators (Sharpe & Van Horne 1998). However, once a predator has been detected, prey animals may increase their movement rate as a predator approaches (Proffitt *et al.* 2009; Middleton *et al.* 2013) to avoid capture (Fischhoff *et al.* 2007) or to move into safer habitats (Fortin *et al.* 2005). Behavioural adjustments in response to the immediate presence of a predator are expected to reduce the catchability of prey as soon as a predator is detected and this is known as behavioural resource depression (Charnov *et al.* 1976; Kotler 1992). For example, plains zebra in Kenya increased their rate of movement and made sharper turns at night when lion predation risk was high as these more erratic movements are thought to reduce detection or capture by lions (Fischhoff *et al.*2007). Similarly, elk in Yellowstone increased their movement rate as predation risk of wolves increased, thereby decreasing their chances of being caught (Proffitt *et al.* 2009; Middleton *et al.* 2013).

This chapter aims to investigate the fine scale spatiotemporal responses of common eland *Tragelaphus oryx* to their major predator, lions *Panthera leo*. Secondly, this chapter aims to investigate where on the landscape eland are most vulnerable to lion predation by assessing the landscape characteristics at eland mortality sites. Eland do not avoid lions at the landscape scale but, at the home range scale, eland avoid dense habitats and areas associated with high levels of long-term male lion predation risk (Chapter two). This chapter thus aims to test the hypothesis that areas avoided by eland at the home range scale represent areas associated with an increased probability predation. Therefore, eland mortality sites (kill sites) are predicted to occur in more dense habitats
relative to the sites where eland were known to occur when alive (live sites), given that lions are
ambush hunters that rely on cover to hunt successfully (Funston et al. 2001; Hopcraft et al. 2005;
Loarie et al. 2013). Furthermore, the level of long-term predation risk is predicted to be higher at kill
sites compared to live sites. Given that eland did not avoid lions at the landscape scale over the full
study period (Chapter two), this chapter also aims to investigate the overlap between eland and lion
space use at finer temporal scales i.e. seasonally and monthly. Spatial overlap between eland and
lions is predicted to be reduced at finer temporal scales compared to overlap observed over the full
study period. At the finest spatiotemporal scale, it is predicted that lions in close proximity to eland
will evoke a behavioural response by eland, demonstrated by a change in their movement rate.
Findings of this chapter will thus shed light on the landscape variables that increase eland
vulnerability to lion predation and the fine scale mechanisms by which predation pressure on eland
may be reduced.

3.2. Methods

3.2.1) Kill site characteristics of herd-associated eland kills

3.2.1.1) Identification of herd-associated eland kill sites

In September 2011 and May 2013, 3 lions (two males and one female) were released into Nyathi and
MZNP, respectively. Lions were fitted with GPS collars (African Wildlife Tracking, Pretoria, South
Africa) by SANParks upon their release. Lion kills were located using the GPS cluster investigation
approach (Tambling et al. 2010; 2012b) with possible kill sites investigated by C.J. Tambling in Nyathi
and by D.B van de Vyver in MZNP. Suspected kill sites were visited on foot and any kills found were
identified to prey species, and sex and age categories if possible. GPS clusters longer than one hour
with no associated kill were assumed to be either lion resting sites or failed hunt attempts (i.e. non-
kill sites, Tambling et al. 2010). The number and location of eland kills made by lions in Nyathi and
MZNP were thus obtained from C.J. Tambling and D.B. van de Vyver, respectively.

In Nyathi, 30 eland kill sites were found between September 2011 and January 2014. Kills sites were
not investigated after January 2014 in Nyathi due to battery failure on the GPS collar on the female
lion in early February 2014. In MZNP, 22 eland kills were found between May 2013 and April 2014.
Kill site analyses were only conducted using data collected from herd-associated kills (i.e. female or
immature individuals), because GPS data representing live eland sites with which to contrast kill site
characteristics were only available for collared female eland. Of the total eland kills found (n = 30),
13 herd-associated eland kill sites were identified in Nyathi and in MZNP, of the total kills found (n =
22), four were herd-associated kill sites. Kill sites from Nyathi included in the analyses were not
restricted to those made during the study period as this would have reduced the sample size. All kills
in MZNP were made during the period of eland observation (as referred to in Chapter two) as lion were reintroduced into MZNP one month before eland were collared.

To investigate eland predation in each reserve during the study period, the total number of eland kills found in Nyathi between March 2013 to January 2014 and in MZNP between May 2013 and April 2014 were compared in terms of the sex of the eland killed and that of the lion present at the kill site. A log-likelihood ratio test (G-tests) was conducted to assess if there was a significant difference between the number of herd- versus non-herd-associated eland kills in each reserves. Similarly, a log-likelihood ratio test (G-tests) was conducted to assess if there was a significant difference between the number of herd-associated eland kills made by male lions compared to the female lion.

3.2.1.2) Comparison of sites where eland are alive and sites where eland are killed

Sites where eland were alive (referred to as live sites) were identified by randomly selecting a set of GPS locations from all collared eland occurring within the population home range in each reserve. The number of live sites selected was based on the number of kill sites identified for investigation, with the minimum number of live sites set as three times the number of kill sites. Live sites in Nyathi (n = 58) and MZNP (n = 31) thus represented sites where eland were known to be alive.

Herd-associated kill sites and live sites were visited between January and May 2014. At all live and kill sites, mean viewshed (the average distance at which sight is blocked by intervening vegetation structures), minimum distance to cover (defined as any structure that could conceal a lion), ruggedness, distance to road, habitat type and level of long-term predation risk from male and female lion was assessed. Lion attacks are more successful at short-ambush distances (Van Orsdol 1984), and vegetation cover is an important factor in hunting success (Funston et al. 2001). Habitats that have good visibility should therefore be safer as they provide detection and evasion of predators and may reduce the risk of attack (Cowlishaw 1997). To measure the viewshed, field assistants, with a white cloth tied around their torso at a height of 1.5 m (approximating the height of an eland’s head), walked away from the observer until the white cloth was no longer visible (Hay et al. 2008). Using a range-finder (Leica Rangemaster 1200 CRF-M), this measure was repeated in 12 directions at 30° increments such that the surrounding line-of-sight obstructions were measured, and then averaged. Minimum distance to cover was defined as the shortest of the 12 measurements and represented potential ambush opportunity for lions. Ruggedness, distance to road, habitat type and level of long-term predation risk were assessed by plotting kill and live sites into ArcGIS 10.1 and extracting the relevant landscape and predation variables for each location. Ruggedness was extracted from a 25 m Digital Elevation Model (DEM, Eastern Cape Parks and Tourism) of each reserve. Distance to road was calculating using the ‘near’ spatial analyst tool in
ArcGIS, providing the distance in meters from each kill site and live site to the nearest frequently used road (see Section 2.2.7.2a). Habitat type and the level of long-term predation risk were extracted from the habitat raster layers (as defined in section 2.2.3.1ii) and the predation risk raster layer (as defined in section 2.2.7.2b).

3.2.1.3) Data analyses

Statistical analyses were only conducted on Nyathi data as the low sample size of herd-associated kills in MZNP (n = 4) did not allow for statistical analyses of these data. Data for each continuous variable (i.e. ruggedness, distance to road, mean viewshed and minimum distance to edge) were checked for normality by examining quantile plots (Zuur et al. 2009). Variance of means between site type (kill site vs. live site) were compared for each variable using F-tests, which revealed that variances were unequal for mean viewshed and minimum distance to edge. Where data were not normally distributed, non-parametric tests were used and variables with normal distribution were analysed using parametric ANOVA and T-tests. Categorical variables (i.e. habitat type and level of long-term predation risk by male and female lion) at kill versus live sites were analysed using Chi-squared tests. Levels of long-term predation risk, ranging from 0-10 were grouped into three broader risk categories; low risk areas (0-2), medium risk areas (3-6) and high risk areas (7-10) (see chapter two section 2.2.7.2b), to allow for an adequate number of kills in each category for analysis.

3.2.2) Space-use overlap

3.2.2.1) Defining eland and lion space use

To assess temporal space use overlap of eland and lion, data analyses were conducted using broad scale GPS data (GPS locations every 6 hours) from collared female eland in Nyathi (n = 4) and MZNP (n = 3) and GPS data from a single male and female lion in each reserve. For details on collaring procedures and GPS data collection, see Chapter two, section 2.2.2. Collared individuals were representative of all eland herds in both sites, respectively (Chapter two). All eland data in each reserve were pooled so that space use overlap with the lions was assessed at the population level. Lion space use was assessed at the sex group level as male and female lion are known to move independently in both reserves (SANParks, unpublished data). Space use by lions was assessed using data from one of the two male lion and the single female lion in each reserve, as males formed coalitions (SANParks, unpublished data).

Overlap of eland and lion space use was assessed at three temporal scales; i) over the full study period (cumulative overlap), ii) seasonally (seasons defined in section 2.2.1.1c) and iii) monthly. The full study period was defined as the length of time for which eland and lion collars were operational at the same time. For each assessment, overlap was estimated at the home range extent (95% UD) and the core area extent (50% UD, Hensman et al. 2013). Eland utilization distributions (UDs) over
the three temporal scales were estimated using the $\alpha$-LoCoH method as described in chapter two, section 2.2.3.1i. Similarly, lion utilization distributions were estimated at the three temporal scales, with the overall and seasonal home range and core areas assessed using the $\alpha$-LoCoH method and monthly UDs assessed as described below in section 3.2.2.2. In Nyathi, the female lion collar stopped data collection in early February 2014. Therefore, the full study period in Nyathi was between March 2013 (when eland collars were deployed) and January 2014 (when the female lion collar ceased working) i.e. an 11 month period. In MZNP, the full study period was between May 2013, when eland collars were deployed, and April 2014.

