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Risk-driven behaviour in the African leopard:how is leopard behaviour mediated by lion presence?

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Risk-driven behaviour in the African leopard:

How is leopard behaviour mediated by lion presence?

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Abstract

Agricultural expansion is restricting many carnivore species to smaller tracts of land, potentially forcing increased levels of overlap between competitors by constraining spatial partitioning. Understanding encounters between competitors is important because competition can influence species densities, distributions, and reproductive success. Despite this, little is known of the mechanisms that mediate coexistence between the African leopard (*Panthera pardus*) and its competitors. This project used GPS radiocollar data and playback experiments to understand risk-driven changes in the leopard's behaviour and movement during actual and perceived encounters with lions (*Panthera leo).* Targeted playbacks of lion roars were used to elucidate immediate and short-lived behavioural responses in leopards when lions were perceived to be within the immediate area. To investigate the post-encounter spatial dynamics of leopard movements, the project used datasets from high-resolution GPS radiocollars deployed on leopards and lions with overlapping territories in the Okavango Delta, Botswana. Leopards were found to adapt behaviours and movements when lions were perceived to be nearby. Specifically, roar playbacks elicited longer periods of vigilance than controls, and movement directions were influenced by speaker locations. Further, leopard movements were quicker and more directional after encountering lions. However, adjustments in behaviour and movement were short-lived. The results provide insights into mechanisms used by the leopard to coexist with its competitors and are a useful case study of the methods that could be used to investigate encounter dynamics within other systems.

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Contents

List of figures

List of tables

Acknowledgements

Chapter 1: General introduction

Global biodiversity is rapidly declining, with extinction rates currently 2-3 times higher than background rates indicated in fossil-records (Barnosky et al., 2011). In recent years, increased public and political awareness of conservation issues has led to global initiatives targeting reductions in the rate of biodiversity loss (Di Marco et al., 2014). Mammals have received much of the attention in conservation literature, research, and funding (Clark and May, 2002). This has occurred for several reasons; carnivores, in particular, play important regulatory and structuring roles within ecosystems by limiting prey species and competitors through predation and competition (Ripple et al., 2014). Typically, they are also charismatic species and provide economic benefits associated with tourism, which provide further incentives for their conservation (Lindsey et al., 2007). Threats to carnivores are exacerbated by aspects of their ecology and life history characteristics (Marco et al., 2014). For example, the wide ranging behaviour of most large carnivores increases the potential for range overlap and conflict with humans, whilst slow life histories and low population densities limit their resilience to anthropogenic disturbance (Carbone et al., 1999; Cardillo et al., 2004; Marco et al., 2014). Agricultural expansion is also restricting many carnivores to smaller tracts of protected land. This constrains spatial partitioning between competitors, forcing more overlap than may have existed previously. Understanding the consequences of this is important because competition can influence species' densities, distributions, and reproductive success (Broekhuis et al., 2013; Creel, 2001; Hayward and Kerley, 2008). Thus, changes in the dynamics of competitor encounters can place protected populations at risk of extinction (Dickman, 1996; Ginsberg et al., 1995).

A key way in which behavioural studies can aid conservation is in understanding the impact that human activities have on animal behaviour (Berger-Tal et al., 2011). The African leopard (*Panthera pardus*) is a useful case study of the question of how competitors could coexist under conditions of enforced proximity because leopards exist within an intact predator assemblage, within which interspecific competition is fierce (Dalerum et al., 2009). Further, research on leopards is also warranted as they have disappeared from an estimated 36.7% of their historical range (Henschel et al. 2008). Leopards have traditionally been assumed to be resistant to interspecific competition and, consequently, have been neglected from interspecific competition studies (Winterbach et al., 2013). However, evidence now suggests that leopards are at risk from dominant competitors - including lions (*Panthera leo*) (Balme et al., 2013; Du Preez et al., 2015). Enforced proximity with lions could change leopard behaviours and impact on reproductive success. From an ecological perspective their survival is important because intact predator assemblages are important for full ecosystem function (Terborgh, 2010). For example, in some ecosystems the combined effects of leopards and lions help to regulate mesocarnivore densities and community structuring (Terborgh, 2010).

Protected reserves may be the key to the survival of leopards because leopards suffer higher mortality rates outside of these areas (Balme et al., 2010). Thus, it is important to understand the factors that facilitate coexistence between leopards and their competitors within protected areas. Understanding how coexistence is facilitated could also lead to the development of tools that allow biologists to manipulate species movements in order to promote conservation outcomes (Ausband et al., 2013; Jackson et al., 2012). Beyond caching prey items in trees, little is known of the mechanisms that mediate coexistence

between the leopard and its competitors (Bailey, 2005; De Ruiter and Berger, 2001; Stein et al., 2015). Our knowledge of interspecific interactions between large carnivores has historically been limited by the difficulties associated with following and observing interactions between free-ranging species. It is only relatively recently that advancement in global positioning systems has enabled researchers to reconstruct the movements of individual animals accurately and, thereby, to investigate the fine-scale dynamics of competitor encounters.

In this thesis, I will investigate the dynamics of leopard - lion interactions within a protected population in order to understand how the leopard's behaviour changes during competitor encounters. I will focus on the leopard's relationship with lions because lions are the largest carnivore competitor with which leopards share their range, and the costs of encountering lions are severe (Balme et al., 2013). I begin by briefly introducing the African large predator guild. I will then provide an introduction to competition, focussing on interspecific competition and the key factors that facilitate coexistence between competing carnivore species. I will discuss the fields of competition and coexistence within the context of large African carnivores in order to provide a concise introduction to coexistence and competitive interactions within the African large predator guild. There will be instances, however, where I refer to other taxonomic groups. This will be necessary because some principles have not been investigated in the context of large African predators. This will lead me to the discussion of one factor, in particular, that can facilitate coexistence: interspecific communication. To date, few studies have investigated interspecific communication between large African carnivores, and so this section will largely draw upon examples from other taxonomic groups. I will then summarise what is known of interspecific

communication between large African predators before moving on to discuss intraguild competition involving the leopard. This will finally lead me into the aims and objectives of this thesis.

The African large predator guild

Species guilds are defined as collections of species, within a community, competing for the same resources (Wilson, 1999). The African large predator guild (herein referred to as *the large predator guild*) represents the last intact guild of large carnivores (Dalerum et al., 2009) and consists of several species: lion, leopard, cheetah (*Acinonyx jubatus*), spotted hyaena (*Crocuta crocuta*), and wild dog (*Lycaon pictus*) (Dalerum et al., 2009; Hayward and Slotow, 2009). The large predator guild is characterised by intense interspecific competition, which has implications for the space use, activity budgets and life history traits of coexisting species (Creel and Creel, 1996; Carbone et al., 1997; Hayward and Slotow, 2009).

Competition

Competition is defined as an interaction, within (intraspecific) or between (interspecific) species, for a limited shared resource, leading to reductions in the fitness of participants (Keddy, 2001). Competition may be categorised as either exploitation or interference competition. Exploitation competition is indirect, involving no aggressive encounters between species, and occurs when access to a limited resource is reduced (Wrangham et al., 1993). In such cases, species respond to resource levels, with competition increasing as resources deplete. In contrast, interference competition occurs in the form of antagonistic interactions, including kleptoparasitism, harassment, and predation. Unlike exploitation

competition, interference competition is independent of resource limitation, and is not necessarily density-dependent (Berger and Gese, 2007).

Interspecific competition intensity increases with resource use overlap (Caro and Stoner, 2003). Since species guilds are a functional classification based on similarities in ecological requirements, guilds are often characterised by intense interspecific competition (Caro and Stoner, 2003). This competition may be manifested in several ways, including kleptoparasitism and harassment, with interspecific predation representing the severest consequence of competition between species (Polis et al., 1989). Large carnivores are particularly vulnerable to interspecific competition because the large costs and benefits of capturing and consuming large prey items predispose species to defend and kleptoparasitise food (Hayward and Kerley, 2008; Palomares and Caro, 1999). Further, the costs of competition are inflated within carnivore guilds because of carnivore species' adaptations for killing: interspecific killings are widespread within communities of carnivore competitors (Palomares and Caro, 1999). Indeed, interspecific predation accounts for up to 68% of species mortality within some carnivore communities (Palomares and Caro, 1999).

The costs of competitive interactions are rarely the same for all individuals involved, and both intraspecific and interspecific interactions show competitive asymmetry. Competitive asymmetry is, however, greater for interspecific interactions because of morphological, behavioural, and life history differences between species, and this is typically manifested as competitive hierarchies within communities of competitors (Keddy and Shipley, 1989). In general, the large predator guild exhibits an asymmetrical dominance hierarchy, with larger species dominating smaller counterparts (Creel and Creel, 1996; Durant, 2000). However, three guild species (lions, spotted hyaenas, and wild dogs) exhibit complex social systems,

and the outcomes of their interactions are often dependent on the contexts of encounters. For example, the outcomes of interspecific interactions between lions and spotted hyaenas are largely dependent on the ratio of attackers to defenders (Cooper, 1991).

Competition outcomes

An early mathematical model of competition (the Lotka-Volterra competition model (Volterra, 1926; Lotka, 1932) distinguished four possible outcomes of competition:

1. species A drives species B to extinction

2. species B drives species A to extinction

3. species A/B drives species B/A to extinction

4. species A and species B coexist

Outcomes 1 and 2 depict scenarios, within a stable environment, in which the less competitive species is driven to extinction. Outcome 3 depicts a scenario where the effects of interspecific competition are greater than those of intraspecific competition for both species, resulting in an unstable equilibrium. In this case, competitive exclusion of one species will occur. This scenario differs from the first two because the exact outcome depends on the species' relative abundances and is susceptible to density-independent effects, which may shift the equilibrium in favour of one species and alter the outcome.

Early models of competition predicted that coexistence was possible only when the effects of intraspecific competition were greater than those of interspecific competition for both species (outcome 4). However, the assumptions of early models limit their application to real world scenarios, and there are systems in which species coexist when interspecific competition appears greater than intraspecific (Creel and Creel, 1996; Durant, 1998; May,

2001). This may be particularly true for rare large carnivore species because large range requirements, low population densities, and mechanisms (such as territoriality) that reduce encounter rates, mitigate the potential for intraspecific interactions. Indeed, within the large predator guild, interspecific competition is fierce, yet competitors can still coexist. Competitive exclusion, for example, has been suggested as the reason why some prey rich areas that support high densities of lions and spotted hyaenas have low densities of cheetahs and wild dogs (Creel and Creel, 1996; Laurenson, 1994). Within the large predator guild, however, there are certain areas where cheetahs and wild dogs coexist with their dominant guild counterparts, even though the strength of intraspecific competition appears weaker than interspecific competition (Creel and Creel, 1996, 2002; Durant, 1998). Thus, there must be additional mechanisms that facilitate species coexistence.

Coexistence of competitors

Competition models have been developed to show that temporal and spatial environmental variability can be important stabilising factors that promote coexistence (Chesson, 1981, 2000). Early models of competition assumed stable environments with homogeneous distributions of risk (Lotka, 1932). However, risk is unevenly distributed across space and time (Chesson, 1985). As such, landscapes may be represented as heterogeneous patches of risk, within which the competitive abilities and densities of competitors fluctuate. Thus, coexistence can be facilitated through *conditional differentiation,* where the competitive abilities of species vary in fluctuating environments (Tilman, 1982).

Spatial heterogeneity is thought to be a stronger stabilising factor promoting coexistence than temporal heterogeneity. Indeed, the role of the latter in facilitating coexistence within the large predator guild is disputed (Chesson, 1985). Traditionally, it was assumed that

asynchronous peaks of diurnal activity periods of cheetahs and wild dogs, with lions and spotted hyaenas, were driven by competitor avoidance (Hayward and Slotow, 2009). However, recent studies support reduced temporal partitioning between guild species, and indicate strong lunar cycle activity associations, suggesting light requirements drive cheetah and wild dog activity patterns (Cozzi et al., 2012). Thus, although temporal activity patterns may be partially influenced by competitor avoidance, it is unlikely that predator avoidance is the primary proximate cause for activity patterns of wild dog and cheetah (Cozzi et al., 2012).

Coexistence may also be facilitated through behavioural strategies that mitigate the levels of competition experienced by inferior competitors. These strategies can also work in conjunction with ecological processes. For example, spatial heterogeneity can promote coexistence by providing inferior competitors with areas of the landscape where the intensity of competition is reduced; thus, species can facilitate coexistence by shifting habitat usage patterns to take advantage of these competition refuges (Durant, 1998). For example, cheetahs mitigate the risks associated with competitive interactions by seeking spatial refuges with low densities of larger competitors, such as lions and spotted hyaenas (Durant, 1998). In this example, however, low lion and spotted hyaena densities are a consequence of low prey densities in the refuge areas. Thus, in some instances, the use of refuges can lead to reductions in foraging efficiency (Durant, 1998; Wirsing et al., 2007; Broekhuis, 2012).

Risk assessment

Mechanisms facilitating competitor coexistence can impose energetic and fitness costs on inferior competitors. In systems where the risk of encountering predators is

heterogeneously distributed across the landscape, species can maximise their fitness by adjusting activity levels to risk. For example, local-scale movement patterns of cheetahs and wild dogs are influenced by predator avoidance, which acts as a partitioning mechanism to facilitate their coexistence with lions and spotted hyaenas (Durant, 1998; Cozzi, 2012; Broekhuis et al., 2013). Further, in both cheetahs and wild dogs, the scale of responses to competitors appears to be mediated by the circumstances of encounters, suggesting that these species have the capacity for facultative risk assessment (Broekhuis et al., 2013).

Risk assessment can be based on assumed risk distributions (predictive) or on the real-time distribution of risk (facultative) (Broekhuis et al., 2013). Facultative assessment allows species to adapt their behaviours in response to changing levels of risk. It can promote the temporary uptake of certain habitats, such as competitor refuges, and it may lead to the uptake of short-lived anticompetitor behaviours (Durant, 1998; Webster et al., 2012). For example, kangaroo rats (*Dipodomys merriami)* reduce foraging behaviours within microhabitats containing predator olfactory cues (Herman and Valone, 2000). Facultative assessment is only possible in species with the capacity to detect predator or competitor presence, and species will often use detection mechanisms intrinsically linked to their sensory systems (Bhatnagar 2008). The assessment of risk from interspecific cues has been identified across several taxa but has largely focussed on the role of semiochemicals in assessment (Amo et al., 2008). However, acoustic cues may also be used to assess risk - particularly in circumstances where visual assessment is constrained. One method, in particular that may facilitate risk assessment is the exploitation of communication networks.

