

The impact of intraguild competition with lion
Panthera leo on leopard *Panthera pardus*
behavioural ecology



Thesis submitted to
THE UNIVERSITY OF OXFORD
in fulfilment for the degree of
DOCTOR OF PHILOSOPHY
by
BYRON D. DU PREEZ
JESUS COLLEGE

Hilary 2014

For my parents and heroes:

DENNIS and GILL DU PREEZ

you made me go to school, and coped with me as a student



“...while the individual man is an insoluble puzzle, in the aggregate he becomes a mathematical certainty. You can, for example, never foretell what any one man will do, but you can say with precision what an average number will be up to. Individuals vary, but percentages remain constant. So says the statistician.”

– Sherlock Holmes, *The Sign of Four* (1890)

ABSTRACT

The impact of intraguild competition with lion *Panthera leo* on leopard *Panthera pardus* behavioural ecology

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Jesus College

Single-species research dominates the field of ecology; however there is a growing appreciation of the importance of a multi-species approach to holistic conservation. Carnivores exert a top-down control on other species, and are vital components of stable ecosystem functioning. Physiologically adapted for predation upon other animals, competition between carnivores can be particularly aggressive; frequently resulting in mortality, and even population suppression. Big cat research has historically focused on those species that are most easily observable; in particular the lion *Panthera leo*. The majority of the Felidae however are secretive and elusive, and receive relatively little scientific attention. In particular, there are few data available that measure the effect of direct intraguild interactions between carnivores. Using leopards *Panthera pardus* as a model species, this research aimed to investigate the impact of lions on the behavioural ecology of a socially subordinate carnivore. Leopards are the most abundant large carnivore in Africa, and have the largest global range of all felids; their ecological niche overlapping with that of both lions and tigers. The knowledge gained from examining their competitive interactions is therefore widely relevant, and may be applicable to other subordinate carnivore species that remain unstudied. Biotelemetry and camera-trap data were modelled using novel algorithms to show that lions impact on leopard population density, demographics and spatial ecology. Faecal analyses suggest that dietary niche segregation may facilitate sympatry. These results indicate the level of impact that large carnivores can exert over smaller species, and the potential for a focus on single-species conservation to undermine holistic conservation. The manifestation of intraguild competition has a significant influence on an animal's ecology; leopards are generalist species that cope with persecution by adapting their behaviour and niche. Ecological specialists may not fare as well under competitive pressure, and proactive conservation initiatives may be required for endangered species.

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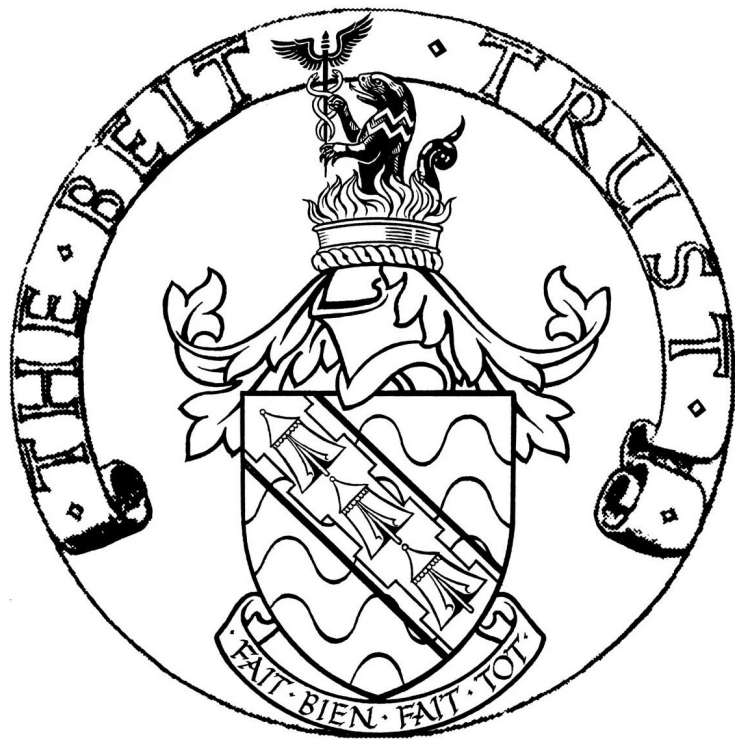
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Acknowledgements

This thesis would never have happened without the help and support of family and friends.

The person whom I would like to thank first and foremost is **Nan Loveridge**. Ma'am, amongst teachers you are unique; never has any other inspired me as you have, and I could not have taken this path without you revealing it to me (and giving a shove). Thank you for your belief in me.

For taking me on as a volunteer during school holidays all those years ago and patiently fielding my incessant questions about lions, eventually offering me the opportunity to do my own research, I will always be grateful to **Andy Loveridge**. (And for the record: I did catch a leopard within the first week; using *my* trap – but thanks for sharing the beers you won off me!).

David Macdonald, I don't know how you do it. Thank you for the constant support and patience that even I could not shake. I appreciate every single reply at 02h00, and every chat that you managed to fit into your ridiculous schedule that always inspired!

The Beit Trust funded my scholarship to Oxford, and without which I would not have been able to undertake this research. The Beit Trust makes a significant contribution to education in Zimbabwe, Zambia and Malawi – and particularly in the field of medicine, which the region so desperately requires. I am indebted to your support over the last five years, and although a lifetime of work would not settle this, I hope to try. The research undertaken in this thesis was funded by **The Darwin Initiative for Biodiversity** Grant 17-031.

Angus Ramsay, you are one of my favourite characters in this world! I treasure your wickedly sharp wit and sense of humour, and one day I hope to have seen

and experienced even the smallest fraction of what you have! Thank you for your constant and fantastic support of this “*jaapie zoo-boy*” that has extended far beyond what you promised. Let’s call it an investment. **Victoria Ramsay**, thank you for providing me with a home away from home during the holidays, for including me in your family’s festivities, and always catering a significant amount of red meat!

Wicks Barton, thank you so much for taking me under your wing, and for always making sure that I was so well looked after! I cannot express how much I have appreciated all your help and encouragement over the last few years. I also really enjoyed all of our correspondence; head’s up though, I think that Angus might have hacked your email account because he always seems to know what’s going on... **Emma Ribeiro**, thank you for always keeping an eye on me, and making sure I stayed on course.

The Buby Valley Conservancy in Zimbabwe is a fantastic realisation of Africa’s wildlife conservation potential, and probably the most efficiently organised wildlife area globally. This is no accident, and BVC is run by the utmost professionalism and dedicated management. Their contribution to conservation is manifest in protecting one of the largest rhino populations in the world; for which they doggedly run a colossal and expensive anti-poaching effort, despite receiving neither direct nor indirect income from having the rhinos on their land. The management of BVC are conservationists of the highest order. I would like to thank **Charles Davy** and the rest of the **BVC shareholders** for allowing me to conduct my research on their conservancy.

Blondie Leathem, you are a legend in Zimbabwean wildlife. If only you would write a book so that not just those privileged enough to share a drink around the fire with you can understand. Thank you for your constant interest in my research, and your eternal enthusiasm. Needless to say that none of this would have been possible with your support – thank you so much. **Katrina Leathem**, thank you for everything; especially ensuring that Paulus and I didn’t regress into complete bachelordom. Your love of animals and ability to connect with wildlife is inspiring. Thank you both for always making me welcome in your home, for providing a venue to watch the rugby, and for all the drinks we shared together.

Heather Green, **Dawn Burnham**, and **Carole Thomas**, thank you all so much for every single bit of administrative help and assistance, and for generally making my time at Oxford a lot less stressful. I cannot tell you how grateful I am for all that you have done for me since before I even arrived at Oxford.

Ullas Karanth, you are a legend in big cat conservation and research, and I am honoured to have been able to discuss my ideas with you. I admire your absolutely practical approach to research, and your complete understanding of the theory.

Tom Hart, thank you for teaching me *R*, for taking an interest in my research, the hours spent working on manuscripts, and for our friendship that has resulted from this. It's been an absolute pleasure working with you, and I always appreciate your help with the statistics (beyond *t-tests*!). I look forward to you visiting Zim and seeing the reality behind the analyses.

Paul Funston, thanks for always helping me so quickly with analyses and questions. I like your non-apologetic attitude towards conservation. I look forward to discussing more ideas with you in the future.

Phil Riordan, thanks very much for mentoring me, always willing to have a chat, and for all the great advice that you've given me. I really appreciate it, thank you.

Jan Kamler, thank you for the hours that we spent discussing my research, and for sharing your extensive knowledge of intraguild interactions. I hope that they find Big Foot for you mate.

Bob Montgomery, thanks for some excellent ideas and helping me to plan my thesis.

Lucy Tallents, thanks very much for all the help that you gave me while I was learning *R*. I appreciate your exceptionally patient tutelage.

WildCRU, I thoroughly enjoyed the tea-time discussions and banter. The range of study species, research talent and nationalities represented by WildCRU is astounding, as is the collective value of their knowledge and skill. Thanks for all the informal discussions that one way or another shaped my research.

Carl Heilbron, thanks for explaining the loop function to me, it revolutionised my data analyses. Come visit me in the mother-land.

Michael Athanson, thank you very much for all your crash-courses in GIS, and for enthusiastically helping me out whenever I had any queries about mapping, even though I used up so much of your time.

Roger and **Jess Parry**, thank you so much for all your help and support of my research. The camera-trapping surveys could not have happened had you not brought the cameras in one by one for me! I wish you the very best of luck with your own research, and I hope that one day I will be able to help you in return.

Gary Cantle, “*Oom*”, thank you for your friendship. Thanks also for all the help that you gave me with building the leopard trap, and the colourful discussions we had regarding its design! You work tirelessly for Hwange’s wildlife under sometimes frustrating conditions, but your efforts are so important – particularly for the elephants that you love so much.

Barry Wolhuter and everyone at The Hide; thanks for your help, especially for allowing me access to your workshop and tools with which to build my leopard trap.

Jane Hunt, thank you for tolerating me as a volunteer for years! Your knowledge and abilities in the bush are famous (she can build a fire in the rain!), and I learnt so much from you.

Stan Cumming and **Nathan Rabinowitz**, thank you both so much for your friendship during my time in Hwange. You guys were amazingly kind and generous, and I appreciate you always trying to get me up to The Falls. I look forward to paying you back soon.

Paul de Montille, thanks for your friendship and all your advice on life in general. You will never know how much it all meant to me. I really enjoyed your company in the bush, and especially your terrible sense of humour.

Chris Foggin, for a lifetime of selfless service to Zimbabwe’s wildlife, and agreeing to be my nominated vet for the Dangerous Drugs Licence, thank you. Thanks to everyone that I crossed paths with on the wildlife capture course, especially my team’s leaders, **Dave Cooper** and **Markus Hofmeyr**, as well as **Pete Morkel** and the late **Woody Meltzer** for taking a special interest in me. **Roxy Danckwerts**, for your lifetime’s dedication to wildlife, allowing me to adopt Diana, and for your friendship and constant support.

Esther van der Meer and **Hans Dullemont**, thanks for your friendship and dedication to Zimbabwe’s ‘other’ carnivores. Best of luck with all of your research, I look forward to watching it develop.

Rosemary Groom, thanks for your help and constant encouragement. What you've achieved is astounding. I look forward to working with you in the future.

Tanith Grant and **Dusty Joubert**, the other two members of Zimbabwe's leopard team, thanks for your constant support and encouragement, and sympathy to the frustrations of working with an animal that is rarely seen. **Guy Balme**, thanks for sharing your thoughts on all things leopard, and for all your comments and advice on my early research plans and articles that resulted in more publications than I could have hoped for.

Ian Howden, thanks very much for donating the rally tyres that were the answer to the incessant punctures that wasted so much of my time. They looked strange on the bakkie, but were just about bulletproof, and saved immeasurable frustration.

Ian Chatterton and **Margot Cunningham** of Installite Contracting, thank you very much for donating the whip antenna that made it so much more efficient to track the collars. Thanks also for providing accommodation whenever I needed to stay in Bulawayo, and for your general support of Zimbabwean conservation efforts.

Terrance and **Corrina Wardley**, thank you so much for hosting Paul and I for the first half of the Kwalusi research. **Norman** and **Denyse Sparrow**, thank you for having Matt and I during the second half of my Kwalusi research. You are the salt of the earth, and I could never repay your generosity.

Matt Trisos, you brought many a laugh and were good fun to work with. Good luck with your own research. Be careful of the donkeys mate, devious buggers!

Enos and **Amurai**, it was a pleasure to work with you. Thank you both so much for all of your help and infinite wisdom of the bush; your tracking abilities and understanding of wildlife are enviable. **Emma**, thank you for your tireless effort in and around the research house – your work ethic and strength to size ratio is incredible – and your lawn was amazing. I thoroughly enjoyed our many and lengthy conversations, though I still don't know what any of them were about! **Benjamin**, thank you for your endless help fixing my tyres and servicing the research vehicle.

Natasha Anderson, thanks for all the drinks and imparting some of your extensive knowledge of everything to do with rhinos. Norman English and Craig Broomberg, thanks for all your help when ‘that side’ of the conservancy. **Craig Botha**, thanks for your friendship and always having me over.

Thanks to all the PH’s that I’ve crossed paths with at BVC, and for all the help and support and genuine interest in the research. In particular, thanks to **Pete Fick, Shaun Buffee, Martin Nel, John Sharp, Mark Brewer, and Ade Langley**. The service you provide in ethical hunting increases the scope of practical conservation initiatives, and you’ve put Zimbabwe on the map for many a philanthropist.

Brian and Sue Trethowan and Paul and Pattie Bristow, thank you all so much for having me over to so many events, for all the food that you sent up to Mazunga, and for generally looking after me in Beit Bridge. I can’t tell you how much I appreciate it.

Mark Bristow, thanks for being a mate. You always chengeta’d me whenever you could, and we shared some great experiences in the bush. Thanks very much for your friendship.

Pete Taylor, thank you for your friendship, shamwari, especially for all the tea! Thanks for coming and visiting me in the field, your love for the bush and Zimbabwe’s wild places is inspiring.

Fritz and Louis von Guionneau, thank you for your friendship and for the great times we had, both in and out of the pool. Thanks for taking me on the annual boys’ trip – that was the experience of a lifetime. **Mr and Mrs von Guionneau**, thanks so much for always looking after me in London.

To all the boys who I had the privilege of playing with for **Ouwpc**, and to the lads who I had the odd pinky with up at **Vinnie’s**, thank you for some awesome memories of Oxford.

Pau-Paul “lion whisperer” Trethowan; mate we had some good times. Thanks for all your help in both the bush and at Oxford. Your D.Phil. is going to be awesome, and I am glad that I was able to watch it develop from the very beginning.

Granny, Gran and Gramps, thanks for all your love and nurturing encouragement of my interest in wildlife.

Lyndsay Nicolson, thank you for always believing in me bird. This last year has been magical.

Mom and dad, thanks for all of your amazing support and constant encouragement. I never could have done this without all of your help. I appreciate every sacrifice that you've made for me.

Finally I thank **JESUS** for hearing my prayers.

Chapter 1

General Introduction

1.1 INTRODUCTION

Prior to widespread extinctions between the Late Pleistocene and the Modern Eras, sympatric carnivore guilds were present on all subpolar continents (Barnosky et al. 2004). Today, the only intact large predator guild remains in Africa (Dalerum et al. 2009). This guild consists of the lion *Panthera leo*, leopard *Panthera pardus*, cheetah *Acinonyx jubatus*, wild dog *Lycaon pictus* and spotted hyaena *Crocuta crocuta*; and presents the only remaining opportunity to understand the complex relationships between the species at the very top of the food chain (Cozzi et al. 2012).

Within the Carnivora, the Felidae are represented by 36 extant species, which naturally occur on every continent except Antarctica and Australasia (Macdonald et al. 2010). Wild felids occupy a wide range of habitats, demonstrating a fantastic array of life histories, with body sizes ranging over three orders of magnitude (Carbone et al. 1999). At one extreme end of the spectrum is the rusty-spotted cat *Prionailurus rubiginosus* at approximately only 1 kg that preys on frogs and mice (Macdonald et al. 2010; Sunquist and Sunquist 2002), and at the other end is the tiger *Panthera tigris* that may weigh up to 325 kg, and is the dominant predator in all ecosystems in which it occurs (Macdonald et al. 2010; Seidensticker et al. 1999). However, despite their discrepancy in size and ecology, both of these species remain “*very distinctly cats*” (Macdonald et al. 2010).

Top predators are keystone species (Gavashelishvili and Lukarevskiy 2008) and a valuable proxy of species richness in wildlife conservation efforts (Berger et al.

2001; Meffe and Carroll 1997). They are therefore useful biological indicators, and protecting high biodiversity sites is a priority of conservation efforts globally (Gavashelishvili and Lukarevskiy 2008). Predators play a vital role in ecosystem functioning and stability (Estes et al. 2011; Karanth and Sunquist 1995; Macdonald et al. 2010; Ritchie et al. 2012; Schaller 1967; Sunquist 1981), and can help reduce the impacts of alien invasive species (e.g. Bonesi and Macdonald 2004), and buffer the potential for disease outbreak and transmission (Pongsiri et al. 2009). The component densities of predator guilds are themselves controlled by the availability of prey (Harihar et al. 2011; Henschel et al. 2011), and the competitive forces between them (Andheria et al. 2007; Hayward et al. 2007; Henschel et al. 2011).

Big cats are facing global population declines (Macdonald et al. 2010), and understanding the threats to carnivores at the species level is vital to development of effective conservation strategies (Olea and Mateo-Tomas 2014). The leading threats to wild carnivores across the planet are habitat loss, human-wildlife conflict, and hunting pressure (Henschel et al. 2011; Macdonald et al. 2010). Large felids are particularly vulnerable to a depleted and inadequate prey base (Carbone et al. 2011), and human-carnivore conflict is a significant threat to their conservation (Inskip and Zimmermann 2009). As obligate carnivores, many felids are highly evolved to exist within specialised and narrow niches, making them particularly vulnerable to environmental change (Macdonald et al. 2010). This vulnerability is concerning because only a small proportion of wild felid ranges are protected (Nowell and Jackson 1996; Ray et al. 2005), and while the more generalist species fare better in heterogeneous landscapes of human use, outside of protected areas even their existence is not guaranteed (Macdonald et al. 2010).

Apart from the obvious primary conservation impacts, anthropogenic habitat destruction and habitat fragmentation can result in increased contact between big cats and people; and may be responsible for predation on livestock, resulting in indiscriminate persecution of carnivores (Ogara et al. 2010). Failure to understand and adequately manage the socio-ecology behind this conflict leads to global under-realisation of felid conservation efforts and potential (Bagchi and Mishra 2006; Ogara et al. 2010).

1.1.1 *Conservation and its paradoxical consequences*

Larger felids receive the most attention in terms of conservation and research (Macdonald et al. 2010). This bias is largely because they are easier to observe, making them popular with tourists, and easier to monitor by ecologists in a wider array of landscapes. Big cats are therefore good examples of ‘umbrella’ species (e.g. Lindsey et al. 2009; Williams et al. 2000), which can potentially enhance the conservation of other biota via their protection and that of their habitat (Andheria et al. 2007).

Predators are often charismatic animals, and powerful icons for fostering public interest to achieve broad conservation aims. Larger carnivores are also often the most at risk of extinction; they are furthest along the strategic biological spectrum, being large in size and ecological requirements, and small in density and reproductive rate (Macdonald et al. 2010). However, predators inherently impact on populations of other animals through their obligate carnivory, and excessive predation can result in prey population declines and loss to biodiversity where

the carnivores exceed their ecological carrying capacity (e.g. Harihar et al. 2011). Large carnivores also impact on smaller carnivore species, which may themselves already be rare or endangered (Caro and Stoner 2003; Creel and Creel 1996; Durant 2000; Palomares and Caro 1999).

In an effort to assess global felid research, Macdonald et al. (2010) report that over 85% of published studies of felids since 1950 mentioned only a single felid species; and indicated an exponential increase in research bias with the body size of the species. Furthermore, the literature is replete with examples of single-species management strategies that have resulted in unpredicted and undesired results that create new conservation issues (see Sinclair and Byrom 2006). There is clearly a large deficit of knowledge on the relationships between many sympatric felids, and carnivores in general. If conservation efforts are to succeed, these data are required.

1.1.2 *In the case of tigers...*

The tiger is the very embodiment of all things wild. With a perfect balance of ferocity and beauty, they capture the spirit of nature, and are one of the world's most celebrated and popular animals (Wang and Macdonald 2009). And rightly so; tigers are a charismatic species that people across the globe can identify with and appreciate [*although, this may be less apparent for those who actually live with them* (e.g. Bagchi et al. 2003; Bagchi and Mishra 2006; Harihar et al. 2011; Treves et al. 2011)].

However, the approach to tiger conservation is dominated by a one-dimensional strategy: increasing tiger abundance. Many global conservation agencies are driven by exploiting the tiger's beauty and plight to receive public donations for its conservation; the long-term ecological stability of the environments receiving tiger conservation attention is a secondary consideration, if considered at all (e.g. Harihar et al. 2011). With the doubling of wild tiger populations by 2022 as a global conservation goal (Asia Ministerial Conference on Tiger Conservation 2010; <http://go.worldbank.org/WW6MUN0YQ0> [accessed 2014-04-21]), some ecologists have concerns that the impact this could have on biodiversity is not fully appreciated (Harihar et al. 2011). Bluntly put, over enthusiasm for tiger conservation could lead to the local extirpation of other rare species (e.g. Odden et al. 2010; Wegge et al. 2009), including leopards (Harihar et al. 2011).

The historical range of tigers has decreased by 93% (Dinerstein et al. 2007), and considerable effort is being made to restore tiger population security and range. However, these efforts do not take into account the impact that this is having on the species over which tigers are dominant, and that have also been historically impacted by habitat destruction and range contractions (Harihar et al. 2011). Though it is undeniable that the conservation of tigers as apex predators is crucial for the ecosystem (Estes et al. 2011; Pace et al. 1999), this closed-minded single-species conservation attitude needs to open up to at least give some consideration to the competitively subordinate carnivores and the value of the environmental services they provide (e.g. Macdonald et al. 2010).

While tiger conservation is a global goal, it has to be considered in the context of

the local ecosystem. Elevating tiger population density to the point of threatening the survival of their prey and competitors or endangering people and their livelihoods cannot be considered a conservation success. In the four years after the successful tiger population recovery at one site, Harihar et al. (2011) reported a sharp decline in the leopard density. Avoidance of tigers in prime habitat exposes leopards to conflict with people on the fringes of those habitats (Harihar et al. 2011; Seidensticker 1976), which can undermine conservation by negatively affecting the attitudes of indigenous people (Macdonald et al. 2010). One potential method of alleviating the impacts of intraguild competition between tigers and mesocarnivores is to augment wild prey populations (Harihar et al. 2011). Realistically though, this may be impractical, and some conservationists suggest that spatial partitioning of management efforts for carnivores may be the most effective solution for the successful conservation of both species (e.g. Harihar et al. 2011).

1.1.3 The direct and indirect impacts of intraguild competition

The ecology of a species is often considered in terms of the ‘niche’ it occupies. The conceptual ecological niche may further be broken down into various measureable dimensions within which each species lies; the breadth of each determining their overlap with sympatric species, and inferring the potential for competition (Pianka 1973). The three main ecological niche dimensions in which segregation occurs are the temporal, spatial and trophic niches. Segregation along any of these dimensions may facilitate coexistence between potential competitors (Chapter 5; *this thesis*),

even where there may be complete overlap of the other two (Pianka 1973).

Intraguild competition between carnivores may involve both resource exploitation, where one species outcompetes another in terms of access to prey, and interference competition, where direct interaction may lead to injury or death (Caro and Stoner 2003; Linnell and Strand 2000; Mills 1991; Palomares and Caro 1999). Utilisation of different food resources reduces the impact of exploitative competition between species, whilst variation in activity periods may help to limit contact between individuals. However, spatial segregation is probably the most effective method of avoiding the more negative consequences of direct competition, because this removes the potential for interaction. Although a species' niche may be well defined, the dimensions of the niche itself are fluid, and may vary in time both within the course of a day or between seasons (Pianka 1973).



Figure 1.1: A pair of camera-traps capture the interaction between a lioness and a leopardess. The leopardess survived this encounter, and was subsequently recorded at the same camera-trap station. Direct avoidance of intraguild interaction reduces aggressive encounters that could lead to injuries or death. [Original figure taken from Chapter 4; *this thesis*]

The level of niche overlap between species reflects the relative level of toleration of one for the other. Closely related species are more ecologically similar and are therefore more likely to compete with one another, which may result in competitive exclusion (Pianka 1973). Intraguild competition leads to direct avoidance (Durant 1998), altered habitat selection (Kamler et al. 2012), changes in behaviour (Berger and Gese 2007; Valeix et al. 2009a; Wang and Macdonald 2009), different activity periods (Valeix et al. 2007), and inefficient foraging (Brown et al. 1999). Intraguild competition between predators may also increase the probability of direct interaction resulting in injury or death (Caro and Stoner 2003; Creel and Creel 1996; Durant 2000; Kamler et al. 2013; Laurenson 1995).

Understanding niches, and their overlaps, may allow predictions of environmental constraints, which are useful where ecologists compare different systems with each other; for example in the case of potential species reintroductions (e.g. Berger and Gese 2007). However, most scientific attention has been focused on the effects that predators have on prey, and little attention is paid to the impact that predators have on each other (Linnell and Strand 2000). In addition, many studies on intraguild relationships have considered exploitative competition, but few have investigated interference competition (Berger and Gese 2007). There is therefore a knowledge gap on the impact of intraguild interactions that undermines the potential for using carnivores to restore ecosystems, and reduces the ability to predict the outcome of carnivore introductions or removal (Ritchie et al. 2012).

Complex and asymmetrical relationships define the ecology of sympatric carnivores (Cozzi et al. 2012); where high levels of intraguild conflict may lead to

the population suppression of subordinate species (Caro and Stoner 2003; Linnell and Strand 2000; Palomares and Caro 1999). For instance, population densities of subordinate carnivores such as cheetah (e.g. Durant 1998, 2000; Laurenson 1995) and wild dog (e.g. Creel 2001; Creel and Creel 1996; Vucetich and Creel 1999) are negatively related to lion density, and these species may face local extinction where lion abundance, and the respective level of persecution, is high. Conversely, the removal of apex predators can release the ecological constraints of smaller carnivores [*mesopredator release*]; (Crooks and Soule 1999)], which may lead to population expansion beyond the ecological capacity, and in turn threaten the conservation status of the species that they prey on (e.g. Creel et al. 2001; Ritchie et al. 2012). Research also indicates that subordinate carnivores behave differently in environments free from intraguild persecution and predation (Crooks and Soule 1999; Marker and Dickman 2005). Some felids, such as leopards, are more adaptable than others, and can alter their behaviour and ecological niche appropriately with respect to varying levels of competition (e.g. Karanth and Sunquist 2000; Seidensticker 1976). Even such robust and adaptable species such as these, however, have their limits; and intense competition ultimately causes population declines (Harihar et al. 2011). Anthropogenic habitat destruction, and resultant fragmentation, forces carnivores into ever-smaller spaces that escalates the probability and magnitude of intraguild and intraspecific competition and interactions, and increases the impact that this has on their behavioural ecology (e.g. Caro and Stoner 2003; Cozzi et al. 2012; Creel 2001).