3.2.2.2) Lion and eland space use overlap at varying temporal scales

Due to the low total number of monthly lion GPS locations acquired (Table 3.1), utilization distributions could not be calculated using the approach used to identify eland UDs (value of $\alpha$ calculated using the auto.a function with a minimum of 15 nearest neighbours), as these parameters overestimated lion space use, given the smaller sample size. The appropriate value of $\alpha$ was identified for each month by first identifying the minimum number of nearest neighbours, and then establishing the best value of $\alpha$ by examining the isopleth area and edge:area curves (Lyons et al. 2014). The isopleth area curve indicates the change in isopleth size as the number of nearest neighbours increases. A sharp increase in isopleth size over two consecutive values of nearest neighbours indicates the point at which the number of nearest neighbours begins to over-estimate the isopleth area (Lyons et al. 2014). The edge:area curve is used to identify the value of nearest neighbours needed to ensure that the core area is properly defined i.e. that the number of nearest neighbours is not too small (Lyons et al. 2014). Using these methods, the number of nearest neighbours used to define monthly lion UDs was reduced to between 6 and 10, depending on the sample size for each month. Defining the value of $\alpha$ in this manner ensured that the monthly utilization distributions of lion, derived from the smaller number of locations, were estimated using an appropriately adjusted number of nearest neighbours and hence, value of $\alpha$. 
Table 3.1 Number of GPS fixes used to define 95% and 50% utilization distributions of eland and lion at different temporal resolution in Nyathi and MZNP.

<table>
<thead>
<tr>
<th>Reserve</th>
<th>Temporal scale</th>
<th>Eland (pooled)</th>
<th>Female lion</th>
<th>Male lion</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nyathi</td>
<td>Overall (11 months)</td>
<td>4718</td>
<td>1564</td>
<td>1808</td>
</tr>
<tr>
<td></td>
<td>Monthly (mean ± SE)</td>
<td>329 ± 26</td>
<td>140 ± 14</td>
<td>138 ± 14</td>
</tr>
<tr>
<td></td>
<td>Wet season</td>
<td>2878</td>
<td>812</td>
<td>1104</td>
</tr>
<tr>
<td></td>
<td>Dry season</td>
<td>1840</td>
<td>752</td>
<td>704</td>
</tr>
<tr>
<td>MZNP</td>
<td>Overall (12 months)</td>
<td>4359</td>
<td>1492</td>
<td>1360</td>
</tr>
<tr>
<td></td>
<td>Monthly (mean ± SE)</td>
<td>360 ± 11</td>
<td>124 ± 6</td>
<td>112 ± 5</td>
</tr>
<tr>
<td></td>
<td>Wet season</td>
<td>2494</td>
<td>819</td>
<td>747</td>
</tr>
<tr>
<td></td>
<td>Dry season</td>
<td>1865</td>
<td>673</td>
<td>613</td>
</tr>
</tbody>
</table>

3.2.2.3) Defining space use overlap

The percent overlap between lion and eland 95% and 50% UDs was assessed using the ‘rgeos package’ (Bivand & Rundel 2013). For each temporal scale, the area of overlap between eland and lion home ranges and core areas was calculated using the gIntersection function in R. The percent of the eland UD overlapped by the corresponding male and female lion UD was calculated by dividing the area of overlap by the total size of the eland UD. The percent overlap at the home range and core area was thus calculated over the full study period, for each season of the study period and for each month in each reserve.

3.2.3) Movement response analyses

3.2.3.1) Defining encounter points and encounter proximities

To assess the fine scale response of eland to lion proximity, changes in the rate of movement before and after lions were within varying distances of eland (i.e. potential lion encounters) were investigated. Eland responses to lions were investigated using eland locations with temporally matching lion fixes (eland and lion locations recorded at the same time) and the distance between them (hereafter referred to as the encounter proximity). To increase the number of simultaneous eland and lion fixes, as well as to assess fine scale eland movement in response to lion proximity, fine scale eland data (GPS locations every hour) were used for these analyses (see section 2.2.2.3). Hourly eland fixes were acquired from all collared individuals in Nyathi (n = 4) and MZNP (n = 3). In Nyathi, eland NF4 was killed by lions in October 2013, resulting in only one week of hourly data collection for this individual. For each reserve, hourly eland GPS locations were pooled, so that
movement responses were assessed at the population level. A schematic diagram is provided (Fig. 3.1) at the end of this section (3.2.3) to provide a simplified outline of the methods detailed below.

Lion GPS fixes in Nyathi were received every four hours, with fixes recorded at 03h00, 07h00, 11h00, 15h00, 19h00 and 23h00. Lion fixes in MZNP were recorded on a six hour schedule, with fixes recorded at 06h00, 12h00, 18h00 and 00h00. Lion locations from one male and one female in each reserve were used for these analyses. The collar on the female lion in Nyathi stopped working in early February 2013, thus analyses in Nyathi were conducted using the first six of the nine weeks of hourly eland GPS locations (n = 2829). Data analyses in MZNP were conducted using nine weeks of hourly eland GPS fixes (n = 4423).

All hourly eland GPS data and female and male lion GPS data from each reserve, recorded in decimal degrees, were re-projected to Universal Transverse Mercator (UTM) [WGS84, zone 35S] for further analysis. Using the date and time of recorded eland GPS locations, temporally matching male and female lion locations were identified in each reserve. In Nyathi, 565 and 592 eland locations had temporally matching female and male lion location data, respectively. In MZNP, 636 and 570 eland locations had temporally matching female and male lion locations, respectively. Eland locations with temporally matching male or female lion locations are hereafter termed potential encounter points. The distance between temporally matching eland and lion points was then measured (hereafter referred to as encounter proximity) using the ‘aspace’ package (Bui et al. 2012) and represented a lion proximity distance for each potential encounter point.

3.2.3.2) Defining movement rates and change in movement rates

Eland movement rate was calculated by summing eland step lengths for 24 hours before and after potential encounter locations, with step length defined as the straight line distance (m) between two successive hourly GPS locations (Middleton et al. 2013). This summation provided a cumulative 24 hour distance before and after each potential encounter point. These cumulative distances were then divided by 24 to calculate the average eland movement rate per hour before and after potential lion encounters. For each potential encounter point, the change in movement rate (hereafter referred to as encounter movement) was calculated by subtracting the movement rate before an encounter point from the movement rate after an encounter point. A positive outcome therefore represented an increase in movement rate following a potential encounter (m/hr before < m/hr after), and a negative value indicated a decrease in movement rate after a potential encounter (m/hr before > m/hr after).

Given that lion locations were obtained every four and six hours in Nyathi and MZNP, respectively, it is acknowledged that the estimated lion proximities provide an incomplete representation of lion and eland interactions. The identified eland and lion GPS points providing simultaneous GPS
locations may not reflect the start point of a movement response by eland, as eland movements may have been influenced by an encounter with a lion that occurred in the hours preceding the identified matched location (i.e. between successive lion fixes). In this way, movements measured ‘before’ a potential encounter may, in fact, have been movement occurring after an unidentified encounter. Measuring the movement response over 24 hours, rather than at a finer temporal scale allowed for cumulative movement patterns to be identified thereby accounting for the coarse nature of the encounter points identified.

3.2.3.3 Identifying eland movement response to lion

To investigate eland movement rates as a function of lion proximity, encounter movement was assessed in relation to a range of lion encounter proximity categories. Prey species alter their behaviour in response to lion presence within 2 km (Fischhoff et al. 2007; Valeix et al. 2009). Using this distance as a baseline, encounter proximities were categorised as < 2 km, 2-4 km, and > 4 km. For each reserve, potential encounter points and their corresponding encounter movement rates were divided into the three proximity categories. An ANOVA was conducted to assess whether encounter movement differed across the three proximity groups. For these baseline proximity distances, no difference was found in the rate of eland movement (see results, section 3.3.3) so the proximity categories were redefined as < 1.5 km, 1.5-3 km and > 3 km. Once again, encounter movement rate was assessed against proximity group using an ANOVA. Encounter movements were found to differ across the redefined proximity categories (see results, section 3.3.3). A Tukey Post-Hoc Test revealed that encounter movement when lion were within 1.5 km was greater than encounter movement observed when lions were between 1.5 km – 3 km of eland and > 3 km from eland in Nyathi, but not in MZNP (see results, section 3.3.3). Proximity distances were redefined to <1 km, 1 km – 2 km and > 2 km to test whether a change in movement rate occurred in MZNP at a closer proximity to lions. However, no movement response was detected (see results, section 3.3.3) for eland in MZNP.

3.2.3.4 Variables that influence eland movement response to lion

Encounter movements were assessed in relation to the sex of the lion encountered, the long-term level of male and female lion predation risk at the encounter point, the habitat type at the encounter point and whether the encounter occurred at night or day. The influence of these variables on encounter movement was investigated for all encounters within 1.5 km of lion as lion within this proximity were shown to influence eland encounter movement (see results, section 3.3.3). Encounters were classified as occurring during the day or night, defined by the time of ecological sunset and sunrise (Nouvellet et al 2008, see section 2.2.7.2i). Encounter points were projected into ArcGIS 10.1 to extract habitat and long-term predation risk data from habitat (see
sections 2.2.3.1ii) and long-term predation risk raster layers (see section 2.2.7.2b). The level of long-term predation risk at the encounter point, ranging from 0-10, was grouped into two broad risk categories; low risk areas (0-4) and high risk areas (5-10) due to the low number of encounter points occurring at locations associated with high levels of long term male predation risk. i.e. in Nyathi and MZNP, the highest level of male lion predation risk at an encounter point was 7 and 8 out of a potential risk level of 10, respectively.

1) Identify temporally matching lion and eland GPS locations  
   = Potential encounter points

2) Calculate distance between temporally matched eland and lion locations  
   = Encounter proximity

3) Calculate eland movement rate 24 hours before and after potential encounter point  
   = meters per hour moved by eland before and after potential encounter point

4) Subtract movement rate (m/hr) before encounter from movement rate (m/hr) after encounter  
   = encounter movement; positive outcome shows increase in movement rate following encounter and negative outcome shows decrease in movement rate following encounter

5) Potential encounter points (1) grouped based on encounter proximity (2) to test effect of lion proximity on encounter movement (4)  
   = movement rate significantly greater when lions within 1.5 km (in Nyathi only)

6) Investigate variables that affect eland movement response to lions within 1.5 km  
   = covariates analysed; habitat type, long-term predation risk, lion gender and time

Fig. 3.1 Schematic diagram of the steps followed to assess the movement response of eland to lions at a fine spatiotemporal scale.
3.2.3.5) Data analyses

Data were tested for normality by examining quantile plots of encounter movement data against encounter distances (Zuur et al. 2009), which revealed that the data were normally distributed. Variances were compared using F-tests which revealed that variances were equal for all two-factor variables. Student’s T-tests were used to test two-factor variables i.e. lion gender (male vs. female), level of long-term predation risk (low vs. high) and time of encounter (day vs. night). ANOVAs were used to assess whether habitat type at the encounter point influenced encounter movement, followed by a Tukey Post-Hoc test in the case that the ANOVA revealed a significant difference between the habitat types.