Interspecific Communication

Communication is traditionally interpreted as a dyadic interaction in which the transmission of information from the sender is perceived by the receiver, changing the receiver's behaviour in a way that is adaptive for at least one of the participants (McGregor 2005). Communication networks can exist when signals are transmitted over distances greater than the average separation between potential recipients (McGregor 2005). Typically, individuals within social groups aggregate and signals are rarely exclusive to conspecifics. Thus, communication is rarely a dyadic interaction and commonly occurs within a social environment of multiple signallers and receivers (Dabelsteen 1992; McGregor and Peake 2000).

Eavesdropping

The transmission of information within communication networks may lead to its interception by unintended receivers. Eavesdropping is the extraction of information from signals directed towards other targets, excluding information not designed for information transfer (Peake, 2005). Eavesdropping may be based on the interception of signals intended for other individuals (interceptive eavesdropping) or may be based on the interception of directed signals intended for conspecifics (social eavesdropping) (Peake, 2005).

Eavesdropping between heterospecifics has been identified across a range of taxa and is particularly well documented within predator-prey systems (Magrath et al., 2015). The interception of interspecific signals can increase the range and volume of relevant information available to eavesdroppers and provide them with competitive advantages (Oliveira et al. 1998; Seppänen et al., 2007). For example, within predator-prey systems,

interspecific eavesdropping may increase the likelihood of detecting predators and reduce the costs associated with information acquisition (Magrath et al., 2015).

Heterospecific signals indicating the presence of predators can lead to behavioural shifts that mitigate the probabilities of encounters, including fleeing to cover or increased vigilance. For example, the targeted playback of baboon (*Papio hamadryas*) alarm calls leads to increased vigilance in impala (*Aepyceros melampus*), which are susceptible to the same terrestrial predators as baboons (Kitchen et al., 2010). In addition, benefits can also be indirect and manifested over a longer time scale (Magrath et al., 2015). For example, heterospecific alarm calls for shared predators can increase a species' foraging efficiency by reducing their investments in antipredator behaviours (Bell et al., 2009). Heterospecific alarm calls can, also, facilitate spatial segregation by providing information on the spatial distribution of risk (Magrath et al., 2015). Thus, interspecific eavesdropping may facilitate species coexistence by providing prey species with information to avoid predators.

Eavesdropping can also facilitate coexistence between interspecific competitors (Durant, 2000; Webster et al., 2012). The interception of interspecific signals can facilitate risk assessment and promote the uptake of risk-sensitive anticompetitor behaviours. For example, wild dogs, who are competitively inhibited by lions and spotted hyaenas, respond to competitor vocalisations by fleeing the area (Creel and Creel, 1996; Webster et al., 2012). Furthermore, cheetahs show increased vigilance and movement distances following lion playbacks, suggesting that fine-scale habitat segregation between cheetahs and lions may be facilitated by the interception of competitor signals (Durant, 2000; Broekhuis, 2012).

Heterospecific signals may also be intercepted by dominant competitors, who benefit from initiating antagonistic encounters, for reasons such as: scavenging opportunities, removal of

a mortality source, or freeing of essential resources (Palomares and Caro, 1999). For example, wild dogs may represent short-term scavenging opportunities for lions, with acoustic experiments showing that lions are highly motivated to approach wild dog rally vocalisations (Webster et al., 2010).

The selective pressures of eavesdropping on subordinate species can lead to adaptations that mediate the interception of information, such as auditory camouflage. As an example, katydid species are predated upon by insectivorous bats who locate katydids from their conspecific signals. However, in the presence of predators, some katydid species display reduced signalling and supplement signals with tremulations that provide auditory camouflage from heterospecifics (Belwood and Morris, 1987).

Conservation applications

Exploiting the communication systems of species could have conservation applications. A novel approach currently under investigation is the strategic deployment of biological signals to manipulate species' space use and promote conservation outcomes. These signals could be used proactively to limit human-wildlife conflict, by restricting free ranging species to protected areas. For example, the deployment of foreign conspecific scent marks into the territories of grey wolves (*Canis lupus*) manipulates pack movements to the extent that individuals show no crossings of scent boundaries (Ausband et al., 2013). Alternatively, biological signals could provide a mechanism by which to return species to protected areas of their range following incursions into human habitations. For example, African wild dogs were found to travel towards core territory areas following exposure to foreign pack scent marks (Jackson et al., 2012). However, such strategies require an intimate knowledge of the communication systems of the target species and their competitors. Knowledge of how

species respond to signals and the motivations behind signal mediated behaviours is essential if communication systems are to be manipulated effectively.

Among mammals, larger species are most likely to benefit from conservation interventions because large home-ranges and an overlap with human resource requirements increase their susceptibility to human-wildlife conflict. However, interspecific communication studies on mammals have largely focussed on microtine rodent species, and communication within higher trophic levels remains relatively unexplored (Herman and Valone, 2000). The African large predator guild is believed to represent the last intact guild of large carnivores (Dalerum et al., 2009) and its members are persecuted for the real and perceived threats they pose to local communities (Gusset et al., 2009). Thus, it is an ideal system in which to test the viability of manipulating species' movements through signal mediated behavioural responses.

The African leopard

Intraguild studies on Africa's large predator guild have primarily focussed on interspecific relationships between lion, spotted hyaena, cheetah, and wild dog. Only recently have researchers begun to consider the effects of intraguild competition on the leopard (Du Preez et al., 2015; Maputla et al., 2015; Vanak et al., 2013). Traditionally, research on the leopard has focused on the species' basic ecology (Balme et al., 2014). Basic ecological work can contribute to informed conservation. However, repetition amongst research topics and a deficiency in applied research explicitly related to conservation represents a failure to address the leopard's conservation needs (Balme et al., 2014). Thus, our knowledge of the mechanisms facilitating coexistence between the leopard and its competitors is poorly understood.

Leopards are smaller than lions and spotted hyaenas but have traditionally been considered resilient to interspecific competition due to their wide habitat tolerance and catholic prey range (Hayward et al., 2006; Kingdon, 2013; Winterbach et al., 2013). Some studies have also referenced leopard behaviour within the Asian large predator guild as justification for its proposed resilience to competition within the African guild (Karanth and Sunquist, 2000; Winterbach et al., 2013). This has largely led to its exclusion from studies of the interactions between African large predator guild competitors. However, the competitive dynamics of large Asian predators are unlikely to be analogous to those of large African predators.

Caro and Stoner (2003) found that leopard home-range and habitat usage patterns, both indicators of potential interspecific competition, directly overlapped with 66 other African carnivore species, thus, making leopards the African carnivore species with the greatest potential for interspecific competition. Incorporating dietary habits into the analysis further identified that leopards were particularly susceptible to kleptoparasitism and exploitative competition (Caro & Stoner, 2003).

Leopards are at risk from dominant competitors that are larger or live in larger, competitively dominant social groups. In the Sabi Sand Game Reserve, for example, lions and spotted hyaenas accounted for 42% of leopard cub mortality, and it is estimated that between 5 to 10% of leopard kills are lost to dominant competitors (Balme et al., 2013). This has shaped aspects of the leopard's ecology (Balme et al., 2007). Leopards are the only guild species to cache prey in trees, and evidence suggests this is an adaptation mediating the costs of interspecific encounters (Stander et al., 1997; De Ruiter and Berger, 2001). For example, in northern Botswana, 75% of leopard kills on the ground were successfully kleptoparasitised by dominant competitors: none were kleptoparasitised when carcasses

were stored in trees (Stein et al., 2015). Furthermore, the density of interspecific

competitors appears to be a major determining factor for whether a carcass is hoisted. In

Kruger National Park - where competitor density is high - 84% of carcasses were stored in

trees; in comparison, only 18% of carcasses were hoisted in the Kalahari Desert, where

competitor density is relatively low (Bothma and Le Riche, 1984; Bailey, 2005). Beyond

caching behaviour, the mechanisms mediating leopard coexistence with other large

carnivores and the consequences of competitive interactions are largely understudied. As a

consequence, empirical evidence on the leopard's role within the guild is lacking and the

conflict it faces is poorly understood.

Leopards may also exhibit negative competitive pressures on smaller members of the large

predator guild. Leopards will consume smaller carnivores, including cheetahs and wild dogs,

more often than expected by the species' abundance (Hayward et al., 2006). Furthermore

telemetry studies indicate that leopards move towards recent wild dog locations, suggesting

they may benefit from initiating interactions (Vanak et al., 2013). However, beyond this, the

relationship between the competitors is poorly understood.

Lions are the largest terrestrial carnivore in Africa and in many ecosystems competitively

inhibit smaller carnivores, such as wild dogs and cheetahs, through kleptoparasitism and

mortality events (Creel and Creel, 1996; Durant, 1998). It has been suggested that lion

population declines may release leopard populations from the regulatory effects of

interspecific competition, but this remains to be tested (Packer et al. 2009). Crude

estimates of abundance, based on the records of professional guides, suggest that at a local

scale leopard and lion numbers are negatively correlated, with recent studies further

suggesting spatial segregation exists between the species (Balme et al., 2013; Du Preez et

al., 2015; Maputla et al., 2015; Vanak et al., 2013). For example, Vanak et al. (2013) found that leopards avoided areas recently occupied by lions. However, this behaviour was absent in the wet season when vegetation characteristics limited visibility, suggesting that either poor visibility precludes the assessment of risk or the risk of detection was sufficiently low to preclude moving away.

Du Preez et al. (2015) found that leopards were more likely to transition into denser habitats when lions were present and found that leopard movement speeds increased with their proximity to lions in open habitats. In contrast, movement speeds did not differ with lion proximity in densely vegetated habitats. That reactions to lions were less pronounced in dense habitats is likely a reflection of the costs and benefits of encountering competitors under different circumstances. For example, the risks and costs of detection may be mitigated in dense habitats that offer suitable ground cover to avoid detection and suitable vertical cover to escape when detected (Du Preez et al. 2015).

Despite these recent advances in our knowledge of lion-leopard interactions several questions remain. In particular, it remains unknown (1) whether spatial segregation between leopards and lions is a mechanism by which leopards avoid aggressive encounters with lions or a by-product of physical confrontations occurring, (2) how leopards behave upon detection of lions, and (3) what information is used by leopards during heterospecific risk assessment.

Acoustic playback experiments allow researchers to quantify animal responses to acoustic information and have been used to study the form and function of acoustic signals in a range of taxa (Fischer et al., 2013). Playback experiments using predator or competitor vocalisations are particularly useful for studying acoustic risk assessment in free-ranging

species because they allow sample sizes and encounter conditions to be controlled. The latter point is important because an individual's response to an acoustic signal may depend on their current situation; thus, playback experiments can be useful in controlling for confounding factors and reducing the noise in animal responses. Acoustic playbacks have recently been used to quantify rarely observed interactions between other guild species (Durant, 2000; Webster et al., 2010, 2012); however, to date this methodology has not been applied to the leopard.

Aims and Thesis Outline

The general aim of my thesis is to understand better how leopard behaviour and movement is influenced by lion proximity. In my thesis I will address the following questions:

1. How does leopard behaviour and activity change immediately after lions are simulated to be within close proximity?

2. How do leopard movements change following naturally occurring encounters with lions?

To address these questions, targeted playbacks of lion roars were used to elucidate immediate and short-lived behavioural responses in leopards when lions were perceived to be within the immediate area. This also allowed me to test whether leopards eavesdrop on competitor vocalisations to facilitate risk assessment. To investigate post-encounter spatial dynamics of leopard movements, I used datasets from high-resolution GPS radiocollars deployed on overlapping populations of leopards and lions. This approach allowed rarely-observed intraguild encounters to be quantified.

The remainder of this thesis has been split into four chapters. *Chapter 2* will focus on providing an overview to this project's study system, starting with an introduction to the study area, and then moving onto the study population. This will be followed by two self-contained data chapters. *Chapter 5* will be the final discussion and will summarise the key findings of this thesis and the broader implications of this research for the fields of competition and coexistence.

Chapter 2: Study system

Study Area

The study area was located in the south-eastern area of the Okavango Delta (19°51'S, 23°65'E) - an inland delta fed by highly seasonal annual precipitation and asynchronous annual flooding (McCarthy et al., 2003). The area has annual precipitation of approximately 450 mm from November until March. Floodwaters from the Angolan highlands arrive several weeks after local rains, peaking in the entry channel between February and May and reaching the delta terminus several months later (McNutt, 1996; McCarthy et al., 2003). Annual inundation areas within the delta are dependent on local precipitation and rainfall in the Angolan catchment area (McCarthy et al., 2003). The asynchrony of local rainfall and the arrival of Angolan floodwaters mean that water is available throughout the year.

The core study area encompassed approximately 2,600 km^2 and was a heterogeneous landscape of habitat types, dominated by areas of mopane and acacia dominated mixed woodland (table 1) (Webster, 2008; Broekhuis et al., 2013). The area included Moremi Game Reserve and adjacent wildlife management areas, NG33 and NG34 (figure 1). Management areas were primarily used for photographic tourism (McNutt, 1996; Lindsey, 2010).