The Felidae are specialised predators that are physiologically evolved to efficiently kill other animals; similar to one another in morphology and ecology, sympatric



Figure 1.2: *This scene records lions chasing down and killing a leopard in open habitat; demonstrating the most aggressive form of intraguild competition between carnivores.* (© Stanslaus Mwampeta, Serengeti Lion Project) [Original figure taken from Chapter 3; *this thesis*]

felids are therefore predisposed to aggressive conflict (e.g. Macdonald et al. 2010). Variation in body size between felids can therefore lead to dominance hierarchies, where larger species subdue the behaviour and abundance of smaller ones (Carbone et al. 1997; Cozzi et al. 2012; Palomares and Caro 1999).

Carnivore competition is unique in a biological sense in that it frequently results in the death of one or both species involved [*‘intraguild predation’*; (Fedriani et al. 2000; Linnell and Strand 2000)]. Palomares and Caro (1999) report 97 interacting carnivore species pairs, of which 27 actively kill other carnivores, and 54 that are susceptible to being killed by other carnivores. Intraguild predation may be particularly prevalent between members of the same family, because they have the greatest levels of niche overlap; e.g. wolves and coyotes (Berger and Gese 2007), wild dogs and jackals (Kamler et al. 2007), jackals and foxes (Kamler et al. 2013), tigers and leopards (Johnsingh 1992; McDougal 1988; Seidensticker 1976), and lions and cheetah (Durant 1998; Laurenson 1995).

However, when considering the impacts of predation, it is not enough to simply consider abundance, as the non-lethal influences on animal behaviour may also impact their ecology (Ritchie et al. 2012), and predator avoidance is important in shaping ecosystems – even where direct killing may in fact be low (Durant 2000; Valeix et al. 2009b). For example, wolves were responsible for a 40% decline in the coyote population density of the Yellowstone National Park, despite the fact that direct predation was apparently uncommon (Berger and Gese 2007).

Habitat loss intensifies intraguild competition (Balme and Hunter 2013; Wang and Macdonald 2009), and with the global range of felids ever decreasing (Nowell and Jackson 1996), the small islands of protected areas may ultimately be all that remains for their guaranteed survival. Understanding intraguild competition is considered vital to the effective management of changing landscapes (Wang and Macdonald 2009), and if competitively superior carnivores are overrepresented in these areas, they may expel subordinate species. Data on intraguild interactions are therefore vital to conservation interventions (Bangs and Fritts 1996; Harihar et al. 2011).

Those studies that deal with competitive interactions between carnivores are largely focused on exploitation competition. Although the phenomenon is often alluded to in the literature (e.g. Bailey 1993; Creel and Creel 1996; Durant 2000; Harihar et al. 2011; Schaller 1972), little direct research has actually been conducted on interference competition. While potential levels and impacts of competition can be theorised, only field studies can demonstrate competition (Caro and Stoner 2003).

With *a priori* evidence of intraguild persecution between terrestrial carnivores (see Palomares and Caro 1999), Caro and Stoner (2003) conducted a meta-analysis of the entire African guild to determine the potential for competition between all sympatric carnivore species, not just those that are easily observed and dominate the literature. Their results were divided into specific risk categories, and these are briefly summarised here. In terms of spatial overlap as a proxy for potential competition with other species, leopards featured in the top five; overlapping 66 other African carnivores. Only small carnivore species had potentially more intraguild spatial overlap than the leopard, and were the Egyptian mongoose *Herpestes ichneumon*, caracal *Caracal caracal* and African wildcat *Felis sylvestris*. The criteria for potential exploitative competition were range, habitat and dietary overlap; in this category, leopards were ranked first – potentially competing for resources with 65 other carnivores. Leopards were also tied for first place in terms of the highest vulnerability to kleptoparasitism by other species. Leopards are therefore the ideal model species with which to investigate the potential impacts of intraguild competition among the higher order carnivores. The outstanding competitor of the leopard that has the most potential to impact its ecology, through both exploitative and interference competition, is obviously the lion.

1.1.4 *The leopard Panthera pardus (Linnaeus, 1758):*

Ecology and Conservation

The leopard has the largest global range of any wild felid (Myers 1986; Ray et al. 2005; Sunquist and Sunquist 2002), extending from the Western Cape of South



Figure 1.3: *The Leopard Panthera pardus*

Africa to the Russian Far East, and is the most abundant big cat in Africa (Henschel et al. 2008; Nowell and Jackson 1996). This expansive range is largely due to the adaptive plasticity of leopards (Bailey 1993; Bertram 1999), and their ability to survive in a wide array of habitats; from rainforests to savannah, and even alpine ridges (Macdonald et al. 2010) – subsisting on anything from invertebrates and rodents up to the size of large antelope (Kingdon and Hoffmann 2013). Leopards consume the greatest variety of prey amongst all large carnivores, with 92 species recorded in sub-Saharan Africa (Hayward et al. 2006). Their adaptability, and secretive nature, allows them to survive even on the fringes of urban areas; closer to human populations than other large carnivores (Gavashelishvili and Lukarevskiy 2008; Hayward et al. 2006; Seidensticker et al. 1990). Female leopards weigh

approximately 35 kg on average, and males 65 kg (Kingdon and Hoffmann 2013), however there is huge size variation within the species, apparently determined by the range in biomass and abundance of available prey (e.g. Martins et al. 2011). A typical leopard may require up to 5 kg of prey per day (Bailey 1993; Stander et al. 1997), and could kill up to 60 animals per year to achieve this (Schaller 1972).

Despite their range and relative success as a species, the abundance of leopards in the wild is in decline (Henschel et al. 2008), and their global range has shrunk by nearly 40% of its historical size (Ray et al. 2005). Nine subspecies of leopards are recognised according to genetic analyses (Miththapala et al. 1996), however all African leopards belong to the nominate form *Panthera pardus pardus* [Linnaeus 1758] (Henschel et al. 2008). Leopards are a vital ecological species, being the apex predator in many areas from which lions and tigers have already been eliminated (Balme et al. 2010a; Harihar et al. 2011; Henschel et al. 2011); however, the conservation status of the leopard is classified as ‘Near Threatened’ by the IUCN (Henschel et al. 2008), recently upgraded from a status of ‘Least Concern’ in 2008. The major threats to leopards are similar to those of other large carnivores, with habitat destruction and depletion of their prey-base at the top of the list (Macdonald et al. 2010; Myers 1986; Nowell and Jackson 1996), and intense competition with bushmeat hunters can have detrimental impacts on leopard populations (Henschel et al. 2011; Lindsey et al. 2011). In addition to being persecuted for both real and perceived predation on livestock (Ray et al. 2005), leopards are also hunted as a trophy species, with sparse data on their populations and high offtake quotas raising concern about the sustainability of this particular form of conservation in some areas (Packer et al. 2009).

In contrast to the complexity of lion sociality (e.g. Schaller 1972), leopards are primarily solitary in nature (Bailey 1993). This however does not mean that they are asocial (Leyhausen 1965, op. cit. Mizutani and Jewell 1998), and they could alternatively be considered as non-cooperative foragers (Mizutani and Jewell 1998). Leopards are territorial, and have a polygynous mating strategy (Bailey 1993). Females defend exclusive home ranges against other females, and a dominant male leopard's territory may overlap several female ranges (Balme and Hunter 2013; Mizutani and Jewell 1998). The size of male leopard ranges increases the difficulty of defence from incursions by other males, however their core areas are largely exclusive (Chapter 4; *this thesis*). According to the resource dispersion hypothesis (Macdonald 1983), female leopard territoriality is most probably based on securing and defending a minimum prey base resource; whilst for male leopards, mating-rights are the desired resource, and his territorial behaviour is likely to be based on the defence and acquisition of sole access to females. This spatial organisation of leopards may be manifested in the fact that leopard density is strongly correlated to prey biomass (Hayward et al. 2006; Henschel et al. 2011); and reduced resource availability may increase the minimum required patch size for females, while males would either have to increase their ranges or reduce their number of mating rights. Despite intrasexual territoriality, interactions between known neighbours are thought to be more amicable than those with unfamiliar individuals (Balme et al. 2010b). Several studies have shown leopards to use both auditory and olfactory stimuli to advertise presence and facilitate mutual avoidance of conspecifics (e.g. Bailey 1993; Bothma and le Riche 1984; Schaller 1972).

The male leopard's contribution to raising offspring is simply to protect his

territory from other males, which would otherwise kill the cubs [*infanticide*’; (Balme et al. 2010a)] to bring the females into oestrus. Territorially established adult male leopards can therefore be considered vital in maintaining population stability and ensuring population recruitment. Leopards exhibit one of the highest levels of infanticide recorded in mammalian carnivores, accounting for the direct mortality of over a third of cubs in some populations (e.g. Balme and Hunter 2013). Whilst lions are infamously infanticidal, solitary felids such as leopards may be even more susceptible to infanticide because they lack cooperative defence (Packer et al. 2009). Leopards also have a relatively long period of cub dependency (Balme and Hunter 2013), and a high level of sexual size-dimorphism (Kingdon and Hoffmann 2013) with males significantly larger than females, which are therefore less able to defend their cubs (Balme and Hunter 2013). Infanticidal species are severely affected by population disturbances (Packer et al. 2009), and even those that are relatively adaptable and robust, such as leopards, may be impacted by relentless infanticide and low recruitment rates (Balme et al. 2009b). Disturbances such as excessive trophy hunting are especially detrimental to leopards, as they lead to a large turnover of dominant males (Packer et al. 2009); although this is often not accounted for by wildlife managers (Balme and Hunter 2013).

Upon independence, male leopards disperse far from their natal range, and may be transient for long periods of time, and even tolerated as such by other males as long as they do not attempt to breed, before securing defensible territories of their own (Bailey 1993; Balme et al. 2009b). Females on the other hand generally establish territories within or adjacent to their mother’s range, and this kin spatial tenure may last for several generations (Balme and Hunter 2013).

**1.1.5 *The lion Panthera leo (Linnaeus, 1758):
Ecology and Conservation***



Figure 1.4: *The Lion Panthera leo*

The IUCN Red List have classified lions as Vulnerable (IUCN 2002), and estimate that less than 25,000 free-ranging lions remain (Bauer and Van Der Merwe 2004) in less than 25% of their historic range (IUCN 2006). Lions were once present throughout Africa, parts of Europe, the Middle East and Asia (Bauer and Van Der Merwe 2004), but their surviving conservation strongholds lie only in parts of eastern and southern Africa (Brassine and Parker 2012; Nowell and Jackson 1996).

Lions are uniquely social felids, with coalitions of up to nine males associated with female prides that may be in excess of 20 individuals (Macdonald et al. 2010;

Schaller 1972). In the 1990's, lions began being reintroduced onto small private areas in parts of their former range, and these relocations were considered 'successful' in terms of high reproductive and survival rates (Miller and Funston 2014). However, this growth rate inevitably led to the potential problem of overpopulation (Funston 2008) and a lack of genetic diversity (Trinkel et al. 2010). These issues in turn required intensive management (Hunter et al. 2007) and reduced the conservation value of the lion populations (Miller and Funston 2014). Translocations were useful for relieving lion population pressure in the late 1990's, however as available space for lion relocations was used up, euthanasia and trophy hunting have taken over as the main methods of lion population control outside of national parks (Miller and Funston 2014).

The lion is the dominant carnivore wherever it occurs (Macdonald et al. 2010), and it is an ideal umbrella species for conservation; being large, charismatic and easily observable (e.g. Williams et al. 2000). In fact, lions are so popular that commercial wildlife ventures risk losing significant market share where they cannot offer them to clients (Lindsey et al. 2007). Lions are therefore often prioritised in conservation, with their charisma exploited to raise the funds so desperately needed to make wildlife areas viable (Lindsey et al. 2007). Lions are also one of the critical trophy species in the safari hunting industry, equalled only in demand by buffalo *Syncerus caffer* and leopard (Creel and Creel 1997), and they are therefore prevalent in both protected areas and private wildlife areas (Packer et al. 2013) where their populations can experience exponential growth rates (Miller and Funston 2014). However, there is little available space remaining for the reintroduction of lion populations in Africa. While the saturation of most wildlife areas on both state

and private land with lions is positive for their future conservation security, as well as that of the species incidentally conserved [e.g. rhino on private conservancies in Zimbabwe; (Lindsey et al. 2009; Suzuki 2001)], there is concern that small and isolated populations are of little conservation value (see Miller and Funston 2014).

The saturation of lion populations within the managed wildlife network also raises concern of the potential for an intense level of intraguild persecution on other carnivores. Lions are aggressively competitive, and have been linked to reductions in wild dog and cheetah abundance (Creel and Creel 1996; Durant 2000; Laurenson 1995) – both of which are already endangered. High lion density could also lead to population declines of ungulate prey (e.g. Wegge et al. 2009), including the endangered roan antelope *Hippotragus equinus* (Harrington et al. 1999). It is therefore critical to holistic conservation that wildlife managers understand the level of impact that lions are able to exert on populations of other animals; particularly on elusive species that are difficult to observe, and that risk declining into oblivion if not carefully monitored.

1.1.6 *Research methods and tools*

Animals that are rare or elusive are difficult to observe, which results in a relative lack of data for those species (e.g. Bagniewska et al. 2013). In fact, there is direct correlation between the ease of research on a particular species, and the number of studies in which it features (e.g. Karanth and DeFries 2010; Macdonald et al. 2010). Leopards are wide ranging, cryptically camouflaged, nocturnal and secretive animals that do not lend themselves to observation, especially over a

large proportion of their range where they are hunted or persecuted. Many leopard studies have employed indirect research methods (e.g. Balme et al. 2009a; Funston et al. 2010; Stander 1998), and the ability to make meaningful inferences from these are limited (Karanth et al. 2003). However, leopard behavioural ecology cannot be properly understood without data on their response to ecological disturbance (Aryal and Kreigenhofer 2009); and in comparison to lions, relatively little is known about leopard behavioural ecology.

Myers (1976) states that “*the basic ecology and behaviour of the leopard are so distinctive that special tools are needed to assess what degree of threat to its existence is tolerable.*” However, technology improves continually, and research tools that were either only a fantasy of field researchers, or prohibitively expensive, just a few years ago are readily available and commonly used in research today. For example, Karanth and Sunquist (2000) used VHF radio-tracking and 100% minimum convex polygons to assess the spatial organisation of leopards, tigers and dholes in India, and concluded that there was no evidence of spatial avoidance or habitat selection based on this. However the temporal resolution of this data precluded calculation of utilisation distributions, and GPS or satellite collars that record high-resolution data at set intervals might have revealed the interspecific spatiotemporal differences that these authors failed to detect with their low-resolution spatial data. More importantly, the data collected was related to, and limited by, the activity periods of the researcher and not the research subject. Similarly, Mills (1991) came to the conclusion that lions have little effect on leopards, without being able to show conclusive evidence of this.

Research methods used in previous felid studies have included: dissection (Karanth et al. 2010); direct observation (Schaller 1972); scat analyses (Hayward et al. 2006); spoor tracking (Funston et al. 2010); call-up surveys (Mills et al. 2001); camera-trapping (Karanth 1995); radio-telemetry (Loveridge et al. 2007); satellite tracking (Martins et al. 2011); and genetic analysis (Miththapala et al. 1996). Indirect methods are cheaper and therefore suitable for limited conservation budgets; however the data they produce is less accurate and less precise, and if not carefully scrutinised can lead to incorrect conclusions. An infamous example of this was the tiger pugmark survey that overinflated density estimates and misled tiger management (Karanth et al. 2003). Distinct from attempting to identify individuals by their pugmarks, felid spoor-tracking data can be effectively used to estimate indices of population density (Funston et al. 2010), which are useful for monitoring population trends within an area over time, while the spoor-transect method itself is cheap and efficient and requires little expertise.

Improvements in ecological modelling and computing power allow complex analyses of the data collected (Karanth et al. 2010), as well as the inclusion of increased ecological information in analyses (Basille et al. 2008). In addition, the reanalysis of historical bio-tracking datasets could allow data-mining them for hidden behavioural signals that were previously unknown. For example, using some ingenuity, Valeix et al. (2009c) analysed simple GPS-collar data to show that water was a key habitat feature that influenced movement patterns of large carnivores, and they were able to detect area-restricted search behaviour near water that was distinct from other signals present in the tracking-data.

Animal movements may be linked to both biotic and abiotic factors, including habitat, predation risk, and anthropogenic influence (e.g. Valeix et al. 2012). Large predators, for example, in both terrestrial (e.g. Broekhuis et al. 2013) and marine (e.g. Weimerskirch et al. 2007) ecosystems have been shown to adopt area-specific behaviour based on resource density. Biotelemetry greatly increases the ability to collect highly detailed spatiotemporal datasets on multiple animals and different species, and the improvement of this technology has opened up an unbiased and relatively uninvasive method of collecting high-resolution data on many elusive and secretive species that are otherwise impossible to observe.

GIS modelling of biotelemetry data further allows highly detailed analyses of the relationship between an animal and its environment (Chapter 3; *this thesis*), as well as spatiotemporal correlation with predators, competitors and prey. Different activities and behaviour may be defined by proxy through analysis of GPS fix patterns, which facilitates the efficient analysis of extensive high-resolution datasets, and allowing the rules of interactions to be defined (Chapter 4; *this thesis*). Behavioural studies by proxy were pioneered in marine systems where observational data is impossible (Hart et al. 2010), and to a large extent, terrestrial ecology lags behind marine biology in terms of remote data collection and analysis ability. Biotracking data may be spatially autocorrelated, which is not a problem in and of itself, but requires some consideration; particularly where the data is used to calculate selection-functions and probabilities related to landscape features and habitat (e.g. Fieberg and Börger 2012). Additionally, analyses of biotracking data may underestimate the strength of interactions, due to contact occurring either inbetween scheduled fixes, or between untagged, and therefore unknown, individuals

(see Creel et al. 2013).

Reliable population estimates are crucial for efficient management of wild populations. Whilst biotelemetry provides highly detailed information on a few tagged individuals, camera-trapping surveys gather data at the ecosystem community level; from which accurate population densities of target species can be calculated (Gopalaswamy et al. 2013; Karanth 1995). Camera-trapping, using capture-recapture modelling, was pioneered by Karanth and Nichols (1998) to monitor tiger populations, and has subsequently and successfully been widely applied to other felid research because of its powerful ability to record and monitor secretive species (Royle et al. 2014; Silver et al. 2004). Camera-trap methods evolve (Chapter 2; *this thesis*), and the theory underpinning the models for analysis improve constantly; with the price of the camera-trap units decreasing, this has become one of the most powerful tools currently available to comprehensively research wild felid populations (Chapter 6; *this thesis*).

Given the range of tools and techniques already available to scientists, and the rate at which technology improves, the future possibilities of ecological research are definitely exciting. However, the most important aspect of any animal research is, and will always be, their welfare; and this should always take priority over research interests, no matter what the conservation status of that species is.

1.1.7 *Study system*

The Buby Valley Conservancy (BVC) is a privately owned hunting conservancy of 3,743 km² located in the Matabeleland South province of Zimbabwe, centred at 30°7'E, 21°30'S, and at an elevation of about 550 m above sea level. The vegetation consists largely of mopane *Colophospermum mopane* and acacia *Acacia* spp. scrub and woodland, traversed by seasonal river-lines and the associated riparian vegetation, with scattered open grassland areas in between. BVC contains the full compliment of historically occurring species, including elephant *Loxodonta africana*, both species of rhinoceros (*Ceratotherium simum* and *Diceros bicornis*), lion, leopard and buffalo. Zimbabwean veterinary legislation pertaining to management of buffalo has resulted in the complete enclosure of BVC by a double fence, which is electrified to contain the elephant. Lions and leopards are the principal large carnivores; and although spotted hyaena, wild dog and cheetah are present, their abundance remains low (B. du Preez, unpublished). There are abundant and diverse herbivore populations; the most conspicuous being zebra *Equus quagga*, wildebeest *Connochaetes taurinus* and impala *Aepyceros melampus*.

The mean annual rainfall between 2007 and 2012 was 351 ± 76 mm, which falls mostly during November through March. May through September are the driest months of the year. Carnivore spatial ecology may be influenced by dry season prey biomass, which is their major limiting resource (Marker and Dickman 2005). However, artificial water points are maintained throughout BVC, which meant that ungulate biomass was not seasonally limited via drought or migrations during the course of this research. The stability of the local ecosystem therefore removed a

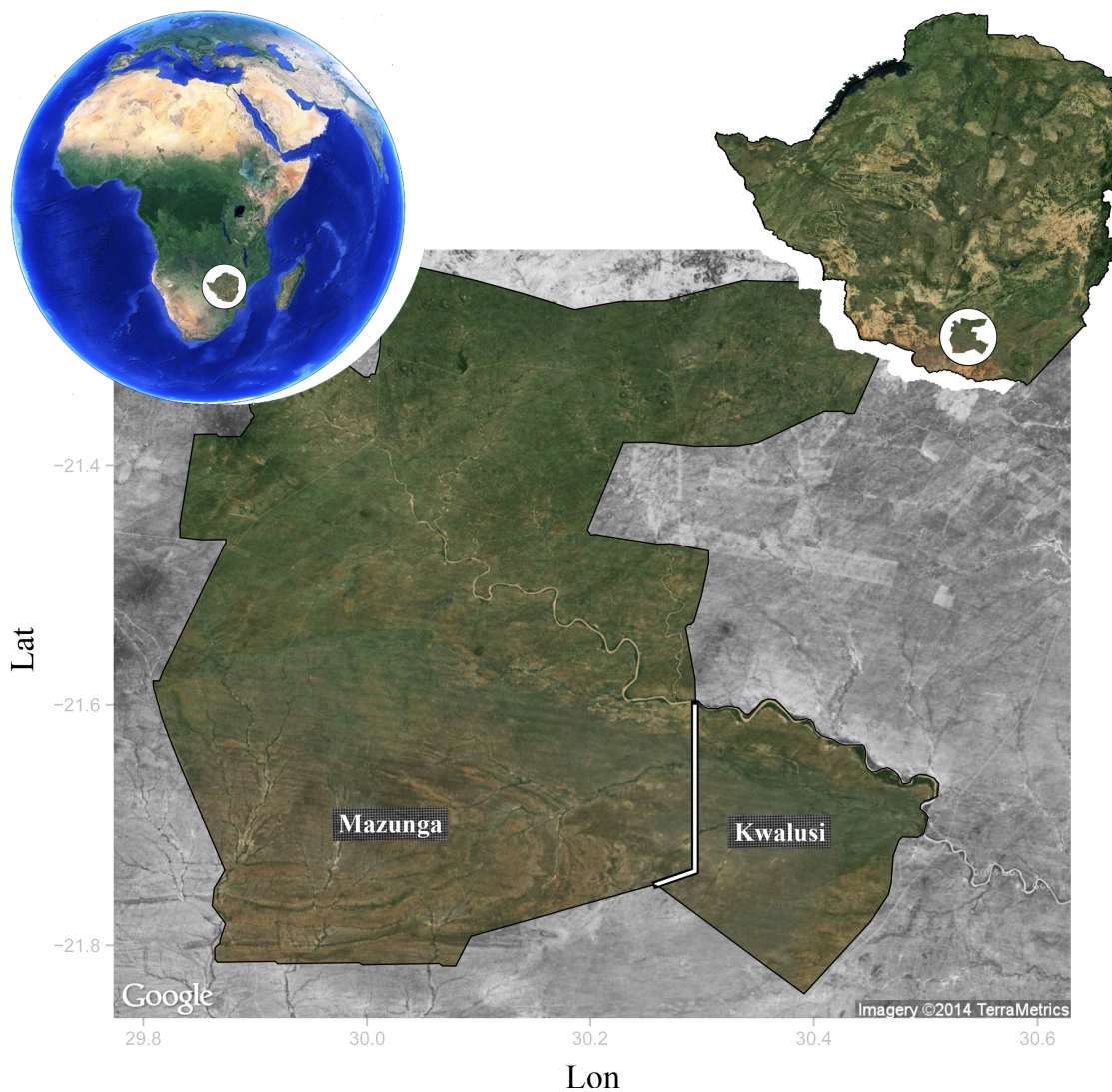


Figure 1.5: *The Bulye Valley Conservancy and its relative size and location within Zimbabwe and Africa (inset). The main study areas, Mazunga and Kwalusi, are indicated on the map, as is the electrified fence (white) that once separated them.*

potentially significant source of variation in terms of prey biomass fluctuations, which thus had no impact on the observed level of intraguild interactions.

All permanent water sources are artificially maintained with boreholes, which can boost ungulate populations by reducing drought–impact, and culling is used as

a tool for population control (K. Leathem, pers. comm.).

BVC was formed in 1994 when neighbouring cattle ranches divested their stock, and were merged and converted into a wildlife conservancy area. Lions were reintroduced to BVC in 1999 having been exterminated by cattle ranchers prior to 1994. The ranchers failed to completely exterminate leopards, which always remained present, but probably at lower densities during the cattle ranching era (K. Leathem, pers. comm.). The Kwalusi area was also a former cattle ranch that was adjacent to BVC, but separated by an electrified fence, and was also converted to a wildlife area in 1994. With congruent landscape, habitat, rainfall and management, Kwalusi maintained the same complement of mega-fauna at similar densities to BVC (Chapter 6; *this thesis*).

However, lions were not reintroduced onto Kwalusi at the same time as they were on BVC; creating a sharp contrast in the leopards' landscape of risk. Kwalusi remained separated from the main body of BVC until the 25th of August 2011, when the electrified fence dividing the areas was removed. The fence removal allowed lions previously confined within the main conservancy to move into and colonise Kwalusi – becoming sympatric competitors with the resident leopards, and changing their landscape of risk. The lion population density within the now continuous area of the expanded Buby Valley Conservancy is currently one of the highest reported in Africa [~ 0.190 lions km⁻²; c.f.: Creel and Creel (1997); Loveridge et al. (2007); Pusey and Packer (1987)].