3.3 Results

3.3.1) Eland kills in Nyathi and MZNP

During the study period, 13 and 22 eland kills were found in Nyathi and MZNP, respectively. The number of herd-associated kills was significantly higher in Nyathi than in MZNP (G = 9.3, df = 1, p =0.002). Of the 13 kills in Nyathi, 4 were adult bulls and 9 were herd-associated eland i.e. adult or sub-adult females and juveniles. In MZNP, only 4 of the 22 kills were female eland with the remaining 18 kills identified as adult bulls. The sex of the lion attributed to majority of the eland kills differed across sites (G = 5.8, df = 2, p= 0.05), with male lions present at 11% and 75% of all herd-associated eland kills in Nyathi and MZNP, respectively. In Nyathi, 22% of the kills were shared.

3.3.1.1) Eland kill site analyses

The level of female lion predation risk at kills sites in Nyathi was significantly higher than at live sites (G=8.38, df = 2, p < 0.05, Fig. 3.1). Almost half of the herd-associated kills (46%) occurred at locations associated with high levels of female predation risk, whereas only 10% of the live sites occurred in high female lion risk areas. Thirty-one percent of kills occurred in low female lion risk areas, whereas 62% of live sites occurred in these low female lion risk areas. The level of male lion predation risk was also significantly higher at kills sites compared to live sites (G = 12.72, df = 2, p < 0.05, Fig. 3.1). Most kills (54%) occurred at locations associated with intermediate levels of male lion risk. Fifteen percent of kills occurred in high male risk areas, whilst no live sites occurred in such high male predation risk areas. The majority of live sites (74%) occurred in low risk areas.
Fig. 3.2 Percent of kill sites (n = 13) and live sites (n = 58) in high, medium and low predation risk areas of the female and male lions in Nyathi.

Fig. 3.3 Percent of kill sites (n = 13) and live sites (n = 58) in open, mixed and dense habitats in Nyathi.
Table 3.2 Average value and test statistics of landscape attributes at herd-associated kill sites (n = 13) and eland live sites (n = 58) in Nyathi.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Kill sites</th>
<th>Live sites</th>
<th>Test statistic</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>Median</td>
<td>SE</td>
<td>Mean</td>
</tr>
<tr>
<td>Ruggedness</td>
<td>12</td>
<td>11</td>
<td>2</td>
<td>10</td>
</tr>
<tr>
<td>Distance to road (m)</td>
<td>916</td>
<td>911</td>
<td>163</td>
<td>676</td>
</tr>
<tr>
<td>Minimum distance to cover (m)</td>
<td>5</td>
<td>2</td>
<td>1</td>
<td>23</td>
</tr>
<tr>
<td>Average view shed (m)</td>
<td>26</td>
<td>6</td>
<td>10</td>
<td>107</td>
</tr>
</tbody>
</table>

The frequency of habitat type at kill sites was significantly different to that at live sites (G = 6.17, df = 2, p < 0.05, Fig. 3.2). The majority of the kills occurred in mixed habitat types (54%) while the majority of live sites occurred in open habitat types (66%). Fifteen percent of kills occurred in dense habitats, with 13% of the live sites occurring in this type of habitat (Fig. 3.2). Average viewshed and the minimum distance to edge at kill sites were significantly lower than at live sites (Table 3.2). The estimated ruggedness and distance to roads did not vary between kill sites and live sites (Table 3.2).

3.3.2) Temporal variation in eland and lion space use overlap

3.3.2.1) Temporal variation in eland and lion space use overlap in Nyathi and MZN

In Nyathi, the long-term overlap (i.e. measured over the full study period) of eland and lion space use at the home range (95% UD) scale was 84% for the female lions and 73% for male lion (Fig. 3.3a). At the core area (50% UD) scale however, there was no long-term overlap with either female or male lions (Fig. 3.3a). At a monthly scale, eland home range overlap with both the female (average = 35 ± 3%) and the male (average = 28 ± 6%) lions was consistently lower than the long-term home range overlap (Fig. 3.3a). Monthly core area overlap with the male lions was minimal (average = 0.5 ± 0.4%) and consistently lower than with the female lion (average = 19 ± 7%). Similarly, on a seasonal scale, home range and core overlap between eland and the female and male lions was lower than the long-term overlap (Appendix 12a). In MZNP, the long-term overlap of eland space use at the home range scale was 53% for the female lion and 52% for the male lions (Fig. 3.3b). At the core area scale, long-term overlap was 4% and 0.7% for the female and male lion, respectively. At a monthly scale, home range overlap between eland and lions was consistently lower for both the female lion (average = 13 ± 4%) and the male lion (11 ± 2%) than the long-term overlap at the home range level. At the core area, monthly overlap was generally lower for both the female (average = 1 ± 1%) and male (average = 1 ± 0.5%) lions than the long-term core area overlap (Fig 3.3b). Similarly, on a seasonal scale, home range and core overlap between eland and the female and male lions was lower than the long-term overlap (Appendix 12b).
Fig. 3.4 Monthly and cumulative percent overlap in space use in eland and lion home range (95% utilization distribution) and core area (50% utilisation distribution) over the full study period in a) Nyathi (no cumulative overlap at the 50% UD) and b) Mountain Zebra National Park.
3.3.3) Eland movement in relation to lion proximity

3.3.3.1) Defining response proximity

In Nyathi, lions may be influencing eland movement rates when the proximity distance between lion and eland is less than 1.5 km (Fig. 3.5), but not at greater distances (i.e. 2 km, Appendix 13). The average change in movement rates (i.e. encounter movement) differed between encounter distances of < 1.5 km, 1.5 km - 3 km and > 3 km ($F_{2,1154} = 8.18, p < 0.001$; Fig. 3.5), with the biggest change in movement rate occurring when lions were within 1.5 km of eland ($1.5 – 3$ $km; p < 0.005$, $>3$ $km; p < 0.005$). In MZNP, eland movement rates were not influenced by the proximity to lions at a $< 1.5$ $km$, $1.5 – 3$ $km$ and $> 3$ $km$ ($F_{2,1203} = 0.236, p = 0.79$, Appendix 14) or at a $< 1$ $km$, $1$ $km$ – $2$ $km$ or $> 2$ $km$ scale ($F_{2,1203} = 0.697, p = 0.49$, Appendix 15).

![Fig. 3.5 Average change in movement rate of eland 24 hours before and after lion encounters within 1.5 km, 1.5 km – 3 km and > 3 km, with a significant increase in movement rate shown (m/hr before < m/hr after) when lions were within 1.5 km (indicated in red).](image)

3.3.3.2) Movement by eland in response to lion within 1.5 km

In Nyathi, 115 encounter points (lions within 1.5 km of eland) were identified, and 58 were identified in MZNP. Average encounter movement did not differ between male and female lions in Nyathi (males: $\Delta$ movement rate = 53 m/hr, female: $\Delta$ movement rate = 28 m/hr, $t = 1.2$, df = 41, $p = 0.21$) or MZNP (males: $\Delta$ movement rate = -7 m/hr, female: $\Delta$ movement rate = 26 m/hr, $t = -1.2$, df = 49, $p = 0.23$).

In Nyathi, the average encounter movement did not differ when eland encountered lions in low or high long-term predation risk areas of both the female (low risk: $\Delta$ movement rate = 39 m/hr, high risk: $\Delta$ movement rate = 21 m/hr, $t = -0.95$, df = 46, $p = 0.35$) and male lions (low risk: $\Delta$ movement rate
rate = 37 m/hr, high risk: Δ movement rate = 22 m/hr, t = -1.28, df = 5, p = 0.25). Similarly, in MZNP, the average encounter movement did not differ when eland encountered lions in low or high long-term predation risk areas of both the female (low risk: Δ movement rate = -5, high risk: Δ movement rate = 51, t = 1.96, df = 28, p = 0.06) and male lions (low risk: Δ movement rate = 5 m/hr, high risk: Δ movement rate = 52 m/hr, t = 1.10, df = 13, p = 0.29).

In Nyathi, the average encounter movement when eland encounter lions at night was significantly greater than average encounter movement in response to lions that were encountered during the day (day: Δ movement rate = 23 m/hr, night: Δ movement rate = 66 m/hr, t = 2.18, df = 43, p < 0.05, Fig. 3.6). In MZNP, encounter movement was not influenced by the time of day at which lions were encountered (day: Δ movement rate = 13 m/hr, night: Δ movement rate = -6 m/hr, t = -0.86, df = 16, p = 0.54). The average encounter movement did not differ when eland encounter lions in open, mixed or dense habitats in Nyathi (open: Δ movement rate = 37 m/hr, mixed: Δ movement rate = 32 m/hr, dense: Δ movement rate = 3 m/hr, F₂ = 0.36, p = 0.7, Appendix 16) and in MZNP (open: Δ movement rate = 20 m/hr, mixed: Δ movement rate = -1 m/hr, F₂ = 0.36, p = 0.7, Appendix 17).

![Fig. 3.6 Average change in movement rate over 24 hours when lions are within 1.5 km in relation to day encounters (n = 85) and night encounter (n = 30) in Nyathi.](image)

3.4 Discussion

3.4.1) Eland predation in relation to patterns of spatial overlap with lions and habitat features

The pattern of spatial overlap between predators and prey influence their encounter rate, predation rates and ultimately, predator-prey populations and community dynamics (Murdoch & Stewart-Oaten 1989, Krivan 1997) and is thus an important aspect of predator-prey interactions. As
expected, eland in Nyathi, were more vulnerable to predation in areas associated with a high level of long-term predation risk, i.e. a high probability of lion presence. Sites associated with high levels of lion activity thus present an increased risk of mortality to eland, whilst areas of low lion activity may act as predator refugia. Similarly, moose *Alces alces* in Canada were most vulnerable to predation in areas of high wolf use (Kunkel & Pletscher 2000). Woodland caribou *Rangifer tarandus caribou* were also more prone to wolf predation when their spatial distribution overlapped with that of wolves (McLoughlin *et al.* 2005). Behaviours that allow these animals to spatially or temporally avoid areas of high predator density thus represent an important antipredator mechanism (Kunkel & Pletscher 2000; James *et al.* 2004; Dussault *et al.* 2005; McLoughlin *et al.* 2005).