Table 1. Summary of the main habitat types within the study area

Habitat type	Characteristic species	Typical density
Floodplain	*Pechuel-loeschea leubnitziae*	Open
Grassland	*Pechuel-loeschea leubnitziae*	Open
Mopane	*Colophospermum mopane*	Medium/dense
Mixed woodland	*Acacia erioloba; A. tortilis; C.mopane; Croton megalobotrys*	Medium/dense
Riparian	*A. nigrescens; Combretum imberbe*	Dense
Swamp	*Panicum repens; Cynodon dactylon*	Open

Adapted from (Broekhuis, 2012; Stein et al., 2015).
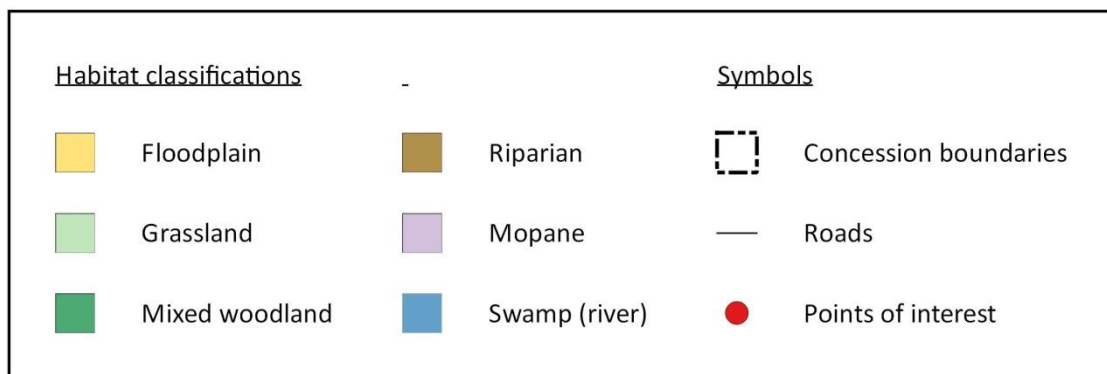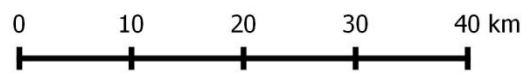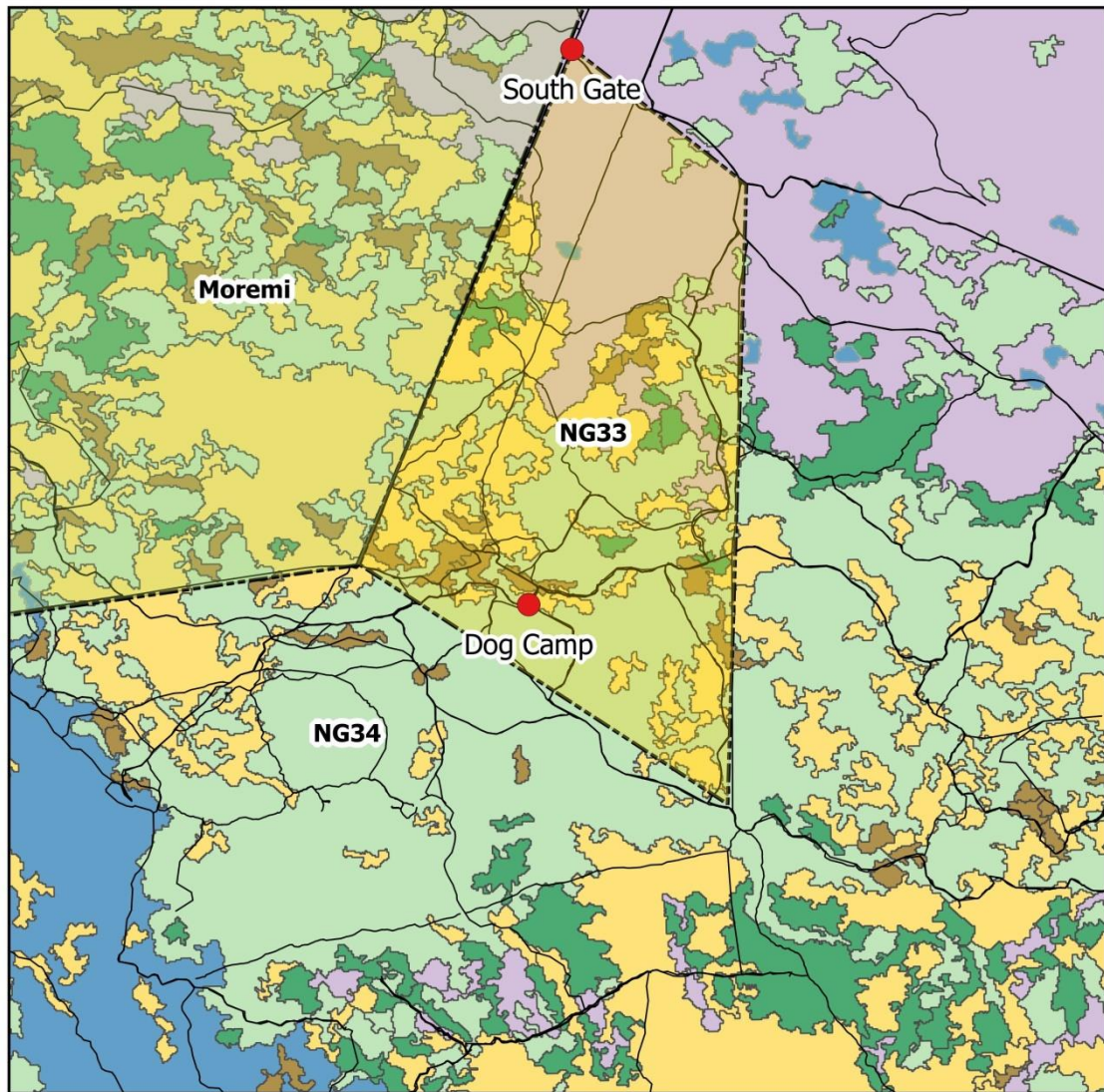
Figure 2. Map of the study area

The Botswana Predator Conservation Trust (BPCT) is a non-government organisation tasked with leading research initiatives on large carnivores in Northern Botswana. This study was based at the trust's field site - centrally located within the study area (figure 1). The BPCT has been operating at the location since 1989 and has developed their camp infrastructure to minimise disruptions to the indigenous fauna and flora. Permanent human populations surrounding the study area were clustered around three villages and estimated at less than 1,000 people (McNutt, 1996).

Study Population

Northern Botswana contains contiguous sympatric populations of all species within the large predator guild and has one of the highest carnivore densities in Africa (Gittleman, 2001). Previous intraguild studies within the area have focussed on the relationships between competitively inferior cheetahs and wild dogs with their dominant counterparts (Webster, 2008; Broekhuis, 2012; Cozzi, 2012). In contrast, there have been relatively few studies on the leopard population within the area, although they appear to show extensive broad-scale spatial overlap with the local lion population. Furthermore, anecdotal accounts of leopard harassment and mortality from lions suggest that interference competition may be acting on leopard populations at the site (K.Rafiq, personal observation).

Large carnivores within the study area have been the focus of a long-term study by BPCT associated researchers. As a consequence, detailed life-histories were available for most large carnivore species within the area, and most species were habituated to research vehicles. Several individuals of each species were also fitted with GPS radiocollars with the capacity to collect high-resolution data on the position, speed, acceleration, and track of individuals (Wilson et al., 2013). Population estimates suggest densities of 5.8 adult lions /

100 km^2 (Cozzi et al. 2013). No leopard density estimates have been completed within the

area. However, recent camera trap studies captured 19 female and 15 male leopards within

the study area over an eight month period (August 2014 to March 2015) (L. Rich,

unpublished data).

Chapter 3: Lion avoidance by leopards: playback experiments reveal leopard behavioural responses to lion proximity

Introduction

Understanding the dynamics of competitor encounters is important for conservation because interspecific competition has implications for the population dynamics, space use, and density of competitors (Broekhuis et al., 2013; Creel, 2001; Hayward and Kerley, 2008). These processes can be affected by both the direct and indirect consequences of competition. Interspecific killings are the severest consequence of physical confrontations between competitors and are ubiquitous amongst terrestrial mammalian carnivores (Donadio and Buskirk, 2006; Palomares and Caro, 1999). The costs or benefits of physical confrontations can indirectly affect species by causing them to adopt behaviours to avoid or initiate encounters. For many animals the risk or fear of predation is heterogeneously distributed across time and space (Laundré et al., 2010). This landscape of fear has implications for the fitness of inferior competitors because it can cause them to adapt their behaviour and space use in response to differing levels of risk (Creel et al., 2013a; Du Preez et al., 2015; Valeix et al., 2012).

Competitively inferior species may facilitate their coexistence with competitors by reducing the probabilities of occupying the same areas as dominants (i.e., avoidance strategies). Alternatively, inferior competitors may reduce the probabilities of physical confrontations when both species are within a detectable distance (i.e., antipredation strategies) (Brodie et al., 1991). For example, to avoid encounters with their two primary competitors, lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*), cheetahs (*Acinonyx jubatus*) increase

their use of prey poor habitats (Durant, 1998). This leads to reductions in foraging efficiency and highlights that adaptations mitigating species vulnerability to competitors may lead to fitness costs (Lima, 1998). Since the risk of encountering competitors is typically heterogeneously distributed across the landscape in both space and time (Chesson, 1985, 2000), species can maximise their fitness through risk-sensitive plasticity in their anticompetitor strategies. However, flexible responses will only be favoured by selection when there are mechanisms facilitating accurate risk assessment (Stankowich and Blumstein, 2005).

The African large predator guild consists of several species, including the lion and leopard (*Panthera pardus*). The guild exhibits a size-mediated asymmetrical dominance hierarchy (Durant 1998; Hayward and Slotow 2009; Webster, McNutt, and McComb 2010); the exact outcomes of encounters, however, are often dependent on the circumstances under which they occur (e.g., Cooper, 1991). In some instances, interspecific competition has been suggested as the proximate cause for the exclusion or near-extinction of competitively inferior species (Creel and Creel, 1996). This has led to it becoming recognised as a key principle for the conservation of large African carnivores (Winterbach et al., 2013).

The leopard has traditionally been considered resilient to the effects of intraguild competition because of its wide habitat tolerance and catholic diet (Ray, Hunter, and Zigouris 2005; Hayward et al. 2006). However, recent evidence suggest that leopards incur negative costs, including mortality and loss of kills, from encounters with larger guild species (Balme et al., 2013). Furthermore, in some areas leopards actively avoid locations recently occupied by lions and show risk-driven avoidance behaviours that are more pronounced in high-risk habitats (Du Preez et al., 2015; Vanak et al., 2013). This suggests that leopards

have the capacity for accurate heterospecific risk assessment, but the cues used in such assessments remain unknown.

The logistical difficulties of observing free-ranging large carnivores have limited our understanding of leopard avoidance behaviours to insights from biotelemetry studies (Du Preez et al., 2015; Maputla et al., 2015; Vanak et al., 2013). Such studies typically use time-referenced locational datasets obtained from GPS radiocollars attached to study animals. Collar power requirements and size/weight limitations limit the frequency at which positional data are recorded, and locational datasets typically comprise of data recorded at frequencies of less than one fix per hour. This has several limitations. In particular, the low resolutions of these datasets make it difficult to discern whether the recorded *avoidance behaviours* are an actual mechanism to avoid areas occupied by competitors (i.e. avoidance strategies) or a consequence of physical confrontations. In addition, radiocollars are poorly suited to capturing immediate and short-lived avoidance behaviours, which may occur between locational fixes. Some behaviours, such as vigilance, vocalisations, and scent-marking, remain cryptic to current remote sensing technologies. Furthermore, to date, there have been no studies on the immediate or short-lived anticompetitor strategies used by leopards to avoid encounters and no empirical studies on whether the species has the capacity for heterospecific risk assessment.

Understanding the dynamics of competitor encounters can provide information on the consequences of enforced proximity between competitors, leading to management decisions that facilitate species coexistence. This is particularly relevant because as species' ranges continue to retract, as a consequence of human activities, the frequency of competitor encounters is likely to increase, and this could place protected populations at

risk (Ginsberg et al., 1995). Large carnivore species are the species most valued by tourists, and so there exists an economic, as well as an ecological, incentive to conserve them (Lindsey et al., 2007). Large carnivores also have important regulatory roles within ecosystems and their loss can reduce biodiversity within a region through mesopredator release (Ripple et al., 2014; Estes et al., 2011; Miller et al., 2001). From an applied management perspective, understanding the cues used to facilitate coexistence could lead to the development of tools with the potential to mitigate human-wildlife conflict. For example, a novel approach under investigation is the strategic deployment of scent marks to create artificial species-specific boundaries (Ausband et al., 2013; Jackson et al., 2012). Understanding the cues used to assess heterospecific risk and species' reactions to that risk are an important step in manipulating the natural communication systems of large carnivores to control their movements.

The aim of this study was to investigate how leopard movement and behaviour are mediated by lion vocalisations. I used targeted acoustic playbacks of lion roars to investigate whether leopards show risk-driven avoidance behaviours when lions are perceived to be nearby. The use of targeted playbacks was preferable to observing naturally occurring encounters for several reasons. In particular, targeted playbacks provided some measure of control over sample sizes and encounter conditions. This was important because interactions between competitors are rarely directly observed by researchers, and the circumstances of encounters are likely to influence the encounter's outcome.

Leopards were predicted to use acoustic cues to assess the risk of encountering lions, and individuals were expected to show avoidance behaviours when lions were perceived to be nearby. In particular, leopards were expected to leave the immediate area following roar

playbacks, and they were expected to show persistent avoidance behaviours, in the form of faster movement speeds, after leaving the experimental site.

Methods

Study area and population

Study site details are provided in *Chapter 2*. One female and one male leopard were fitted with very high frequency (VHF) radiocollars supplied by Sirtrack and African Wildlife Technologies (AWT), respectively. A second male was fitted with an AWT GPS radiocollar. Individuals were immobilised by a registered veterinarian in compliance with Botswana legislation before being fitted with radiocollars. Immobilisations took place from 2013 until 2014 - all before the onset of this project. All three radiocollars emitted high frequency radio signals that allowed individuals to be located using a handheld receiver (Communications Specialist R-1000 Telemetry Receiver) and directional antenna (RA-XXX Yagi antenna).

Playback protocol

Targeted playbacks were carried out from February until May 2015. Playbacks were of three types: lion roars, southern ground hornbill calls (*Bucorvus leadbeateri)*, and dummy playbacks. Hornbill playbacks were used to control for speaker-induced disturbance effects. Dummy playbacks, where experimental equipment was deployed but no sound played, were used to control for observer disturbance effects.

Roar recordings were supplied by the Botswana Predator Conservation Trust and were collected by associated researchers in 2013 and 2014. Recordings were made using a

Marantz PMD660 solid-state recorder linked to a Sennheiser ME66 shotgun microphone. Leopards may behave differently to male and female lions; as a consequence, only roar recordings of male lions were used. Roars are long distance communication calls with several functions including territorial maintenance and mate attraction (Pfefferle et al., 2007; Schaller, 1976). The playback of non-resident males could have introduced stress into the local lion population and altered community dynamics. To limit disturbance to the local population, selected recordings were further limited to males who were residents in the playback areas at the time of experiments. Hornbill recordings were obtained from public-domain videos hosted on the video sharing website YouTube.

All recordings were processed in the open source digital audio editing software Audacity (Audacity Team, 2015). Recordings that showed excessive background noise were filtered to remove frequency bands falling outside the noise profile of the desired call. The amplitudes of recordings were standardised, and five seconds of silence were added to the beginning and end of each recording (as recommended by Fischer et al., 2013). These files were then transferred to a solid-state media device (internal memory of Samsung I9300).