What distinguished BVC as an ideal field research site was the effective lion enclosure of the Kwalusi area, which allowed simultaneous monitoring of two leopard

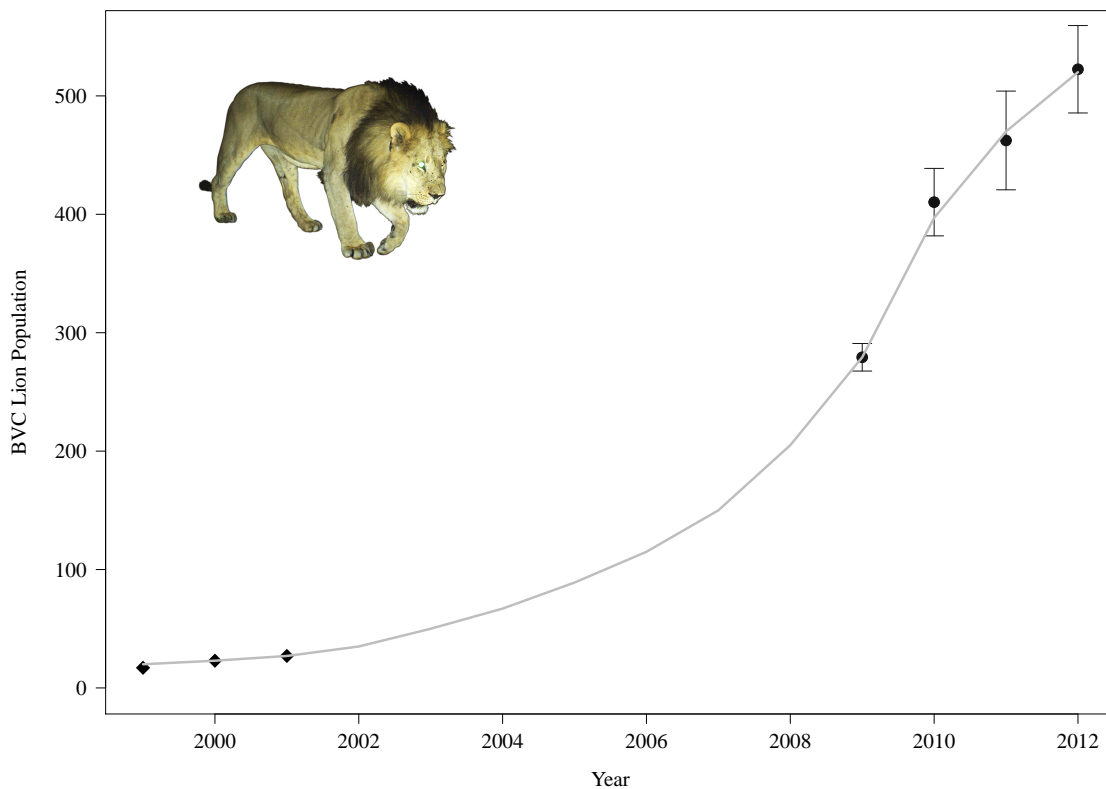


Figure 1.6: *The Buby Valley Conservancy lion population has experienced exponential growth since the reintroduction of just 17 individuals in 1999. [Original figure taken from Chapter 6; this thesis]*

subpopulations within the greater conservancy area: one that was sympatric with lions, and one that was not sympatric with lions. This allowed the testing of direct and indirect intraguild competition hypotheses regarding the introduction of a superior carnivore, whilst also having access to a control population. Although comparative studies can indicate strong effects of risk, *in situ* environmental studies are required to measure their strength (Creel et al. 2013), and the ability to compare independent ecosystems that are otherwise similar is one of the most powerful tools available to ecologists (Pianka 1973). Reintroduction of species into their historical areas allows rare opportunities to experimentally test the impacts

of predators on an ecosystem. For example, wolf reintroduction to the Northern Rocky Mountains was shown to affect elk group size, vigilance, foraging behaviour, habitat selection and diet (see Creel et al. 2013).

1.1.8 *Thesis structure and broad research aims*

Within practical limitations, this thesis aims to comprehensively investigate the impact of lions on leopard behavioural ecology. These two top-order carnivores were chosen chiefly because they exhibit both a large degree of generalist behaviour, and occupy fairly broad ecological niches within which they extensively overlap one another. They are therefore the ideal model species on which to test intraguild competition, and the direct implications of this relationship may be relevant to the conservation and management of other ecosystems, as well as to understanding competition between other species that are not so amenable to research.

There has never previously been a study directly and simultaneously conducted on the competitive relationship between lions and leopards. Most intraguild interactions have been inferred through qualitative rather than quantitative research (Palomares and Caro 1999), and carefully conceived behavioural experiments are essential to competently understand the phenomenon (Palomares and Caro 1999). *In situ* experiments of competition produce the most conclusive evidence (Wiens 1989), and their advantage over comparative studies is due to the inclusion of proper controls (Bonesi and Macdonald 2004). Field based tests of competition, however, are rare due to the practical constraints of effectively separating ecological variables (Bonesi and Macdonald 2004). The main themes of this research are

briefly described here:

Chapter 2 – *To bait or not to bait: a comparison of camera-trapping methods for estimating leopard *Panthera pardus* density*

Leopards are a highly sought after trophy species in Africa, although their populations are not monitored in most areas. Zimbabwe sets the highest leopard quota in Africa, but actual offtake does not reflect this, and the number of successful hunts has steadily declined in recent years. Accurate data on leopard populations is therefore urgently needed, particularly where they are harvested.

Camera-trapping is a powerful tool for non-invasively researching populations of rare and elusive felids, allowing accurate calculation of population density, and monitoring trends. However, unbaited camera-trapping is plagued by low capture rates, affecting the accuracy of the resultant density calculations. In addition, dependent cubs are underrepresented in the data, precluding an accurate description of demographic structure.

Here, the data quality of a novel baited camera-trapping method was compared against the traditional unbaited camera-trapping method from two survey areas within our study site. Baited camera-trapping significantly increased leopard capture rates, as well as recording dependent cubs which the unbaited method entirely failed to detect. In addition, the baited method was more cost effective. Using baits to increase capture rates of leopards is more efficient than the unbaited method, and has the potential to accurately survey unmonitored populations;

including where their density is too low to determine accurately via other means. These data are required for management of leopard populations, especially where harvested, and may be applied to improve monitoring efforts of other big cat species.

[*Published:* Biological Conservation **176** (2014) 153–161]

Chapter 3 – *The impact of risk on animal behaviour and habitat-transition probabilities*

Lions and leopards coexist in space, and compete for resources. While direct killing of leopards by lions has been recorded, avoidance behaviour is an important part of leopard ecology that is difficult to measure through direct observation. Using tracking data from simultaneously collared lions and leopards, the effect of lion proximity on the behavioural ecology of leopards was investigated. Proximity to lions was shown to influence leopard habitat use, transition probability, and behaviour. Visual observation data suggest that lions and leopards infrequently come into direct contact; however, tracking data indicates that avoidance is based on relative habitat cover and detectability, and as a result the two species are often located within close proximity.

Finding new signals of interaction and avoidance within two well-studied predators with relatively small sample sizes suggests that this approach may have value to other systems, such as predator/prey interactions, or relationships between sympatric species, and at a scale hitherto not possible. This could be used to investigate the cost-benefits of animal foraging where competitive exclusion may

occur, and is relevant for the large number of animals that are difficult to observe.

[*In Press: Animal Behaviour*]

Chapter 4 – *Detecting signals of intraguild interaction: measuring the impact of a large carnivore on subordinate predator spatial ecology*

The interaction between top- and subordinate predators can greatly influence the success and distribution of the later, and may have conservation implications. In Africa, the conservation of declining lion populations is sometimes prioritized to the detriment of smaller carnivores. Despite both felids having extensive range overlap in Africa, the intraguild interaction between lions and leopards has been poorly studied. Biotelemetry is increasingly used in large mammal research, and a method to quantify interactions may be widely applicable; particularly for species that are impossible to observe. However, there is currently neither an efficient nor automated method of detecting interactions from biotelemetry data.

With a sympatric sample of 15 leopards and 21 lions tagged with GPS biotelemetry collars, the confounding signals of interaction were identified, and a dynamic interaction index was developed to test response strength against expected values. When spatial overlap between species is sufficient for a large number of direct interactions, leopards actively avoided lions at both the landscape and patch level; and where leopards are more vulnerable to detection they showed a stronger negative response to lions. While such aggressive interactions have been observed in the past, these results demonstrate a method to extract coordinated behaviour from simultaneously tracked species. This method has the potential to be applied to

other studies of remotely tracked elusive species, for which observational data is impossible, to help model how population changes of one species can influence the behaviour of other guild members.

[*In Review: Behavioural Ecology*]

Chapter 5 – *Dietary niche differentiation facilitates coexistence of two large carnivores*

An animal's diet is an important attribute of its niche, and affects the role that it plays in the ecosystem. Comparing the diets of sympatric species reveals the level of dietary niche overlap between them, which can be used to gauge the potential for competition, as well as each species' vulnerability to competitive exclusion. Because of a morphology adapted to predation, sympatric carnivores have particularly aggressive competitive interactions; the scale of which may be directly related to the amount of overlap in the prey species that they both consume.

The diets of sympatric populations of lion and leopard were analysed and compared to test for possible mechanisms of competitive avoidance between them. After controlling for prey handling ability, there was still a significant difference in mean prey body size preference between the carnivores, despite a relatively high level of dietary niche overlap. Where intraguild competitors overlap spatiotemporally, dietary niche segregation such as this may be a mechanism through which competition is avoided and, in the case of carnivores, could reduce the frequency of potentially costly interactions.

[*In Review: Journal of Zoology*]

**Chapter 6 – Experimentally testing an intraguild hostility hypothesis:
the impact of lions *Panthera leo* on leopards *Panthera pardus***

The impact of lions on the density and age-class structure of leopard populations was investigated using the baited camera-trapping survey method (described in Chapter 2; *this thesis*) at both a control site and a neighbouring experiment site where lions were originally absent but later introduced. Many current conservation efforts are single-mindedly focused on increasing apex predator density, while few measure the impact that this has on the conservation of less conspicuous species, including both subordinate carnivores and prey species. Leopard density was calculated using spatially explicit capture-recapture models, and was compared between sites and seasons using a Before-After-Control-Impact-Pairs experimental design to test the impact of lions on the leopard population.

This study showed that lions negatively affect the density, cub survival and recruitment rates of leopard populations, suggesting that some leopard populations in competition for resources with lions are not self-sustaining. Whilst leopards are still thought to be abundant throughout their current range, the effect of competition with lions on populations of endangered carnivores, such as cheetah and wild dog, may be of great concern.

[*In Review: The American Naturalist*]

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Chapter 2

To bait or not to bait: a comparison of camera-trapping methods for estimating leopard *Panthera pardus* density

Byron D. du Preez, Andrew J. Loveridge and David W. Macdonald

PUBLISHED in *Biological Conservation*:

du Preez, B.D., Loveridge, A.J., Macdonald, D.W., 2014. To bait or not to bait: A comparison of camera-trapping methods for estimating leopard *Panthera pardus* density. *Biological Conservation* (176), 153-161.

Authorship: Collected the data: BdP. Analysed the data: BdP. Produced first manuscript: BdP. Contributed to revisions: BdP, AJL and DWM. Oversaw the project: AJL and DWM

2.1 ABSTRACT

Leopards have the largest natural distribution of felids, but have lost a third of their historical range, and their current CITES status is ‘Near Threatened’. Leopards are a highly sought after trophy species in Africa, although their populations are not monitored in most areas. Zimbabwe sets the highest leopard quota in Africa, but actual offtake does not reflect this, and the number of successful hunts has steadily declined in recent years. Accurate data on leopard populations is urgently needed, particularly where they are harvested.

Camera-trapping is a powerful tool for non-invasively researching populations of rare and elusive felids, allowing accurate calculation of population density, and monitoring trends. However, unbaited camera-trapping is plagued by low capture rates, affecting the accuracy of the resultant density calculations. In addition, dependent cubs are underrepresented in the data, precluding an accurate description of demographic structure.

We compared baited and unbaited camera-trapping methods and resultant data quality from two survey areas within our study site. Baited camera-trapping significantly increased leopard capture rates, as well as recording dependent cubs, which the unbaited method failed to detect. In addition, the baited method was more cost effective. Using baits to increase capture rates of leopards is more efficient than the unbaited method, and has the potential to accurately survey unmonitored populations; including where their density is too low to determine accurately via other means. These data are required for management of leopard populations, especially where harvested, and may be applied to improve monitoring efforts of other big cat species.

2.2 INTRODUCTION

Leopards *Panthera pardus* subsp. have the most expansive natural range of any large felid (Sunquist and Sunquist 2002), with patchy distribution from the Western Cape in South Africa to the Russian Far East (Henschel et al. 2008; Nowell and Jackson 1996). This vastness reflects their adaptability to diverse habitats and a varied diet (Hayward et al. 2006), and enables them to occupy a wide array of anthropogenic landscapes (Henschel et al. 2008). However, leopards have been eradicated from an estimated 36.6% of their historical range (Ray et al. 2005), and CITES have listed them as ‘Near Threatened’; elevating their status from ‘Least Concern’ in 2008 (Henschel et al. 2008). Leopards are an important apex predator in many ecosystems, including many from which previous incumbents of the role, such as lions *Panthera leo* and tigers *Panthera tigris*, have gone locally extinct (Balme et al. 2010a; Henschel et al. 2008). Despite the species’ global range, few ecological data are available for the majority of extant leopard populations, which inhibits assessment of the impact of current management practices (Balme et al. 2009b). This constraint on evidence-based management may be particularly disadvantageous where leopards face the dual challenges of being hunted for trophies and coexisting with their own predators.

Hunting tourism creates financial incentives for the conservation of large areas of land in Africa (Lindsey et al. 2006; Packer et al. 2009), and was the driving force behind the development of the wildlife industry in Zimbabwe (Lindsey et al. 2005). Leopards are one of the most popular trophy-hunting species in Africa (Grobbelaar and Masulani 2003; Lindsey et al. 2007; Turnbull-Kemp 1967), and in 1983 CITES

issued Zimbabwe with 80 permits per year to hunt male leopards. In 1992 this quota was increased to 500 leopards per annum following Martin and de Meulenaer (1988), whose calculations were based on the flawed assumption that leopards occurred at the highest possible density in all habitats (Daly et al. 2005; Marker and Dickman 2005; Norton 1990), and used rainfall data to estimate abundance; calculating what seems likely to have been an over-estimate of Zimbabwe's leopard population at 16,064.

In reality, there is no reliable estimate of the national leopard population abundance, trends or distribution in Zimbabwe (Lindsey and Chikerema-Mandisodza 2012), and leopard numbers are not monitored in most of the areas in which they are hunted (Balme et al. 2010a). Nonetheless, more leopards are hunted in Zimbabwe than in any other country (Lindsey et al. 2007). Between 578 and 882 (663.7 ± 38.8) leopard hunting permits are issued annually in Zimbabwe (Lindsey and Chikerema-Mandisodza 2012), despite the fact that the actual number of successful hunts per year (261.0 ± 16.4) never meets this allocation [*Appendix 2.8.1*] (<http://www.unep-wcmc-apps.org/citestrade/> [accessed 2014-01-25]). The repeated failure to achieve the annual quota in the face of intensive effort may suggest that there are insufficient leopards to meet the quota, and raises the fear that leopard hunting in Zimbabwe may be unsustainable and, with continuing habitat loss, is becoming progressively more so. Indeed, the annual leopard trophy offtake in Zimbabwe has steadily declined over the last decade, despite quotas remaining large [*Appendix 2.8.1*]. This decline is worrying because harvesting an excessive amount of males has been demonstrated to result in elevated levels of infanticide (Balme et al. 2010b; Packer et al. 2009; Whitman et al. 2004),

and accurate data on leopard population density is therefore urgently required to facilitate responsible management.

Data on leopard numbers are essential to determining a sustainable quota (Balme et al. 2010a). Insofar as sustainable offtake through harvest is often calculated as a percentage of the total estimated population size (e.g. Martin and de Meulenaer 1988), the essential data for informed management is that of abundance (Stander 1998). However, carnivores are inherently difficult to count, and leopards are particularly elusive, occurring at low densities, being cryptically coloured, solitary by nature, and mostly nocturnal (Bailey 1993; Balme et al. 2009a; Davidson and Romañach 2007; Funston et al. 2001). Methods such as strip counts and aerial surveys to obtain population estimates are therefore inappropriate, but measures of relative abundance may suffice to reveal trends, and to compare populations between sites, habitat types and larger regions (Balme et al. 2009a; Karanth et al. 2011a). To date, no rigorous scientific research has been undertaken with which to estimate Zimbabwe's national leopard population abundance and justify the current quota (Balme et al. 2010a). There is not only an urgent need for this research, but also for a method of accurately estimating leopard population density that is both relatively cheap and easily undertaken, particularly in hunted areas where populations experience the direct effects of trophy hunting.

Karanth (1995) pioneered camera-trapping as a method of estimating tiger population size using a closed capture-recapture model. Camera-trapping as a method is rapidly evolving; technology improves, and capture-recapture theory and statistical models are continuously being refined (e.g. Efford 2013; Gopaldaswamy

et al. 2012). Nonetheless, the central problem remains of securing an adequate sample of individuals. Carnivores necessarily occur at low densities, even in the most productive habitats, and therefore their photographic capture probability is correspondingly low (Karanth et al. 2011a). Increasing capture probabilities allows more individuals in the sampled population to be captured, as well as increasing capture frequencies (Karanth et al. 2011a). The more target animals that are photographed, and subsequently the more often that the same individuals can be repeatedly photographed, the more robust the population density estimate will be (Maffei et al. 2011). Methods of increasing capture probability and frequency thus merit attention.

An obvious approach to increasing capture probability and frequency is by using baits at the camera sites to attract the animals. However, baited camera-trapping is mentioned, but not adequately dealt with, in the literature (Karanth and Nichols 2002; Karanth et al. 2011a,b; Nichols and Karanth 2002). Karanth et al. (2011a) stress the need to increase capture probability and frequency as the primary consideration of camera-trapping surveys, to improve the accuracy of the resultant density estimation, and to this end sanction the use of bait for increasing detections. We compared the quality of data produced by both baited and unbaited camera-trapping surveys in terms of total leopard captures and demographic representation, and weighed these against cost and effort. The data from each survey were analysed using spatially explicit capture-recapture (SCR) models, and the quality of the resultant data were compared between methods.

2.2.1 *Study site*

The Buby Valley Conservancy (BVC) is a privately owned hunting conservancy of 3,743 km² located in the Matabeleland South province of Zimbabwe, centred at 30°7'E, 21°30'S, and about 550 m above sea level. The mean annual rainfall between 2007 and 2012 was 351 ± 76 mm, which falls mostly during November through March. May through August are the driest months of the year.

Both baited and unbaited camera-trapping surveys were conducted to investigate the leopard population at two study sites within BVC; Mazunga and Kwalusi (Figure 2.1). Between May and August 2012, a 50-day unbaited survey and a 50-day baited camera-trapping survey were conducted at each site, with no temporal overlap between methods. The Kwalusi baited camera-trap survey ran from May 11 to June 29, and the unbaited survey from July 9 to August 27. The Mazunga unbaited survey ran from May 1 to June 19, and the baited survey from July 10 to August 28.

2.3 METHODS

Despite the use of bait, the fundamental principles of the camera-trapping method for collecting SCR data with which to calculate density [see *Appendix 2.8.2*] are the same for both methods, and were adhered to in this study.

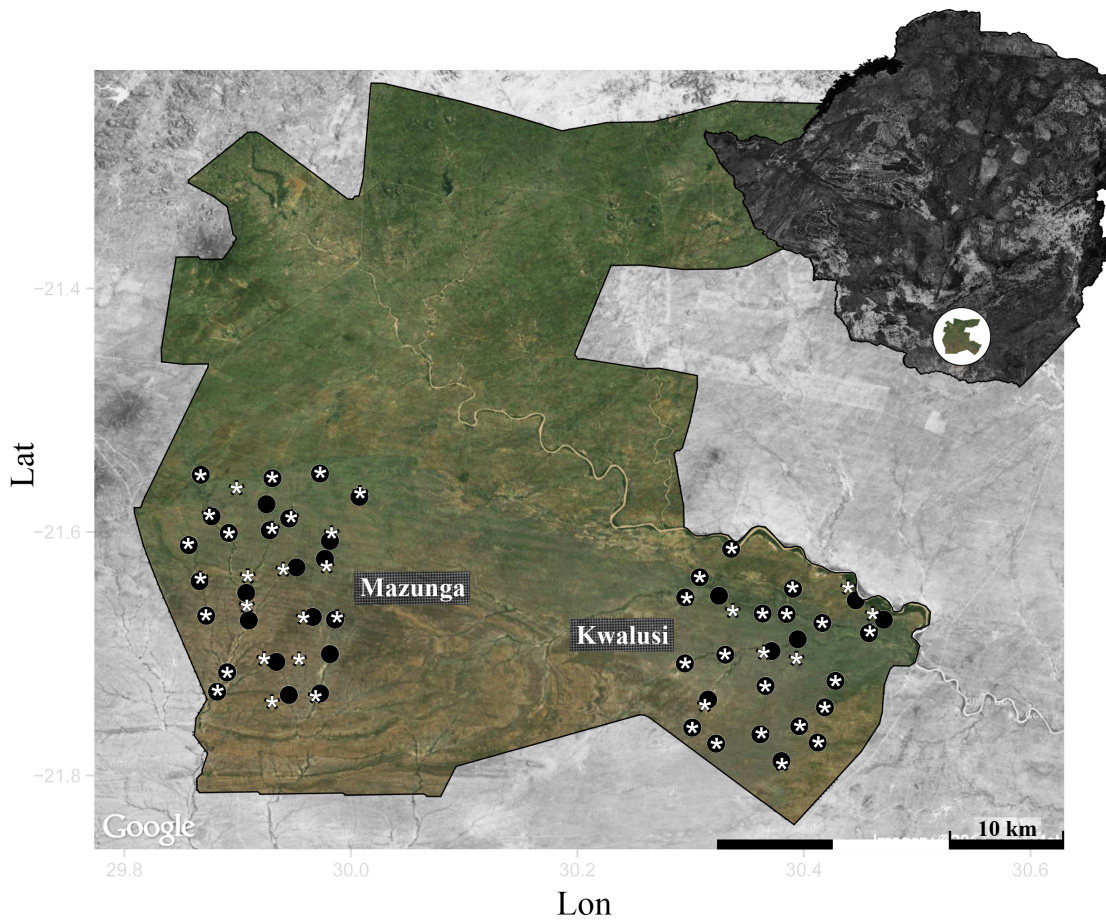


Figure 2.1: Map of the Bulye Valley Conservancy, and its relative size and position within Zimbabwe (inset top right). The white stars indicate the position of the baited camera-trap locations, and the black points represent the unbaited camera-trap locations, in both the Mazunga (west) and Kwalusi (east) survey areas.

2.3.1 Sampling occasion

Each sampling occasion was defined as the 24-h period beginning and ending at midday, because leopards are mainly active between dusk and dawn (Balme et al. 2009a; Karanth and Sunquist 2000; Martins and Harris 2013; Ramesh et al. 2009), and the chosen sampling occasion therefore represents the active period of

the leopards' diel cycle. The infrequent cases in which individual leopards were recorded within three hours both before and after midday were not considered separate sampling occasions. Leopards were identified based on their unique pelage spot or rosette patterns, and a reference database containing each individual was maintained.

2.3.2 *Camera-trap placement and spacing*

The survey area throughout which camera-traps are deployed often attains the shape of an irregular polygon, however the more circular the area, the more tractable it is for analysis, and survey designs that have high perimeter-to-area ratios should be avoided (Karanth et al. 2011a). The entire survey area needs to be covered by camera-traps, and there can be no large gaps between the cameras in which an individual of the target-species could exist for the entire duration of the survey without any chance of encountering a camera-trap (Karanth et al. 2011a; Maffei et al. 2011; Nichols and Karanth 2002).

Siting camera-traps relies heavily on preliminary reconnaissance of survey areas to find areas of concentrated target species use (Karanth and Nichols 2002). The requirement to ensure that every individual in the survey area has a chance of encountering a camera during the survey determines the distance between camera-traps and defines the maximum size of an area to be sampled by each camera-trap (Maffei et al. 2011). Therefore, the minimum average home range size of the target species in the survey area is what determines the maximum spacing of camera-traps necessary to avoid gaps in the effective trapping area and make certain that each

individual animal is potentially exposed to a trap (Karanth et al. 2011a; Maffei et al. 2011). As a rule of thumb, using minimum female home range area to space cameras ensures that other social classes in the population, such as transient juveniles and adult males whose home ranges may be 3-10 times larger (e.g. in the case of tigers (Smith 1993)), have a reasonable chance of encountering a number (≥ 1) of traps (Karanth et al. 2011a).

Tracking data from leopards in BVC indicated home-range sizes for females of $61 \pm 13\text{km}^2$ ($N = 7$) and males of $154 \pm 21\text{km}^2$ ($N = 8$), and camera-trap spacing was based on a modest female leopard home-range size of approximately 40 km^2 . Camera-traps were deployed at ≥ 2 per the equivalent area of a female leopard home range, aiming for a sufficiently high density to ensure that no home range would be unpopulated by traps, and that every individual has a chance of capture (Dillon and Kelly 2007; Karanth et al. 2011a), but also low enough to maximise the area surveyed (Karanth et al. 2011b).

With the goal of placing ≥ 2 cameras per female leopard home range, a 40 km^2 range translates into a trapping area of 20 km^2 per camera. If this was circular, the radius of the trapping area would be approximately 2.5 km. Therefore if traps are set at a maximum distance of 5 km apart, there is minimal risk of missing leopards whose territories could lie in the interstices of the effective trapping area of each camera. In reality, our radio-tracking data revealed that leopard territories are generally not circular, configured to encompass water holes and favoured habitat. Nonetheless, the optimal placement, and maximum spacing of camera-traps at 5 km, ensures that all resident animals have a chance of capture, and there is almost

certain to be at least two camera-traps per home range (see Figure 2.1; *and see Appendix 2.8.5*).

2.3.3 *Unbaited camera-trap siting and setup*

A Google Earth satellite map was investigated at a scale of approximately 1:40,000 for preliminary selection of the unbaited camera-trap survey sites. Junctions between roads and riparian habitat belts, and river confluence sites were marked first, as these effectively covered two paths of the sort known to be used by leopards (Bailey 1993; Stander 1998). Dry riverbeds in dense riparian vegetation and dry riverbeds near, or leading towards, permanent water were selected next, as tracking data showed a preference for this habitat (B. du Preez, unpublished data). Finally, road junctions, and roads leading towards permanent water were marked, as big cats are known to utilise roads on which to travel long distances (Funston et al. 2010; Stander 1998). In each study area, 75-100 candidate sites were thus marked, and then each was explored on foot to assess the feasibility of setting up a camera-trap station. Both fresh and old leopard sign, such as spoor and scats, were recorded to gauge frequency of use and likelihood of encountering a leopard at each site.

Those sites surviving this scrutiny were then replotted onto a GIS map. A buffer with a 2 km radius (so as to ensure that maximum spacing was not violated) was placed around each potential site, mindful of ideal positioning and a regular survey area shape. 25 Final camera-trapping locations were then selected for each unbaited survey site.

Cameras were housed in protective camera cases (Cuddeback Bear Safes) attached to wooden poles approximately 1.5 m in length, in order to facilitate optimal positioning. Unbaited camera-trap stations consisted of a pair of camera-traps, one of each model, planted on opposite sides of a path at least 3 m wide, facing inwards to capture both sides of a leopard as it walks down the path, and slightly offset from one another so that the flash from one camera would not overexpose the image recorded in the other.

Each unbaited camera-trapping pair consisted of two different models, either a Cuddeback Capture or Cuddeback Attack (Cuddeback, WI, USA). Unbaited camera sites were serviced once a week, and all SD memory cards and batteries were changed.