The spatial overlap between herd eland and the female lion, shown by the lack of avoidance of high risk areas within eland home ranges at a broad temporal scale (Chapter two) and the high monthly overlap at the core area, thus likely contributed largely to the increased predation pressure on herd-dwelling eland in Nyathi by the female lion. Similarly, in Addo Main Camp section, the core area of a buffalo herd overlapped a male lion coalitions’ core area by 65% for a period of 4 months, over which time herd buffalo predation was significantly higher than previously recorded (Tambling *et al.* 2013). Male lions were not found to contribute largely to herd eland predation in Nyathi, with this reflecting the spatial asynchrony in time between eland and male lions’ space use. At a broad temporal scale this was shown by the avoidance of male lion high risk areas by eland within their home range (Chapter two), and at a finer temporal scale, by the low monthly overlap between eland and male lion core areas. The low number of eland kills attributed to the male lions may thus be the result of effective predator avoidance whilst failure to avoid areas associated with high levels of female lion risk resulted in increased predation on herd eland by the female lion.

Similarly, elk in Chequamegon National Forest in Wisconsin, USA, reduced predation pressure by selecting areas within their home ranges that were spatially distant from the core area of wolf territories (Anderson *et al.* 2005). Conversely, elk in Yellowstone did not avoid the core areas of wolf territories (Fortin *et al.* 2005). Such contrasting prey behaviours thus challenge the common assumption that predator distribution drives predation risk and hence the distribution of prey (Kauffman *et al.* 2007). This emphasises the importance of considering the influence of landscape and habitat features on the spatial distribution of predation risk (Hebblewhite *et al.* 2005; Hopcraft *et al.* 2005; Kauffman *et al.* 2007). The effect of lions on prey populations is largely determined by landscape features through the mechanisms of habitat-dependent prey vulnerability and predator hunting success (Gorini *et al.* 2010). The dynamics of predator-prey interactions are thus largely affected by fine scale differences in landscape characteristics (Hopcraft *et al.* 2005) as spatial
heterogeneity is an important factor affecting the rate at which a predator can kill and consume its prey (Gorini et al. 2010). Predator-prey interactions may thus vary largely between heterogeneous landscapes and more spatially homogenous landscapes (Gorini et al. 2010). For example, in Etosha National Park, characterised by a relatively homogenous landscape, lion hunting success was most strongly influenced by co-ordinated group hunts and lioness group size, with habitat type having little effect on hunting success (Stander & Elbon 1993). Conversely, studies conducted in less homogenous environments have shown little influence of lion group size on hunting success, but a large influence of habitat features (Schaller 1972; Von Olssol 1984; Funston et al. 2001; Hopcraft et al. 2005; Laorie et al. 2013).

Eland kills occurred most frequently in mixed habitat types, most likely due to the cover provided by vegetation structures (Loarie et al. 2013), as shown by the significantly shorter viewshed and minimum distance to cover at eland kill sites. The risk-associated influence of these habitat features is consistent with the stalking hunting strategy of lions (Von Olssol 1984; Prins & Jason 1988; Funston et al. 2001; Loarie et al. 2013). Patches of high female lion predation risk located in the eland home range occurred largely in mixed habitat. Sites of high female lion risk thus represent areas in the eland home range of both a high probability of encountering the female lion and an increased probability of mortality given an encounter. This may have contributed further to the high proportion of herd-dwelling eland killed in Nyathi by the female lion. Given that eland vulnerability to lion predation was influenced by both the long-term lion activity in an area and the habitat structure, predation risk in Nyathi should thus be considered a function of both lion distribution and habitat features (Kauffman et al. 2007).

Despite the increased risk of predation associated with mixed habitats, eland were shown to select these habitats in both Nyathi and MZNP (Chapter two). Dense habitats were predominantly avoided by eland herds (Chapter two). The small number of kills found in dense habitats in Nyathi reflects the limited use of this habitat by eland (Chapter two) and shows that avoidance of dense habitats effectively limited predation. The selection for mixed habitats may thus reflect the outcome of the trade-off between safety from predation and access to vegetation on which to browse (Sinclair 1985; Lima & Dill 1990). In Alberta, Canada, caribou were preyed upon by wolves most frequently in well-drained uplands yet avoidance of these areas was not absolute and some caribou individuals actively selected uplands (McLoughlin et al. 2005). This was attributed to the abundance of forage resources associated with this habitat type (McLoughlin et al. 2005). Use of these risky areas thus represented a trade-off between energy intake and predation risk. Similarly, elk in Yellowstone increased their use of open areas in winter after wolves were reintroduced, despite these areas being more risky.
than forested areas (Kauffman et al. 2007). Again, this seemingly dangerous habitat selection indicated that, during winter, elk in Yellowstone faced a clear trade-off between forage quality and predation risk (Kauffman et al. 2007).

Although eland predation was lower in open habitats than mixed habitats, potentially explaining the strong selection for this habitat type in Nyathi (Chapter two), open habitats did not provide complete safety from predation. This is largely due to the increase in eland vulnerability to ambush predation at the ecotone between open habitats and more dense habitats, as demonstrated by all eland kills located in open habitats occurring within a short distance of the habitat edge. The safety benefits provided by open habitats thus appear to be lost at the interface between open and denser habitats. Buffalo were similarly killed by lions on open plains when within 100 m of ecotones between open and dense habitats in Lake Manyara National Park, Tanzania (Prins & Iason 1988). Similarly, forest edges are associated with an increased risk of predation for mule deer *Odocoileus hemionus* under predation pressure from ambush hunters such as mountain lions *Felix concolor* (Altendorf et al. 2001) and pumas *Puma concolor* (Laundré & Hernández 2003).

The data thus show that predation risk for eland is a function of not only the spatial distribution of lions but also of habitat features that rendered eland more or less vulnerable to lion predation once encountered (Hebblewhite et al. 2005). Integrating the probability of lion presence and habitat features thus represents the landscape of fear experienced by eland in Nyathi (Laundré et al. 2001; 2010). Areas of high long-term lion activity in mixed habitats characterise high risk areas while areas of low lion activity in habitats of limited structural cover represent sites of refugia. The spatial scale of safe and risky patches influences the ability of prey to manage the risk of predation while foraging, moving and selecting habitats (Brown & Kotler 2004). Thus, the mosaic of risky and safe areas available to eland in Nyathi, given the fine scale spatiotemporal variation in lion presence and habitat heterogeneity, indicates that eland may reduce the risk of predation through fine scale movements, which may be as effective as broad scale avoidance (Hebblewhite & Merrill 2009a, 2009b). For example, despite considerable predation risk from wolves at a broad scale, resident elk in Banff National Park, Canada, adopted fine scale trade-offs that allowed them to reduce predation risk to the same degree as migratory elk that reduced the risk of predation through broad scale avoidance (Hebblewhite & Merrill 2009a).

Unlike in Nyathi, most of the eland killed in MZNP were adult bulls (assumed not to be herd-dwelling animals), killed by male lions. Similar to observed eland predation in MZNP, males of prey species are often preferentially killed by lions (Hirst 1969; Rudnai 1974; Schaller 1972; Prins & Iason 1988). For example, in Nairobi National Park, male eland killed by lions represented 89% of all eland killed
over a four year period, even when the population was female dominated (Rudnai 1974). Eland exhibit sexual segregation where females and young often occur in large, mobile herds in open habitats (Hillman 1988). Herd-associated eland thus reduce predation risk by selecting habitats that reduce the hunting success of lions (Funston et al. 2001) and by occurring in large groups that offer increased vigilance (Hamilton 1971). Conversely, mature males spend most of their time alone or in small bachelor groups which are much less mobile and occupy dense habitats which offer better forage but are associated with increased predation risk (Hillman 1988). Individuals that occur alone or in small bachelor groups may be easier to capture due to lower group vigilance (Hamilton 1971). Furthermore, in the Kruger National Park, South Africa, and Lake Manyara National Park, Tanzania, bachelor buffalo Syncerus caffer males experienced predation risk up to four times and three times higher, respectively, than that of female buffalo in herds, due to their selection of denser habitats (Prins & Iason 1988; Hay et al. 2008). The higher proportion of male eland kills compared to herd-dwelling eland in MZNP may thus reflect the tendency for male eland to select dense, and thus more dangerous, habitats (Hillman 1988). In MZNP, areas associated with high levels of male lion activity occurred in these dense habitats along the Wilgeboom River (Chapter two). Similarly, all male eland kills located in MZNP were found in dense habitats along the river and in (or near) drainage lines (D.B. van der Vyver, Personal observation). Male eland may have selected these areas as they retain more moisture, and thus provide better forage, particularly during the dry season, as seen with male buffalo in Kruger National Park (Macandza et al. 2004; Hay et al. 2008). MZNP is fairly seasonal and generally drier than Nyathi, particularly in the dry season (Appendix 11). Male eland may thus have accepted increased levels of predation risk to increase energy intake during the dry season. Bachelor males of several sexually dimorphic ungulates trade-off safety for better forage quality outside the breeding season (Miquelle et al. 1992; Main et al. 1996; Bleich et al. 1997; Hay et al. 2008). This may be driven by males seeking to optimise their body condition so as to be more competitive for mating opportunities (Miquelle et al. 1992; Main et al. 1996; Bleich et al. 1997).

The limited predation on herd-dwelling eland in MZNP may indicate that herd-associated eland effectively minimised predation. Only 2% of the herd-associated eland home range in MZNP consisted of dense habitats (Chapter two). Their use of dense areas, associated with an increased probability of predation by lions (Funston et al. 2001; Hopcraft et al. 2005; Loarie et al. 2013), was thus minimal. Unlike the male eland that appeared to use these dense habitats, indicated by the number of male eland kills located in such areas, female eland in herds with young likely avoided these areas due to the increased predation risk in these habitats. Females with offspring are thought to select predator-safe habitats even at the expense of forage quality given the increased vulnerability of young animals to predation (Miquelle et al. 1992; Main et al. 1996; Bleich et al. 1997;
Barten et al. 2001). There was a high degree of spatial asynchrony in time between herd-associated eland and lions in MZNP, as shown by the low monthly overlap at both the core and home range level, thus encounter rates were likely low. Furthermore, larger group sizes provide increased vigilance and thus increases early predator detection (Hamilton 1971).