Roar exemplars consisted of a single bout of adult male roars, with mean playback duration of 53.3 ± 1.8 seconds (standard error) (range: 45 - 58 seconds). Hornbill exemplars consisted of several discrete bouts, with mean playback duration of 39.6 ± 0.3 seconds (range: 39 - 40 seconds). In total there were six roar and three hornbill exemplars, which were randomly alternated between successive experiments.

Playbacks were conducted through a loudspeaker (Tannoy CPA 12 studio) linked to an amplifier (Kicker Impulse car amplifier) by approximately 100 meters of speaker cable. The amplifier was powered by a 12 volt car battery and operated from within the research

vehicle. Speakers were concealed behind available vegetation approximately 50 m from resting leopards - with distances verified using a handheld rangefinder (wildgame halo XRT; ± 1 m accuracy up to 500 m). A handheld GPS unit (Garmin etrex 10) was used in areas where vegetation density precluded rangefinder use. Speakers were placed approximately north of target individuals to reduce bias in placing speakers within certain vegetation types. Research vehicles were then manoeuvred into positions that allowed the speaker, leopard, and area in-between to be observed.

All playbacks were standardised to 110 dB, which is within the natural sound pressure levels of lion roars (Webster et al., 2012); peak levels were checked using a handheld sound level meter (Extech 407730 digital sound level meter; ± 2 dB accuracy). Playbacks were conducted in the 90 minutes preceding sunset. This is when leopards and lions are likely to become active and so may naturally expect to encounter one another, and there was sufficient light remaining for observations (Hayward and Slotow, 2009). Playbacks were carried out to target leopards that were fully at rest, and behaviours were recorded for at least five minutes prior to the onset of experiments to ensure that this was the case. One exemplar was played twice during each experimental session, with a three minute interlude between playbacks. Dummy playbacks were considered to commence at an arbitrary time, decided prior to the onset of the experimental session.

Focal animal sampling was used to monitor changes in leopard behaviour during sessions (Altmann, 1974). In particular, changes in the leopard's behavioural state and orientation of their head were noted. This continued until the animal had left the experimental site, which was defined as a circle with a radius of 50 m, centred on the leopard's resting location at the onset of experiments, or until 60 minutes had elapsed from the beginning of the first

playback. Upon leaving the experimental site, leopard departure times and movement directions (relative to the speaker's location) were recorded. Individuals were then followed until low light levels precluded further observations. Positional fixes were recorded at a minimum of 15 minute intervals whilst the animal was moving and their location 60 minutes after the onset of playbacks was noted.

Additional measurements were taken to contextualise the circumstances of playback encounters. Overall vegetation density was assigned to one of three categories: low, intermediate, and high density areas. These classifications were based on the amount of vegetation that would obscure the visibility of a standing leopard in the area between the leopard's resting location and the vegetation behind which the speaker was hidden. In low density areas there was no vegetation that limited visibility; intermediate density areas had vegetation that slightly limited visibility; and in high density locations the area was completely obscured by vegetation. Further, visibility at the leopard's exact playback resting location was used as a proxy for risk of detection by competitors. I defined visibility as the number of squares (6 x 6 cm) on a 66 x 66 cm wooden board attached to poles 63 cm from the ground (mean height of male and female leopards) visible at a distance of 5 m (Estes, 1992). Visibility was calculated 0, 90, 180, and 270 ° relative to the speaker's direction, and the mean of these values was used to quantify the risk of detection for that location. Furthermore, stomach distension was used as a proxy for hunger levels and scored into one of three categories following Bertram (1975). Finally, the presence or absence of the leopard's preferred prey, impala (*Aepyceros melampus*), within 100 m of the experimental site was noted.

Challenges in finding target animals meant that replication was unavoidable, and four leopards were sampled during the study. However, I took several steps to mitigate the effects of pseudoreplication. To avoid subjects associating the arrival of a vehicle with a playback, a minimum of two weeks lapsed between successive playback experiments (extended to four weeks for playbacks of the same type) and playbacks were interspaced with a minimum of two non-experimental observational sessions. Furthermore, different exemplars were used when individuals were presented with multiple playbacks from the same category. Individuals were only subjected to playbacks from the same category twice. Finally, pseudoreplication was also mitigated *post hoc* by including leopard identity as an explanatory variable in models.

Statistical methods

General linear models were used in the analyses of post-playback leopard vigilance levels, response latencies (i.e. the time between playback onset and the first orientation towards the speaker), movement latencies, and distances travelled. An information theoretic approach was applied to the analyses, and the corrected Akaike's information criterion (AIC$_c$) was used to rank competing models (Burnham and Anderson, 2002). Sample sizes limited model explanatory factors to playback category and leopard identity. Three models were defined *a priori*:

1. Response variable ~ playback category + leopard identity

2. Response variable ~ playback category

3. Response variable ~ 1

Model 1 assumed that the leopard's post-playback behaviour (the response variable) was influenced by playback category and leopard identity. Leopard identity was included as a *post hoc* control for pseudoreplication. Model 2 assumed that the leopard's behaviour was influenced by playback category alone. The third model represents the null model, where neither playback category nor leopard identity explains post-playback leopard behaviour.

Models within six AIC$_c$ units of the best fit model were retained, which provided a 95% confidence of the best fit model being considered, and models within two AIC$_c$ units were assumed to be as good as the best fitting model (Burnham and Anderson, 2002; Richards, 2005).

Individuals were defined as vigilant when heads were raised and fixed in one direction with eyes wide open or when individuals were visually scanning the landscape (Treves, 2000). Post-playback vigilance levels were represented as the proportion of time spent vigilant. This allowed me to control for differences in post-playback time spent at the experimental site. Proportions were transformed using the logit transformation (as recommended by Warton and Hui, 2011) before being incorporated into models as the response variable.

If no post-playback vigilance behaviours were observed, response latency was set to the duration of time the leopard spent at the experimental site - up to a maximum value of 3600 seconds. When there were no post-playback movement behaviours, movement latencies were set to 3600 seconds. Right censoring of the latency response variables necessitated the use of censored regression models (Henningsen, 2010). Distances travelled were the straight line distances between the experimental sites to the individual's location at the time of interest. I compared the mean distances travelled for each playback category. Distances were calculated for the 60 minutes after the beginning of the first playback and 15

minutes after the commencement of movement. The former allowed me to detect

differences in distances travelled over a relatively short post-playback time-scale. This

allowed me to look at whether roar playbacks induced leopards to leave the area. In

contrast, comparing the distances travelled once leopards had begun moving was important

because it controlled for time lags between playbacks beginning and leopards moving.

Distances were only available for the 15 minute period after movement began because

leopards were typically lost soon after.

Fisher's exact test was used to investigate whether playbacks provoked movement

responses; paired t-tests were used to compare vigilance levels in the first and second

halves of post-playback time spent at the experiment site. Circular statistics were used to

analyse post-playback movement directions of leopards (Pewsey et al., 2013). In particular,

the Rayleigh test was used to test for uniformity in post-playback movement directions

against the alternative hypothesis of a unimodal distribution, with specified mean direction.

This mean direction was the mean movement direction for that particular playback

category.

Analyses were carried out in the open source software environment for statistical

computing 'R' (version 3.2.0) (R Development Core Team, 2015) . The packages 'MuMIn'

(Barton, 2015) and 'circular' (Agostinellli and Lund, 2013) were used for information

theoretic and circular statistical analyses, respectively.

Results

Leopards typically responded strongly to lion roar playbacks. In particular, response

latencies were shorter following roar playbacks than either control (table 1), with the best

fitting model (AIC_c weight = 0.956) including only playback category (table 2). Although

leopards spent a greater amount of time vigilant after roar playbacks and were vigilant for

approximately three times longer than controls (table 1), the null was the best supported

model. However, the model containing playback category was within 1 AIC_c unit of the null,

suggesting a possible influence of playback type. Vigilance levels increased immediately

after roars began. Leopards showed heightened vigilance during their remaining time at the

experimental site, and vigilance levels were similar in the first and second halves of the

post-playback time leopards spent in the area (paired t-test$_6$ = 1.99, p = 0.943) (figure 1).

Table 1. Post-playback vigilance levels, response latencies, and movement latencies

	Playback category								
	Lion			Hornbill			Dummy		
	N	Mean	SE	N	Mean	SE	N	Mean	SE
Time spent vigilant (%)	7	49.53	12.70	6	16.12	9.63	6	12.50	4.98
Latency to response (s)	7	11.29	3.41	6	1204.17	757.63	6	2888.17	321.10
Latency to movement (s)	7	1428.86	584.19	6	2434.67	610.11	6	2664.83	335.77

Table 2. Information theoretic models fitted to post-playback response variables

Response	N	Model	AICc	Δ AICc	Weight	df
Vigilance	19	null	103.012	-	0.613	2
		category	103.974	0.965	0.378	4
		category + individual	111.443	8.431	0.009	7
Response latency	19	category	261.932	-	0.956	4
		null	268.906	6.975	0.029	2
		category + individual	270.259	8.327	0.015	7
Movement latency	19	null	262.946	-	0.825	2
		category	266.148	3.202	0.166	4
		category + individual	272.169	9.223	0.008	7
Distance (15 minutes) [a]	14	null	175.742	-	0.961	2
		category	182.165	6.423	0.039	4
		category + individual	201.459	25.717	< 0.001	7
Distance (60 minutes) [b]	19	null	269.675	-	0.937	2
		category	275.082	5.407	0.063	4
		category + individual	284.398	14.723	0.001	7

[a] This is the leopard's distance from the experimental site 15 minutes after the onset of movement.

[b] This is the leopard's distance from the experimental site 60 minutes after playbacks have commenced.
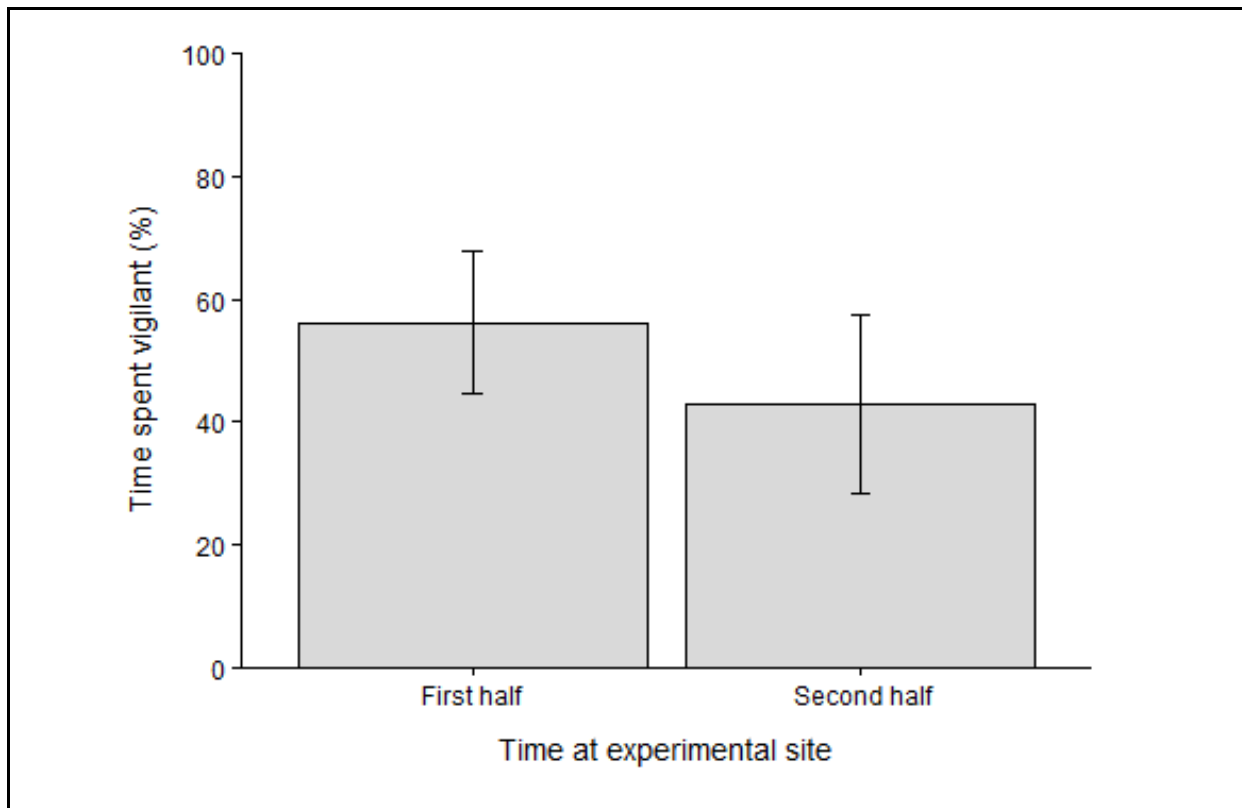
Figure 1. Post-roar playback time spent vigilant in the first and second halves of the leopard's remaining time at the experimental site. This figure shows that mean vigilance levels (± standard error) are not strongly affected by time spent at the experimental site following roar playbacks.

Leopards were more likely to move away immediately, that is within 15 minutes, after hearing lion roar playbacks compared to controls; however, this was not-significant (Fisher's exact test, p = 0.2953) (table 3). Furthermore, whilst movement latencies were typically smaller after roar playbacks (1428 ± 584 seconds) than either hornbill (2434 ± 610 seconds) or dummy (2664 ± 336 seconds), the null was the best data supported model (AIC$_c$ weight = 0.825).