2.3.4 *Baited camera-trap siting and setup*

For siting of the baited camera-traps, the full length of every road in each study site was first driven by motor vehicle, and suitable sites for baiting leopards were marked on a GPS. These included junctions between roads and riparian habitat belts, dense vegetation near permanent water, rocky outcrops, river tributaries near roads, dense riparian vegetation near roads, and permanent water. Sites near roads were a prerequisite due to the necessary ease of access for replacement of baits, which were bulky and cumbersome to transport (approximately 25 kg each, but frequently up to 50 kg when supplies allowed). For bait we used quartered zebra carcasses donated for research by the BVC management. Leopard sign was again recorded to aid in site selection. Following the same spacing justifications

as for the unbaited survey, camera-traps were deployed at ≥ 2 per the equivalent area of a modest female home range (40 km^2) so that all individuals had access to multiple stations.

Tall trees at each trap location were selected, and baits of approximately 25 kg were hung from a branch so that the lowest part of the bait was at least 2 m from the ground. A forked pole of 3-4 m in length and at least 250 mm in diameter at the base was placed against the tree under the bait, approximately 2 m high, and acted to facilitate and guide the leopards' access to the bait. A single camera-trap was set up perpendicular to the right hand side of the pole, approximately 3 m away. This placement of the camera-trap in relation to the pole ensured that the right flank of each leopard was photographed as it used the pole to access the bait (Figure 2.2). This setup requires only half the number of cameras used in the unbaited survey to cover at least the same area, whilst also improving capture probability through the use of an attractant. Baits were secured with nylon ropes so that leopards (and lions) were unable to remove them, and feed out of sight of the camera. Baits were hung at the camera-trap sites at least a week before the survey commenced so as to avoid recording any adjustment lag of habituation to a novel situation by the leopards.

Approximately half of the baited camera sites were serviced every day. Because of the increased probability and frequency of capture, due to the attraction to baits and subsequent feeding on them, SD memory cards were changed during each service, and batteries were tested for remaining charge and replaced if less than half power remained. If more than half of the bait had been consumed, a fresh bait



Figure 2.2: *Camera-trap capture of male leopard 11K04M03 ('Mazino') detected during two different years using a baited camera-trap setup (this illustrates the ease of identification using the baited camera-trap setup. However only survey data from 2012 is presented in this study). The pole on which the leopards are standing allows precise positioning of the subject relative to the camera, resulting in a clear broadside photograph that is easily identifiable and comparable.*

was added to the remaining piece. Baits were replaced if they were rotten. Due to the sensitivity of leopards in hunted areas to human scent on baits (K. Leathem, pers. comm.) we used intestines, stomach contents and blood to cover our scent on and around the bait tree.

The camera-trap models used were either Cuddeback Capture or Cuddeback Attack, which were alternated between the baited survey sites, as only one camera was required per site. Both models required four D-cell batteries and stored images on SD memory cards.

2.3.5 *Camera-trap data analysis*

Closed-population SCR analyses were used to model the camera-trap data and calculate the population density estimates and standard errors for each survey [see *Appendix 2.8.3 for details of model definition*]. The camera-trap data were analysed using the packages *SPACECAP* version 1.0.6 (Gopaldaswamy et al. 2012) and *secr* version 2.5 (Efford 2013) in *R* (*R* 3.0.1, *R* Core Team 2013).

See supplementary information for details on *SPACECAP* and *secr* SCR model specification used in our analyses. Comprehensive description and instruction can be found in Gopaldaswamy et al. (2012) for *SPACECAP*, and Efford (2013) for *secr*.

To ensure that the baits were not influencing leopard ranging behaviour and overinflating density estimates by attracting leopards from outside of the survey area, a sample of GPS-collared leopards ($N = 10$) were monitored before, during and after the surveys to test for differences in area occupancy, and indicate whether the baits were affecting the wider population behaviour. The collared individuals included both male ($N = 6$) and female ($N = 4$) leopards, with ranges that lay either inside, outside, or straddling the boundary of the camera-trap survey areas [see *Appendix 2.8.5*]. A one-sample *t*-test was used to determine whether the difference between the size of the home ranges during the baited and unbaited periods was significantly different to zero. All individuals were adult leopards between the ages of 4-7 years.

2.3.6 *Survey method cost comparison*

Regarding the calculation of the cost of each survey method, a 10% contingency for failure and destruction were added to the costs of the equipment used in each survey, and the cost of vehicle fuel used for each method was averaged between sites. The cost of bait was not included in the survey expenses, as this was donated by the BVC management. Each bait was replaced approximately every 4 days, however they were checked every second day. Each baited survey therefore required about 300 baits of around 10 kg, and although the baits were provided free of charge to this study, the potential cost of these may need to be factored into other studies that are not so fortunate. In addition, although servicing the baited camera-traps required only one person, similar to servicing the unbaited camera-traps; the baited surveys involved approximately 36 man-hours per week and an additional 10 collecting the baits, compared to only 12 h per week for the unbaited surveys.

2.4 RESULTS

2.4.1 *Comparison of capture frequency and probability between survey methods*

More individuals were captured, and at a greater frequency, when conducting baited surveys than unbaited surveys (Figure 2.3). The mean number of leopard captures per day was significantly higher in the baited surveys than the unbaited surveys (Independent two-group t -test: $t_{132.32} = 21.9041$, $P < 0.001$); with mean

(\pm SE) leopard detections of 10.600 ± 0.379 and $8.020 (\pm 0.397)$ per day in the Kwalusi and Mazunga baited surveys respectively, compared with just 2.362 ± 0.189 and 1.806 ± 0.148 for the unbaited surveys.

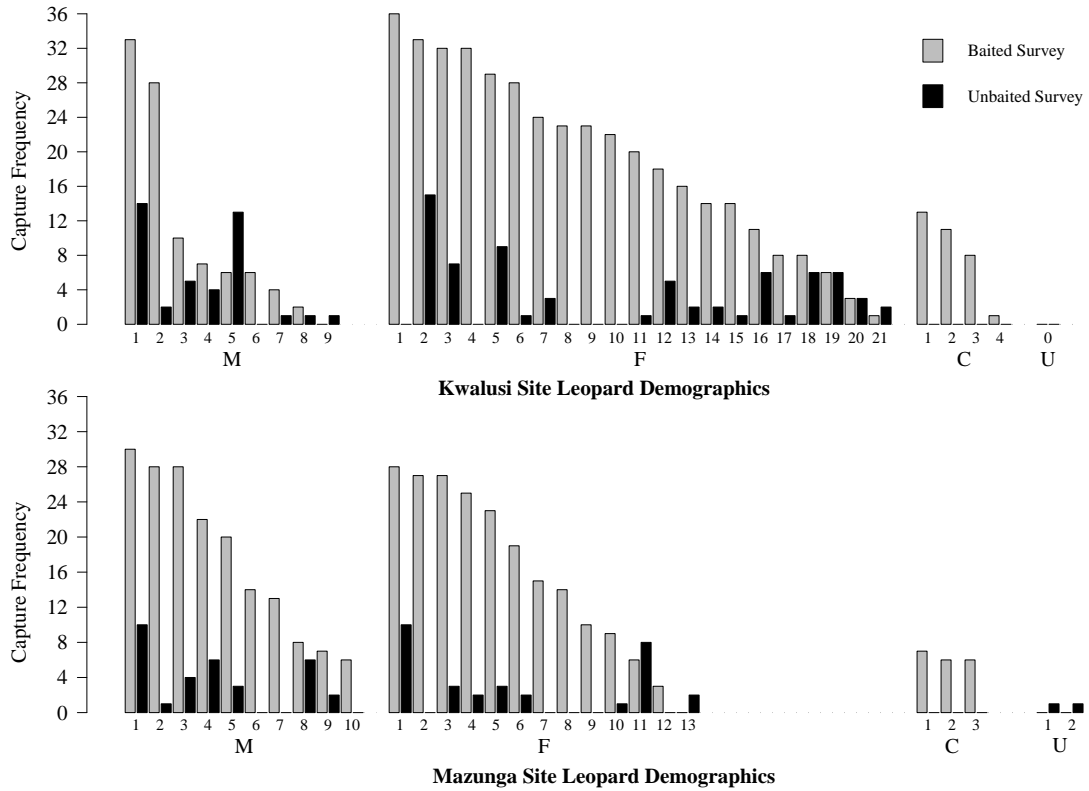


Figure 2.3: Comparison of capture success for all demographics at both sites between unbaited (black bars) and baited (grey bars) camera-traps. Each number on the x-axis refers to a single individual leopard within the relevant demographic class; M = male, F = female, C = cub, and U = unidentifiable. No leopards were detected in both the Kwalusi and Mazunga survey sites. Data are ordered by capture frequency within demographic classes, recorded during baited surveys.

33 Individuals were captured a total of 530 times in the Kwalusi baited survey, while only 24 individuals were captured on 111 occasions in the respective unbaited survey. This result was mirrored at the Mazunga site, where 25 individuals were

recorded 401 times in the baited survey, whilst only 17 were detected 65 times during the unbaited survey (Figure 2.3). There were two unidentifiable detections in the Mazunga unbaited survey when only one camera in the pair was operational, and the leopard walked too close to it in both instances to allow identification from the resultant photograph.

An obvious absence in a comparison of the results between methods is that whilst cubs were recorded during the baited surveys (7 cubs, 52 separate trapping-occasions) (e.g. Figure 2.4), none were recorded during the unbaited surveys.



Figure 2.4: *Examples of small cubs (left) and large cubs (right) captured during baited camera-trap surveys. Large cubs were recorded in 2011 but not 2012, and the image is used here as an example. No cubs were detected at all during unbaited surveys.*

2.4.2 *SCR submodels*

A comparison of the *scr* submodels using Akaike's Information Criterion (AIC) (Burnham and Anderson 2002; Karanth et al. 2011b) showed that the site

behavioural response ($g0 \sim bk$) submodel followed by the site transient response ($g0 \sim Bk$) submodel fitted the baited survey data best, while the sex model ($g0 \sim Sex$, $sigma \sim Sex$) followed by the site behavioural response ($g0 \sim bk$) submodel fitted the unbaited data best. Based on the AIC results, the *secr* behavioural response submodel was therefore used to analyse the baited survey data, and the sex model was used to analyse the unbaited data. The *SPACECAP* trap response model was used to analyse the baited survey data, and the null model analysed the unbaited data, and these submodels were comparable between SCR packages.

The site behavioural and site transient response models take into consideration leopard behaviour (e.g. Karanth et al. 2011a,b), and indicate site affinity (e.g. Royle et al. 2011; Wegge et al. 2004), whilst the sex model considers difference between sexes in terms of capture probability and frequency, in relation to differences in territory sizes and ranging behaviour between the sexes (Martins and Harris 2013).

The *SPACECAP* trap response submodel is comparable to the *secr* transient and behavioural response submodels, whilst the *SPACECAP* null model and *secr* base model are comparable. The outputs of both SCR models were therefore comparable. The density estimates calculated at both sites were slightly higher for the baited survey data than the unbaited data (Table 2.1).

Table 2.1: *Comparison of the baited and unbaited camera-trap survey results between sites and SCR models. The results are presented as leopard density, and the standard error of the estimate, per 100 km². The baited surveys were analysed without the dependant cub capture-recapture data, as no cubs were detected during the unbaited surveys.*

	Unbaited survey (leopards 100 km ⁻²)		Baited survey (leopards 100 km ⁻²)	
			<i>Independent adult leopards only</i>	
	<i>SPACECAP</i>	<i>secr</i>	<i>SPACECAP</i>	<i>secr</i>
Kwalusi	5.284 ± 0.885	5.462 ± 1.139	5.993 ± 0.912	6.112 ± 1.155
Mazunga	2.791 ± 0.593	2.783 ± 0.717	3.478 ± 0.626	4.596 ± 1.008

2.4.3 *Leopard ranging behaviour*

There was no significant difference in the areas occupied by GPS-tagged leopards between the baited survey period and periods of the same duration outside of the baited surveys (one-sample t -test: $t_8 = 1.585$, $P = 0.152$); indicating that the baits had no significant influence on ranging behaviour and did not attract neighbouring leopards into the survey area. Visual inspection of the location of each leopard's home range confirms that the baits did not affect the location of the ranges during the survey period (Figure 2.5). Every collared leopard that was detected during the baited survey was also recorded in the respective unbaited survey.

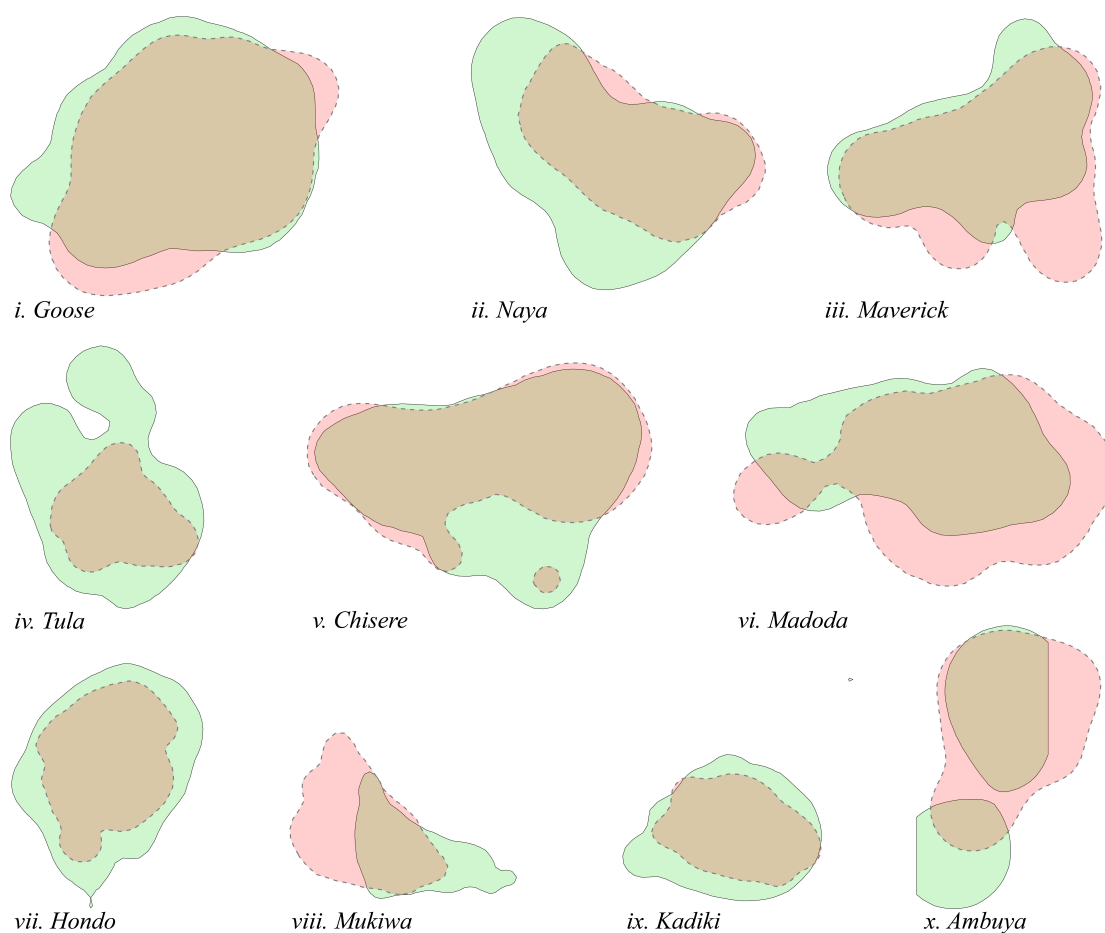


Figure 2.5: Comparison of the 95% home range kernel size and location for each of ten satellite-collared leopards between both baited (green/solid outline) camera-trap survey periods and unbaited (red/dashed outline) survey periods of equal length. The area of overlap of the baited/unbaited survey ranges is indicated by darker shading. The nicknames of each individual (which aid in identification and communication between field researchers) are indicated under the respective range, by the roman numerals i to x.

2.4.4 Camera-trap failure and causes

In total there were 240 camera-trap failures in the Kwalusi baited survey, and 260 in the Mazunga baited survey, resulting in 1010 and 990 effective trap-nights

respectively for each site. There were 149 and 189 failures of individual camera-traps during the Kwalusi and Mazunga unbaited surveys respectively, however only three nights in total were lost in Kwalusi, and four in Mazunga, when both cameras in a pair had failed (in all instances this was due to elephants destroying both of the cameras in the pair). ‘Failure’ considered not only the proper functioning of the camera itself, but that of the site in the case of the baited surveys; as if the bait was finished, the site was necessarily inactive. The reasons for failure were similar between sites, but different between the methods. The failures were mostly biological in the baited surveys, and mechanical in the unbaited surveys [*Appendix 2.8.4*].

The two camera models differed in their failure rates; Cuddeback Capture models were more susceptible to failure than the Cuddeback Attack; with 268 faults compared with 70 during the unbaited surveys. The reason for this differential failure between camera-trap models was not clearly apparent.

2.4.5 *Comparison of cost between methods*

Despite lower capture rates, the cost of the unbaited survey method (US\$26,507.88) was nearly double that of the baited method (US\$13,858.33) (Table 2.2).

Table 2.2: *Cost comparison between baited and unbaited survey methods.*

Equipment		Per Trap Site	US\$ ea.	Required	Sub-Total	10% Contingency	Total
<i>Baited Survey Expenses</i>							
Camera	<i>Capture</i>	<i>1</i>	327.05	<i>25</i>	8,176.25	817.63	8,993.88
Batteries	D Cell	<i>8</i>	8.51	<i>200</i>	1,702.00	170.20	1,872.20
SD Card	2 Gigabyte	<i>2</i>	11.77	<i>50</i>	588.50	58.85	647.35
Protective Case	<i>Bear Safe</i>	<i>1</i>	47.10	<i>25</i>	1,177.50	117.75	1,295.25
Vehicle	Fuel	-	-	-	1,049.65	-	1,049.65
							13,858.33
<i>Unbaited Survey Expenses</i>							
Camera	<i>Capture</i>	<i>1</i>	327.05	<i>25</i>	8,176.25	817.63	8,993.88
Camera	<i>Attack</i>	<i>1</i>	348.49	<i>25</i>	8,712.25	871.23	9,583.48
Batteries	D Cell	<i>16</i>	8.51	<i>400</i>	3,404.00	340.40	3,744.40
SD Card	2 Gigabyte	<i>4</i>	11.77	<i>100</i>	1,177.00	117.70	1,294.70
Protective Case	<i>Bear Safe</i>	<i>2</i>	47.10	<i>50</i>	2,355.00	235.50	2,590.50
Vehicle	Fuel	-	-	-	300.93	-	300.93
							26,507.88

Italic text = official model names; Italic numbers = quantity; Bold numbers = survey total cost; Normal numbers = US\$ cost

2.5 DISCUSSION

Advances in camera-trap technology and capture-recapture modelling in recent years have opened up a non-invasive means of researching large elusive mammals that would otherwise be impossible (Foster 2008). The addition of baits to the camera-trap survey greatly improved the quality of data collected over that of the traditional unbaited method; the number of individuals detected increased by $\times 1.4$ and $\times 1.5$, and the frequency of detections increased by $\times 4.8$ and $\times 6.2$, in Kwalusi and Mazunga respectively. These improved data increase confidence in the resultant density estimation, as well as provide a detailed snapshot of the population demographics. Increased detections may be particularly useful in conservation efforts; as investigation of accurate density and demographic data could potentially reveal trends over time that are related to changes in the species' environment –

such as trophy hunting offtake levels or predator density.

Capture-recapture theory and assumptions were originally developed for estimating the abundance of small animals with small home ranges that occur in large numbers at high densities; circumstances very different to those of large carnivores (Foster 2008). Species management policy is, or should be, heavily influenced by estimates of their population abundance, with critical consequences for rare felids (Karanth and Nichols 2002). Increasing capture probabilities allows more individuals to be sampled from the population, and increases the recapture rates of known animals, improving the accuracy and precision of the capture-recapture model calculations (Karanth et al. 2011a).

Small sample sizes, inherent to unbaited camera-trapping surveys, reduce the ability to identify the source of variation in capture probability that is required in order to select the correct submodel to analyse the data (Karanth and Nichols 1998; Nichols and Karanth 2002). The results demonstrate the value of using bait in increasing the detectability of leopards. Insofar as lessons learnt from our study of leopards can be transferred to this species elsewhere, and indeed to other big cats, we conclude that baiting the camera-trap stations is advantageous as it greatly increases capture probabilities and frequencies of the animals. A considerable additional benefit of using baits was that this facilitated the recording of dependent cubs when their mothers brought them to the baits; not a single camera-trap detection of a leopard cub was recorded in 2,500 unbaited camera-trapping occasions.

It may be possible that baits could attract individuals from outside of the survey

area, and thereby inflate the population density estimate; however this depends on the distance over which the baits are actually detectable, and which would need to be greater than the buffer between the periphery cameras and the boundary of effective trapping area (ETA). This is a considerably large distance given the size of leopard ranges and the need to ensure that animals living outside of the ETA are unlikely to encounter traps (calculation of the ETA is integrated into the SCR modelling framework; see Efford (2013) and Gopalaswamy et al. (2012)). From a sample of GPS collared leopards both inside and outside of the survey areas, we have shown that the presence of the baits did not influence leopard spatial behaviour.

That there was no significant difference in either the size or location of the leopard home ranges during the baited surveys (Figure 2.5) indicates that whilst the presence of the baits is enhancing capture probability and frequency of the population within the survey area, it is not attracting animals from outside of the survey area and inflating the resultant density calculations. This stable range size corresponds with the territorial behaviour of leopards, and the fact that both sexes defend home ranges against conspecifics of the same sex (Bailey 1993; Balme and Hunter 2013). Assuming that the baits could actually be detected from outside of the ETA, it may be possible that natural territorial behaviour and defence would prevent significant changes in leopard spatial behaviour by effectively creating a ‘biological barrier’ to the influx of conspecifics into the baited survey area.

Taking the mean of the density estimates from both survey sites and SCR models results in a total leopard population abundance estimate of 227 ± 39 from the

baited survey data, and 201 ± 38 from the unbaited surveys, for the greater BVC area. The similarity of these abundance estimations may be partly due to both a healthy leopard population at BVC, as well as the robustness of the SCR method to the relatively poorer unbaited survey data. However, at least 20 recaptures are required to ensure an accurate result using SCR models (Efford et al. 2004); and the value of the improved capture probability and frequency produced by baited survey method may be particularly apparent where a species' population density is too low to achieve adequate detections and recaptures from an unbaited survey.

Unbaited camera-traps record only a single image as the target animal walks past, whilst baited camera-traps take many photographs of the cat while it feeds, and these additional images greatly improve the accuracy of individual recognition as they provide many examples for comparison. The actual setup of the camera-trap with regard to the bait is not necessarily rigid however, and may be specifically tailored to the behavioural ecology of the target species; for example Ngoprasert et al. (2012) used a baited camera-trap setup, involving three cameras per site, to record the chest markings of Asiatic bears for SCR estimation of their population density.

The leopard identity references gathered in the baited surveys considerably assisted in identifying individuals in many of the suboptimal images recorded in the unbaited surveys. Broadside photographs recorded during baited surveys not only allow accurate identification of photo-captured animals, but also facilitate in precise determination of sex and age-class categorisation (Figures 2.2 and 2.4). Accurate identification and demographic classification of target animals is assumed,

and taken for granted in camera-trapping analyses; however, without a clear view of the genitals of some species, including leopards, young males are nearly indistinguishable from adult females (e.g. Balme et al. 2012). The inability to correctly identify an individual would result in an inaccurate population density estimation; with potentially dire consequences for rare species.

2.6 CONCLUSION

Here we have demonstrated a method that clearly improves the capture probability and frequency of leopards. It is possible that the baited camera-trap survey method would work equally well for other species that can be attracted with the use of baits or lures, and may be particularly advantageous in improving density estimates of rare carnivores. We therefore recommend the use of baits, where possible, in camera-trap surveys of other carnivore species that are uniquely marked and amenable to individual identification.

Any method used to estimate population abundances needs to balance time, expense and rigor (Balme et al. 2009b). Despite the extra effort required to undertake a baited survey, under our circumstances it cost less than conducting an unbaited survey, and the improvement in the quality of the data obtained is invaluable. Half the amount of camera-traps and associated equipment were required for the baited surveys, which only required a single camera-trap per site, and although this meant that they were more susceptible to missed trap nights through failure, they nonetheless recorded more individuals with greater frequency than did the unbaited cameras, whilst also requiring less expense per

survey. Management of leopard, and indeed other big cat populations, would benefit from the quality of data recorded by baited camera-trapping surveys, particularly with regard to managing sustainable offtake.

2.7 Acknowledgements

We would like to thank the BVC Management for allowing us to conduct the research, Blondie Leathem for his support, Paul Trethowan and Matt Trisos who helped in the field, and Paul Trethowan for a critical reading of the manuscript. Dusty Joubert conceived of the baited camera-trap setup. This project was sponsored by The Darwin Initiative for Biodiversity Grant 17-031. D.W.M. gratefully acknowledges the support of the Robertson and Recanati-Kaplan Foundations. B.dP. would like to thank The Beit Trust for scholarship funding and support. We would also like to thank two anonymous reviewers who provided useful and critical comments on an early draft of the manuscript.