It should be noted that eland kills that were successfully located in MZNP and Nyathi may not be a full representation of all eland kills that occurred, as smaller kills (i.e. eland juveniles and calves) are often consumed entirely by lions or scavengers and therefore may not be located using the GPS cluster investigation methods (Tambling et al. 2010; 2012b).

3.4.2) Movement in relation to lion proximity

In Nyathi, lions within 1.5 km evoked a behaviourally-mediated movement response in eland. At a fine spatiotemporal scale, male and female lions caused equally strong behavioural response in eland. Furthermore, the level of long-term predation risk was not an important driver of the behavioural response of eland to the close proximity of lions while the time (i.e. day versus night) was shown to affect the response. At a fine scale, the movement response of eland to lions thus appear to be in agreement with the risky times hypothesis which stipulates that prey species engage antipredatory behaviours only when predators are present, regardless of previous presence or absence of predation risk in the area (Creel et al. 2008). The fine scale behavioural responses of eland to lions thus differed to those observed at a broad scale, which appeared to be more supportive of the risky space hypothesis in that eland were shown to avoid areas based on long-term background levels of predator presence (Creel et al. 2008; Chapter two).

When lions were detected within 1.5 km at night, eland increased their rate of movement more than when detected at close proximity during the day. Lions are more active at night and have higher hunting success under the cover of dark (Funston et al. 2001). The level of threat perceived by eland at night may thus be higher than during the day, as reflected by their increased movement rate in response to lions at close proximity at night. Although time of day did not influence eland resource selection at the home range scale (Chapter two), results from this chapter indicate that eland are sensitive to fine scale temporal variation in predation risk, and respond accordingly. Similarly, plains zebra (Equus quagga) Ol Pejeta Conservancy, Kenya, increased movement rates and made sharper turns at night, when predation risk was highest (Fischhoff et al. 2007).

Eland predation in Nyathi was habitat-specific, with eland more vulnerable to predation in habitats providing structural complexity. The behavioural movement response of eland to lions at close proximity was, however, not influenced by habitat type. Conversely, elk movement in response to
wolf presence in Yellowstone was habitat dependent, with movement rates being faster in forested areas than on open grasslands (Proffitt et al. 2009). The lack of a habitat-specific movement response by eland to lions at close proximity indicates that, at a fine scale, eland behaviour is influenced by predation risk regardless of the surrounding habitat features and their influence on lion lethality. The indirect effects of predation are therefore not reduced in open habitats despite such habitats being associated with decreased predation risk. Thus, when lions are in close proximity to eland in Nyathi, eland perceive an increased level of threat and respond by increasing their rate of movement regardless of lion gender, background levels of predation risk or habitat type. Such fine scale movement by eland may be an important predator avoidance technique, allowing eland to move away from approaching lions, given that lion hunts are more successful when they utilise an ambush hunting strategy at close range (Funston et al. 2001). Thus eland movements in response to lions at a fine spatiotemporal scale may represent an important mechanism by which eland dynamically maintain a safe distance between themselves and detected lions or move into safe habitats when lions are detected (e.g. Valeix et al. 2009).

These analyses reveal that once eland acquire a signal of lion presence, they respond through behaviourally-mediated adjustments in their movement rate. The movement rate of elk in Yellowstone similarly increased when wolves were nearby (Proffitt et al. 2009; Middleton et al. 2013). The proximity at which wolves were reported as causing a behavioural responses in elk, however, varied, with Middleton et al. (2013) reporting that elk were only affected by wolves within 1 km, whilst Proffitt et al. (2009) and Liley & Creel (2008) found that elk were sensitive to wolf presence up to 5 km and 3 km away, respectively. In Hwange National, Zimbabwe, lions within a 2 km radius influenced the habitat preference of both grazers and browsers (Valeix et al. 2009). Similarly, plains zebra displayed intense vigilance when lions were within 2 km (Périquet et al. 2012).

The quantification of a prey's perceptual range (or the range within which signs of predators can trigger a response) is important when investigating the impact of predators on prey species as behaviourally-mediated responses by prey are dependent on preys’ spatial and temporal perception of risk (Latombe et al. 2013; Barnier et al. 2014). The perceptual range of prey is thus important because behavioural responses to variation in predation risk carry costs through their influence on prey energetics and physiology (Barnier et al. 2014). Behavioural responses such as habitat shifts and increased vigilance are often associated with decreased energy gains (Brown & Kotler 2004). For example, zebras in Hwange which had been in close proximity to lions had a lower quality diet (Barnier et al. 2014). Behavioural adjustments by eland when lions are in close proximity may thus carry nutritional and energetic costs which may translate into changes in prey population.
demographics over time (see Creel & Christianson 2008). The strength of these nonlethal effects of predation are influenced by the rate at which eland and lion encounter one another on the landscape, with low encounter rates predicted to limit the indirect effects of predation (Brown 1999; Middleton et al. 2013).

Given the discrete nature of the lion GPS location data (lion locations recorded every 4 hours in Nyathi), the frequency and strength of antipredatory responses by eland in Nyathi, where high spatial overlap between lions and eland exists, were likely underestimated by this study (see Creel et al. 2013). In MZNP, the lack of a change in eland movement rates in response to lions at close proximity however, is potentially largely a reflection of the low spatial overlap at the monthly scale and thus a low encounter rate. Eland in MZNP were largely spatially temporally separated from lions, so that fine scale responses to lions were not relied on to reduce predation risk. Eland in Nyathi are thus probably more affected by the indirect effects of predation than eland in MZNP.

Results from this chapter indicate that eland experience increased levels of predation in denser habitats, with a short distance to cover shown to be common across all eland kill sites. Avoidance of core areas of lion territories was apparent in both study sites, except in the case of the female lion in Nyathi. Consequently, herd-associated eland predation was highest in Nyathi and is attributed predominantly to the female lion. At the finest spatiotemporal scale, eland avoid close-range encounters with lions by increasing their rate of movement when lions are in the immediate vicinity (i.e. within 1.5 km), with movement rates particularly heightened when lions are detected at night. These fine scale responses of eland to lions likely represent essential antipredator behaviours that allow eland and lions to co-exist, particularly where eland and lion space use overlap. The nutritional and energetic costs of behaviourally-mediated responses that reduce the risk of predation may have adverse effects on eland populations, particularly in Nyathi, where the landscape is dominated by risky habitats. In Nyathi, eland home ranges are thus limited by the low availability of preferred habitats, which overlapped with lion territories, thereby increasing the rate of lion-eland encounters. Confirmation of this would however require further research aimed at investigating the long-term effect of indirect predation on eland population dynamics.
Chapter 4

Concluding discussion

This study set out to investigate how eland *Tragelaphus oryx* respond to lions *Panthera leo*, their major predator, at multiple scales to contribute to the larger field of how predators and prey interact. Specifically, the study aimed to assess the antipredatory avoidance mechanisms employed by eland on both spatial and temporal scales. In terms of exploring predator-prey interactions, the eland-lion system is particularly relevant. This is because of the preference of lions for eland as a prey species in terms of their body size (Hayward & Kerley 2005). Furthermore, eland are not swift runners, and although they are known to actively defend themselves and their calves against lions (Estes 1991), observed population declines (Tambling & du Toit 2005; Louw *et al.* 2012; SANParks, unpublished data) indicate that this may not be an effective antipredatory strategy. This suggests that eland have to employ alternate antipredatory behaviours to persist under predation pressure.

Eland are nomadic, known to move vast distances and range extensively (Schaller 1972), and are the African antelope with the largest home ranges (Hillman 1988). Given that large scale movements allow prey species to avoid predators (Schaller 1972; Bergerud *et al.* 1984; Fryxell *et al.* 1988), it was hypothesised that elands’ primary antipredatory mechanism is that of landscape scale avoidance of predators such that other antipredatory strategies may not be under strong selective pressure (Brodie & Formanowicz 1991; Louw *et al.* 2012). A lack of investment in fine scale escape strategies may thus increase eland vulnerability to predation where their nomadic behaviour is compromised.

In the current context of wildlife populations largely restricted to small, fragmented conservation areas in South Africa, into which apex predators are increasingly being reintroduced (Hayward *et al.* 2007), a need exists to understand how eland populations cope with predation pressure when their natural, large scale movement is restricted. Severe declines in eland populations following lion reintroductions in several small reserves across South Africa (Tambling & du Toit 2005; Louw *et al.* 2012; SANParks, unpublished data) emphasise the relevance of this study from a wildlife management perspective. Furthermore, there exists a dearth of research on the response of African bovids to predator reintroductions (Tambling *et al.* 2012a). This is a problem given the diversity of African bovids and predators and the increasing number of large carnivore reintroductions in Africa (Hayward *et al.* 2007).

Predator reintroductions provide a powerful natural experiment to study antipredator responses (Tambling *et al.* 2012a). This study provides one of the first assessments of antipredator responses of eland at multiple scales and thus contributes to our understanding of eland ecology and the
conditions required for eland persistence under predation pressure in spatially limited reserves. Eland responses to predation risk were investigated through

1. Determining eland habitat selection at the landscape scale (2nd order) and the drivers of eland resource selection at the home range (3rd order, Chapter two).

2. Investigating fine scale lion-eland interactions in terms of the patterns of spatial overlap at multiple temporal scales, and the behaviourally-mediated movement response of eland to lions at a fine spatiotemporal scale (Chapter three).

3. Determining common features across sites of eland mortalities to assess where on the landscape eland are failing to avoid predation (Chapter three).