Table 3. Leopard movement directions (relative to speaker locations) within 15 minutes of playbacks commencing

Playback category	Movement Direction		
	Toward	Away	None
Lion	0	3	4
Hornbill	1	0	5
Dummy	0	0	6

Initial movement directions following roar playbacks were typically away from the speaker (mean direction of 174.44°, relative to speaker) (Rayleigh's $Z_{0.786}$, p = 0.0019) and never towards the speaker (figure 2). In contrast, movement directions were uniformly distributed for hornbill (Rayleigh's $Z_{0.4619}$, p = 0.1008) and dummy playbacks (Rayleigh's $Z_{0.2947}$, p = 0.1825) (figure 2). However, 15 minutes after the onset of movement the leopard's initial preferred movement bearing directly away from the roar location was gone, and movement directions were uniformly distributed for roar (Rayleigh's $Z_{0.2243}$, p = 0.2245), hornbill (Rayleigh's $Z_{0.3233}$, p = 0.2265), and dummy (Rayleigh's $Z_{0.0684}$, p = 0.4376) playbacks (figure 3).
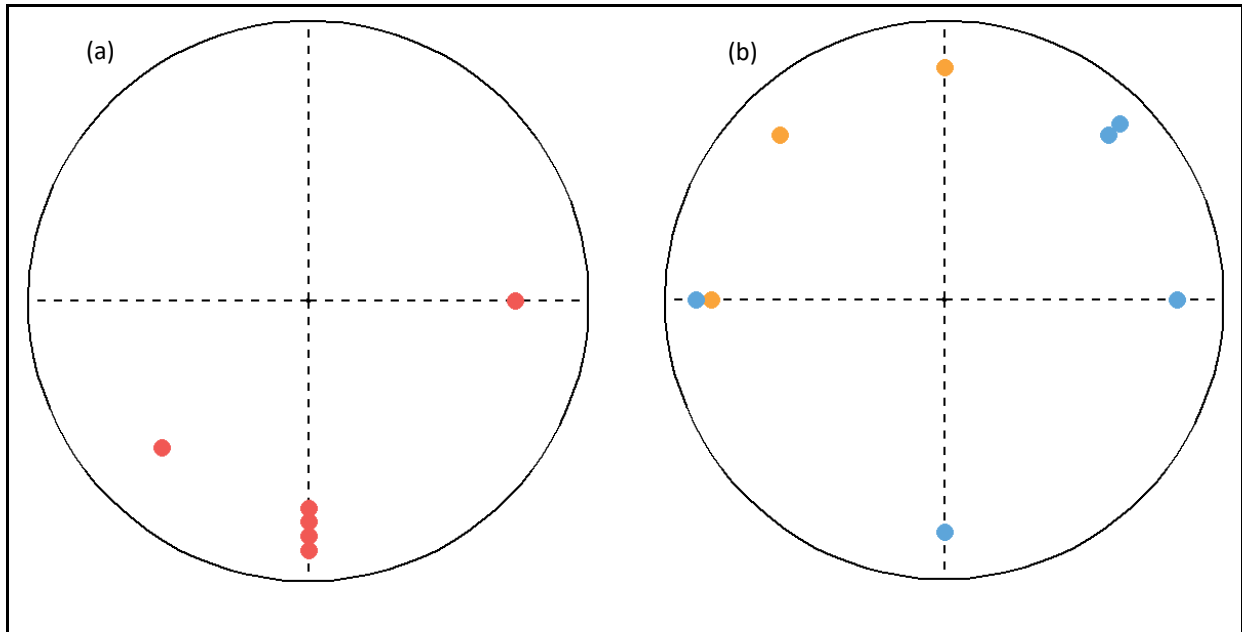
Figure 2. Initial movement directions of leopards following playbacks. This figure shows the initial bearings of movement (relative to speaker locations) of leopards following roar [a] (red), hornbill [b] (orange) and dummy [b] (blue) playbacks. Movement directions were recorded for all moving leopards regardless of the length of time after playbacks that movement began. Instances where leopards did not move, (roar: n = 1, hornbill: n = 3; dummy: n = 1) are not shown on this figure. Figures are centred on the leopard's experimental location, with the speaker location north of the centre. Distance travelled is not represented on this figure.
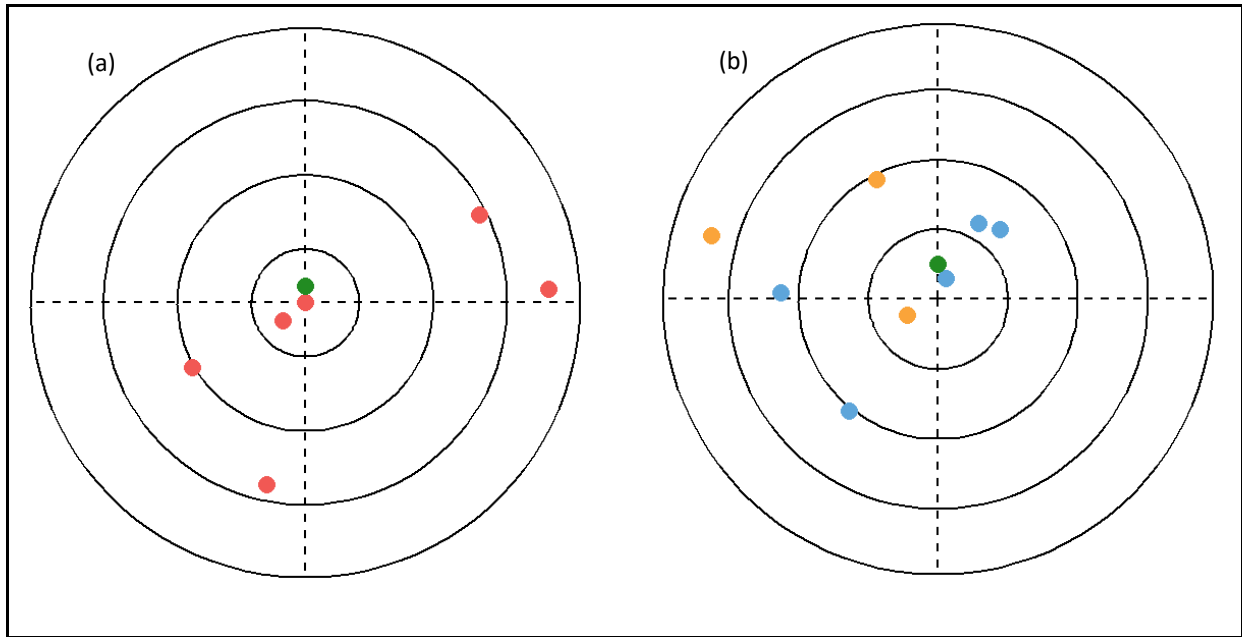
Figure 3. Leopard locations 15 minutes after leaving the experimental site. This figure shows the locations of leopards 15 minutes after leaving the experimental site following roar [a] (red), hornbill [b] (orange) and dummy [b] (blue) playbacks, relative to the speaker's location (green). Circular grid lines delineate distances of 100 m. Figures are centred on the leopard's experimental location. Instances where leopards did not move, (roar: n = 1, hornbill: n = 3; dummy: n = 1) are not shown on this figure.

Mean movement distances 15 minutes after the onset of movement were similar across all playback categories (figure 4a), as were distances from the playback site 60 minutes after the onset of playbacks (figure 4b). Indeed, the best fitting models for movement distances 15 minutes after the onset of movement and 60 minutes after the onset of playbacks were the null models (AIC$_c$ weights = 0. 961 and 0.937, respectively) (table 2).
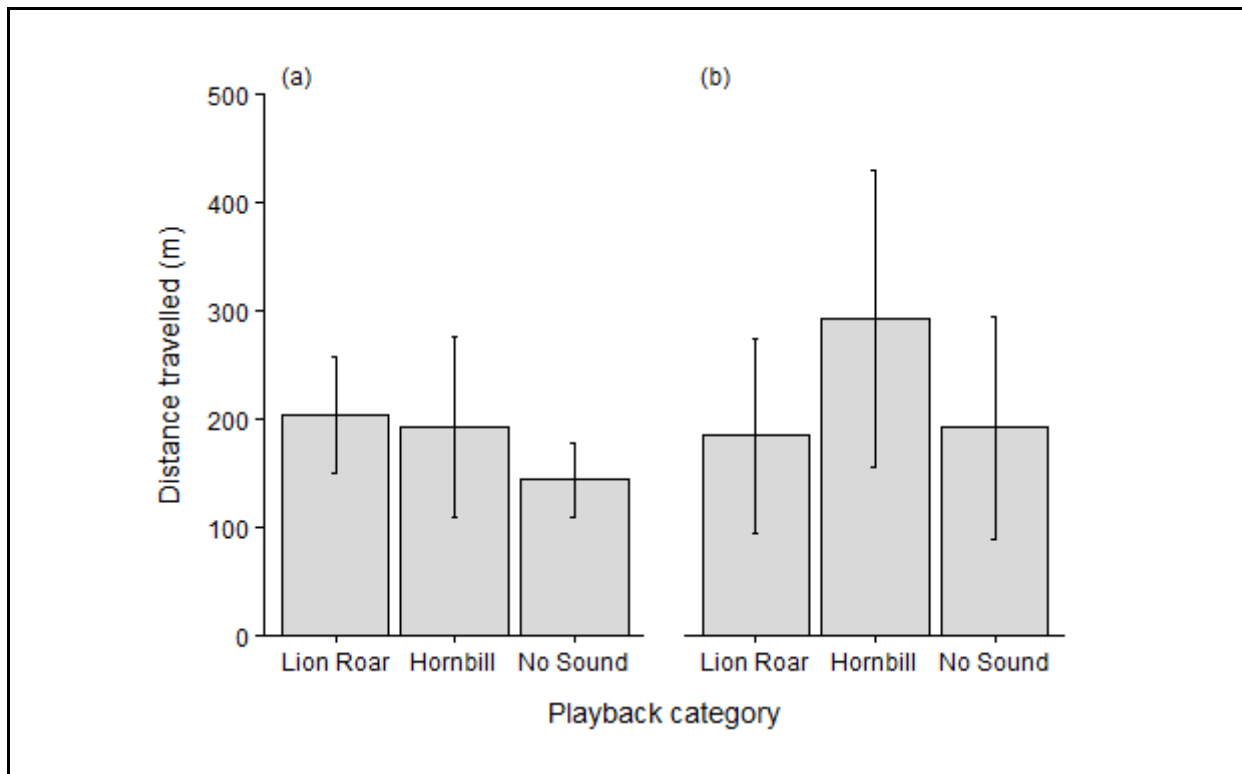
Figure 4. Mean (± standard error) leopard distances (m) from experimental sites following playbacks. Shown are the post-playback distances travelled for each playback category 15 minutes after movement begins (a) and 60 minutes after the onset of playbacks (b).

Discussion

The results of this study challenge the traditional assumptions that leopards are unaffected by interspecific competition and offer insights into risk-mediated anticompetitor strategies. Sample sizes were limited by the logistical challenges of locating uncollared leopards. However, I overcame the potential issues of repeated sampling by using different exemplars and long temporal interludes (Fischer et al., 2013). The results presented offer key insights into risk-driven behavioural changes in leopards.

Risk assessment

That leopards showed heightened anticompetitor responses to lion roars suggests that heterospecific acoustic cues are used in facultative risk assessment. However, the results do not preclude additional stimuli from facilitating assessment. Indeed, species will often use multiple competitor detection mechanisms that are intrinsically linked to their sensory systems (Bhatnagar, 2008; Kats and Dill, 1998). The risk of mortality from encountering competitors suggests that carnivores may primarily rely on cues facilitating detection at distance (Palomares and Caro, 1999). Furthermore, trade-offs may exist in the reliability and associated risk of using different methods of detection under different conditions. For example, acoustic cues can be detected at distance but the signaller's exact location is often uncertain: visual cues are better indicators of an animal's exact location but require competitors to be within relatively close proximity (Bhatnagar, 2008).

Typically, leopards avoid open habitats that are well suited to long distance visual detection and instead prefer intermediate or densely vegetated areas (Balme et al., 2007; Hayward et al., 2006). As a consequence, leopards may primarily rely on acoustic and olfactory cues to detect competitors, since their preferred habitats limit visibility. In this study, leopards adopted anticompetitor behaviours in response to competitor acoustic cues, either remaining in the cover of their resting location and showing increased vigilance or moving away. Thus, individuals relied primarily on acoustic cues to assess risk and did not move towards vocalisations in order to achieve visual contact.

The inability to differentiate between null and playback category models for vigilance may be a consequence of the small sample size. However, the results provide weak support that resting leopards increase vigilance when lions are perceived to be nearby. Vigilance is typically defined as a '*motor act, which corresponds to a head lift interrupting the ongoing activity*' (Quenette, 1990). Consequently, increased vigilance has energetic costs and fitness implications as it precludes other activities, including resting - the basal metabolic state (Toïgo, 1999). Furthermore, increased vigilance can induce endocrinology stress responses with potential fitness implications, although this remains poorly understood in free-ranging carnivores (Becker, 2002; Wingfield et al., 1997).

Individuals did not consistently retreat following roar playbacks. This is in contrast to African wild dogs (*Lycaon pictus*), which typically flee from the targeted playback of lion roars (Webster et al., 2012). The exact strategy employed by individual leopards may reflect a trade-off in the costs and benefits of different responses under different conditions (Broom and Ruxton, 2005; Cooper Jr. and Frederick, 2007). The distance at which an individual flees from a competitor or predator is typically smaller for cryptic than non-cryptic species (Stankowich and Blumstein, 2005). It may be that leopards typically remained at the experimental site following roar playbacks because their cryptic colouration and solitary nature facilitated the use of crypsis as an anticompetitor strategy. In contrast, the social nature of wild dogs is partially maintained through bouts of prolonged vocalisations, which may preclude the use of crypsis (Webster et al., 2010). Furthermore, although wild dogs occur in packs, their smaller size makes them particularly susceptible to mortality from lions, and so the risks of encountering lions may be greater for wild dogs

than leopards (Creel and Creel, 1996). Also, unlike leopards, wild dogs cannot climb trees to escape from competitors (Bailey, 2005).

All of this study's playbacks were in intermediate and densely vegetated areas, which is a reflection of the leopards' preference for these areas rather than a conscious bias. The presence of suitable cover in these areas likely facilitated the effectiveness of cryptic behaviours. Within open habitats crypsis may be a less viable strategy as the lack of ground cover (to avoid detection) and vertical cover (to escape from competitors when crypsis fails) increases the risks and costs of cryptic behaviour (Bothma, 1998). Crypsis may also have been preferred because the risk of predation was not perceived to be immediate. Non-proximate detection mechanisms do not indicate whether detected competitors are aware of the detector's presence. Lions, however, do not typically vocalise whilst stalking. As such, roars likely represent instances where lions remain unaware of the leopard's presence. In these instances, the optimal strategy for leopards may be to remain in cover and either await visual contact before fleeing, or simply move away from the last known direction of the lion when movement does become necessary.

Leopards may be expected to exhibit stronger responses to lion olfactory cues than to lion roars, since body odours may still be detected when lions are engaging in predatory behaviours. On three occasions leopards were clearly observed to sniff the air following roar playbacks, suggesting olfactory cues may be used in risk assessment. Whilst acoustic cues provide locational information only whilst the competitor is vocalising, body odours may represent a continuous source of positional information. The leopard's increased vigilance following auditory cues may increase its sensitivity to additional cues, and pre-exposure to one cue may facilitate heightened responses to others. It would be interesting

to pair olfactory competitor cues with playback experiments to see how multi-modal information influences risk perception.