2.8 APPENDICES

2.8.1 *Zimbabwe National Leopard Offtake*

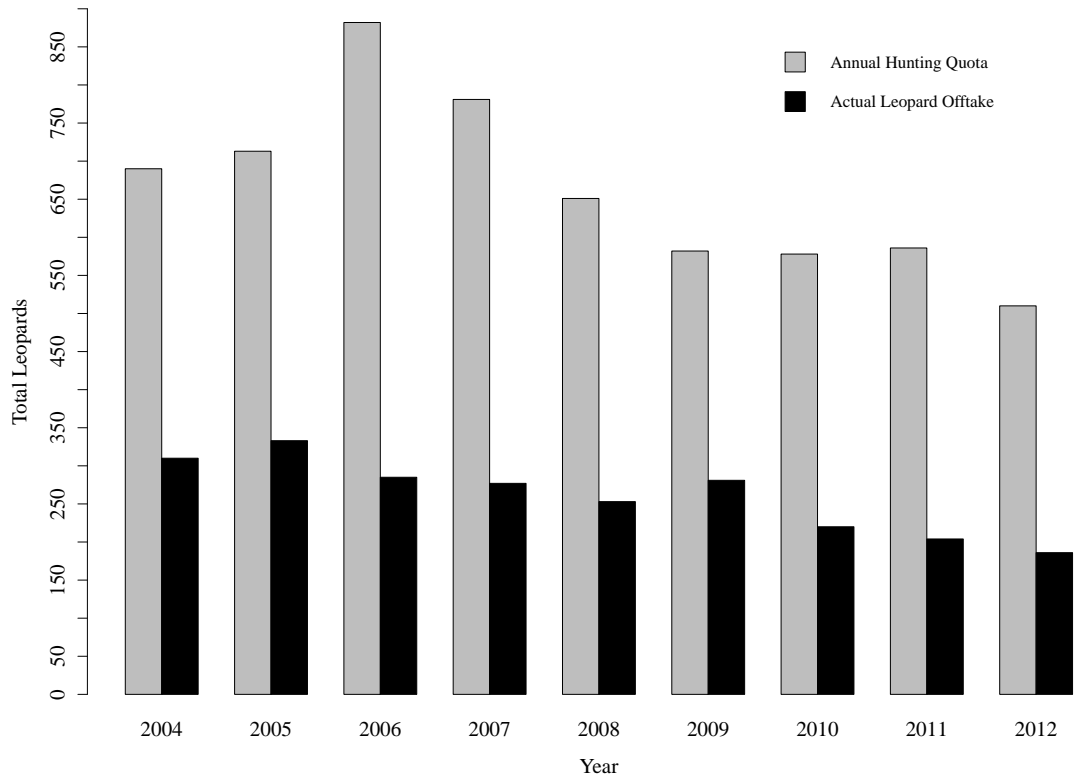


Figure 2.6: *Discrepancy between annual leopard hunting quotas and actual offtake* (<http://www.unep-wcmc-apps.org/citestrade/> [accessed 2014-01-25])

2.8.2 *Theory and Assumptions of Spatially Explicit Capture-Recapture Modelling*

Capture-recapture analysis is based on comparing the ratio of previously known individuals to newly recorded animals over two or more trapping occasions in a closed population to estimate abundance (Foster 2008; Nichols and Karanth 2002). The most basic models, the Peterson-Lincoln and Chapman estimators, use two trapping periods to calculate the sampled population size (Karanth et al. 2011a; Krebs 1999). However, the more trapping occasions that are undertaken, the more reliable the estimate will be (Foster 2008), as well as allowing a greater scope to model the data (Nichols and Karanth 2002). Multiple occasion models can be classified by the assumptions they make about capture probability, which may vary with time, individual behaviour and response to the capture experience (Foster 2008). Spatially explicit capture-recapture (SCR) models are the most recent form of capture-recapture modelling, and have been specifically developed for camera-trapping surveys of felids (Gopalaswamy et al. 2013).

The major improvement of SCR modelling over traditional capture-recapture analysis is that it does not use ad hoc methods of estimating the effective sampling area in order to calculate density (Efford 2013; Gopalaswamy et al. 2013). SCR modelling uses a grid of theoretical home-range centres within suitable habitat of the target species, and calculates the probability of capture at each of these centres as a declining function of the distance from the camera-trap locations (Efford 2013). This declining probability is similar to the detection function used in distance sampling, which is a common method used to estimate ungulate density (Buckland et al. 1993). There are several such parametric detection probability functions that may be used in SCR to describe declining capture probability, but the two most commonly used in open-source SCR packages such as ‘*SPACECAP*’ (Gopalaswamy et al. 2013) and ‘*secr*’ (Efford 2013), are the Half-Normal and Negative-Exponential (see Efford 2013).

The overriding assumption behind capture-recapture modelling is that even though not every animal in the survey area may be recorded, each individual in the target population has an equal chance of being captured, and that this probability is greater than zero (Karanth et al. 2011a; Karanth et al. 2011b). This is achieved with carefully considered survey designs and optimal trap placement and spacing, if possible based on *a priori* knowledge of the species’ behavioural ecology and minimum home-range size (Karanth and Nichols 2002). Another important assumption, pertaining to unique capture-histories, is that the animals can be individually identified throughout their lives from first capture (Foster 2008).

Closed-population models assume that there is no change in absolute numbers over the sampling period, and the sampling period should therefore be as short as possible, largely determined by the target species' biology (Karanth and Nichols 2002; Nichols and Karanth 2002; Otis et al. 1978; White et al. 1982; Williams et al. 2002). Longer surveys increase the chance of births, deaths, immigration and emigration within the study population, which break the closure assumption and affect the model accuracy (Karanth et al. 2011a). In reality, closure cannot be tested (Otis et al. 1978; White et al. 1982) due to the fact that these events are unpredictable, no matter how short the survey (Foster 2008). However it is acceptable to assume demographic closure of the population as long as the trapping period remains appropriate for the species, which in the case of big cats is generally recognised to be about two months (Balme et al. 2009; Foster 2008; Karanth and Nichols 1998; Silver et al. 2004). Therefore, sampling periods of 30 – 60 days are likely to satisfy the conditions of minimum and maximum survey time for a closed-population study of species such as leopards (Balme et al. 2009; Nichols and Karanth 2002), and Karanth et al. (2006) found that although their tiger population had high mortality, recruitment, and turnover rates, assuming demographic closure within this timeframe was acceptable. Camera-trap surveys of leopards have generally followed these closure periods (e.g. Balme et al. 2009; Grant 2012; Henschel and Ray 2003).

In contrast, open-population models assume that the population experiences gains, losses, or both, during sampling (Nichols and Karanth 2002). Open-population models are therefore appropriate for longer survey periods, and may be useful for calculating survival rates and recruitment (Nichols and Karanth 2002). Open-population models, however, are less robust than closed-population models, as they cannot account for individual capture heterogeneity (but see Gardner et al. 2010; Karanth and Nichols 2002). In long-term capture-recapture studies, it may be possible to merge both a closed-population model, for abundance and density estimation, with the annual recruitment and survival calculations of the open-population model, using Pollock's Robust Design (but see Gardner et al. 2010; Pollock et al. 1990), but this was not necessary to achieve the aims of this study.

2.8.3 *SCR Model Definition*

R Package ‘SPACECAP’

SPACECAP uses SCR modelling in a Bayesian framework (Royle et al. 2009) to estimate population density from camera-trap survey data (Gopalaswamy et al. 2013). The program requires three input files that are specifically formatted to be read into the *SPACECAP R* package graphic user interface (GUI), which is where the user defined model selection is specified. A habitat suitability mask of potential home range centres, which assumes that the entire area covered by the mask is viable habitat for the target species, buffers the camera-trap survey area and needs to be wide enough that there is no chance that animals living outside the buffer could encounter a camera. We set the buffer to 25 km based on GPS telemetry data of leopards and that the maximum straight-line length within any leopard home-range in BVC was 21.3 km. The habitat suitability mask was created in ArcMap 10.1 (ESRI), and only the area that fell within the BVC boundary fence was considered suitable. The potential leopard home range centre ‘pixel’ grain was set to 1 km² based on the relatively large average leopard home range size (see Gopalaswamy et al. 2013). Under ‘Model Definition’ we selected: ‘Trap response present’, due to the attraction of the bait; ‘Spatial Capture-Recapture’, because of the benefits of this method already discussed; and the ‘Half Normal’ detection function. For the Markov-Chain Monte Carlo (MCMC) parameters the number of iterations was set to 50,000, the burn-in period was set to 1,000, the thinning rate to 1, and the data augmentation value to 350 (see Gopalaswamy et al. 2013 for details). The MCMC algorithm was assessed to ensure convergence through examination of the N-super distribution (Noss et al. 2012).

One of the major drawbacks of the Bayesian modelling framework implemented in *SPACECAP* is the length of time that it takes to analyse the results, which for our data took up to 60 hours per survey.

R Package ‘secr’

secr considers three parameters when modelling the capture data; animal density (D), encounter rate ($g\theta$), and the scale parameter of declining capture probability with increased distance from the trap (σ) (Efford 2013). *secr* implements generalised linear models that allow the user to define the detection submodels to be fitted to the data (Efford 2013), and while *SPACECAP* is rather inflexible with regard to model definition, *secr* provides the user with a wide range of available predictor

variables for creating the detection submodels (see Efford 2013), which can be used to address a variety of questions. These predictor variables include behavioural response to the trap (b), individual heterogeneity ($h2$), variation between sampling periods (T), or user defined covariates such as age and sex (see Efford 2013 for a comprehensive list). *secr* fits the models by numerically maximising the likelihood (Efford 2013).

As with *SPACECAP*, *secr* requires specifically structured input files. However an advantage of *secr* over *SPACECAP* is that it allows the user to include additional covariates to the capture input file, such as the sex- and age-classes, which can be taken into account by the detection submodels and fitted to the data. *secr* requires two input files; the first is the individual capture histories, to which the covariate columns can be added, and the second is the camera-trap locations (see Efford 2013). A habitat mask can be easily created within *secr*, and if not specified by the user, *secr* will automatically generate one (Efford 2013). Where a more detailed mask is required, this can be created in GIS software. The same habitat suitability mask may in fact be used by both *SPACECAP* and *secr* packages for the analyses, which is what we did.

2.8.4 Camera-Trap Causes of Failure

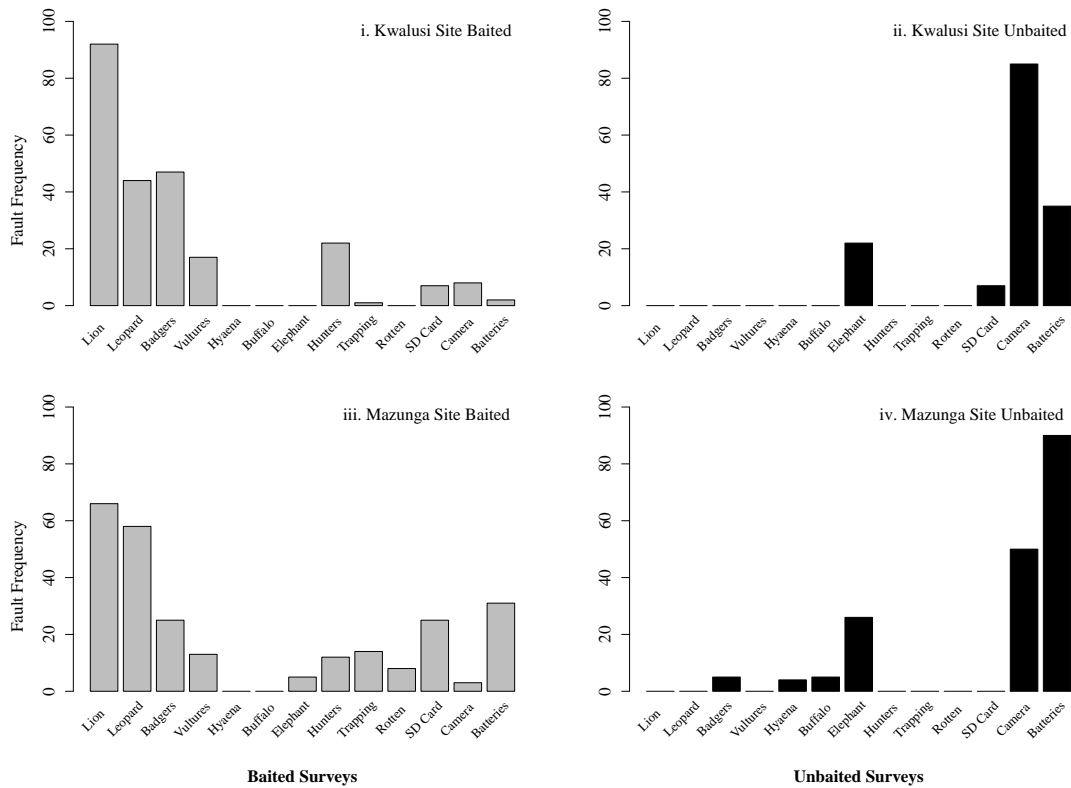


Figure 2.7: Histograms of the frequency of the reasons for camera failure for each survey method (grey = baited surveys, black = unbaited surveys). Lion = finished bait. Leopard = finished bait. Badgers = finished bait/dug out camera-traps. Vultures = finished bait. Hyaena = dug out camera-traps. Buffalo = knocked over camera-traps. Elephant = pulled out camera-traps. Hunters = removed baits. Trapping = leopard capture operations. Rotten = unusable bait. SD Card = run out of storage space. Camera = flash or PIR sensor failure/distance to animal too small/great (unbaited survey).

2.8.5 *Leopard home-range comparison between baited and unbaited periods*

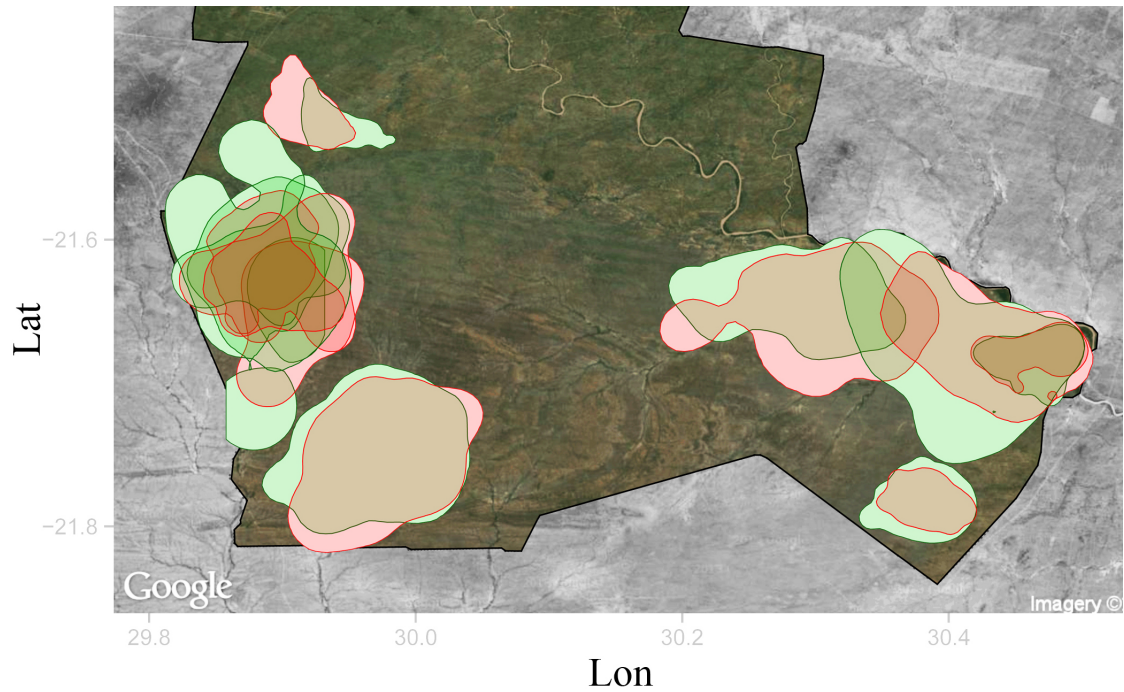


Figure 2.8: *In situ* 95% kernel isopleths of the leopard home ranges between baited (green) camera-trapping survey periods and unbaited (red) periods of equal periods of time. The data represents ten leopards with satellite biotelemetry tags. The Buby Valley Conservancy, in which both surveys were conducted, is represented by the coloured background map on top of which the kernels lie.

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Chapter 3

The impact of risk on animal behaviour and habitat transition probabilities

Byron du Preez, Tom Hart, Andrew J. Loveridge and David W. Macdonald

IN PRESS: *Animal Behaviour*

Authorship: Collected the data: BdP. Analysed the data: BdP and TH. Produced first manuscript: BdP. Contributed to revisions: BdP, TH, AJL and DWM. Oversaw the project: AJL and DWM

3.1 ABSTRACT

Lions *Panthera leo* and leopards *Panthera pardus* coexist in space, and compete for resources. While direct killing of leopards by lions has been recorded, avoidance behaviour is an important part of leopard ecology that is difficult to measure through direct observation.

Using tracking data from simultaneously collared lions and leopards, we investigate the effect of lion proximity on the behavioural ecology of leopards. We show that proximity to lions influences leopard habitat use, transition probability, and behaviour. Within enclosed habitats, lions are allowed to get closer to leopards before leopards engage a flight response. Visual observation data suggest that lions and leopards infrequently come into direct contact. However, tracking data indicates that avoidance is based on relative habitat cover and detectability, and as a result the two species are often located within close proximity.

Finding new signals of interaction and avoidance within two well-studied predators with relatively small sample sizes suggests that this approach may have value to other systems, such as predator/prey interactions, or relationships between sympatric species, and at a scale hitherto not possible. This could be used to investigate the cost-benefits of animal foraging where competitive exclusion may occur, and is relevant for the large number of animals that are difficult to observe.

3.2 INTRODUCTION

Predators can influence the ecology and population dynamics of other species not only through direct killing, but also indirectly by eliciting behavioural changes in response to risk (Creel et al. 2013; Laundre et al. 2001; Valeix et al. 2009b). The impacts of predators are typically measured in terms of total individuals killed (Lima 1998), or biomass consumed (e.g. Bodendorfer et al. 2006; Hayward et al. 2007b; Karanth and Sunquist 2000). However, the indirect effects of predation, including behavioural modifications that result in ecological niche shifts, can affect the fitness, demographics and population density of a species (Creel et al. 2013). Ungulate distribution and habitat selection is influenced by the risk of predation, and they avoid areas of high predation risk and habitats that reduce their ability to escape (Laundre et al. 2001; Valeix et al. 2010), even though this behaviour negatively affects their rate of food ingestion and nutrient quality (e.g. Creel et al. 2013; Hernandez and Laundre 2005). If predation risk is high, it can eventuate in ecological niche shifts that negatively affect the population dynamics of the subordinate species (Brown et al. 1999; Spitz et al. 2006).

Aggressive intraguild interactions between terrestrial carnivores have been well documented (e.g. Creel et al. 2013; Harihar et al. 2011; Kamler et al. 2007; Kamler et al. 2013; Karanth and Sunquist 2000; McDougal 1988; Palomares and Caro 1999), and as with herbivores, dominant carnivore species may also indirectly affect subordinate carnivore species by inducing behavioural adjustments associated with risk (e.g. Brown et al. 1999; Laundre et al. 2001). It is therefore conceivable that subordinate carnivores incur significant costs as a result of increased vigilance,

avoidance behaviour, kleptoparasitism, and restricted use of shared habitats (e.g. Creel et al. 2013; Lima 1998; Valeix et al. 2010). These costs have been less well researched, but understanding the effects that predation and competition for resources have on the behaviour and distribution of key species is fundamental to informed management (e.g. Funston et al. 2013), especially as protected areas, which are limited in size, become increasingly isolated (Lindsey et al. 2011).

Interpreting the indirect impacts of predation on an animal's behavioural ecology requires insight into the circumstantial decisions that an individual faces, which may be reflected in its activity and habitat use (Basille et al. 2008; Jessopp et al. 2013), because where an animal is and what it is doing are influenced by its need for both short- and long-term risk avoidance (Lima 1998; Valeix et al. 2009a; Whitehead and Jonsen 2013). Variation in risk between habitats, and the effect this has on behaviour, therefore requires serious consideration (Lind and Cresswell, 2005; Lone et al., 2014). Spatial heterogeneity of habitat and vegetation density influences the distribution of risk within the landscape (Laundre et al. 2001; Valeix et al. 2009b), and because predation risk influences habitat selection (Creel and Winnie, 2005; Valeix et al., 2009b; Valeix et al., 2009c) it is thus important to take into account different habitat types when investigating interspecies interactions. Determining habitat use and transition rates between habitat types with regard to predator proximity is therefore informative regarding the impact of risk on behavioural ecology.

However, unbiased observation of wild animals, and in particular nocturnal predators, is difficult (e.g. Broekhuis et al. 2013; Funston et al. 2001; Hart et al.

2010; Jessopp et al. 2013), and attempts to do so may affect their behaviour or expose their position to potential predators or prey. At the landscape level, quantification of the behavioural response to predator proximity via direct observations is virtually impossible (Valeix et al. 2010), however, biologgers are commonly and increasingly used in ecological studies. These biologgers are able to record large time-referenced datasets on location, body orientation and temperature (amongst other parameters); from which utilisation distributions, habitat selection, speed of movement, and distances between individuals can be determined.

Inferring patterns of animal behaviour indirectly is limited insofar as it precludes highly detailed description of activity. However, even broad behavioural classification is insightful when related to the environment and distance from predators (e.g. Broekhuis et al. 2013; Milinski and Heller 1978), and investigating the transitions between behavioural states, rather than focusing on them individually, may allow identification of the environmental factors that induce changes in behaviour (Bagniewska et al. 2013; Hart et al. 2010; Krebs and Davies 1991). For example, consider the transition of Adélie penguins *Pygoscelis adeliae* between water, where they forage but are also at risk of predation by leopard seals *Hydrurga leptonyx*, and ice, on which they generally are safe from predation (Ainley et al. 2005); although movements between environments occur frequently, the probability of transition from water to land may be directly related to the presence and proximity of seals, i.e. the behavioural change points are coincident with a predator.

Using biotelemetry track-data from both species, we aimed to investigate the effect of lion *Panthera leo* predation risk on the behavioural ecology of leopards

Panthera pardus; specifically, how the presence and proximity of lions influenced leopard behaviour and habitat-transition probability. Lions and leopards are morphologically similar intraguild competitors that have extensive range and habitat overlap in Africa (Bauer et al. 2013; Henschel et al. 2008), as well as overlap in prey-species utilisation (Bodendorfer et al. 2006; Ogara et al. 2010). Leopards are solitary in nature, and smaller than lions [*leopards: females 35-50 kg, males 50-75 kg*; vs. *lions: females 140-160 kg, males 180-240 kg*; (Kock et al. 2006)], and leopards are consequently at risk of aggressive persecution by the physically and numerically dominant carnivore (e.g. Bonesi and Macdonald 2004; Kamler et al. 2007; Kamler et al. 2013; McDougal 1988) [*see Appendix 3.8.1*].

Studies of diving animals have used Hidden Markov Models (HMMs) to calculate the probability of transiting between as few as two dive states to accurately determine environmental predictors of behaviour (Bagniewska et al. 2013; Hart et al. 2010; Jessopp et al. 2013). Specifically, Hart et al. (2010) linked dive depth and duration to hidden behavioural states that were classified as either foraging or not foraging, and investigated the transitions between these states and the environmental conditions that triggered them. HMMs assume that the system is Markovian, with distinct states where the transition from time step t to $t+1$ is conditional on the state at t rather than previous states, and estimate the unknown states and the transition probabilities between them (Bagniewska et al. 2013). As Markov Chain analyses consider state persistence and transitions between states, this makes them ideal for analysis of non-independent temporal data such as movement trajectories (Hart et al. 2010; Patterson et al. 2009). Markov Chain analyses control for variables such as different amounts of habitat

and density of predators, prey and competitors; and allow direct comparison of behaviour between habitat types and different areas.

Here we employed a Markov Chain analysis of relatively high-resolution track [i.e. the same GPS fix-rate used for detecting dynamic interactions between big cats (e.g. Benhamou et al. 2014)] and environmental data to investigate behavioural changes in two terrestrial predators. This study is inspired by the pioneering work of Brown et al. (1999) and Laundre et al. (2001) regarding the ecological concept of fear, but is novel in that we had access to leopard populations both with and without lions present, as well as before and after the introduction of lions. A Markov Chain analysis of this system is appropriate as it measures and removes the confounding effects of spatial autocorrelation, habitat variability and prey density, and focuses on the behavioural changes that occur when leopards come into close proximity to lions.

In the field of large-mammal ecology, properly controlled, large-scale *in situ* experimental manipulations are rare, and notoriously difficult to carry out (Bonesi and Macdonald 2004; Creel et al. 2013). We took advantage of a unique opportunity to experimentally test the impact of lions on leopard behavioural ecology when an electrified fence that had historically excluded lions from a section of our study site (hereafter ‘Kwalusi’) was removed (see Figure 3.1). Lions were present and abundant in the area adjacent to Kwalusi (hereafter ‘Mazunga’), and the fenced enclosure effectively created a sharp contrast in competition and predation by lions on an otherwise contiguous population of leopards. The fence was removed 18 months after the study began, allowing lions to move into and colonise the

Kwalusi area, rapidly balancing their density between the two sites (du Preez et al. 2014a). We thus compared, at the individual level, the behaviour of the leopard subpopulations with and without the risk of predation by lions, as well as the effect of the removal of the fence and rapid introduction of lions on the leopard population. Where lions were present, we also assessed the variation in predator proximity and resultant level of leopard response, so as not to simply dichotomise risk into only predator present/absent classes (e.g. Creel et al. 2007; Creel et al. 2013).

Lions represent a significant source of mortality for leopards (Bailey 1993; *and see Appendix 3.8.1*), and leopards are likely to actively avoid lions so as to reduce risk. However, avoidance behaviour may be a trade-off between running away, thereby alerting lions to their presence, and hiding, thereby risking close-quarter detection. Leopard behaviour and habitat use is thus likely to reflect both the real and perceived risk associated with lions (e.g. Brown et al. 1999; Laundre et al. 2001). We therefore expect to find changes in the transition rate from open to closed habitat and a change in behaviour within each habitat when lions are present compared to when they are absent. Moreover, as this behaviour is lion-moderated and based on detection of lions, we would expect leopard behaviour to change based on the proximity of the nearest tracked lion.

Because of the potentially lethal consequences of interaction with lions, and the differing amounts of available cover between habitat types (and therefore differential levels of detection risk and potential for escape), we hypothesise firstly that (H_1) leopard habitat-transition probability would increase from more-open habitat types

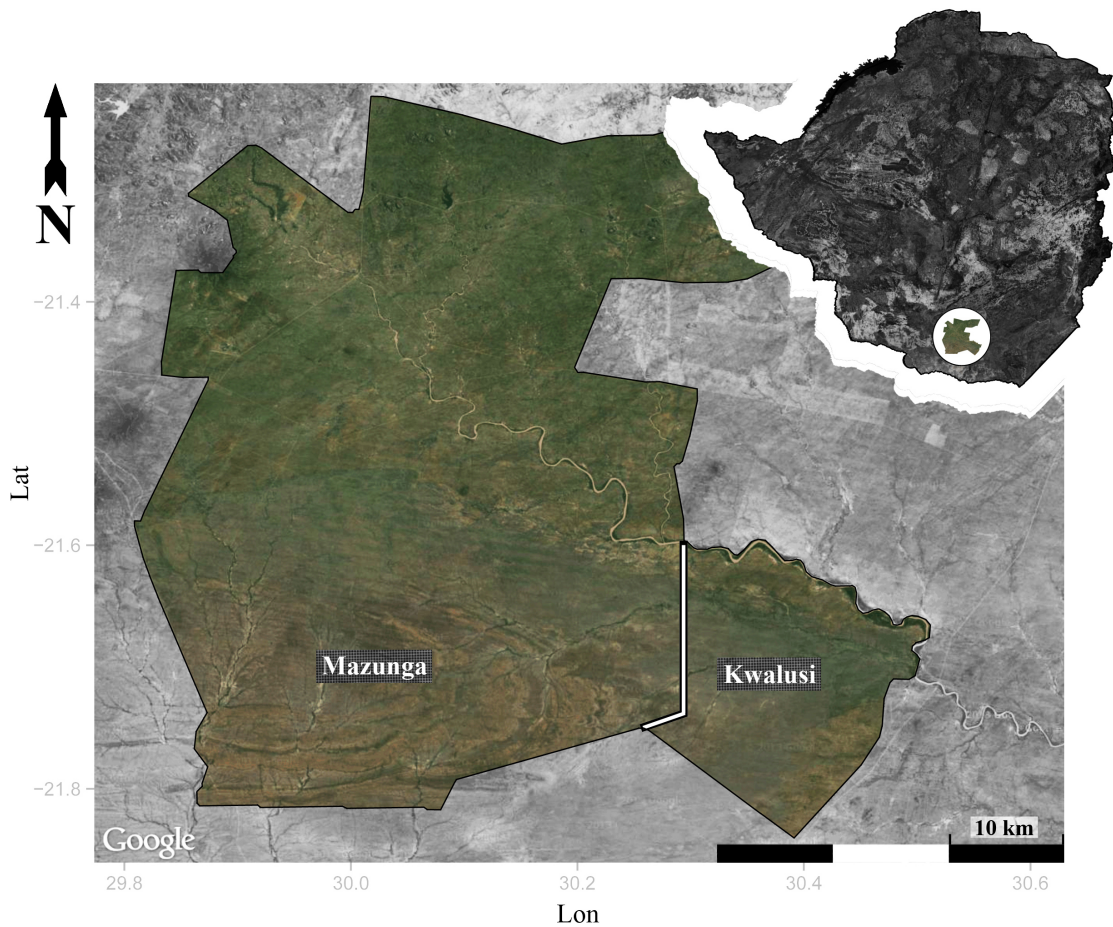


Figure 3.1: Map of the 3,743 km² Bulye Valley Conservancy where the research was conducted, and its location and relative size within Zimbabwe (inset top right). The Mazunga (control site) and Kwalusi (experiment site) areas are indicated on the map. The black-and-white line indicates the electrified fence that excluded lions from the Kwalusi area east of the fence (the ‘exclosure’).

to more-closed habitat types where lions are present. Secondly, we hypothesise that (H₂) leopard behaviour between each habitat type would differ in areas where lions are present. Finally, as detection probability and the relative level of risk are an inverse function of distance (related to habitat density), we hypothesise that (H₃) leopard behaviour is dependent on the proximity of lions.