4.1 Study limitations

It is important that findings from this study are interpreted in the light of a number of limitations pertaining to the data collected and the study design used. The most pertinent limitation to this study was the small sample size in terms of the number of eland individuals collared in each reserve (n = 3). For analyses such as home range estimation and resource selection functions (Chapter two), a small sample size is cautioned against if population-level inferences are the objective (Leban et al. 2001; Börger et al. 2006). Although the number of collared individuals was small, the regular monitoring of eland herds, particularly in the case of the Nyathi population, confirmed that all eland herds were represented by at least one collared individual, and that the herds were generally stable despite occasional fission-fusion movements between herds (personal observation). Thus, the strong herd-forming tendencies of female eland and the small number of eland herds (confirmed by extensive camera trapping across Nyathi, Craig Tambling, unpublished data) in each reserve increased the capacity of the small sample to be considered representative of the herd eland population in Nyathi and MZNP, respectively. Nonetheless, population-level inferences from this study should be considered cautiously (Hebblewhite & Haydon 2010).

The limitations of a small sample size are again considered in terms of the number of reserves (n = 2) in which lion-eland interactions were investigated. Furthermore, the sample reserves were not matched in size (Nyathi = 14 000 ha, MZNP = 28 000 ha) or underlying vegetation type, with Nyathi dominated by thicket vegetation while MZNP is predominantly Nama-Karoo and grassland vegetation (Chapter two). Given the opportunity presented by Nyathi and MZNP as study sites to investigate the dynamic interactions between lions and eland in small reserves, it was not possible to deal with these constraints. Generalisations of the study results beyond the boundaries of the study sites investigated should thus be considered cautiously (Bissonette 1999). However, the study sites investigated presented an interesting opportunity to investigate predator-prey interactions in two
distinct systems of contrasting environmental conditions and ecological processes (Laundré et al. 2014). To address the constraints of a small reserve sample size, future studies of this nature should be conducted across a number of sites where eland and lions co-exist in different sized areas and with different habitat features (e.g. biomes, productivity etc.).

At the species level, the study was limited in that only female eland were collared such that sex-specific responses to predation risk could not be assessed. Eland are sexually dimorphic both morphologically and behaviourally (Underwood 1975; Hillman 1988). Furthermore, lion predation is often not equal across sex classes within a prey species (Mills & Shenk 1992; Rudnai 1974, Chapter three). However, female eland were collared specifically due to their stronger herd-forming tendencies which helped effectively deploy the small number of GPS collars available for the study. To make species-level inferences regarding the effect of lions on eland in small reserves, this study should be repeated with collars deployed on both female and male eland, and the sex-specific strategies explored.

Despite these limitations, this study provided important insights into the impact of predation risk on eland at multiple scales. This emphasises the relevance of a multi-scale research approach (Johnson 1980; Wiens 1989; Caro 2005; Hebblewhite & Merrill 2007). In addition, this study provides valuable insight on how to take research in this field forward. Particularly, the use of GPS technology to collect movement data from coexisting predator and prey species at the same time provides a powerful technique for assessing prey species’ responses to mobile predators at multiple spatial and temporal scales.

4.2 Synthesis of results

Prey avoidance of predators is scale-dependent, driven by the dynamic interactions between predators, prey and their environment (Johnson et al. 2002; Creel et al. 2005; Dussault et al. 2005; Kittle et al. 2008; Hebblewhite & Merrill 2007;2009; Courbin et al. 2013; Latombe et al. 2013). The main prediction of this study was that eland avoid lions at a broad spatial scale, however, findings of this study did not support this prediction. At a finer scale, eland avoided lions. Eland avoidance of lions was scale-dependent and not ubiquitous, similar to the avoidance strategies of many prey species in response to their major predators ([elk Cervus elaphus, Creel et al. 2005]; [moose Alces alces, Dussault et al. 2005]; [plains zebra Equus quagga Fischhoff et al. 2007]). Prey responses to predators may also be site-specific due to the complex biotic and abiotic interactions that influence predator-prey dynamics (Hopcraft et al. 2010). In this study, there was a large disparity in the proportional representation of different habitat types (based on vegetation structure) at the landscape scale and seasonal variation between the two study sites. Common across both reserves
however was the presence of lions at low densities. Thus, eland responses to lions differed between the two reserves studied, driven largely by variation in landscape scale variables.

Spatially, prey avoid areas of high predator activity, reducing their probability of encountering predators on the landscape (Anderson et al. 2005; Dussault et al. 2005; Valeix et al. 2009; Thaker et al. 2011). For prey of territorial predators, such as lions, areas of high use may be fairly predictable and thus avoidable by prey (Thomson et al. 2006). At a broad spatial scale, prey may avoid predator home ranges so that predators and prey are spatially separated, a behaviour that allows caribou Rangifer tarandus caribou, for example, to minimise wolf predation (Seip 1991; Rettie & Messier 2000; James 2004). Broad scale spatial avoidance of this nature is often not possible however, for example, wolves Canis lupus occupy essential winter feeding grounds for elk in Yellowstone National Park (Moa et al. 2005). Avoidance of wolves would thus expose elk to increased risk of starvation (Fortin et al. 2005; Moa et al. 2005). Avoidance of predators at finer scales is thus an important mechanism allowing prey to balance food and safety (Creel et al. 2005; Fortin et al. 2005; Fischhoff et al. 2007). Eland in both study sites had considerable home range overlap with lions but avoided areas of high lion activity within their home ranges (Chapter two). In both study sites, this avoidance was lion gender-specific with areas of high male lion activity avoided whilst areas of high female lion activity were not avoided. Thus, the interaction between the female lion and eland in Nyathi and MZNP represented a case where prey do not avoid areas of high predator activity (Fortin et al. 2005; Moa et al. 2005; Kittle et al. 2008; Theuerkauf & Rouys 2008). At the finest spatiotemporal scale, eland increased their rate of movement when lions were detected in the immediate vicinity (i.e. within 1.5 km), particularly at night (Chapter three). This response is similar to that of elk to wolves and represents fine scale spatial avoidance of predators (Liley & Creel 2008; Proffitt et al. 2009; Middleton et al. 2013). At this fine spatial scale, eland were sensitive to temporal variation in predation risk, a response that was not revealed at the home range scale as time of day was not an important driver of eland resource selection (Chapter two).

Temporal variation in predation risk influences the antipredatory responses of prey at multiple scales (Lima & Bednekoff 1999). The relationship between eland and lions supports the idea that the spatial relationships between predator and prey are dependent on both the spatial and temporal scales at which they are investigated (Johnson et al. 2002; Anderson et al. 2005; Creel et al. 2005; Heithaus & Dill 2006; Hebblewhite & Merrill 2007; 2009). Investigating prey responses to predators at multiple spatiotemporal scales provides dynamic and comprehensive insight into predator-prey interactions. Over a broad temporal scale (i.e. the full study period), lion home ranges were not avoided, however core use areas of eland and lions were spatially separate (Chapter three).
corroborated the finding that eland avoided areas of high predator activity within their home range (Chapter two). At a finer temporal scale (i.e. monthly), overlap between eland and lion home ranges was largely reduced, except in the case of the female lion in Nyathi (Chapter three). Eland and lion space use was predominantly asynchronous in time when investigated at a finer temporal scale. At a broad spatiotemporal scale, the spatial coincidence between predators and prey may be interpreted as the predator having succeeded in its attempt to occupy areas where prey are abundant (Sih 2005; Heithaus & Dill 2006). However, at finer spatiotemporal scales, the spatial overlap between predators and prey may be minimal, indicating that prey have achieved their goal of avoiding areas of high predator activity (Sih 1984). Asynchronous space use at finer spatiotemporal scales may be due to prey abundance being less predictable and antipredatory behaviours being more effective at finer scales (Heithaus & Dill 2006). The considerable overlap between eland and the female lion in Nyathi at the monthly scale but not at the broad temporal scale suggests that either the female lion was not perceived as a major threat, and therefore not avoided, or the temporal resolution used to assess fine scale space use overlap was too coarse to detect avoidance.

In agreement with several studies investigating the spatial distribution of predation risk (Hopcraft et al. 2005; Bergman et al. 2006; Kauffman et al. 2007), eland predation risk was a function of both lion distribution and habitat features (Chapter three). Some habitats are more dangerous than others, determined predominantly by the structural cover they provide (Mysterud & Østbye 1999; Loarie et al. 2013) and how this affects the hunting strategy of the predator (Preisser et al. 2007) and the escape tactics of the prey (Lima 1992; Heithaus et al. 2009; Wirsing et al. 2010). Consequently, prey reduce predation risk by avoiding risky habitats on the landscape (Dussault et al. 2005; McLoughlin et al. 2005; Valeix et al. 2009; Thaker et al. 2011; Tambling et al. 2012a). Consistent with the ambush hunting strategy of lions, habitats that reduce visibility and provide cover for stalking are more risky than open habitats for lion prey species (Funston et al. 2001; Hopcraft et al. 2005; Hay et al. 2008; Burkepile et al. 2013; Loarie et al. 2013). Patterns of eland habitat selection at the landscape and home range scale showed that the spatial distribution of eland in Nyathi was largely influenced by habitat-dependent predation risk as eland in Nyathi avoided dense habitats and selected open and mixed habitat types (Chapter two). These results suggest that eland in Nyathi faced a trade-off between forage acquisition and predation risk given that their selection of mixed habitat types probably provided an increased abundance of browse yet exposed them to increased predation risk (Chapter three). The spatial distribution of eland in MZNP was unaffected by variation in habitat types but was influenced by seasonal variation in rainfall (Chapter two). Thus, eland in Nyathi and MZNP respond to a landscape of fear model, which states that where risky habitats predominate,
(Nyathi), top-down forces are stronger than bottom-up effects, whereas on landscapes comprising predominantly safe habitats (MZNP), bottom-up factors are more important (Laundré et al. 2014).