Although three out of seven roar playbacks provoked an immediate movement response, in only one case did the leopard depart from the experimental site completely. In this instance, a female leopard immediately fled the area after hearing the roar and took refuge in a tree approximately 280 m from the playback site. This was the only instance a roar playback was carried out to a female leopard. It is possible that the leopard's departure from the experimental site may have been linked to differences in the life-history traits of males and females. For example, female leopards are smaller than males, and so may be less able to defend themselves during physical confrontations with lions. In another instance, a male leopard fled to a distance of 70 m before tentatively returning to his experimental site location - frequently stopping and focussing in the roar direction as he returned. The final case involved movement further into the thicket whilst the leopard remained close to the experimental site.

The heterogeneity of leopard responses to lion roars supports the idea that risk is context dependent, and that anticompetitor behaviours change with circumstance. Unfortunately, the small sample size limits what can be said about which factors are most influential. However, sexual size dimorphism, habitat characteristics, and the presence of defendable resources are likely to alter the costs and benefits of different strategies. Greater sample sizes would elucidate under which contexts different avoidance behaviours are initiated.

Although leopards did not typically leave encounter sites immediately after roar playbacks, initial movement directions away from the speaker likely reflect their spatial perception of risk. Individuals may limit encounter probabilities by avoiding areas where competitors were last identified. However, leopard locations 15 minutes after the onset of movements were uniformly distributed around speaker locations. This suggests that in this instance the leopard's perception of risk is limited to the competitor's last known location. This is likely to have occurred because there was no information available on the perceived competitor's movement direction - since playbacks were performed from a stationary speaker. That leopards moved away from playback locations has implications for bio-management strategies looking to manipulate carnivore movement by manipulating the target species' perception of risk (see below). It would be interesting, however, to repeat the playback experiments with mobile speakers. This would provide further insights into the leopard's cognitive ability to map risk spatially and would show how competitor movement directions influence fine-scale movement behaviours of leopards.

Although it was predicted that leopards would move greater distances following roar playbacks, our results suggest otherwise. However, this is to be expected if leopards rely predominantly on crypsis to avoid competitors in intermediate and densely vegetated areas. Du Preez et al. (2015) found that leopards travel similar hourly distances in the presence and absence of lions within intermediate and densely vegetated areas. Within open habitats, however, hourly distances travelled were greater in the presence of lions. This is likely a reflection of the risks associated with different habitat types: within open areas the increased risk of detection may preclude crypsis as a viable avoidance strategy. In such

instances, leopards can use quick highly directional movements to minimise exposure times and avoid encounters (Du Preez et al., 2015).

The results of Du Preez et al. (2015) suggest that habitat type influences which avoidance strategy is used. This has implications for landscape restoration and habitat conversion strategies as changes in community dynamics, such as encounter frequencies between competitors, could lead to possible extinction events (Dickman, 1996). For example, phototourism is an important income generator for many sub-Saharan countries and contributes to conservation efforts (Bushell and Eagles, 2006; Lindsey, 2010). Wildlife phototourism is viable only in areas offering good densities of visible wildlife (Goodwin and Leader-Williams, 2000), and in some instances landowners may be tempted to increase the availability of open areas to increase visibility. However, increasing the availability of open areas may impact leopard populations by increasing their susceptibility to competitor mortality events. Large carnivores are typically the species most valued by tourists (Lindsey et al. 2007); strategies that increase densities of visible wildlife could negatively impact tourism by reducing densities of the most sought after species. Understanding how species utilise different habitats is essential if habitat conversion strategies are to maintain biodiversity.

The Du Preez et al. (2015) study, with the exception of this current study, uses the highest GPS resolution (one local fix per hour) of any study investigating interspecific interactions between the African leopard and its competitors. However, along with other telemetry studies that suggest segregation between leopards and lions, it still has several limitations that are imposed by the large time gaps between locational fixes (Vanak et al., 2013; Maputla et al., 2015; Du Preez et al., 2015). For example, the limited resolution precludes

the distinction between behaviours based on the real-time risk of encountering competitors and those based on the predicted distribution of risk.

Although several studies have shown that other African large predator species display risk-driven anticompetitor behaviours, none, to the best of my knowledge, have quantified their direct-associated costs. However, understanding the costs of competition is vital for informed conservation. This is particularly relevant in a society where habitat reductions restrict competing species to shared, increasingly isolated areas (Ray et al., 2005). Future studies would benefit from including quantitative measures of the costs associated with encounters. Giving up densities at kill sites, in the presence and absence of competitor cues, could provide a simple measure to quantify foraging costs as encounter risk increases. Alternatively, the energetic costs of encounters could be quantified using multi-sensor radiocollars fitted with electrocardiogram recorders (Duriez et al., 2014). This approach would provide greater insights into changes in an individual's perception of fear over time and would allow the costs of remotely captured encounter events (see *chapter 4*) to be quantified.

Implications for bio-fence management

In some areas of Africa, leopards account for the highest number of livestock losses attributable to large carnivores, which leads to their active persecution (Schiess-Meier et al., 2007; Gusset et al., 2009). Carnivores that cross into or reside in community areas are particularly susceptible to retaliatory or pre-emptive killings from land owners (Kissui, 2008). Furthermore, leopards at the boundaries of protected areas may suffer higher mortality rates than those at the core, which can put protected populations at risk (Balme et al.,

2010). Thus, reducing levels of human-leopard conflict is essential in ensuring the long-term viability of the species (Winterbach et al., 2013).

A common strategy to reduce conflict is to use physical barriers to separate carnivores from human populations. However, fences are sometimes undesirable, for reasons including aesthetics and financial limitations (Creel et al., 2013b; Packer et al., 2013). Furthermore, the efficacy of physical barriers varies by species and is particularly low for leopards (Hayward et al., 2007; Cozzi et al., 2013). Another common strategy is the removal of 'trespassing' carnivores from areas where conflict may arise. Translocations, however, require large investments in time and resources, and they may not be viable for rural communities (Treves and Karanth, 2003). They are also of limited efficacy due to the possible return of translocated individuals or the take-over of their former range by conspecifics (Weise et al., 2015).

A novel approach currently under investigation is the use of naturally occurring biological signals to manipulate large carnivore movements and promote conservation outcomes (Jackson et al., 2012; Ausband et al., 2013). Such strategies could be proactive or reactive. Proactive strategies involve restricting carnivore movements to protected areas: reactive strategies involve relocating carnivores to protected areas following incursions into human habitations and employing signals to encourage them to remain there. For example, Jackson et al. (2012) found that wild dog packs resting at the peripheries of their home range boundaries would move towards the core areas of their territory after being exposed to the scent marks of stranger packs.

That leopards preferred cryptic behaviours after hearing lion roars suggests that lion roars may not be effective signals to relocate leopards to core territory areas. Other competitor

cues, however, could still be used as a reactive signal-based strategy to manipulate leopard movements. Further, the costs and benefits of cryptic avoidance strategies are likely to differ between resting and moving individuals. Thus, the results of my study do not rule out the possibility of using lion calls to prevent moving leopards from entering undesirable areas. In this case, it would be important to consider the intraspecific effects that these signals may have on individuals from the donor species. For example, using lion roars to repel leopards may attract lions, which is clearly an undesirable outcome. In some areas, leopards maintain discrete territorial boundaries with same-sex conspecifics (Bailey, 2005). Thus, intraspecific cues may be more effective in proactively manipulating leopard movements.

Understanding the feasibility of conservation strategies relying on biological signals requires a sound understanding of the communication systems of the species involved as well as the dynamics off intraspecific and intraguild interactions. Knowledge of how species respond to competitor cues and the motivations behind intraguild encounters is particularly relevant for the development and effective deployment of biologically-relevant boundaries.

Conclusion

Understanding the dynamics of competitor encounters and the mechanisms facilitating coexistence is important for conservation because competitive interactions can have negative costs for inferior competitors. This is particularly relevant in ecosystems where the availability of suitable habitats is decreasing, increasing the potential for encounter events. The low sample sizes of this study limit what can be said of the factors influencing risk-driven avoidance behaviours. However, within habitats with suitable vegetation cover - habitats perhaps most typical for leopards - resting leopards do appear to rely on crypsis to

avoid encounters with lions. The results have implications for projects looking to manipulate leopard movements using naturally occurring signals, and they provide the basis for future studies interested in understanding the anticompetitor strategies used by the African leopard.

Chapter 4: Spatial dynamics of leopard movements following naturally occurring encounters with lions

Introduction

Physical confrontations between species with overlapping resource requirements can be costly to some or all participants (Polis et al., 1989). As a consequence, species often have anticompetitor adaptations to reduce the probabilities of confrontations. Some species rely primarily on avoidance mechanisms that reduce the probabilities of competitors occupying the same immediate areas at the same time (Brodie et al., 1991). For example, sympatric jackal species, *Canis adustus* and *Canis mesomelas,* show differentiation in habitat use (Loveridge and Macdonald, 2003). Other species may rely on anticompetitor mechanisms that reduce the probabilities of physical confrontations when both species occupy the same area (Brodie et al., 1991)**.** For example, cheetah (*Acinonyx jubatus*) show increased vigilance when lion (*Panthera leo*) are perceived to be nearby (Durant, 2000).

Species may also mitigate the costs associated with physical confrontations after they have been initiated. The costs and benefits of engaging with or fleeing from competitors, post-detection, are likely to depend on circumstances of the encounter, such as the competitor species involved or presence of valuable resources (Webster et al., 2012). Unfortunately, investigating the encounter dynamics between free-ranging carnivores can be challenging for several reasons, including the attitudes of local communities to large carnivores and the ecology of the involved species.

For example, the large home-ranges utilised by carnivores and the logistical challenges in coordinating research activities over these spatial scales restrict the number of naturally occurring encounters observed. As a consequence, relative to the mechanisms mediating confrontations, the dynamics of competitor encounters are poorly understood, and our understanding of post-encounter behaviours is primarily based on experimental approaches that have simulated the presence of competitors (Creel, 2001; Durant, 2000; Webster et al., 2012). This approach is useful in quantifying avoidance behaviours when competitors are perceived to be nearby; however, it provides little insight into the dynamics of naturally occurring interspecific interactions.

Remote sensing technologies that record the locations of individuals over time (e.g., GPS radiocollars) are increasingly used in ecological studies (Cagnacci et al., 2010). Formerly, technological limitations often led to limited fix rates, and this precluded the identification of competitor confrontations and the detailed analysis of post-encounter behaviours. However, recent advancements in GPS radiocollar technologies provide the capacity to collect high-resolution (five-minute intervals between locational fixes) positional data in a power-conservative manner (Wilson et al., 2013). Such high-resolution datasets from potential competitors with overlapping home-ranges have the potential to capture and describe interspecific encounters accurately.

In this study, datasets from custom built, high-resolution GPS radiocollars were used to investigate the dynamics of interspecific interactions between the African leopard (*Panthera pardus*) and African lion. Traditionally, leopards have been assumed to be resistant to the effects of interspecific competition (Winterbach et al., 2013). This has largely led to their exclusion from studies interested in the mechanisms mediating physical confrontations

between large African predators. However, lions represent a significant source of leopard mortality, and recent telemetry studies suggest that leopards avoid areas occupied by lions (Du Preez et al., 2015; Maputla et al., 2015; Vanak et al., 2013).

In the previous chapter, I investigated how leopards respond to the threat of nearby lions, simulated to be in proximity through targeted acoustic playbacks. The purpose of this chapter is not to carry out an exhaustive analysis of encounter dynamics within the leopard-lion dyad; instead, I focus on the leopard and how properties of its movement, such as speed, direction, and tortuosity, change following encounters.

As lions represent a major source of leopard mortality, it was predicted that leopards would travel greater distances in the time following lion encounters, relative to when lions were absent (Balme et al., 2013). It was also predicted that leopards would alter movement bearings to avoid prolonged encounters with competitors. Finally, tortuosity, which in this context refers to the linearity of movement paths, is a key component of animal movement and changes under different behavioural processes (Benhamou, 2004). For example, lion movements are highly directional in areas where they are at risk of encountering humans (Valeix et al. 2012). Thus, it was hypothesised that, following lion encounters, leopards would display highly directional (less tortuous) movement paths and would travel at greater speeds.

This is the first study investigating the detailed dynamics of interspecific interactions involving the African leopard. It is also one of the first to use high-resolution GPS radiocollars to elucidate the consequences of interspecific interactions between Africa's large predators. The results will aid conservationists by providing information on the potential costs of enforced proximity amongst competing terrestrial carnivores. This is

important as changes in community dynamics that elevate competition levels can place inferior competitors at risk of localised extinction events (Dickman, 1996; Jackson, 2014). In addition, the results will have applications in applied conservation management, particularly by informing management strategies based on controlling carnivore movements by manipulating a species' perception of risk (Ausband et al., 2013; Jackson et al., 2012)

Methods

Study area and data collection

Study site details are provided in *Chapter 2*. In 2012, nine lions (two males and seven females) and two leopards (both male) were fitted with radiocollars developed by the Royal Veterinary College's (RVC), University of London, Structure and Motion Laboratory (Wilson et al., 2013). Study animals were tranquilised by a qualified registered veterinarian, in compliance with Botswana law and fitted with radiocollars whilst immobilised. All immobilisations were coordinated by academics associated with the Botswana Predator Conservation Trust and were carried out prior to my involvement in the project.

Radiocollars were species-specific and designed to minimise the discomfort of study animals. Each collar was also fitted with a high speed transceiver allowing collar instructions to be uploaded, and data downloaded, remotely - minimising animal disturbance. Radiocollars included the capacity to record data on the position, speed, acceleration, and track of individuals. The inclusion of an accelerometer and gyroscope allowed radiocollar operating instructions to change with the animal's behaviour. This allowed power to be conserved until data collection was initiated by behaviours relevant to the specific questions being asked. Furthermore, high efficiency solar cells extended collar operational times

before battery exhaustion. Default radiocollar operating instructions were set to record the locations of individuals at thirty minute intervals. However, when animals were active, as detected by accelerometer and gyroscope force measurements, operating instructions shifted to record GPS positional fixes at an accelerated rate of one fix every five minutes. GPS fixes were accurate to within < 10 m (Wilson et al., 2013).