3.3 METHODS

3.3.1 *Study site*

The Buby Valley Conservancy (BVC) is a privately owned wildlife conservancy of 3,743 km² located in the Matabeleland South province of Zimbabwe, centred at 30°7'E, 21°30'S, and about 550 m above sea level. The mean annual rainfall between 2007 and 2012 was 351 ± 76 mm, which fell mostly during November through March. May through August are the driest months of the year. The vegetation consists largely of mopane *Colophospermum mopane* and acacia *Acacia* spp. scrub and woodland, transected by seasonal river-lines and associated riparian vegetation, with scattered open grassland areas in between. BVC contains full compliment of endemic megafauna, including elephant *Loxodonta africana*, both species of rhinoceros (*Ceratotherium simum* and *Diceros bicornis*), lion, leopard and buffalo *Syncerus caffer*. Zimbabwean veterinary legislation pertaining to management of buffalo results in the complete enclosure of BVC by a double fence. Lion and leopard are the principal large carnivores; and although present, the abundance of spotted hyaena *Crocuta crocuta*, wild dog *Lycaon pictus* and cheetah *Acinonyx jubatus* remain low (B. du Preez, unpublished data). There are abundant and diverse herbivore populations, especially zebra *Equus quagga*, wildebeest *Connochaetes taurinus* and impala *Aepyceros melampus*. All permanent water sources are artificially maintained with boreholes, and culling is used as a tool for ungulate population control (K. Leathem, pers. comm.). On the 25th of August 2011 the fence separating the Kwalusi management section from the main

body of the conservancy was removed, and as a result lions were able to enter and colonise this area (see Figure 3.1).

3.3.2 *Leopard and lion capture methods, permission and ethical statement*

Captured leopards and lions were handled by project staff qualified by attendance at Zimbabwe's Physical and Chemical Capture of Wild Animals Course and held valid drugs licences [*B. du Preez; Dangerous Drugs Licence No. 600131*]. The animals were captured under permit from the Zimbabwe Parks and Wildlife Management Authority (23(1)(C) (ii) 13/2008) and with permission from the landowner and conservancy management, following the ASAB/ABS recommendations for the Use of Animals in Research.

Adult lions were darted remotely using a Dan-Inject (DAN-INJECT ApS, Sellerup Skovvej 116, Børkop, Denmark, DK 7080) CO₂ propelled 1.5 ml dart, which delivered drugs intramuscularly either to the shoulder or rump of the animal. Lions were darted strictly during the coolest part of the day, either at dawn or dusk. Leopards were trapped in cages measuring $1.500 \times 0.750 \times 0.600$ m, with a 2×2 cm wire mesh that prevented body parts from getting caught, and a door-stopper, combined with a lock, to prevent complete closure causing injury to the tail. Traps were positioned at midday when leopards are least likely to be active, and were set in the late afternoon, before the evening peak in leopard activity. Leopards were trapped at night, and the traps were checked at first light

each morning. The traps were covered before the leopard was darted through the mesh using the Dan-Inject at a pressure of 4 bars, and the animal was left in the trap until completely immobilised. Subadult leopards that were caught were darted in the trap so that they could be safely removed without causing injury to themselves or research staff, but were not collared. Captured leopards that were not collared were visually monitored after capture until they had moved off on their own initiative and were no longer visible, and approximately 8 hours later they were then physically tracked on foot until it was clear that they had left the area and were moving with consistent stride and directionality. Small cubs were not able to trigger the trap, and leopard trapping was strictly done in conjunction with camera-trap surveys so that specific animals could be targeted, which prevented heavily pregnant females and those with dependent cubs from being captured. Only adult animals of both species were collared. Lions in late stage pregnancy were not captured, and although impossible to detect early pregnancy, the drugs are extensively used by veterinarians, and have no known effects on fetuses.

The capture drugs used to immobilise the animals were a combination of a dissociative anaesthetic (Zoletil; lion dosage: 1.445 ± 0.157 (range: 1.042 – 1.786) mg/kg; leopard dosage: 2.752 ± 0.181 (range: 2.400 – 3.000) mg/kg; manufactured by Virback RSA, Halfway house, South Africa), and a sedative (Xylazine; lion dosage: 0.578 ± 0.063 (range: 0.417 – 0.714) mg/kg; leopard dosage: 1.310 ± 0.156 (range: 1.000 – 1.500) mg/kg; manufactured by CP Pharma, Germany), which was reversed with an α -2 antagonist (Atipamezole; lion dosage: 0.058 ± 0.006 (range: 0.042 – 0.071) mg/kg; leopard dosage: 0.131 ± 0.016 (range: 0.100 – 0.150) mg/kg; manufactured by Novartis, Isando, South Africa) administered intramuscularly

within 60 minutes of immobilization. Doses were calculated for each species and sex separately, and animals were monitored until they'd made a full recovery and had left the area [*up to 5 hours, but usually less than 3*]. Collared animals were monitored via radio-tracking for the next 48 hours after capture to ensure that there were no lingering effects. No adverse effects from the drugs were observed, and none have been reported in the literature.

The lion collars weighed 1.10 kg, and the leopard collars 0.65 kg, which represents 0.69% and 1.30% of the body weight of the smallest individual collared of each species respectively. GPS-collars were replaced approximately 18 – 24 months after deployment, when the batteries began to fail (which was indicated by noticeably weaker VHF signal detection). Recollaring of known individuals allowed long-term population monitoring.

3.3.3 *Leopard and lion at BVC*

Although the abundance of each carnivore is irrelevant to the Markov Chain analysis, both lion and leopard density at each study site, and before and after the removal of the enclosure fence, are provided simply to indicate the potential for competition between them. Lion density was measured both inside and outside of the enclosure, before and after the fence was removed, using spoor transects (Funston et al. 2010; Stander 1998). In 2011 there were 0.000 ± 0.000 lions km^{-2} detected inside the Kwalusi enclosure (460 km^2), and 0.202 ± 0.018 lions km^{-2} in the adjacent Mazunga area ($2,293 \text{ km}^2$). In 2012, after removal of the fence, the lion density had increased to 0.202 ± 0.020 lions km^{-2} at the enclosure site, and had

remained at a similar density of 0.187 ± 0.012 lions km^{-2} in the surrounding area (du Preez et al. 2014a). Leopard density was calculated using spatially explicit capture-recapture modelling of camera-data, and the adult density at Kwalusi was 0.054 ± 0.011 leopards km^{-2} in 2011 before lions were present, and 0.061 ± 0.011 leopards km^{-2} in 2012 when lions were present, and at Mazunga was 0.046 ± 0.010 leopards km^{-2} in both 2011 and 2012 (du Preez et al. 2014a).

3.3.4 *GPS radio-telemetry tagging*

Between 2010 and 2013, 21 lions (9 female and 12 male) and 15 leopards (7 female and 8 male) were fitted with custom-built GPS radio-telemetry collars (Africa Wildlife Tracking, Pretoria, South Africa). Six leopards were collared at the Kwalusi site whilst the area was lion free, and an additional leopard was collared after the fence had been removed and lions entered. Eight leopards were collared at the Mazunga site. The number of collared leopards at each site represents approximately 26% of the standing Kwalusi leopard population and 38% of the standing Mazunga leopard population (du Preez et al. 2014b).

All collars simultaneously recorded a GPS positional fix hourly from 16h00 – 08h00 when the animals were most active, and then every two hours at 10h00, 12h00 and 14h00 during the heat of the day when both lions and leopards are least active (e.g. Bothma et al. 1984; Cozzi et al. 2012; Valeix et al. 2010). This fix schedule was a compromise between the resolution of the data and the life span of the collar batteries, which in our case lasted for approximately 18 – 24 months before they needed replacement. GPS-collar data were analysed to determine

habitat use, transition between habitats, and behaviour within each habitat type. All statistical analyses were done in *R* (*R* 3.0.1, *R* Core Team 2013).

We conducted a static test of horizontal GPS-collar location accuracy in riparian habitat to ensure that the circular error probable (CEP) was not adversely affected by the density of the vegetation (e.g. Rempel and Rodgers 1997). Five GPS-collars were placed in a fixed location within riparian habitat and left for one week, after which the 50% CEP for each GPS-collar was calculated. This resulted in a mean \pm standard error 50% CEP of 9.94 ± 0.89 m, which we considered to be acceptable for our study (e.g. Agouridis et al. 2004; D'eon et al. 2002; Rempel and Rodgers 1997).

The maximum precision of the GPS-collars we used is approximately 2.5 m (M. Haupt, Africa Wildlife Tracking, pers. comm.), and to help assess the accuracy of each locational fix, the horizontal dilution of precision (HDOP) value is coincidentally recorded. The HDOP values may be multiplied by 2.5 m to calculate the potential error of the fix, and for our data the mean \pm standard error of the HDOP values recorded were in grassland 2.10 ± 0.09 , in scrub 2.17 ± 0.08 , and in riparian habitat 2.19 ± 0.09 . We compared the mean HDOP values for each individual animal in each habitat type, and tested these for a significant difference using a general linear mixed-effects model, with individual included as a random effect. Although the mean HDOP value increased slightly with habitat density, there was no significant difference in HDOP between each habitat type ($F_{2,98} = 0.287$, $P = 0.752$, $R^2 = 0.01$, power = 0.096).

3.3.5 *Habitat use*

Habitat classification was performed in ArcMap 10.1 (ESRI), using a BingTM (Microsoft Corporation 2013) satellite map at a scale of 1:40,000. Description of cover regarding risk of detection needs to be objective (Jones 1968), and therefore the area within the study site was classified into one of three broad habitat types derived from the satellite imagery, based on relative vegetative density: (i) grassland, characterised by containing neither ground nor vertical cover, (ii) scrub, characterised by containing ground cover but not vertical cover, and (iii) riparian habitat, characterised by providing both ground and vertical cover (in the form of trees, up which leopards can find refuge from lions) (e.g. Calenge et al. 2005; de Knegt et al. 2011; Godvik et al. 2009). Habitat classification into broad categories was relatively straightforward as all three habitat types differ obviously from one another in terms of species composition and vegetative density, and are thus visually distinguishable.

The points of greatest change in vegetation cover and composition defined the ecotones between habitat classes (Fortin and Drapeau 1995), and shapefiles for each were created in ArcMap. The resulting habitat map was ground-truthed by inspecting random GPS points *in situ* and comparing these to the digital map to ensure classification consistency. GPS tracking-data for each individual were then imported into ArcMap, merged with the habitat map (using the ‘Merge’ function in the ‘Geoprocessing’ menu), and the habitat class attribute for each GPS fix was extracted by the habitat shapefile it was located within (using ‘Extract’ under ‘Spatial Analyst Tools’ in the ArcMap Toolbox).

3.3.6 *Habitat-to-habitat transition probability*

A habitat-transition matrix of five consecutive GPS fixes was created for each individual GPS fix location, with each matrix consisting of the fix datum at t along with the two previous (t_{-1} , t_{-2}) and two subsequent (t_{+1} , t_{+2}) fixes for each individual leopard [see R script in Appendix 3.8.2]. Five was the lowest number of consecutive fixes required to create a transition matrix. The reason that we used the minimum amount of fixes possible was because the aim was to show very short-term behavioural encounters, so we wished to avoid any averaging effect of a longer moving window.

The proportional transition probability of the animal either staying in the same habitat, or moving to a different habitat type was thus calculated [i.e., a dependency metric (see Jessopp et al. 2013)]. With three different habitat types there are nine possible ‘transitions’; one from each habitat to either the same habitat or one of the other two habitat types. The mean likelihood of each possible transition to and from each habitat class for each individual could then be related to environmental predictors, such as varying proximity to lions.

The distance of each individual to every other simultaneously collared animal was determined for every fix datum [see R script in Appendix 3.8.3], and the habitat-transition probabilities to and from each habitat class were compared at varying distances (100 m intervals) between leopards and lions. Thus the relationship between the proximity to lions, and leopard habitat use, behaviour and transition probabilities could be determined. A general linear mixed-effects

model, with a single fixed effect of lion presence, was used to determine difference in habitat-transition probabilities between the areas with and without the risk of lion predation. To remove any pseudoreplication, individual was included as a random effect.

A large proportion of direct interactions between species could be missed as a result of the hourly resolution of the collar data, and detections of interaction between individuals would be reduced because of avoidance behaviour occurring between scheduled fixes (Creel et al. 2013). Investigating predator-prey dynamics with GPS-collar data therefore likely underestimates the ‘predator-effect’ because encounters both between fixes and with uncollared predators go undetected. If the frequency of interactions between predators and prey is underestimated, then the level of anti-predator response in the population will be underrated (Creel et al. 2013). To reduce the observed impact of unknown lions on the analysis of leopard behaviour, only leopard data collected within 1,000 m of collared lions were considered for comparison between the areas where lions were either present or absent. Lions are aggressively territorial, and neighbours largely avoid each other because direct interactions can result in injury or death (e.g. Benhamou et al. 2014). A threshold distance of 1,000 m from known lions was therefore chosen within which to measure leopard behaviour, because this distance is great enough that it allowed a large sample of leopard data to be investigated, whilst also small enough to prevent the effect of unknown lions, which were unlikely to be frequently within 1,000 m of territorially dominant individuals (see Mosser and Packer 2009), from influencing leopard behaviour.

3.3.7 *Generalised transitions between open and closed habitat types where lions are present*

Transitions between habitats could be directionally generalised in terms of movement between open and closed types; e.g. from grassland to scrub would be considered moving from open to closed habitat, while riparian to scrub would be a closed to open direction. The *open-closed/closed-open* directionality of habitat-transition at varying distances to lions was therefore determined at varying lion proximity to investigate further the relative importance of and habitat density and transitions between habitats by leopards for reducing risk.

Leopard habitat-to-habitat transition probabilities were calculated at increasing distance from the nearest known lion within 100 m intervals. The mean likelihood of a leopard remaining in any particular habitat type versus moving to a different habitat type at t_{+1} was determined for each interval and individual leopard. The mean probabilities of leopards moving from closed to open (scrub \rightarrow grass, riparian \rightarrow scrub, riparian \rightarrow grass) and open to closed (grass \rightarrow scrub, grass \rightarrow riparian, scrub \rightarrow riparian) habitat types at varying proximity to lions were thus calculated, and the effect of lion proximity on leopard habitat-transition direction was tested using a polynomial analysis with the *lm* function in *R*.

3.3.8 *Habitat specific leopard behaviour*

As a proxy for leopard behaviour within each habitat class, the straight-line distance between consecutive hourly fixes was calculated, and was defined as ‘step-length’ (Fieberg and Börger 2012; Valeix et al. 2010). This is effectively a proxy for the speed ($v = d/t$) at which a leopard moves within each habitat type, and is indicative of a latent behaviour (e.g. Bagniewska et al. 2013; Hart et al. 2010; Whitehead and Jonsen 2013). Lion step-lengths are known to be short when foraging, but long and highly directional when avoiding danger such as people or other lions (Valeix et al. 2012). Similarly, as lions represent a source of risk to leopards, leopard habitat-specific step-lengths were determined at varying distances from lions, and compared to those at the Kwalusi site when lions were absent.

3.4 RESULTS

3.4.1 *Leopard habitat-transition probabilities in the presence and absence of lions*

The mean probability of every possible habitat-to-habitat transition for each collared leopard was calculated both in the absence (Figure 3.2a) and presence of lions (Figure 3.2b), between which there was a difference in risk of predation. A general linear mixed-effects model, with individual included as a random effect, was used to test the effect of lion presence on each leopard habitat-transition probability, which showed a significant increase in the probability of leopards transitioning from

grassland to scrub where lions were present ($F_{1,7} = 10.019$, $P = 0.016$, $R^2 = 0.589$, power = 0.866).

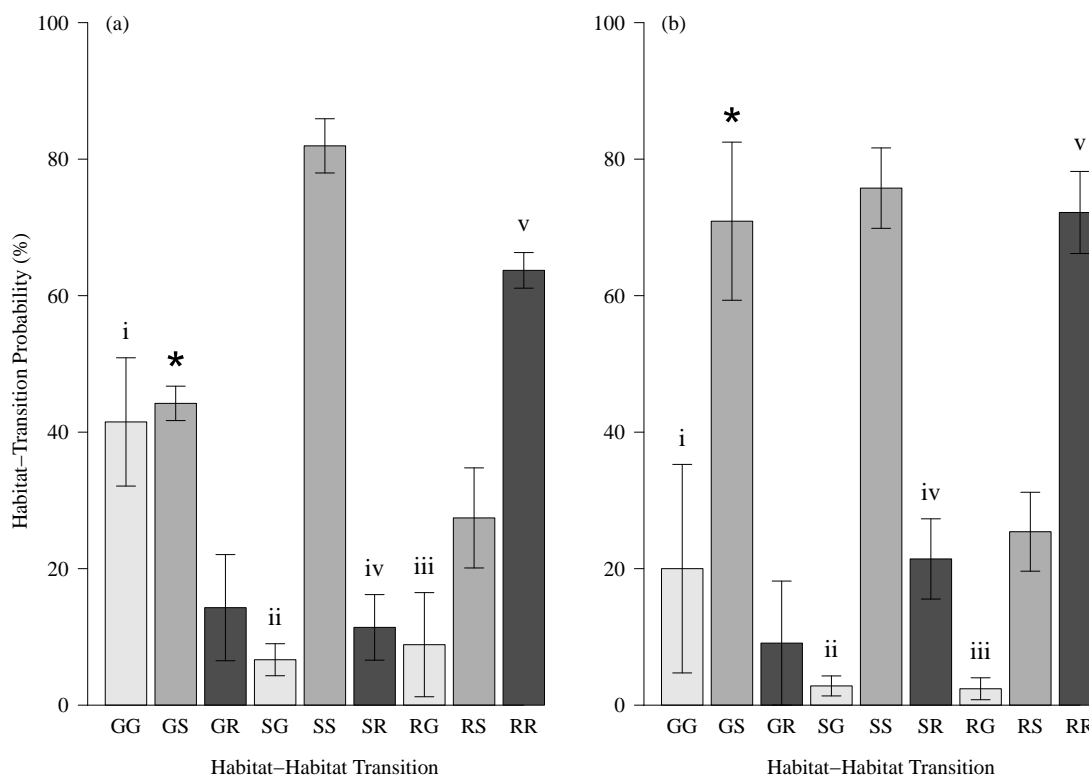


Figure 3.2: Leopard transition probabilities to and from each habitat type, both where lions are absent (Figure 3.2a), and present (Figure 3.2b). The solid bars indicate the mean probability averaged across individuals for each habitat type, and the error bars represent the standard error of the mean. G = grassland; S = scrub; R = riparian; GG = grassland-to-grassland transition; GS = grassland-to-scrub transition, etc. An asterix (*) above the corresponding bars on Figs. 3.2a & 3.2b indicates where a particular habitat-transition is significantly different between the areas present and absent lions. Roman numerals i – iii above the corresponding bars on Figs. 3.2a & 3.2b indicate where lions had a negative effect on habitat-transition probability, and Roman numerals iv and v indicate where lions had a positive effect on habitat-transition probability, as predicted based on relative habitat density.

Although non-significant [see Table 3.1 in Appendix 3.8.4 for statistical results],

there was a lower mean probability of leopards transitioning from all other habitats (riparian, scrub and grassland) to grassland habitat, and a greater mean probability of leopards transitioning from scrub to riparian habitat, and remaining in riparian habitat, where lions were present.

3.4.2 Transitions between open and closed habitats where lions are present

There was a relatively low likelihood of leopards moving from closed to open habitat types, except when at close proximity to lions (Figure 3.3), which had a significant influence on the probability of leopards transitioning out of the particular habitat type they were located within ($F_{1,18} = 9.528$, $P = 0.001$, $R^2 = 0.641$, power = 0.997). There was no significant influence of lion proximity on the probability of leopards transitioning in the direction of open to closed habitat ($F_{1,18} = 0.254$, $P = 0.621$, $R^2 = 0.014$, power = 0.079), which remained relatively high at all distances from lions.

3.4.3 Comparison of leopard habitat-specific behaviour with and without lions

There was no difference in mean leopard step-lengths between habitat types where lions were absent ($F_{2,14} = 0.060$, $P = 0.924$, $R^2 = 0.008$, power = 0.059), nor where lions were present but when their proximity to the leopards was not

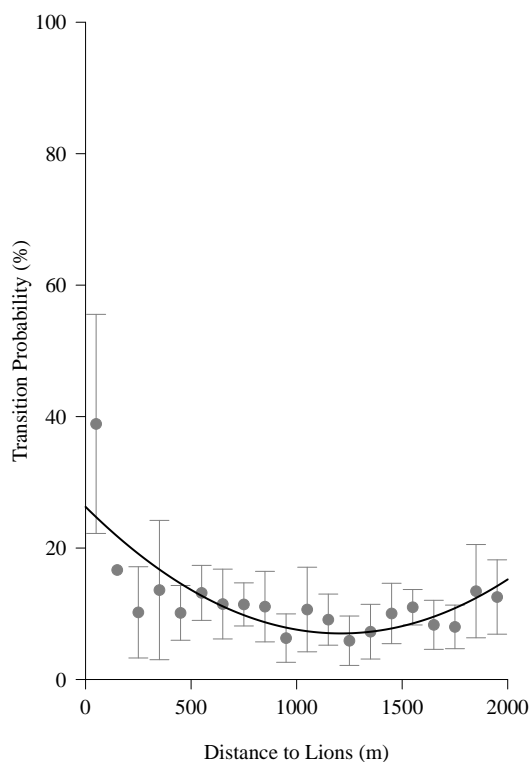


Figure 3.3: *The probability of leopards moving in the direction of ‘closed’ to ‘open’ habitat at varying proximity to lions. Points indicate the mean transition probability, averaged across each individual leopard, and the error bars indicate the standard error of the mean. The curve represents the quadratic polynomial of the general linear model.*

accounted for ($F_{2,19} = 2.286$, $P = 0.079$, $R^2 = 0.191$, power = 0.553). However, when leopard behaviour was examined within 1,000 m from lions, there was an increase in leopard step-length in grassland habitat, which was significantly greater than the step-lengths in both scrub and riparian habitat types ($F_{2,12} = 4.022$, $P = 0.046$, $R^2 = 0.401$, power = 0.704) (Figure 3.4).

The relationship between leopard step-length in grassland habitat and lion proximity was therefore investigated further; leopard data were divided into 100

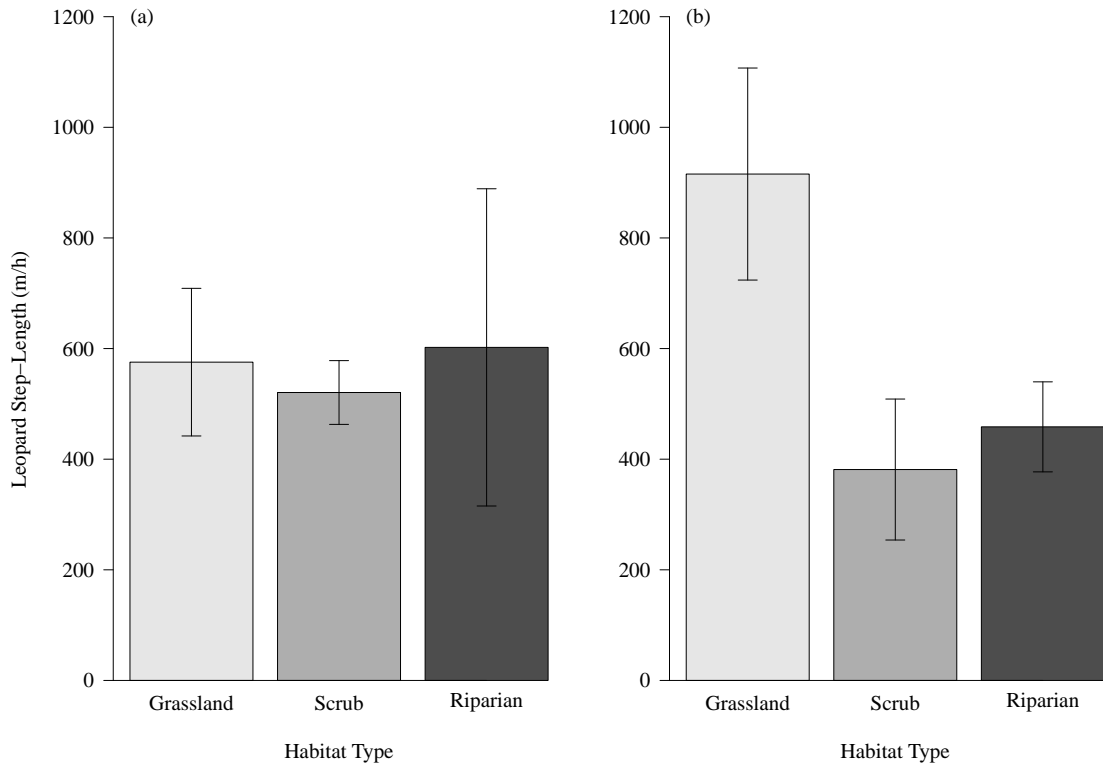


Figure 3.4: *The average hourly distance ('step-length') moved by leopards in each habitat type, compared between where lions are absent (Fig. 3.4a) and when they are present (Fig. 3.4b). The solid bars indicate the mean probability averaged across individuals for each habitat type, and the error bars represent the standard error of the mean.*

m intervals from the nearest similarly collared lion, and the mean step-length for each interval was determined. A general linear mixed-effects model, with individual included as a random effect, showed that leopard step-length was significantly related to their distance from lions ($F_{1,13} = 12.686$, $P = 0.003$, $R^2 = 0.494$, power = 0.942) (Figure 3.5).