The findings of this study indicated that eland use different cues to determine the strength of their antipredatory response at different spatiotemporal scales (e.g. Creel et al. 2014). At a broad scale, eland responded to the spatial variation in predation risk (i.e. long-term lion activity and habitat type, Chapter two), consistent with the ‘risky space’ hypothesis (Creel et al. 2008). Responses to long-term spatial variation in risk were proactive and allowed eland to minimise their risk of predation using background levels of risk as cues (Creel et al. 2014). At a fine scale however, the strength of the antipredatory response was determined by temporal variation in predation risk (i.e. diurnal versus nocturnal) whilst the long-term spatial variation in predation risk did not affect the strength of the response (Chapter three). Antipredatory responses at a fine scale appeared to be consistent with the ‘risky times’ hypothesis (Creel et al. 2008) and were more reactive in that they allowed eland to reduce the risk of capture using lion presence as a cue (Creel et al. 2014). Consistent across all scales, eland revealed threat-sensitive predator avoidance (e.g. Thaker et al. 2010) as the strength of their antipredatory response was influenced by the level of risk perceived. Threat-sensitive predator avoidance (McNamara & Houston 1987; Lima & Dill 1990; Sinclair & Arcese 1995) may represent an important mechanism by which eland are able to balance the cost and benefits associated with food acquisition and predation risk.

Where prey do not effectively avoid predators, or are unable to do so, they may experience increased rates of predation (Tambling & du Toit 2005; Theuerkauf & Rouys 2008; Louw et al. 2012; Tambling et al. 2013). This was demonstrated by the interaction between the female lion and eland in Nyathi (Chapter two and three), where considerable overlap at a monthly scale and failure to avoid areas of high female lion activity within eland home ranges at a broad temporal scale resulted in the highest proportion of herd-associated eland kills being attributed to this lion (Chapter three). These results are consistent with red deer Cervus elaphus being unable to avoid wolves, resulting in them being preyed upon more frequently than other prey species in the Białowieża Forest, Poland (Theuerkauf & Rouys 2008). Ultimately, where eland do not effectively avoid predators, they may experience increased vulnerability to predation. Where predators and prey home ranges overlap, the spatial scale of safe and risky patches influences the ability of prey to mitigate predation risk as they move through their home ranges (Brown & Kotler 2004). In the case of Nyathi, the highly heterogeneous landscape of risk at a fine spatial scale, as well as the high availability of alternative prey (Craig Tambling, unpublished data) and low lion density most likely played a large role in
inhibiting excessive predation of eland, despite the considerable spatial overlap between eland and lions.

4.3 Eland and lions in small reserves; the way forward

Predators are unable to regulate prey populations where prey migrate seasonally (Schaller 1972; Sinclair et al. 1985; Fryxell et al. 1988; Mills & Shenk 1992). However, where prey populations are resident, predators can regulate and even limit prey populations (Sinclair et al. 1985; Hunter 1998; Power 2002; Louw et al. 2012). In small reserves, predator-prey dynamics are affected by the spatial limitations imposed by fences which restrict the movement of ungulates (Ben-Shahar 1992). Predation effects are thus generally more pronounced in small, fenced reserves than in larger areas (Louw et al. 2012) and there is potential for large predators such as lions to negatively affect prey populations (Power 2002; Druce et al. 2004; Tambling & du Toit 2005; Louw et al. 2012). Prey populations that may be vulnerable to the adverse effects of predation in small reserves are those that; i) are most selected for by lions (Power 2002), ii) occur at low densities (Fryxell et al. 1988) or iii) experience a break-down in their antipredatory strategies (Tambling & du Toit 2005; Louw et al. 2012).

Eland populations across South Africa exist in fenced reserves (IUCN 2008). Large scale spatial avoidance of predators is thus likely to be hindered in most eland populations. However, this study has shown that eland respond to predation risk in ways that allow them to avoid predators at multiple scales. The contrasting environmental conditions between the reserves investigated influenced the nature of the lion-eland interaction and the scale at which antipredatory mechanisms were most effective. A key contribution of this study is that it sheds light on important and unresolved aspects of predator-prey interactions in small reserves that require future research, particularly if conservation and management efforts are to restore ecological integrity to previously disturbed systems (Hayward et al. 2007).

Three factors appear to be important in lion-eland interactions in small reserves; 1) the abundance of vegetative cover on the landscape, which determined, 2) the size of the area of suitable habitats available to eland, and 3) the lion density within eland home ranges. The size of the reserve may not be an important variable influencing eland antipredatory mechanisms, as eland can effectively avoid lions at fine spatiotemporal scales and therefore do not require extensive space to reduce their risk of predation. The density of lions at the scale of eland home ranges may be an important factor influencing the ability of eland to employ fine scale avoidance strategies. The results of this study reflect prey responses to predators at low densities. Where eland have undergone rapid population declines due to predation in small reserves, predator densities have been substantially higher.
than in Nyathi and MZNP at the time of this study. This supports the idea that lion density is an important variable that may compromise the ability of eland to effectively avoid lions at a fine scale. Lions in small, enclosed reserves commonly experience rapid population growth (Druce et al. 2004; Hayward et al. 2007; Kettles & Slowtow 2008). Lion densities within reserves are therefore not regulated by natural processes such as starvation, disease and infanticide (see Kettles & Slotow 2008), putting increased pressure on ungulate populations that may become increasingly unable to effectively avoid lions (Tambling & du Toit 2005). The impact of lion density on vulnerable prey species such as eland (Louw et al. 2012) therefore requires further investigation and suggests an important way forward for research aimed at investigating the conditions required for predator and prey species to be sustained in small reserves.

Forage heterogeneity may interact with predation risk to influence prey behaviour and distribution (Winnie et al. 2008). Particularly in the case of large herbivores, bottom-up forces play a large role in population regulation (Sinclair et al. 2003; Radloff & du Toit 2004), spatial distribution (Sinclair 1977; Morgantini & Hudson 1985; Prins 1996) and group sizes (Winnie et al. 2008). Eland are known to be selective feeders (Underwood 1975; Watson & Owen-Smith 2000; 2002) and given their large body size, require large amounts of food (Watson & Owen-Smith 2000). The spatial distribution of eland is thus likely to be largely affected by bottom-up factors, as seen in MZNP. Results from Nyathi indicated that eland traded-off safety for forage, reflected by their selection for mixed habitat types. Eland responses to predation risk are thus likely to vary depending on the productivity and spatiotemporal variation in forage quality and quantity within reserves. Future research that will increase our understanding of how bottom-up and top-down factors interact to affect eland distribution, behaviour and population dynamics will contribute largely to management efforts aimed at establishing stable lion-eland interactions in small reserves.

Prey population declines related to predation in small reserves have been attributed to the direct effects of predation (Power 2002; Tambling & du Toit 2005; Louw et al. 2012) i.e. the impact that predators have on prey populations through killing and removing them from the system (Lima 1998a). Eland populations in both study sites were not under immense predation pressure given that they were able to avoid the direct effects of predation to a large degree. This was reflected by both eland populations (Nyathi and MZNP) being stable and not declining over the study period (personal observation). The indirect effects of predation may affect prey populations to as great or greater an extent, than the direct effects (Peckarsky et al. 1993; Boonstra et al. 1998; Preisser et al. 2005; Creel & Christianson 2008). In the case of Nyathi, eland may be trading-off access to forage for safety.
(Chapter two). Over extended periods, such trade-offs can result in a decrease in the body condition of breeding females thereby decreasing the reproductive capacity and growth rate of the population (Edwards 1983). Failing to recognise such indirect effects of predation on prey populations can lead to prey population declines being incorrectly attributed to bottom-up limitations (Creel & Christianson 2008), which would largely misguide conservation and management efforts in small reserves. Research on the effects of indirect predation on prey population dynamics in an African context is largely lacking (but see Barnier et al. 2014). Additional research that increases our understanding of the indirect effects of predation on African ungulates is thus needed, particularly given that many African systems have multiple predators with varying hunting strategies, thereby affecting prey behaviour to a potentially larger extent than in single predator systems (Thaker et al. 2011).

This study revealed that eland responses to lions were lion gender-specific (Chapter three). The mechanisms of this gender-dependent predator avoidance are unclear and introduce an important phenomenon for future research to explore. Investigating the role of sexually dimorphic morphology and behaviour on the variable hunting strategies employed by male and female lions will increase our understanding of the variable direct and indirect effects that sexually dimorphic predators may have on prey species. Furthermore, further research is needed to assess whether predator gender-specific responses by prey are restricted to sexually dimorphic predators or is common across all predators.

4.4 Eland traits; the role of predation

The findings of this study indicate that the antipredatory strategies employed by eland differ from those typically used by other members of the Tribe Tragelaphine (Estes 1991). Elands’ morphological, physiological and behavioural traits have likely been largely affected by predation from lions, given that, in their adult form, eland are an unattainable prey item to other large African carnivores, unlike the smaller Tragelaphines that may be preyed upon by a range of predators (Owen-Smith & Mills 2008). In comparison to the other African bovids, eland are distinct, being the largest and slowest member of the Tragelaphines, and antelope, in Africa (Estes 1991), as well as the widest-ranging in terms of the extensive home ranges they occupy (Hillman 1987). Due to their large-scale, irregular movements eland are one of the few bovids described as nomadic (Estes 1991; Augustine 2010). Furthermore, eland are the only member of the Tribe Tragelaphini to form large herds, commonly of up to 100 animals (Estes 1991). The eland is also the only Tragelaphine that ventures onto open plains and avoids dense habitats, unlike other Tragelaphine species which rely heavily on cover (Estes 1991). Tragelaphine antipredatory strategies are typically based on
concealment (i.e. standing still in cover), which their markings are adapted for, and failing that, abrupt flight when faced with predators (Estes 1991). Given their slow evasive speed and bulk, escape from large, co-operative hunters such as lion at close range is likely to prove difficult, if not fatal. Both males and female eland have horns, unlike other sexually dimorphic Tragelaphines, including the elands’ closest relative, the greater kudu *Tragelaphus strepsiceros*. Eland thus appear to be adapted to different antipredatory strategies to those observed in their closest relatives.

Considering these vast discrepancies between eland and other Tragelaphine antelope, it is easy to understand the taxonomical uncertainty surrounding the eland (Underwood 1975). Eland can hybridise with greater kudu, hence they have been classified as a Tragelaphine (Underwood 1975). Eland habits and habitat preferences are different to other extant Tragelaphini antelope however, as described above, which is why it was previously classified in a separate genus: *Taurotragus* (Ansel 1971), which included the common eland (*Taurotragus oryx* Pallas) and the giant eland (*Taurotragus derbianus* Grey). Estes (1991) suggests; “Apparently the eland has substituted size and cooperative maternal defence for speed to protect itself and its offspring against predation. Eland fear only man…” (pp. 192). Despite this, eland population crashes (Tambling & du Toit 2005; Louw *et al.* 2012 SANParks, unpublished data), and the results of this study show that elands’ size and its apparent active defence mechanisms do not exclude it from predation from lions and that man is by no means all that an eland fears.