Data were recorded for a mean of 195 days for lions (n = 9; SD = 97.48 days; range: 50 – 276 days) and for a mean of 174 days for leopards (n = 2; SD = 35.36 days; range: 149 – 199 days). However, taking into account that interactions could only be recorded when both participants had functional radiocollars, there was a mean of 127 days (SD = 62.93; range 50 – 198 days) where lion radiocollars were functioning at the same time as at least one leopard radiocollar with which they could have an encounter.

Encounter definition

For simplicity, encounters were assumed when distances between competitors were less than the detection distance for either species (Lima and Dill, 1990). Previous measurements made during a brief pilot study suggested that 200 m was the maximum distance at which leopards may be able to see a standing lion within intermediate density habitats (K.Rafiq, unpublished data). Consequently, a detection radius of 200 m was assumed for both species. Thus, encounters were defined as occurring when the distance separating competitors was less than 200 m. These assumptions carried a number of limitations. In particular, detection distances likely change with properties of the habitat, for example, decreasing in densely vegetated areas. Thus, there may have been instances where competitors were less than 200 m apart and remained unaware of the other's presence and distances greater than 200 m where they were visible to one another. However, these

assumptions were necessary as the resolution of locational fixes made it difficult to completely differentiate between actual and near encounters.

Data extraction

Locational data were extracted for two hours either side of each leopard-lion encounter. The data were extracted using coding developed by the RVC in the Perl and 'R' programming languages. Instances where the same competitors met multiple times were only considered as separate encounters if they were separated by 12 hours. The encounter location for each individual was defined as the locational fix where the individual was closest to its competitor.

Encounter data were plotted, and each encounter was visually assessed to identify erroneous locational fixes that may have resulted in false encounters being extracted. False encounters were typically characterised by single erroneous locational fixes that had deviated several kilometres from preceding and succeeding locations. Erroneous locational fixes were identified and removed if they would have required individuals to exceed maximal sprint speeds, 60 km per hour and 59 km per hour, for leopards and lions respectively (Bro-Jørgensen, 2013).

Radiocollars were not standardised to record locational fixes at the same times as other collars. Thus, interpolated points were used to provide greater accuracy in defining encounter locations. Interactions were linearly interpolated at 5 second intervals between raw locational fixes. Interpolations were carried out by the RVC using the Perl and 'R' programming languages. The encounter locations of each individual were then recalculated using interpolated points to identify the locations at which individuals were closest to

competitors. Encounter sites were defined for each encounter as the midpoint between competitor encounter locations. Analyses were conducted on datasets containing raw and interpolated locational fixes.

<u>Response variables</u>

Four response variables were used in the analyses: distance from encounter site, movement speed, movement bearing, and tortuosity. Distances from encounter sites were calculated as the straight line distances. Pre- and post-encounter movement speeds were the mean speeds travelled between successive coordinates at five minute intervals in the thirty minutes before and after encounters. Distances and mean movement speeds were also calculated for two hours post-encounter.

Pre- and post-encounter movement bearings were the mean bearings between successive interpolated points at five minute intervals in the thirty minutes before and after encounters. Circular statistics were used to calculate the movement bearings. Changes in pre- and post-encounter bearings for each leopard were then converted into ratios, which standardised the extent to which individuals continued on pre-encounter bearings. Values of one indicated post-encounter bearings remained the same: values close to zero indicated individuals travelling on opposite bearings (formula 1).

$$Change\ ratio\ = \frac{360 - x\ (if\ x > 180);\ x\ (otherwise)}{180}$$

Formula 1. Formula used to calculate the change ratio for pre- and post-encounter movement bearings, where x is the absolute value of the pre-encounter bearing minus the post encounter bearing.

The straightness index, which is the ratio of the straight line distance between points *A* and *B* and the path length travelled to reach point *B* from point *A*, was used as the measure of

path tortuosity. This was the preferred tortuosity metric for two primary reasons. First of all, the straightness index is a reliable tortuosity measure when animals are expected to be undertaking orientated movements, as may be the case when carnivores are at risk from competitors (Benhamou, 2004; Valeix et al., 2012). Secondly, as opposed to other measures of tortuosity, the straightness index is intuitive to interpret, with higher values indicating more directional (less tortuous) movements (Benhamou, 2004).

<u>Controls</u>

The locational data for leopard movements during the same four hour period on the day before encounters took place were used as controls. Movements occurring the day after encounters were not used as controls because these may have been affected by the encounter on the previous day. Locations of the nearest radiocollared lions during this four hour window, for each control, ranged between 1309 - 12,140 m; thus, it can be assumed that the controls represent leopard movements in the absence of radiocollared lions. The two hours either side of each control 'encounter' were classified as pre-encounter and post-encounter, respectively. Response variable values were calculated for my control datasets and compared to leopard responses during lion encounters using paired t-tests. Paired t-tests were also used to compare lion speeds pre- and post-encounter.

Analyses were carried out in the open source software environment for statistical computing 'R' (version 3.2.2) (R Development Core Team, 2015). All mean values are reported with the standard error. I report absolute p-values to aid transparency of the results, since several p-values came close to the assumed significance threshold of 0.05.

Results

In total, 21 interspecific encounters were extracted, occurring over seven pairwise

combinations between two leopards and six lions (figure 1). The mean separation distance

between competitors at the point of encounters was 93.38 ± 13.75 m.
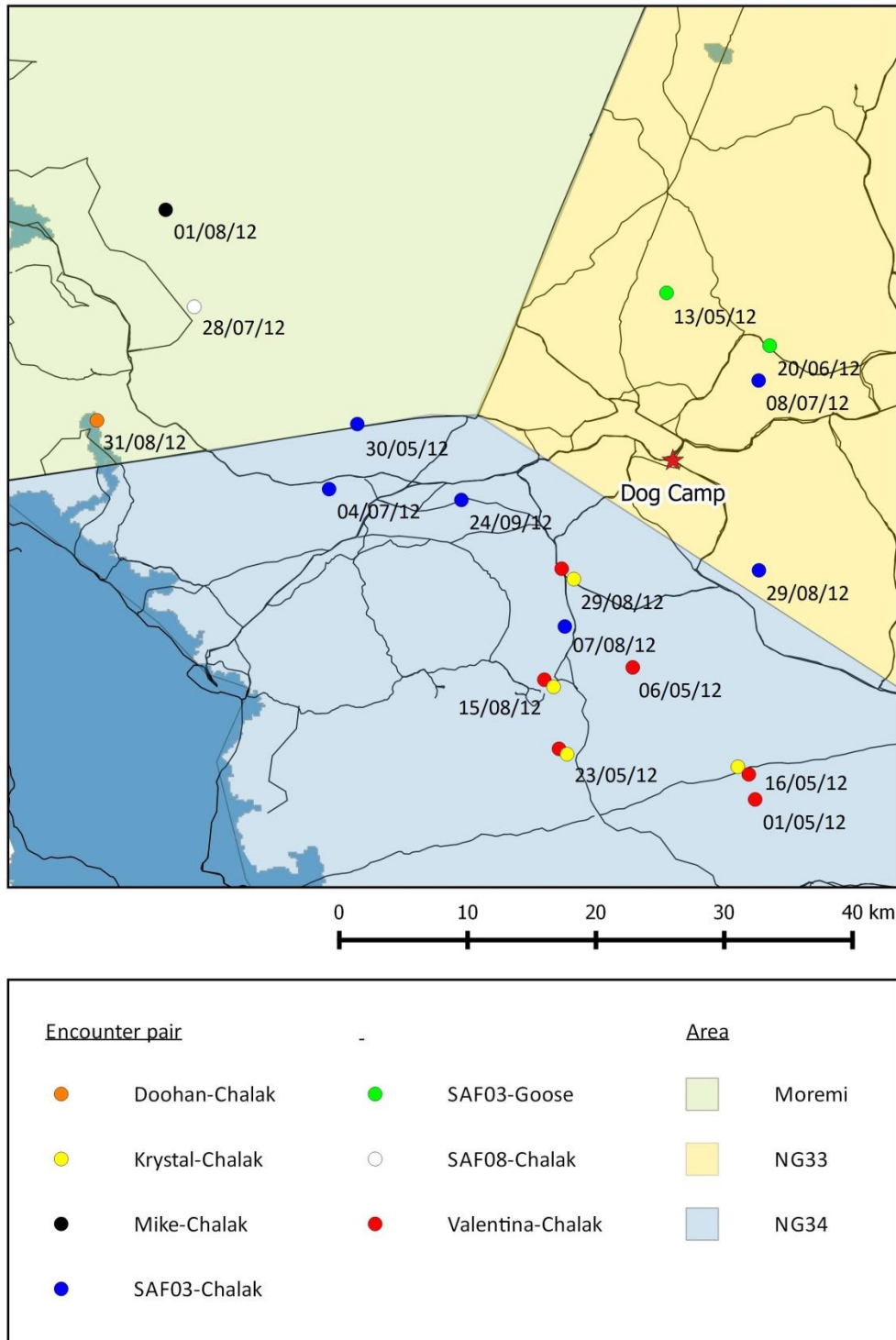
Figure 1. Encounter sites for all RVC radiocollar identified lion - leopard interactions. Lion names are reported first in the encounter pairs. Individuals Doohan and Mike are adult male lions: the remaining lions are adult females. Both leopards, Goose and Chalak, are male.

Distance travelled & movement speeds

Thirty minutes after encounters, leopards were located significantly further from lion encounter locations (654.72 ± 97.67 m) than controls (358.88 ± 78.09 m) (paired t-test$_{20}$ = 2.0918, p = 0.049). Leopard mean velocities over this period also tended to be higher following lion encounters (2.38 ± 0.37 km/h) than controls (1.32 ± 0.28 km/h), but this was not-significant (paired t-test$_{20}$ = 2.0495, p = 0.054). Encounter site approach speeds did not differ between lion encounters (1.97 ± 0.36 km/h) and control encounters (1.85 ± 0.29 km/h) (paired t-test$_{20}$ = -0.33073, p = 0.744).

Two hours after encounters, leopards were found further away from lion encounter locations (1853.30 ± 255.45 m) than controls (1172.98 ± 253.87 m); however, this difference was not significant (paired t-test$_{20}$ = 1.7067, p = 0.103). Furthermore, although mean velocities in the two hour period after lion encounters (2.18 ± 0.3 km/h) were higher than controls (1.32 ± 0.28 km/h) this difference, again, was not significant (paired t-test$_{20}$ = 1.8409, p = 0.081).

Movement bearings

Leopards did not significantly change their mean movement bearings in the thirty minutes after an encounter had taken place (paired t-test$_{19}$ = 0.78956, p = 0.440) or in the two hours after an encounter had taken place (paired t-test$_{15}$ = 0.49215, p = 0.630), compared to control encounters. The mean movement bearing change in the thirty minutes following lion encounters was 40.93° and in the two hours following lion encounters was 62.46°.

<u>Tortuosity</u>

Leopard paths thirty minutes after lion encounters were less tortuous (0.93 ± 0.02) than controls (0.81 ± 0.04) (paired t-test$_{20}$ = 2.3489, p = 0.029). In contrast, there was no difference in tortuosity for leopard paths in the time period two hours after encounters (0.69 ± 0.06) compared to controls (0.75 ± 0.05) (paired t-test$_{20}$ = -0.89296, p = 0.383).

Discussion

This is the first study of whether the fine-scale movements of leopards are mediated by lion encounters. In spite of its preliminary nature, several points of interest arise from the analysis. The results suggest that encounters with lions change the spatial dynamics of leopard movements over the short-term, but that leopard movements are not significantly affected over the long term, even only two hours after encounters. Following lion encounters leopards were found to adapt properties of their movements (i.e., path tortuosity) that allowed them to increase their distance from the encounter location. Although there was a non-significant increase in tortuosity, increases in velocity may have been an artefact of less tortuous trajectories resulting in larger distances between successive fixes.

The previous chapter suggested that resting leopards primarily rely on crypsis when lions are nearby. Similar preferences for crypsis from moving radiocollared leopards would be seen as reductions in their movement distances; however, my results suggest that moving leopards prefer to leave areas occupied by lions. The preference of flight or cryptic responses is based upon the economics of engaging in different strategies under different circumstances (Ydenberg and Dill, 1986). Resting is the activity associated with the lowest energy expenditure. As such, the metabolic costs of movement may preclude fleeing

behaviours for resting leopards until risk is imminent. For example, leopards may rely primarily on crypsis until just prior to when competitors approach to a distance that limits the leopard's chances of successfully fleeing if detected. In contrast, moving leopards may incur relatively little additional costs from increased speeds and less tortuous trajectories, increasing the viability of fleeing strategies.   Thus, there is a trade-off between the costs associated with fleeing versus the risk of hiding and having to confront competitors if detected.

Interestingly, in five instances, which represent 24% of encounters, leopards remained within 25 m of the encounter site thirty minutes after encounters had begun. On three of these occasions pre-encounter speeds suggest leopards were resting prior to encounters occurring. In the final two cases, mobile leopards encountered predators at a mean distance of 34 m, at which point movement ceased. These five instances could represent encounters where leopards were relying on crypsis to avoid detection; alternatively, individuals may have taken refuge in trees after being detected by competitors. This highlights a key limitation of using GPS radiocollar datasets to capture interactions between species: it is difficult to differentiate between behaviours with similar activity signatures. Another limitation is that it is difficult to identify the underlying motivations for behaviours. Thus, whether behaviours are a reflection of antidetection strategies or a reaction to detection by competitors is unknown. For example, Du Preez et al., (2015) suggested that leopards were more likely to move into denser habitats when lions were nearby compared to when lions were absent. Since, however, their results were based on hourly locational fixes from radiocollared leopards and lions, it is unknown whether transitions into denser

habitats occurred because leopards were seeking, pre-emptively, to avoid encounters or whether they had been detected by lions and were fleeing.

The fact that changes in post-encounter movement properties were less detectable over longer post-encounter time periods suggests that lion-mediated behaviours of leopards are relatively short-lived. This has implications for low-resolution GPS radiocollar studies (e.g., Maputla et al., 2015; Du Preez et al., 2015). In particular, in studies relying primarily on radiocollars with large time gaps between fixes, competitor mediated behaviours may be underestimated or undetectable due to their dilution with pre-encounter behaviours. Employing a sliding window approach across different timescales to high-resolution GPS datasets could elucidate the scale at which changes in spatial properties persist.