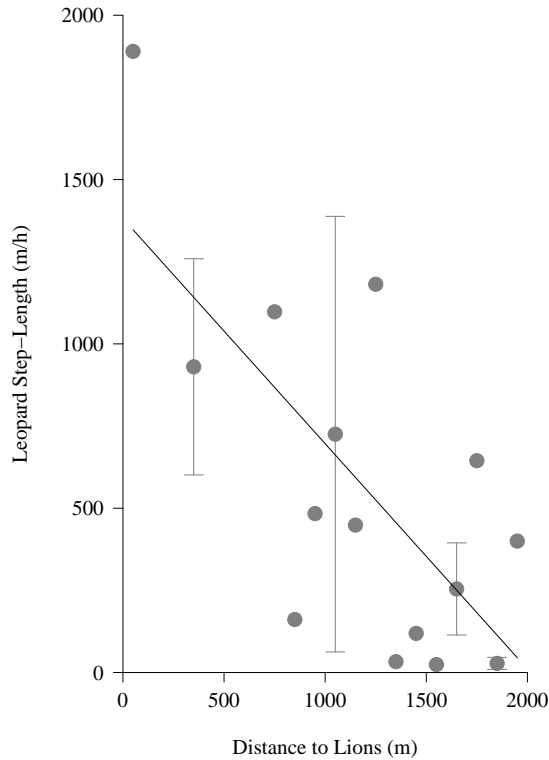


Figure 3.5: *Leopard step-length in grassland habitat at varying proximity to lions. Points indicate the mean step-length, averaged across each individual leopard, and the error bars indicate the standard error of the mean. The black line represents the linear model.*

3.5 DISCUSSION

Here we used Markov Chain analyses to investigate the track-data of sympatric carnivores, which allowed us to detect new signals of interaction between two relatively well-studied species, and reveal the impact of one species on the habitat-transitions and behaviour of the other. Markov Chain analyses account for the serial dependence of track-data, and directly link behaviour to environmental data in an integrated manner (Patterson et al. 2009). The Markov Chain analysis

facilitated the identification of transition-points between leopard behavioural states in relation to the proximal cause of lion risk, and thus removed the effects of confounding variables such as prey density and the presence of other carnivores.

Investigating the impact of one species on the behaviour of another is important, because the cost of habitat-transitions when avoiding predators could lead to reduced foraging efficiency, fitness, and ultimately population density; whilst failure to avoid predators altogether may result in mortality. Predators, and the risk and fear of encountering them, therefore have a significant impact on the behavioural ecology of a species (e.g. Brown et al. 1999; Laundre et al. 2001). In this study, the existence of the lion enclosure and its subsequent removal provided an unprecedented opportunity to determine the impact of lions on leopard behaviour by simultaneously comparing neighbouring leopard subpopulations under differing levels of risk, where part of this variation was experimentally manipulated, part natural.

Animal movement and behaviour are influenced by environmental circumstances, and may be impacted by both habitat characteristics and predation risk (e.g. Valeix et al. 2010). A typical anti-predator response may be indicated by retreat to safe habitat (Sih 1997), and our results show that leopard behaviour and transition probabilities are related to the proximity of lions; leopards transition to denser habitat types to reduce risk. Reactions to lions were greatest in grassland habitat, where leopard behaviour changed when at closer proximity to lions, as indicated by the increase in their speed of movement. This response occurs because within a landscape where there is the threat of predation, faster, straight-line movement

in open areas reduces exposure time and risk of detection (e.g. Valeix et al. 2010; Zollner and Lima 2005).

Where lions were present, leopards demonstrated a significantly increased probability of transitioning from open grassland habitat to the denser scrub habitat, which offers more ground cover where they are able to hide. Similarly, leopards also showed a reduction in transition probability from all habitat types to grassland, and an increase in transition probability to riparian habitat. Open habitat types, particularly grassland, are likely to be dangerous areas where lions are a concern for leopards, as such habitats provide neither substantial ground cover nor trees up which to escape, and lions can outrun leopards (L. Hunter, unpublished data, *op. cit.* Balme et al. 2007). Where there is predation risk, leopards are therefore likely to have an increased probability of transitioning out of grassland habitat and into denser habitats that provide relatively more safety from detection and avenues of escape, and this was confirmed by the comparison of the leopard habitat-transition probabilities between the sites of lion presence/absence, as well as increased step-length in open areas so as to reduce the time exposed to risk. With nowhere to hide in grassland habitat, this response is also likely to be stronger at closer proximity to lions, which was also shown by the analysis of step-length versus distance to lions. Similarly, even though predation risk does not ultimately affect long-term herbivore habitat selection, it has been shown that they may still exhibit short-term ‘risk-sensitive’ behaviour in the vicinity of lions (Valeix et al. 2010). For animals at risk of predation, the non-lethal effects of predators on their behavioural ecology may have a greater impact on their population dynamics than mortality alone (Brown et al. 1999).

Scrub and riparian habitat appeared to be equally adequate regarding their use by leopards in the presence of lions, as there was little difference in leopard behaviour and transition probabilities between them. This finding confirms a previous study of habitat use by leopards for hunting, in which areas of intermediate ground cover were found to be optimal (Balme et al. 2007), and it is likely that where the available ground cover is adequate for leopards to escape being detected by their prey, this cover may also aid in their concealment from predators. However, if leopards are detected by lions at close proximity in scrub habitat where there are no trees up which to climb, then leopards may still have little chance of safely escaping. If a leopard were hiding from a lion that was on a convergent trajectory, it would therefore need to weigh the costs of remaining concealed and thereby risking detection at close proximity, or breaking cover and alerting the predator to their presence (e.g. Broom and Ruxton 2005).

Cryptic animals at risk of predation, including subordinate carnivores such as the leopard in this context, are likely to be wary of and detect larger and more numerous predators before they themselves are detected (Broom and Ruxton 2005; Brown et al. 1999). One strategy to minimise risk, upon detection of a predator, is to immediately leave the general area before they themselves are detected; even if this means crossing exposed habitat to reach safety. Leopards may also employ a multistage, or ‘sophisticated’, anti-predator response where possible (e.g. Hemmi and Pfeil 2010); relying on camouflage and cryptic behaviour (Caro 2014) until the risk of detection is imminent, and then ‘flushing’ – rather than breaking cover early and risk alerting an otherwise unaware predator (Broom and Ruxton 2005). This would explain the pattern observed in the ‘*closed* → *open*’ habitat-transition

probability, which showed a low probability of transition from closed to open habitat types, except when at close proximity to lion where there was a significant increase in the transition probability out of the immediate area and habitat.

Leopards displayed significantly different (H_1) habitat-transition probabilities and (H_2) behaviour between the areas of lion presence and absence, as well as (H_3) increased step-length at closer proximity to lions. We therefore show that lions do affect the behavioural ecology of leopards, and accept our hypotheses. However, we also note that the true scale of the observed effects was possibly masked by the presence of uncollared lions, as well as the unrecorded interactions between GPS fixes, and may therefore be even greater than was actually shown.

Sexually size-dimorphic male and female leopards are likely to behave differently (e.g. Loarie et al. 2013; Valeix et al. 2010) as they have different energy requirements, access to prey types, and home range sizes (Bailey 1993), and therefore subsequently differing levels of predation risk. Generalist populations may also contain individual specialists, and behavioural differences may result in variation of response measurements (e.g. Bagniewska et al. 2013). However, despite these influences, the general pattern of leopard habitat-transitions and behaviour related to lion presence remained clear in this study. Fifteen tagged leopards and 21 lions provided sufficient data to investigate predation risk at a range of distances between the species, despite the interspecies encounter frequency being low.

In addition to considering leopards at the population level, an interesting example of one GPS-collared male leopard allowed the simultaneous investigation of behavioural differences at the individual level between areas with and without

lions, as this individual utilised both sides of the electrified fence whilst it was in place. This leopard was able to freely cross the fence, and displayed different behaviour between areas where lions were present and absent. The behavioural differences shown by this individual between areas of risk reflect similar differences detected at the population level, and suggest an individual ability to adapt to the immediate level of risk [see *Appendix 3.8.5 for a comprehensive description and analysis of this individual's habitat-transitions and behaviour at both sites of lion presence/absence*].

While reducing risk can lead to a lower probability of mortality in the short-term, this may still not prevent significant levels of interspecific killing in the long-term (Lima 1998), as competitors with a large niche overlap will have correspondingly large frequencies of encounter. This is particularly relevant in protected areas, which are of limited size and increasingly isolated (Lindsey et al. 2011), and where the potential for dispersal away from high-risk areas is reduced. The BVC lion population has increased from just 17 individuals (of which only 5 were female), reintroduced to the area in 1999, to an estimated 523 ± 37 in 2012 (du Preez et al. 2014a). This equates to a current lion density of 18.950 ± 1.340 lion 100 km^{-2} , which is one of the highest reported in Africa (Creel and Creel 1997), and is still increasing (du Preez et al. 2014a). Similarly, additional interactions with other intraguild competitor species may also affect the behavioural ecology of leopards (e.g. Vanak et al. 2013). However, here we were specifically interested in the potential impact of the burgeoning lion population; the presence and influence of other carnivore species would not affect the Markov Chain analysis of behavioural switches related to lion predation risk that we present here.

3.6 CONCLUSION

Detecting new signals of interaction and avoidance between two relatively well-studied species indicates the wide applicability of this method to the ever-expanding field of biotelemetry. Investigation of behavioural transitions, with regard to the environment and varying proximity to other species, provides information not only on the location of an animal or its mean habitat use, but also on why that animal is where it is, and doing what it is doing. The Markov Chain technique that we have presented here could be further developed and applied to management of sensitive species, or highlight areas of potential conservation value, as well as allow accurate predictions of interspecies interaction and habitat use in unstudied areas.

3.7 Acknowledgements

We would like to thank the BVC shareholders and management for allowing us to conduct the research, Blondie Leathem for his constant support, Paul Trethowan who helped in the field, and Mark Jessopp for early discussions on the concepts of behavioural-transitions. This project was funded by The Darwin Initiative for Biodiversity Grant 17-031. D.W.M. gratefully acknowledges the support of the Robertson and Recanati-Kaplan Foundations. B.dP. would like to thank The Beit Trust for scholarship funding and support.

3.8 APPENDICES

3.8.1 *Lion-leopard intraguild predation*



Figure 3.6: *Image series of lions chasing, catching and killing a leopard in grassland habitat* (© Stanslaus Mwampeta, Serengeti Lion Project)

3.8.2 R script – habitat-transition matrix

```

BehavTrans <- CollarData

### TRANSITION LOOP
for(i in 3:(length(BehavTrans[,1])-2)){
  Cat.trans <- data.frame()
  Cat.trans[1,"Code"] <- BehavTrans[i-2,"Habitat.Type"]
  Cat.trans[2,"Code"] <- BehavTrans[i-1,"Habitat.Type"]
  Cat.trans[3,"Code"] <- BehavTrans[i-0,"Habitat.Type"]
  Cat.trans[4,"Code"] <- BehavTrans[i+1,"Habitat.Type"]
  Cat.trans[5,"Code"] <- BehavTrans[i+2,"Habitat.Type"]
  probvect<-NULL
  for(j in 1:length(Cat.trans$Code)){
    ifelse(Cat.trans$Code[j]=="G" & Cat.trans$Code[j+1]=="G", probvect[j]<-1,
    ifelse(Cat.trans$Code[j]=="G" & Cat.trans$Code[j+1]=="S", probvect[j]<-2,
    ifelse(Cat.trans$Code[j]=="G" & Cat.trans$Code[j+1]=="R", probvect[j]<-3,
    ifelse(Cat.trans$Code[j]=="S" & Cat.trans$Code[j+1]=="G", probvect[j]<-4,
    ifelse(Cat.trans$Code[j]=="S" & Cat.trans$Code[j+1]=="S", probvect[j]<-5,
    ifelse(Cat.trans$Code[j]=="S" & Cat.trans$Code[j+1]=="R", probvect[j]<-6,
    ifelse(Cat.trans$Code[j]=="R" & Cat.trans$Code[j+1]=="G", probvect[j]<-7,
    ifelse(Cat.trans$Code[j]=="R" & Cat.trans$Code[j+1]=="S", probvect[j]<-8,
    ifelse(Cat.trans$Code[j]=="R" & Cat.trans$Code[j+1]=="R", probvect[j]<-9,
    NA)))))))))
  # CALCULATE TOTAL FIXES RECORDED IN EACH HABITAT
  l1<-sum(Cat.trans$Code=="G")
  l2<-sum(Cat.trans$Code=="S")
  l3<-sum(Cat.trans$Code=="R")
  # CALCULATE PROBABILITY OF MOVING FROM THE HABITAT TYPE AT [j] TO THE HABITAT TYPE AT [j+1]
  p1<-sum(probvect==1)/(length(Cat.trans[,1])-1)
  p2<-sum(probvect==2)/(length(Cat.trans[,1])-1)
  p3<-sum(probvect==3)/(length(Cat.trans[,1])-1)
  p4<-sum(probvect==4)/(length(Cat.trans[,1])-1)
  p5<-sum(probvect==5)/(length(Cat.trans[,1])-1)
  p6<-sum(probvect==6)/(length(Cat.trans[,1])-1)
  p7<-sum(probvect==7)/(length(Cat.trans[,1])-1)
  p8<-sum(probvect==8)/(length(Cat.trans[,1])-1)
  p9<-sum(probvect==9)/(length(Cat.trans[,1])-1)
  # ASSIGN HABITAT TRANSITION PROBABILITIES TO NEW COLUMNS
  BehavTrans[i,"GG"]<-dp3(p1)
  BehavTrans[i,"GS"]<-dp3(p2)
  BehavTrans[i,"GR"]<-dp3(p3)
  BehavTrans[i,"SG"]<-dp3(p4)
  BehavTrans[i,"SS"]<-dp3(p5)
  BehavTrans[i,"SR"]<-dp3(p6)
  BehavTrans[i,"RG"]<-dp3(p7)
  BehavTrans[i,"RS"]<-dp3(p8)
  BehavTrans[i,"RR"]<-dp3(p9)
}
print(i)
print(length(BehavTrans[,1])-i)
}

# REMOVE THE FIRST AND LAST 2 LINES OF EACH CAT
for(i in 1:length(BehavTrans[,1])){
  if(BehavTrans[i,"CatName"]!=BehavTrans[i+1,"CatName"]){
    BehavTrans[c(i-1,i,i+1,1+2),c("GG","GS","GR","SG","SS","SR","RG","RS","RR")]<-NA
  }
  print(length(BehavTrans[,1])-i)
  print(i)
}

```

3.8.3 *R* script – simultaneous distances between simultaneously collared animals

```

CollarData <- BehavTrans
CollarData$RowNumber <- c(1)
Interaction <- merge(CollarData[1,],CollarData[1,],by="RowNumber",all.x=T)

# DISTANCE LOOP
for(i in 1:length(CollarData[,1])){
  Alphacat <- CollarData[i,]
  Betacats <- CollarData[(CollarData$Realtime==Alphacat$Realtime),]
  Alphacat[(1:length(Betacats[,1])),] <- Alphacat[1,]
  Alphacat$RowNumber <- c((1:length(Betacats[,1])))
  Betacats$RowNumber <- c((1:length(Betacats[,1])))
  AlphaBeta <- cbind(Alphacat,Betacats)
  AlphaBeta <- merge(Alphacat,Betacats,by="RowNumber",all.x=T)
  Interaction <- rbind(Interaction,AlphaBeta)
  print(i)
  print(length(CollarData[,1])-i)
  print(CollarData[1,"Year"])
}

# UTM DISTANCE CALCULATION
Interactions$CatDistUTM <- sqrt( (((Interactions$UTM.E.x) - (Interactions$UTM.E.y))^2) +
(((Interactions$UTM.N.x) - (Interactions$UTM.N.y))^2) )

# REMOVE ALL ZEROS
Interactions <- Interactions[Interactions[,"CatDistUTM"]!=0,]
Interactions$Row <- c(1:length(Interactions[,1]))

# CLOSEST LION TO LEOPARD
LEOPsvLIONS <- Interactions[order(Interactions$Realtime.x),]
MIN <- data.frame()
MINLEOPvLION <- data.frame()
for(i in 1:length(levels(LEOPsvLIONS$CatName.x))){
  LEOP <- LEOPsvLIONS[(LEOPsvLIONS$CatName.x==unique(unlist(LEOPsvLIONS$CatName.x))[i]),]
  for(j in 1:length(LEOP[,1])){
    MOMENT <- LEOP[(LEOP$Realtime.x==unique(unlist(LEOP$Realtime.x))[j]),]
    MIN <- MOMENT[which.min(MOMENT[,"CatDistUTM"]),]
    MINLEOPvLION <- rbind(MINLEOPvLION,MIN)
    print(j)
    print(length(LEOP[,1])-j)
    print(unique(unlist(LEOPsvLIONS$CatName.x))[i])
    print("Min distance to lions Loop")
  }
}

```

3.8.4 Results of all statistical tests

Table 3.1: Comparison of leopard habitat-transition probabilities between areas of lion presence versus lion absence

Habitat-transition		P-value	F-statistic	Power	Effect-size (R^2)
<i>From</i>	<i>To</i>				
Grassland	Grassland	0.247	1.598	0.237	0.186
Grassland	Scrub	0.016 *	10.019	0.866	0.589
Grassland	Riparian	0.698	0.164	0.068	0.023
Scrub	Grassland	0.196	1.924	0.280	0.161
Scrub	Scrub	0.404	0.759	0.139	0.071
Scrub	Riparian	0.216	1.746	0.259	0.149
Riparian	Grassland	0.388	0.825	0.147	0.084
Riparian	Scrub	0.831	0.048	0.055	0.005
Riparian	Riparian	0.260	1.446	0.222	0.138

* denotes a significant result

Table 3.2: Comparison of leopard habitat-transition probabilities versus lion proximity between open habitat and closed habitat types

Transition Direction		P-value	F-statistic	Power	Effect-size (R^2)
<i>From</i>	<i>To</i>				
Closed	Open	0.001 *	9.528	0.997	0.641
Open	Closed	0.621	0.254	0.079	0.014

* denotes a significant result

Table 3.3: Comparison of leopard step-length between habitats where lions are present versus where lions are absent

Step-length	P-value	F-statistic	Power	Effect-size (R^2)
<i>Lions</i>				
Absent	0.942	0.060	0.059	0.008
Present	0.046 *	4.022	0.704	0.401

* denotes a significant result

3.8.5 *Case study of a single male leopard (LM4) simultaneously occupying territory both inside and outside of the enclosure*

Electric fences may affect species differently; where the same fence may be a barrier to lions, but permeable to leopards (e.g. Balme et al. 2010; Cozzi et al. 2013; Hayward et al. 2007a). In this study, one collared male leopard (LM4) held a territory that spanned both sides of the electrified fence while it was in place. On the west side of fence, lions were present at a high density (0.202 ± 0.018 lions km^{-2}), whilst to the east inside the fence they were absent. LM4's GPS-collar was active from 24th of October 2010 to the 1st of June 2011, while the electrified fence was in place, and his territory was approximately elliptical in shape, lying between 30.17635° and 30.39665° longitude, -21.69321° and -21.59940° latitude, and is centred at 30.31375° longitude and -21.64788° latitude (Figure 3.7).

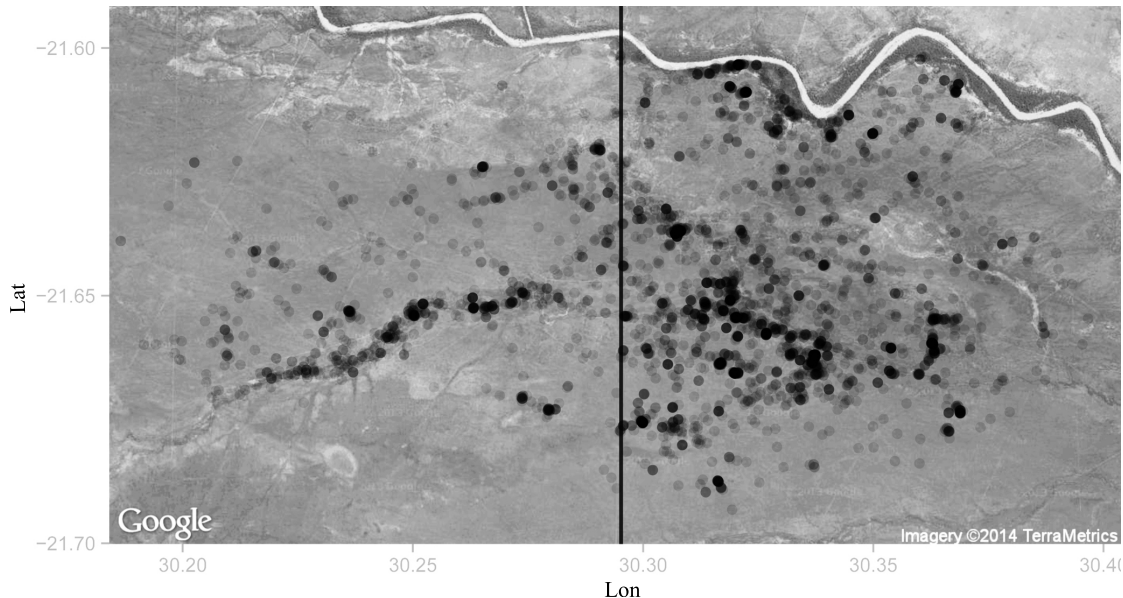


Figure 3.7: *Male leopard LM4's GPS data whilst the electrified fence (black line) was in place. Lions were present on the western side of the fence, but excluded from the eastern side. LM4 crossed the fence freely, but the pattern of habitat use on either side was different; generally spread out in the east, but clustered along a riparian habitat belt in the west.*

The electrified enclosure fence is orientated almost perfectly north-south along the longitude 30.29521° , and this is close to the line that bisects LM4's home range. Only 812 collar fixes (21.2%) for LM4 were recorded where lions were present,

whilst 3013 fixes (78.8%) were recorded where lions were absent.

The obvious difference in the pattern of LM4's GPS-collar fixes on either side of the fence, concentrated along a riparian belt in the west where lions were present, and more generally spread out in the east where lions were absent (see Figure 3.8), indicates that this leopard altered his habitat use and behaviour based on risk. To explore the risk-dependent behavioural differences further, LM4's collar data were divided by the side of the fence they lay on, and his habitat-specific behaviour (Figure 3.9) and transition probabilities (Figure 3.10) between either side of the fence were compared. Similar to the population level differences, LM4 exhibited increased step-length in open habitat types, and a greater probability of transitioning to denser habitat types on the side of the fence where lions were present.

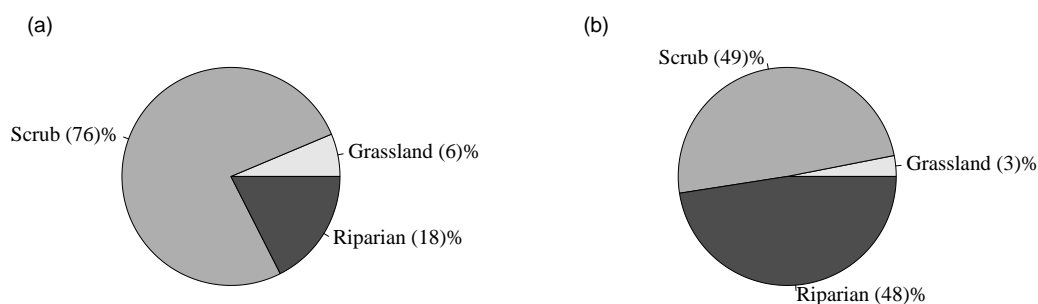


Figure 3.8: Comparison of habitat use by male leopard LM4 between the enclosure, without lions (Figure 3.8a), and the other side of the fence with lions (Figure 3.8b).

LM4's habitat use within the enclosure site, where there are no lions, is dominated by scrub (Figure 3.8a), however outside of the enclosure, where lion risk occurs, riparian habitat becomes more important (Figure 3.8b).

Similar to the pattern displayed in habitat use, LM4's habitat-specific behaviour is different on either side of the fence (Figure 3.9), reflecting the same differences at the leopard population level between where lions are present and absent. There is little difference in step-length between habitats within the enclosure (Figure 3.9a), however where lions are present there is a significant increase in step-length in both grassland ($F_{1,214} = 43.807$, $P < 0.001$, $R^2 = 0.170$, power = 1) and scrub habitat ($F_{1,2693} = 151.886$, $P < 0.001$, $R^2 = 0.053$, power = 1) (Figure 3.9b).

Analyses of LM4's habitat-transition probabilities on either side of the fence,

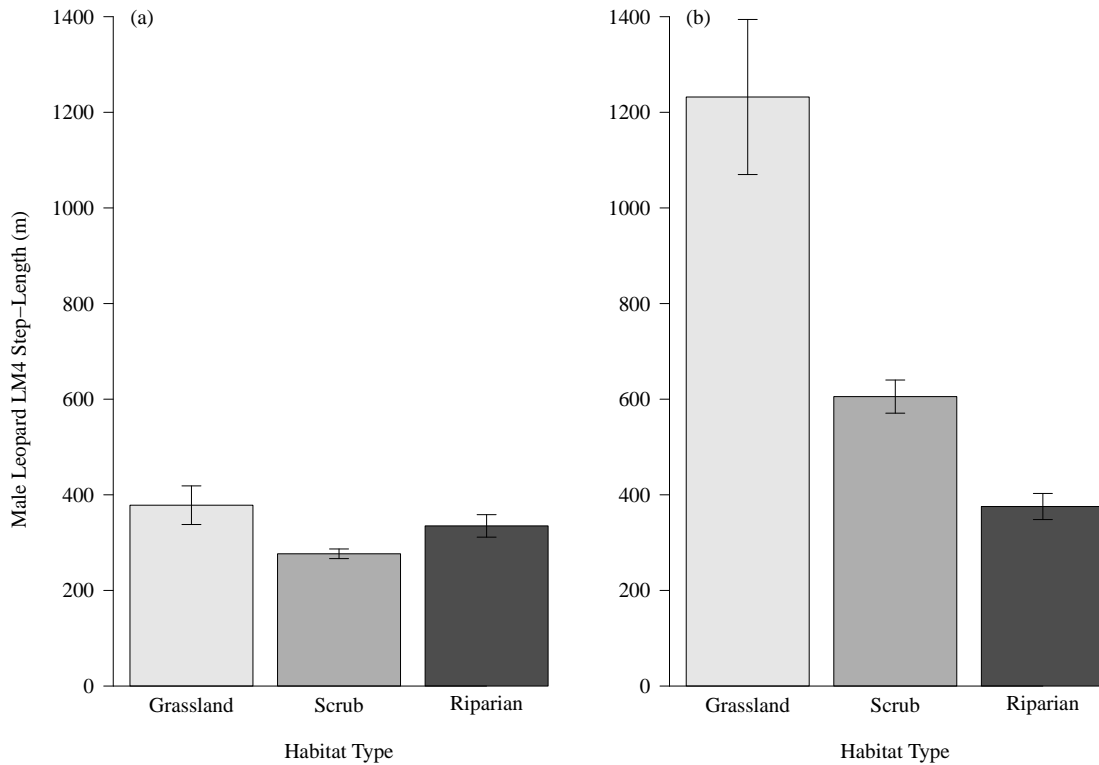


Figure 3.9: *LM4's average hourly distance moved ('step-length') in each habitat type where lions are absent compared with where they are present.*

with and without lions (Figure 3.10), are again reflective of the pattern exhibited at the population level. There was a similar reduction in the probability of remaining in grassland habitat (from 52.3% to 21.3%; $F_{1,428} = 35.243$, $P < 0.001$, $R^2 = 0.076$, power = 1), but a greater probability of transition to riparian habitat from grassland (from 6.1% to 47.4%; $F_{1,428} = 132.503$, $P < 0.001$, $R^2 = 0.236$, power = 1) and scrub (from 8.9% to 19.4%; $F_{1,3199} = 85.113$, $P < 0.001$, $R^2 = 0.026$, power = 1) and remaining there (from 62.5% to 72.5%; $F_{1,1395} = 21.910$, $P < 0.001$, $R^2 = 0.015$, power = 0.997) when lions were present.