Eland underwent rapid population declines following the arrival and swift expansion of western settlers and their guns, a predator to which they were unaccustomed (Skead 2007). Several historic records make reference to vast herds of eland encountered on open plains, and inevitably, the ease with which they were chased down on horseback and shot in large numbers (Skead 2007). This exemplifies the significance of the evolutionary arms-race where, through natural selection over time, interactions between predator and prey species drive the evolution of specific antipredatory traits that allow prey species to reduce predation pressure from their natural predators (Dawkins & Krebs 1979). Potentially, the lack of knowledge and understanding regarding eland interactions with its major natural predator is derived from eland in open systems effectively avoiding lions such that it has been assumed that eland are unaffected by predation and unafraid of lions (Hillman 1988; Estes 1991). To the contrary, it may be suggested that much of elands’ morphological, physiological and behavioural traits have been shaped by coevolution with its natural predator. Its large body size, although excluding it from predation by smaller carnivores, does not protect it from lion predation (Hayward & Kerley 2005). It does however allow eland to be largely water-independent, which in
turn allows them to exploit open, arid habitats and range extensively (Hillman 1988; Augustine 2010) thereby avoiding predators at a broad (Fryxell et al. 1988) or finer scale. Thus, perhaps the lion-eland interaction has played a large role in shaping the unique traits and behaviours of the eland antelope at an evolutionary scale. These traits have historically allowed eland to mitigate predation from territorial predators that require cover to hunt, yet did little to protect them from wide-ranging humans with long-range weapons (Skead 2007), and they frequently collapse in small fenced reserves.

### 4.5 Conclusion

This study of the lion-eland system provided an opportunity to increase our understanding of the dynamic nature of predator-prey interactions at multiple scales and across different systems. The study allowed for prey responses to be assessed over a range of spatiotemporal scales and emphasised the value of such an approach. This study has contributed substantially to our understanding of the antipredatory strategies employed by eland. Furthermore this study has brought to light several important aspects of eland-lion interactions that require further research. More specifically, this study has highlighted the need for a multifaceted approach in order to assess the dynamic and various ways in which predators impacts prey behaviour and populations given the increasing number of predator reintroductions into small reserves in South Africa.
References


Appendices

Appendix 1 Candidate suite of *a priori* models (based on previous studies on ungulate resource selection and field observations) developed to assess resource selection function parameters of eland with reserve (n=2) and eland individual (n=7) as random effects.

**Models including female lion risk**

1. State~ Female_risk + (1|Eland_ID) + (1|Reserve)
2. State~ Female_risk + Open + (1|Eland_ID) + (1|Reserve)
3. State~ Female_risk + Dense + (1|Eland_ID) + (1|Reserve)
4. State~ Female_risk + Mixed + (1|Eland_ID) + (1|Reserve)
5. State~ Female_risk + Open + Dense + (1|Eland_ID) + (1|Reserve)
6. State~ Female_risk + Open + Dense + Ruggedness + (1|Eland_ID) + (1|Reserve)
7. State~ Female_risk + Ruggedness + (1|Eland_ID) + (1|Reserve)
8. State~ Female_risk + Dist_TR + Time_day + (1|Eland_ID) + (1|Reserve)
9. State~ Female_risk + Open + Dense + Time_day + (1|Eland_ID) + (1|Reserve)
10. State~ Female_risk + Open + Dense + Ruggedness + Time_day + (1|Eland_ID) + (1|Reserve)
11. State~ Female_risk + Time_day + (1|Eland_ID) + (1|Reserve)
12. State~ Female_risk + Time_day + Mixed + (1|Eland_ID) + (1|Reserve)

**Models including male lion risk**

13. State~ Male_risk + (1|Eland_ID) + (1|Reserve)
14. State~ Male_risk + Open + (1|Eland_ID) + (1|Reserve)
15. State~ Male_risk + Dense + (1|Eland_ID) + (1|Reserve)
16. State~ Male_risk + Mixed + (1|Eland_ID) + (1|Reserve)
17. State~ Male_risk + Open + Dense + (1|Eland_ID) + (1|Reserve)
18. State~ Male_risk + Ruggedness + (1|Eland_ID) + (1|Reserve)
19. State~ Male_risk + Dist_TR + Time_day + (1|Eland_ID) + (1|Reserve)
20. State~ Male_risk + Open + Dense + Time_day + (1|Eland_ID) + (1|Reserve)
21. State~ Male_risk + Open + Dense + Ruggedness + Time_day + (1|Eland_ID) + (1|Reserve)
22. State~ Male_risk + Time_day + (1|Eland_ID) + (1|Reserve)
23. State~ Male_risk + Time_day + Mixed + (1|Eland_ID) + (1|Reserve)

**Models including male and female lion risk**

25. State~ Male_risk + Female_risk + (1|Eland_ID) + (1|Reserve)
26. State~ Male_risk + Female_risk + Open + (1|Eland_ID) + (1|Reserve)
27. State~ Male_risk + Female_risk + Dense + (1|Eland_ID) + (1|Reserve)
28. State~ Male_risk + Female_risk + Mixed + (1|Eland_ID) + (1|Reserve)
29. State~ Male_risk + Female_risk + Open + Dense + (1|Eland_ID) + (1|Reserve)
30. State~ Male_risk + Female_risk + Open + Dense + Ruggedness + (1|Eland_ID)+ (1|Reserve)
31. State~ Male_risk + Female_risk + Ruggedness + (1|Eland_ID)+ (1|Reserve)
32. State~ Male_risk + Female_risk + Dist_TR + Time_day + (1|Eland_ID)+ (1|Reserve)
33. State~ Male_risk + Female_risk + Open + Dense + Time_day + (1|Eland_ID)+ (1|Reserve)
34. State~ Male_risk + Female_risk + Open + Dense + Ruggedness + Time_day + (1|Eland_ID) +
   (1|Reserve)
35. State~ Male_risk + Female_risk + Time_day + (1|Eland_ID)+ (1|Reserve)
36. State~ Male_risk + Female_risk + Time_day + Mixed + (1|Eland_ID)+ (1|Reserve)

Models including no lion risk parameters

37. State~ Altitude + (1|Eland_ID)+ (1|Reserve)
38. State~ Altitude + Open + Dense + (1|Eland_ID)+ (1|Reserve)
39. State~ Ruggedness + Altitude + (1|Eland_ID)+ (1|Reserve)
40. State~ Open + Dense + (1|Eland_ID)+ (1|Reserve)
41. State~ Time_day + (1|Eland_ID)+ (1|Reserve)
42. State~ Open + Dense + Time_day + Ruggedness + (1|Eland_ID)+ (1|Reserve)
43. State~ Dist_TR + Time_day +(1|Eland_ID)+ (1|Reserve)
44. State~ Mixed + Time_day +(1|Eland_ID)+ (1|Reserve)
45. State~ Open + Time_day +(1|Eland_ID)+ (1|Reserve)
46. State~ Dense + Time_day +(1|Eland_ID)+ (1|Reserve)
Appendix 2 Home ranges (95% isopleth) of NF1, NF2 and NF3 during a) the dry season and b) the wet season in MZNP
Appendix 3 Home ranges (95% isopleth) of MF1, MF2 and MF3 during a) the dry season and b) the wet season in Mountain Zebra National Park (MZNP).
Appendix 4 Distance to tourist road (plotted at time t and t + 1) of the four collared eland in Nyathi, with only eland NF4 showing temporal autocorrelation.

Appendix 5 Probability of eland presence (n = 7) at the three defined habitat types during the day and night in Nyathi and Mountain Zebra National Park, with all other modelled variables held at their mean, determined using generalised linear mixed effects models. Error bars represent standard error.
Appendix 6 The relationship between ruggedness and the probability of eland presence (n=7) in open and dense habitat types in Nyathi and Mountain Zebra National Park, determined using generalised linear mixed effects models. Red lines represent 95% confidence intervals.

Appendix 7 The relationship between long-term risk of predation from female lions (proportional to the likelihood of female lion presence) and the probability of eland presence (n = 4) in open, mixed and dense habitat types in Nyathi determined using generalised linear mixed effects models. Red lines represent confidence intervals.
Appendix 8 The relationship between ruggedness and the probability of eland presence (n = 4) in open, mixed and dense habitat types in Nyathi determined using generalised linear mixed effects models. Red lines represent 95% confidence intervals.

Appendix 9 Probability of eland presence (n = 4) at the three defined habitat types during the day and night in Nyathi, with all other modelled variables held at their mean, determined using generalised linear mixed effects models. Error bars represent standard error.
Appendix 10 Probability of eland presence (n = 3) at the three defined habitat types during the day and night in Mountain Zebra National Park, with all other modelled variables held at their mean, determined using generalised linear mixed effects models. Error bars represent standard error.

Appendix 11 Mean monthly and seasonal rainfall in Nyathi and MZNP during the study period (March 2013 – May 2014, SANParks, unpublished data).
Appendix 12 Seasonal and cumulative overlap of eland and female and male lion home ranges (95% UD) and core use areas (50% UD) over the full study period in a) Nyathi and b) Mountain Zebra National Park (MZNP).
Appendix 13  Average change in movement rate of eland 24 hours before and after lion encounters within 2 km, 2 km – 4 km and > 4 km in Nyathi, with no significant increase in movement rates shown.

Appendix 14  Average change in movement rate of eland 24 hours before and after lion encounters within 1.5 km, 1.5 km – 3 km and > 3 km in MZNP, with no significant increase in movement rates shown.
Appendix 15 Average change in movement rate of eland 24 hours before and after lion encounters within 1 km, 1 km – 2 km and > 2 km in MZNP, with no significant increase in movement rates shown.

Appendix 16 Average change in movement rate when lions are within 1.5 km in relation to open (n=87), mixed (n=23) and dense (n=5) habitat at encounter location in Nyathi.
Appendix 17 Average change in movement rate when lions are within 1.5 km in relation to open (n=87) and mixed (n=23) habitat at encounter location in Mountain Zebra National Park (no encounter points occurred in dense habitats).