That leopards did not significantly change their post lion encounter bearings suggests that individuals do not typically change their final destination after encountering lions; rather, they change the route taken, as suggested by reductions in the tortuosity of movement paths, and the time taken to arrive. This may have implications for the reproductive success of leopards if by taking these alternative paths they are prevented from carrying out important ecological functions. For example, route deviations may hinder territorial defence if it results in leopards depositing scent marks in suboptimal locations where conspecific competitors are less likely to encounter them (Gosling and Roberts, 2001). In order to understand the individual costs related to changes in movement properties, it would first be important to understand the drivers of fine-scale leopard movements outside of interspecific encounters and also the scale of route deviations in relation to territory sizes.

That leopards did not appear to change their final destination also has implications for conservation strategies interested in exploiting competitor avoidance behaviours to control leopard movements. In particular, the results suggest that simulating the presence of lions would not deter leopards from entering undesirable areas. As such, lions may not be a suitable candidate species from which to develop communication based management tools to control leopard movements. However, the results do suggest that leopards are affected by lion proximity in the short-term and appear to adopt anticompetitor behaviours to avoid encounters. Thus, I recommend further work is needed on the responses of mobile leopards to potential indicators of risk, such as competitor vocalisations or recently deposited scent marks, before completely dismissing the use of lion cues in excluding leopards from undesirable areas.

Comparisons of my results with other intraguild studies suggest that lion space use is a stronger driver of movement in other guild species, such as cheetah and wild dog (*Lycaon pictus*), than in leopards (Broekhuis et al., 2013; Creel, 2001). This is likely to occur because of life history and ecological differences between the species. For example, leopards are the only guild species that routinely use trees as a vertical refuge from competitors (Bailey, 2005). This may allow them to persist in closer proximity to lions or show depressed anticompetitor behaviours, relative to other guild species, because upon detection they can avoid the major costs of encounters, such as injury and mortality, by climbing a tree. This could be investigated by applying additional remote sensing technologies, such as satellite imagery and aerial drone photography, to radiocollar datasets in order to incorporate environmental properties into movement models. The inclusion of these variables could also elucidate other environmental properties driving competitor mediated behaviours (Kerr

and Ostrovsky, 2003). Indeed, other studies have found that habitat characteristics play a role in how strongly leopards respond to competitors: leopards in Zimbabwe showed greater responses to lions, in the form of faster movement speeds, within open habitats relative to densely vegetated areas (Du Preez et al., 2015). Understanding how environmental properties facilitate coexistence would be useful to land managers and practitioners of landscape restoration strategies because it would allow them to understand how habitat characteristics can promote or hinder coexistence between competitors. This is important because large carnivores play important structuring and regulatory functions in ecosystems and their removal can lead to biodiversity loss (Ripple et al., 2014).

The inclusion of competitor movements into leopard movement models would further elucidate the circumstances under which certain anticompetitor strategies are preferred. Such analyses are likely to involve complex mathematical movement models that may traditionally have deterred many ecologists (Patterson et al., 2008). However, in recent years, there has been an increased focus on the promotion of collaborations between ecologists and information scientists, and the development of interdisciplinary research networks to support such collaborations (Demšar et al., 2015). This sets the scene for an exciting period of research in ecology, wherein new interdisciplinary methods are being developed to analyse the near-continuous ecological data now available.

Conclusion

This is the first study to use near-continuous radiocollar data to investigate the dynamics of naturally occurring interactions between competing large predators. The results suggest that leopard movements are influenced by lion proximity but that this effect is short-lived. This has implications for conservationists interested in manipulating leopard movements by

simulating the presence of their competitors. The preliminary analysis conducted in this study provides the basis for future projects interested in modelling the processes influencing leopard movements, and provides an insight into the novel data that can now be collected thanks to recent advances in GPS technologies.

Chapter 5: Final discussion

Interspecific competition is now recognised as an important consideration for conservationists because of the impact it has on species' densities and distributions (Winterbach et al., 2013). Across sub-Saharan Africa, large carnivores are experiencing range retractions due to human activities (Ray et al., 2005). This has implications for the coexistence of competing carnivores because restricting competitors to small, shared tracts of protected land may reduce the effectiveness of mechanisms facilitating their coexistence and may increase the frequency of antagonistic encounters. This can place protected populations at risk of localised extinctions (Ginsberg et al., 1995). Understanding how human activities are impacting animal behaviour is one of the key ways in which behavioural ecology can aid conservation (Berger-Tal et al., 2011).

Traditionally, the indirect effects of antagonistic encounters have rarely been considered for carnivore competitors occupying the same trophic levels and, prior to this study, little was known of the encounter dynamics between the leopard and its competitors. I addressed this deficit by using data derived from advanced GPS radiocollar technology and field-based experiments. As well as elucidating the dynamics of leopard-lion encounters, the results of my thesis also contribute to our broader understanding of competition and the mechanisms

that facilitate species coexistence. In this chapter, I will summarise the key results of my thesis in the context of the leopard before addressing the broader contributions of my work in the field of coexistence. This will be followed by a concise summary of future research directions and a brief conclusion.

Chapter summaries

The aim of my thesis was to understand how leopard behaviour and movement are mediated by competitor encounters. *Chapter 3* investigated risk-driven behavioural changes in leopards by simulating the presence of adult male lions through targeted acoustic playbacks. Previous studies on risk-driven behaviours have predominantly focussed on interactions between trophic levels, and interspecific eavesdropping within competitors is poorly documented (Oriol-Cotterill et al., 2015). *Chapter 3* addressed these deficits and found experimental evidence that leopards adapted their behaviours when they perceived lions to be nearby. The results also suggested that leopards have the capacity for heterospecific risk assessment and suggested that leopards use acoustic competitor cues to assess competitor risk.

Chapter 4 used high-resolution GPS radiocollars to investigate the spatial dynamics of leopard movements after naturally occurring lion encounters. Previous studies of leopard movements when lions were nearby used radiocollars with large intervals between locational fixes (Du Preez et al., 2015; Maputla et al., 2015). This limited the resolution of captured movements and meant that actual encounters between species could not be reliably identified. My findings were that, following lion encounters, leopards adapted movement properties that allowed them to quickly increase their distance from the encounter location. Changes in movement properties were, however, short-lived and it is

likely that behavioural shifts continue only until the immediate risk of encountering lions has passed.

My thesis was the first detailed investigation of how fine-scale leopard behaviours and movements are mediated by lions and provides compelling evidence that leopards show risk-driven plasticity in their behaviours to avoid costly interspecific encounters. Overall, the results of my thesis suggest that leopards may be more affected by interspecific competition than previously thought. The data also highlight the plasticity of leopard responses to competitor risk and confirm that leopards are capable of subjective risk assessment. This opens up several future research directions, including on leopard cognitive abilities and the feasibility of manipulating leopard movements through the strategic deployment of competitor signals. In *Chapters 3* and *4*, I interpreted my results in the context of the leopard-lion dyad. In the next section, I consider the broader implications of the results and methods used, and I then move on to consider future research directions arising from my work.

Implications beyond the leopard-lion dyad

The results of this study advance our knowledge of coexistence by providing insights into the mechanisms that species use to facilitate their coexistence with larger competitors. Coexistence can be facilitated by both broad-scale behaviours occurring when competitors are not within the immediate area, and fine-scale behaviours occurring during encounters or when competitors are nearby. Fine-scale behaviours of wide ranging carnivores are, however, difficult to quantify as they are rarely directly observed by researchers and, by definition, occur over short time periods that were typically undetectable by former GPS technologies. Although some studies have used playback methodologies to measure

species' responses to competitors (Durant, 2000; Webster et al., 2010, 2012), many studies typically focussed on broad-scale behaviours easily detectable by former technologies (Berger and Gese, 2007; Cozzi et al., 2012; Durant, 1998). This has limited our understanding of species' responses during near-miss or actual competitor encounters and how these behaviours might facilitate coexistence.

The results presented in my thesis address the lack of knowledge of fine-scale anti-competitor behaviours and provide evidence of *in situ* heterospecific risk assessment in a large terrestrial mammal. This is significant because whilst the assessment of predation risk has been identified across several taxa, most studies have focussed on risk assessment within microtine rodent species (Amo et al., 2008; Herman and Valone, 2000). Thus, my thesis was one of the limited number of studies to show that large carnivores also have the capacity for heterospecific risk assessment, and one of the first to show heterospecific risk assessment outside a predator-prey system (*cf*. Durant, 2000; Webster et al., 2012). The behavioural consequences of antagonistic interactions have been well described in predator-prey species but relatively rarely have been considered for competitors. However, the results of my thesis support the notion that some principles originally developed for predator-prey interactions may also apply to interactions between competing species occupying the same trophic levels (Oriol-Cotterill et al., 2015). This may be particularly true for competing carnivores because interspecific killings are widespread within this taxonomic group and are analogous to predation in predator-prey systems (Palomares and Caro, 1999).

Future research

Leopards, spotted hyaenas, and wild dogs

Time and financial constraints precluded the inclusion of spotted hyaenas in this study. In addition to lions, spotted hyaenas also pose a risk to leopards through kleptoparasitism and mortality events, but the dynamics of their competitive relationship with leopards is poorly understood (Bailey, 2005; Balme et al., 2013). Although the mechanisms to assess competitor risk may be similar, the leopard's behavioural responses to lions and spotted hyaenas are likely to differ because the level and type of risk presented differ between species (Durant, 2000; Webster et al., 2010, 2012). For example, lions are stalking predators relying on short bursts of speed whilst hunting: spotted hyaenas are coursing predators with greater stamina (Kingdon, 2013). Thus, relying on crypsis until competitors are near may be a poor strategy when dealing with spotted hyaenas because the species' grater stamina may increase the risk of capture for leopards. Alternatively, that the leopard's body mass is comparable to that of the spotted hyaena may mean that leopards perceive spotted hyaenas to be a lesser threat than lions. Leopards may, thus, adopt more aggressive behaviours when encountering spotted hyaenas than lions. The methods used in my thesis could be easily adapted to investigate the spatial-dynamics of encounters within the leopard-spotted hyaena dyad.

The methods could also be applied to consider the leopard's relationships with smaller guild species. For example, African wild dogs are the smallest species within the guild and their persecution by lions and spotted hyaenas is well documented (Creel and Creel, 1996; Carbone et al., 1997). However, the leopard-wild dog dyad has received little research attention despite the fact that they have a 67% overlap in preferred prey species, which

indicates a high potential for interspecific competition (Hayward and Kerley, 2008).

Leopards have been known to kill and consume adult wild dogs more often than expected

by wild dog abundance (Hayward et al., 2006), but anecdotal accounts of wild dog packs

mobbing individual leopards suggest that dominance within the dyad may change between

encounters (McNutt, personal communication). Although individual wild dogs are

approximately half the weight of an adult male leopard, wild dogs occur in social groups,

which increases their competitive dominance (Kingdon, 2013).   Consequently, a leopard's

motivation to engage in or avoid encounters is likely to change with the biomass of the

competing group. Although, the costs of lion and spotted hyaena encounters may be

greater for leopards and wild dogs, encounters between the two may still have implications

for the reproductive success of the individuals involved. Reduced tracts of shared,

protected areas may lead to an increase in encounter frequencies between leopards and

wild dogs, and disturb the processes that facilitate their coexistence. Thus, their

relationship warrants further investigation.

Encounter dynamics within other competitor systems

Across the globe, expanding human activities are restricting species to increasingly smaller

tracts of land (Prugh et al., 2008). This may limit spatial partitioning between competitors,

force more overlap than may have existed previously, and increase the frequency of

encounters. In turn, this may limit the effectiveness of broad-scale coexistence mechanisms

such as spatial partitioning, and risk-driven behavioural shifts may become more important

in maintaining coexistence between species. Leopard responses upon encountering lions

are likely to be species and system specific. This means that the behavioural responses of

leopards cannot be extrapolated to other competitor systems. My thesis does, however,

stand as a useful case study for the use of playback experiments and high-resolution radiocollars in quantifying competitor responses during encounters. The methods employed throughout this study could be used to study coexistence within other competitor systems. Acoustic playbacks offer a promising method to simulate interspecific interactions rarely observed by researchers, and high-resolution radiocollars allow fine-scale movements to be quantified during naturally occurring encounters. These methods are particularly valuable for cryptic or difficult to observe species and could provide greater insights into the mechanisms facilitating their coexistence with competitors.

<u>Developing signal-based management tools</u>

The work presented in my thesis will also inform the development of conservation strategies focussed on manipulating carnivore movements through manipulation of their perception of risk. Although there was no evidence to support the use of lion vocalisations to stop leopards from entering undesirable areas, further research into leopard responses under different situations and to different competitor cues is needed. In particular, it would be interesting to see if the results of my thesis extend to open habitats where the risk of detection is higher and, thus, crypsis a less viable strategy. High-resolution GPS radiocollars, similar to those used in *chapter 4,* could be used to identify whether competitor densities and distributions form natural barriers to leopard movements. This would allow an ideal competitor species to be identified from which a signal-based management tool could be developed.

Once a candidate species has been identified, experimental approaches, similar to those from *chapter 3,* could be used to identify the cues used to maintain spatial segregation between the competing species. *Chapter 3* focussed on the use of acoustic cues in risk

assessment, but olfactory and visual cues may also facilitate assessment and, consequently, could help maintain spatial or temporal segregation between competitors. Unlike acoustic signals, chemical signals can persist in the environment once signallers have left the area. This means that chemical signals could provide contextual information on the density and distribution of competitors. Two important considerations for future olfactory studies would be the type of chemical cue used and the method of presentation. Cue selection is important because different signals provide different information and thus may provoke different responses. For example, competitor body odours may be more likely to elicit anticompetitor behaviours than scent marks because they indicate that a competitor is nearby. To avoid cueing the animals, presentation protocols should limit the association between the signal and the presence of researchers. This is true for all studies where animals are presented with novel stimuli, but it is particularly relevant for olfactory studies because chemical signals are traditionally presented to the targets manually. In contrast, acoustic playback studies typically operate speakers from locations that minimise the association between the stimulus and the observer's presence.

Conclusion

In summary, leopard movements and behaviours were influenced by the perceived and actual presence of lions, but this behaviour was relatively short-lived. Crypsis appeared to be the preferred strategy for resting leopards, whilst moving leopards preferred to change properties of their movement that allowed them to quickly move away from the threat. Both resting and moving leopards showed plasticity in their response to lions, and comparisons with other studies suggest that habitat type may play a key role in influencing responses (Du Preez et al., 2015). The results presented provide insights into fine-scale

behaviours facilitating coexistence, and my thesis is a useful case study of the methods that

could be used to investigate encounter dynamics within other competitor systems.

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