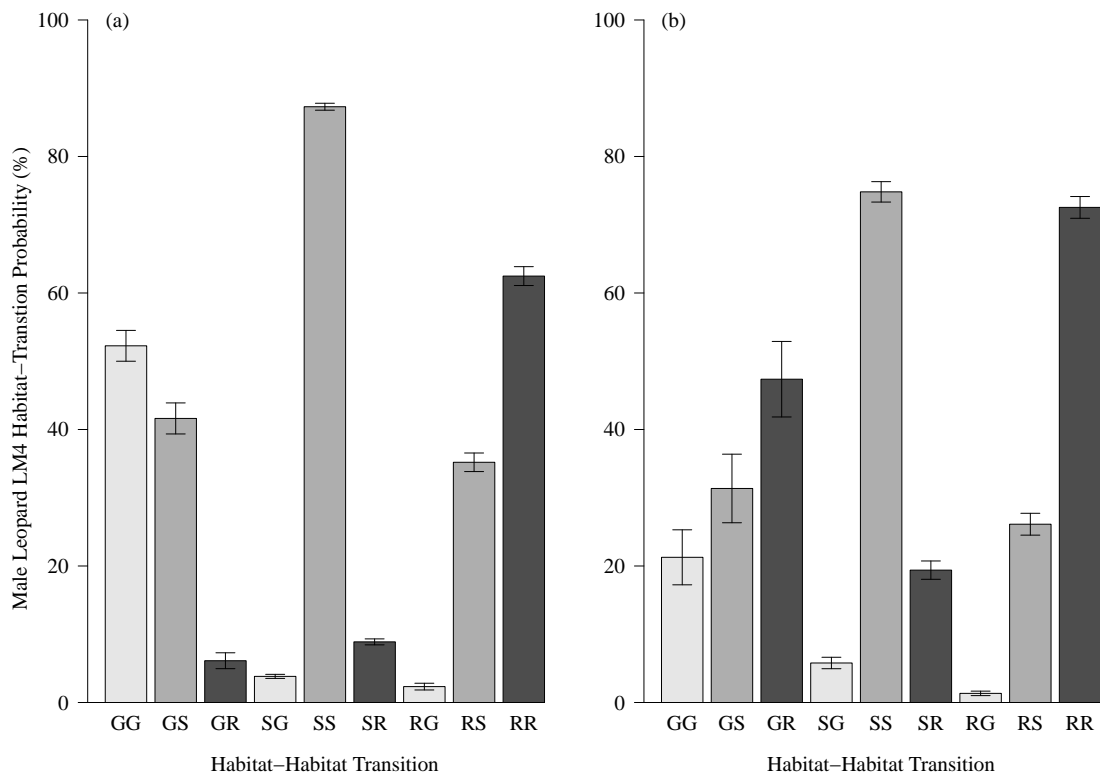


Figure 3.10: *LM4's habitat-to-habitat transition probabilities on either side of the electrified fence between areas where lions were absent (Figure 3.10a) and where lions were present (Figure 3.10b).*

To demonstrate the differential permeability of the fence, Figure 3.11 shows the GPS data of a lioness FL3, who was collared approximately two months before the removal of the fence, which while in place prevented her entry into the enclosure. After the fence's removal, FL3 entered the enclosure, colonising an area in the northwest corner that was originally occupied by LM4.

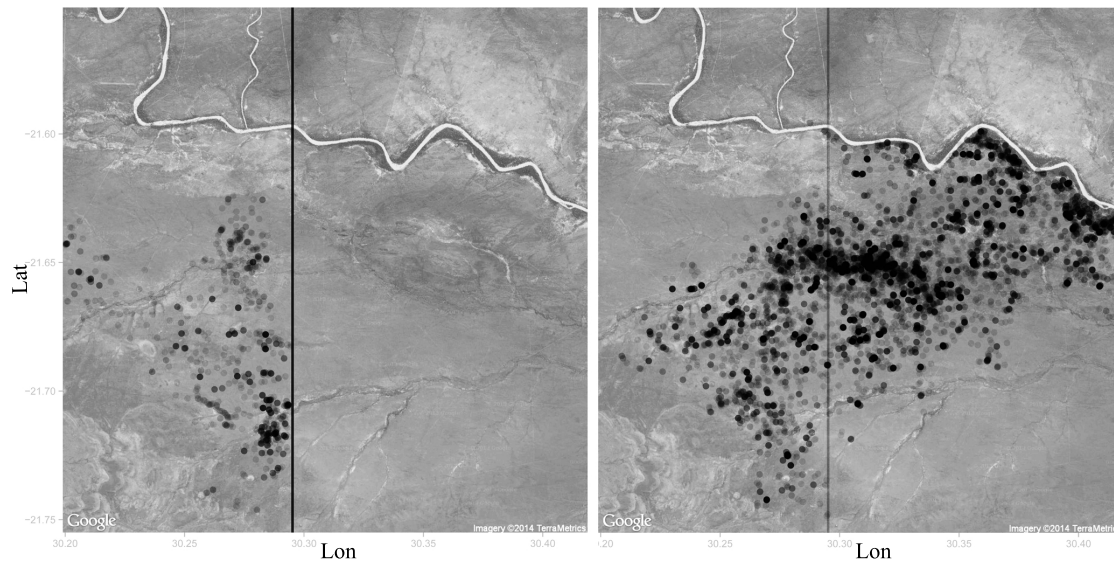


Figure 3.11: *Left: GPS data for a lioness, FL3, up to the day before removal of the electrified fence (dark grey); and Right: FL3's data after removal of the electrified fence (original position indicated in light grey), showing her colonisation of the area within the original enclosure in which LM4 once inhabited before his disappearance after the removal of the fence and entry of the lions.*

3.8.6 Results of LM4's statistical tests

Table 3.4: Comparison of leopard LM4's step-length between habitats where lions are present versus where lions are absent

LM4 Step-length	P-value	F-statistic	Power	Effect-size (R^2)
<i>Lions</i>				
Absent	<0.001 *	8.266	0.962	0.005
Present	<0.001 *	32.863	1.000	0.075

* denotes a significant result

Table 3.5: Comparison of leopard LM4's step-length in each habitat type between where lions are present versus where lions are absent

LM4 Step-length	P-value	F-statistic	Power	Effect-size (R^2)
Grassland	<0.001 *	43.807	1.000	0.170
Scrub	<0.001 *	151.886	1.000	0.053
Riparian	0.373	0.795	0.145	0.001

* denotes a significant result

Table 3.6: Comparison of leopard LM4's habitat-transition probabilities between areas of lion presence versus lion absence

LM4 Habitat Transition		P-value	F-statistic	Power	Effect-size (R^2)
<i>From</i>	<i>To</i>				
Grassland	Grassland	<0.001 *	35.243	1.000	0.076
Grassland	Scrub	0.060	3.570	0.472	0.008
Grassland	Riparian	<0.001 *	132.503	1.000	0.236
Scrub	Grassland	0.010 *	6.707	0.736	0.002
Scrub	Scrub	<0.001 *	90.641	1.000	0.028
Scrub	Riparian	<0.001 *	85.113	1.000	0.026
Riparian	Grassland	0.140	2.181	0.315	0.002
Riparian	Scrub	<0.001 *	18.106	0.989	0.013
Riparian	Riparian	<0.001 *	21.910	0.997	0.015

* denotes a significant result

3.9 LITERATURE CITED

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Chapter 4

Detecting signals of intraguild interaction: measuring the impact of a large carnivore on mesopredator spatial ecology

Byron du Preez, Tom Hart, Andrew J. Loveridge and David W. Macdonald

IN REVIEW: *Behavioural Ecology*

Authorship: Collected the data: BdP. Analysed the data: BdP. Produced first manuscript: BdP. Contributed to revisions: BdP, TH, AJL and DWM. Oversaw the project: AJL and DWM

4.1 ABSTRACT

Interaction between predators can greatly influence the success and distribution of the smaller species, and may have conservation implications. In Africa, the conservation of declining lion *Panthera leo* populations is sometimes prioritized to the detriment of other carnivores. Despite both felids having extensive range overlap in Africa, the intraguild interaction between lions and leopards *Panthera pardus* has been poorly studied.

Biotelemetry is increasingly used in large mammal research, and a method to quantify interactions may be widely applicable; particularly for species that are impossible to observe. However, there is currently neither an efficient nor automated method of detecting interactions from biotelemetry data.

We tagged a sympatric sample of 15 leopards and 21 lions with GPS biotelemetry collars, with which we identify the confounding signals of interaction and develop an index to test the response strength against expected values. We show that when spatial overlap between species is sufficient for a large number of direct interactions, leopards actively avoided lions at both the landscape and patch level; and that where leopards are more vulnerable to detection they showed a stronger negative response to lions. While such aggressive interactions have been observed in the past, our results demonstrate a method to extract coordinated behaviour from simultaneously tracked species. This method has the potential to be applied to other studies of remotely tracked elusive species, for which observational data is impossible, to model how population changes of one species can influence the behaviour of other guild members.

4.2 INTRODUCTION

An understanding of interspecific competition is a vital component of basic behavioural ecology, and an important element of conservation under scenarios of changing habitat use or fragmentation where animals may come into increasing contact with each other. How two species interact can have important implications for conservation; historically, where conservation of lion *Panthera leo* has been prioritised, sympatric mesopredators such as cheetah *Acinonyx jubatus* and wild dog *Lycaon pictus* have declined (Creel and Creel 1996; Laurenson 1995). But is this decline due to spatiotemporal avoidance, the result of direct interaction leading to injury and mortality, or a combination of both?

Large carnivores persecute smaller members of the guild, impacting their survival, abundance, distribution and behaviour (Fedriani et al. 2000; Harihar et al. 2011; Kamler et al. 2007a; Kamler et al. 2007b; Seidensticker 1976). This harassment is largely due to the fact that species within the same Family tend to have similar ecological requirements and constraints, which naturally results in competitive interference and exploitation (Caro and Stoner 2003; Macdonald et al. 2010; Macdonald and Sillero-Zubiri 2004; Mills 1991). Lions have been reported killing both cheetah (Durant et al. 2004; Laurenson 1995) and wild dog, effectively suppressing their population numbers (Creel and Creel 2002); and tigers *Panthera tigris* reduce leopard *Panthera pardus* abundance, sometimes lethally, where these species overlap in range (Harihar et al. 2011; Karanth and Sunquist 2000; Macdonald et al. 2010; McDougal 1988; Seidensticker 1976).

Direct persecution frequently results in the death of subordinate carnivores (Kamler et al. 2007b; McDougal 1988; Palomares and Caro 1999; B. du Preez, pers. obs.). However, even the sub-lethal effects of competition may accumulate and influence behavioural ecology, as intraguild interaction also manifests indirectly, and avoidance of larger carnivores can affect a species' habitat use (Schaller and Crawshaw 1980), temporal activity (Karanth and Sunquist 2000; McDougal 1988; Seidensticker 1976; Seidensticker et al. 1990), diet (Harihar et al. 2011; Mondal et al. 2011) and even fertility (Watts and Holekamp 2008). The trade-off between predation and starvation (Cozzi et al. 2012; Roth and Lima 2007) is therefore challenging for subordinate carnivores, but important to define for effective conservation.

Direct competition has traditionally been inferred by observation (Ropert-Coudert and Wilson 2005), but this is not possible in studies of elusive species. For example, lions and leopards are presumed to have aggressive interactions based on anecdotal accounts (e.g. Bailey 1993) and relative body sizes following the general trend in intraguild competition (Caro and Stoner 2003; Palomares and Caro 1999). However, the extent to which these species interact, and the impact that this has on their behavioural ecology, has previously not been examined and quantified with rigour.

While interspecies interactions may be impossible to quantify through observation, the increasing number of biotelemetry studies with simultaneously tracked individuals means that it may be possible to determine the behavioural rules of interspecies engagement, and detect interactions by data-mining their biotelemetry

tracks. The dynamic response of one animal towards another during interaction is particularly important where this could have negative consequences for one or both individuals involved.

Within a species, the effect of one individual on the movement on another has been investigated in lions (Benhamou et al. 2014), and studied experimentally by the simultaneous release of paired pigeons (Biro et al. 2006), however the behavioural impact of direct interactions between species has never been analysed and described using track data. Interspecies interactions may have a significant impact on a species' behaviour, and without accounting for these in spatial and behavioural analyses it would not be possible to comprehensively understand the reasons behind the decisions that an animal makes, and that are reflected in the biotelemetry data we collect. The major problem with existing interaction algorithms remains being able to distinguish actual interactions between individuals from separate random movements. Even the most advanced methods so far use *ad hoc* application of a 'critical distance' of interaction; within which it is assumed that the animals are interacting, and outside of which are not (Benhamou et al. 2014; Long and Nelson 2013). This method is obviously flawed.

Although the detection of dynamic interactions in behavioural and spatial analyses is important, it may be difficult to prove from tracking studies. Similarly, birds are often presumed or demonstrated to follow fishing boats (Valeiras 2003), but fishing boats may well use bird aggregations as a cue to locate shoals of fish (Tremblay et al. 2009), so it is therefore vital to rigorously test the direction of interaction. Here we set out to define the conditions necessary to infer interaction,

devise a metric, and then test for interaction between wild populations of lions and leopards.

When directly observing interactions between individuals or species, we would be able to infer that the animal has detected and responded to another animal by posture, movement, aggression, and vocalisation (Macdonald et al. 2010); any inference of detection and response from telemetry will be far less sensitive. Whilst posture is increasingly being recorded through triaxial accelerometry, vocalisations are rarely recorded in tags, and facial characteristics signifying aggression have never been remotely inferred without direct observation. Researchers need to ensure that inferences made from changes in posture and movement are directly linked to the presence of another animal if we are to conclude that an apparent interaction is real. Here we define an interaction as a non-random measurable change in behaviour, in terms of speed and direction of movement, between two or more animals in relation to one another.

The impact of intraguild competition by lions on leopard behavioural ecology has previously not been directly investigated. The range of leopards in Africa completely envelopes that of lions (Bauer et al. 2013; Henschel et al. 2008; Nowell and Jackson 1996), and where these ranges intersect there is further overlap between the carnivores in terms of competition for habitat and prey (Macdonald et al. 2010; Radloff and du Toit 2004). Interactions with lion may have a significant impact on leopard behavioural ecology, as unlike the dispersed sociality of tigers (Sunquist 1981) lions are typically gregarious (Bygott et al. 1979; Mosser and Packer 2009; Schaller 1972).

Here we quantified the spatial impact of lions on leopards at two temporal levels: ‘*long-term*’, with regard to the distribution of leopard territory and core areas; and ‘*short-term*’, with regard to direct interaction between individuals [e.g. *Appendix 4.8.1*]. Long-term avoidance of conflict, by avoiding areas heavily utilised by lions, is a predictive reduction of risk, while short-term avoidance can be described as more of a reactive response (Broekhuis et al. 2013). Analyses of static interactions consider how different individuals utilise the same space, whilst investigation of dynamic interaction describes how the spatiotemporal behaviour is affected (Long and Nelson 2013; Macdonald et al. 2010). A sample of animals including both species was investigated at the individual level by testing for both static and dynamic interaction between all species/sex pair combinations that had overlapping simultaneous spatiotemporal tracking data. With the *a priori* knowledge that carnivore guild interactions are aggressive, and potentially lethally so (see Palomares and Caro 1999), we therefore hypothesise that the smaller leopard would avoid both static and dynamic interaction with lion.

4.3 METHODS

4.3.1 *Study site*

The Buby Valley Conservancy (BVC) is a 3,743 km² wildlife conservancy located in southern Zimbabwe, geographically centre at 30°7'E, 21°30'S, and approximately 550 m in elevation. The mean annual rainfall was 351 ± 76 mm between 2007 and 2012, which fell mostly during November through March, with May through August

being the driest months. The vegetation is dominated by mopane *Colophospermum mopane* and acacia *Acacia* spp. scrub and woodland, traversed by seasonal drainage-lines and the associated riparian vegetation, and with dispersed open grassland habitat in between.

4.3.2 *Track data*

From 2010 to 2013, a total of 21 lions (9 female and 12 male) and 15 leopards (7 female and 8 male) were fitted with biotelemetry collars (Africa Wildlife Tracking, Pretoria, RSA) that simultaneously recorded GPS fixes on the hour from 16h00 – 08h00 when the animals were most active, and then every two hours, at 10h00, 12h00 and 14h00, during the day when both species are least active (Bothma et al. 1984; Cozzi et al. 2012; Valeix et al. 2009a). This fix schedule was a compromise between the resolution of the data and the life span of the collar batteries (e.g. Benhamou et al. 2014; Hayward and Slotow 2009; Loarie et al. 2013) [*see Appendix 4.8.2 for an ethics statement and detailed description of the capture, handling and tagging of lions and leopards*]. All statistical analyses involving GPS collar data were done in *R* (*R* 3.0.1; *R* Core Team 2013).

4.3.3 *Static interaction*

Home range overlap indices are useful indicators of the potential for direct interaction between individuals, and therefore the relative impact of one on the other. Static interaction occurs when animals utilise the same space and their

ranges overlap. However, simply considering overlap in terms of a two dimensional area could indicate large overlap between neighbouring individuals, even when the probability of locating both of them simultaneously in the same general space may in fact be low (Fieberg and Kochanny 2005). Defining the utilisation density (UD) is the most appropriate method for describing spatial use of the home range (van Winkle 1975). The UD transforms the spatial data into a three dimensional probability distribution, so that every ' x,y ' location is defined by the probability of locating the animal there (Fieberg and Kochanny 2005).

The UD is therefore a useful determinant of habitat and resource selection (Millspaugh et al. 2006), but it also provides a more informative measure of overlap between individuals by enabling calculation of the utilisation distribution overlap index (UDOI) (Fieberg and Kochanny 2005). The UDOI compares the UD between the intersecting and exclusive areas of two home ranges in a similar manner to the Hurlbert index of niche overlap (Calenge 2014). The UDOI will be 0 for home ranges that do not overlap, and 1 if the UDs of both animals are uniformly distributed and have 100% overlap. Values of less than 1 indicate less overlap than expected relative to uniform spatial distribution, while UDOI values of more than 1 indicate non-uniform distribution and greater than expected overlap (Fieberg and Kochanny 2005).

Static interaction was considered at the 95% UD isopleth for each individual, in which direct interaction may be avoided though temporal segregation in the use of that area (e.g. Kamler et al. 2012). It was then recalculated at the 50% UD isopleth, or 'core' area of the home range, which is where the animal concentrates

its activity (Kamler et al. 2012). Non-overlapping core areas indicate a long-term, or predictive, risk avoidance strategy (Kamler et al. 2007a; Kamler et al. 2012; Valeix et al. 2009b).

It is often not logistically possible to simultaneously tag all individuals of both species within the study area, and though static interaction between two individuals could be low, nothing is known about the distribution of the 3rd, 4th... n^{th} neighbours. However, exploring the UDOI's between and within species for the pairs of known individuals reveals the pattern of attraction or avoidance. Territorial species actively defend their core home ranges (50% isopleth) from conspecifics, and the area between the 50 and 95% isopleths, which is less strongly defended, may act as a buffer between conspecific neighbours. This heterogeneous landscape of dominant species' usage could provide a fugitive subordinate species some area of relatively low risk (Kamler et al. 2012).

Every possible species/sex pair combination for lion and leopard with temporally overlapping collar data was investigated for spatial overlap at both the 95% and 50% UD isopleth levels, using a UDOI calculated in the *kerneloverlap* function of the package *adehabitatHR* (Calenge 2014) in *R*. The *kerneloverlap* function produces three indices: one for each of the animals in their exclusive area, and one for the area of overlap. These indices are comparable: the larger value between the shared and exclusive range for each individual indicating its preferred spatial distribution with regard to the other animal.

Home range is a classic metric of resource overlap, however it is a static measure; saying nothing about the temporal overlap or exclusion of one animal by another.

Both lions and leopards range over vast areas [*BVC*: leopardess = $61 \pm 13 \text{ km}^2$; leopard = $154 \pm 21 \text{ km}^2$; lioness = $151 \pm 27 \text{ km}^2$; lion = $287 \pm 78 \text{ km}^2$], and even when there is a large UDOI between individuals, they may still spend most of their time far enough apart that they are not directly influencing one another.

4.3.4 *Establishing spatiotemporal avoidance*

Here we aimed to determine whether there were any patterns of spatiotemporal association between the species, and whether there was an active response by leopards to the location of lions. We first calculated the distance of each fix for every leopard to the nearest known lion. We then selected 100 of these separation distances at random, divided them into 100 m bins, determined the total number within each bin, and calculated the average per bin for each individual leopard. To establish whether any observed spatial separation between the species was active on the part of the subordinate animal, for each leopard we then overlaid an evenly spaced grid of the same number of artificially simulated ‘lion’ fixes over the range of the actual lion data closest to each leopard at each fix. We then calculated the distance of each leopard fix to each location on the grid, randomly selected one result for each leopard fix datum, and randomly selected 100 simulated distances, divided them into the same 100 m bins, and calculated mean counts per bin for each individual as before. The mean of the real and simulated counts for each individual leopard per separation distance bin could then be compared using a linear model, and a significant difference would indicate that leopards were actively avoiding lions spatiotemporally [*see Appendix 4.8.3*].

4.3.5 *Dynamic interaction*

Static interaction metrics are useful for examining the potential for direct, or dynamic, interaction between animals (Long 2012); dynamic interaction can be considered as the dependency of the position or movement of one or both individuals with regard to the other (Doncaster 1990; Macdonald et al. 1980), and described by indices of either attraction or repulsion. Dynamic interaction analyses are more informative than static interaction analyses for investigating the direct impact of one animal on another (Fieberg and Kochanny 2005; Kamler et al. 2007a; Kamler et al. 2007b).

Long (2012) reviewed several different methods of quantifying dynamic interaction; from simple comparisons of the spatial distribution and positional separation between a pair of individuals (e.g. proximity analysis, coefficients of association, and Doncaster’s non-parametric test of interaction) to advanced analysis of their simultaneous trajectories and deviation from the mean path vectors (e.g. Shirabe’s correlation coefficient (Shirabe 2006)). Long and Nelson (2013) advanced on the Shirabe statistic by separating the independent effects of speed and direction from the movement data. Similarly, Benhamou et al. (2014) created a dynamic interaction function to test for correlation in the inter- and intragroup movement of lions.

Unfortunately, none of these indices consider the distance between the individuals and instead require *ad hoc* implementation of a homogenous ‘critical distance’ of interaction. However, in heterogeneous environments, where detectability may vary

from hundreds of metres down to nearly zero (see O’Kane et al. 2014), based on habitat features and even wind direction, defining a critical distance is impractical.

To resolve this deficiency we created our own dynamic interaction-reaction function, the ‘Action-Index’ (AI). This index takes into account both the proximity of individuals and the magnitude and direction of their movement vectors to calculate each individual’s relative displacement with regard to the other.

4.3.6 *The Action-Index of dynamic interaction*

The AI first isolates and investigates pair combinations with simultaneously recorded spatial data, and it then employs a dynamic interaction function to consider the individual reaction of each animal in a pair to the other during each ‘interaction’; describing the movement vector in terms of distance and direction moved in relation to those of the other animal, and the spatial separation between them. Unlike both the Shirabe and the Long-Nelson indices, the spatial separation between individuals is an integrated function of the AI.

The AI itself is composed of two component indices; the Orientation-Index and Reaction-Indices [*Appendix 4.8.4*]. The Orientation-Index describes the affinity of the interaction in terms of either attraction or repulsion, calculating an index of the relative orientation of each individual after interaction; the sign of the index indicates the direction and strength of the interaction. The magnitude of the interaction is determined by the size of the distance between the individuals, as a function of the model denominator. The Reaction-Indices compare the length and

direction of each individual's movement trajectory during interaction in relation to the other; describing the response vector of each animal separately in terms of whether it moves towards or away from the other [see *Appendix 4.8.4 for a detailed description of the Orientation- and Reaction-Indices*].

The Orientation-Index and Reaction-Indices are informative when investigating each interaction in isolation, however for analysing large data sets it is useful to separate actual interactions from random noise. This distinction is achieved by combining these indices (which becomes the Action-Index) and calculating their product; smaller indices will be expressed as small decimal numbers, which when multiplied together approximate zero. A result of zero for either of the indices, separately or when combined, indicates no reaction. Spatial proximity is taken into account by incorporating the distance between individuals in the denominator of the model. Indices approximating zero may result from large spatial separation between animals, which at greater distances from one another may not even be aware of the other's presence. Alternatively, where two individuals do not react to one another's presence, the ratio of the *reaction:separation* distances would reflect this by resulting in a small index. Combining the indices simply involves multiplying one by the other to create the Action-Indices for animals *A* and *B* (Equations 4.1 and 4.2):

$$\Delta A = \left(\frac{(B_{\text{vec}} - A_{\text{vec}}) + (d_t - d_{t+1})}{(d_t + d_{t+1})} \right) \times \sqrt{\left(\frac{d_t - d_{t+1}}{d_t} \right)^2} \quad (4.1)$$

$$\Delta B = \left(\frac{(A_{\text{vec}} - B_{\text{vec}}) + (d_t - d_{t+1})}{(d_t + d_{t+1})} \right) \times \sqrt{\left(\frac{d_t - d_{t+1}}{d_t} \right)^2} \quad (4.2)$$

The Action-Indices (ΔA and ΔB) are a product of the Reaction-Indices and the positive Orientation-Index (made so by squaring and then square rooting), which therefore acts to preserve the directionality of each individual's reaction. This directionality indicates the asymmetry of interactions; one animal may be displaced more than the other, which may chase the first for a short distance and so have a positive Reaction-Index, while the overall Orientation-Index for the interaction is negative (e.g. Figure 4.1). These indices are directly comparable for interactions between all possible species/sex pair combinations.

As already stressed, determining indices of dynamic interactions usually requires *ad hoc* definition of a critical distance that approximates a tolerance threshold between animals (e.g. Long 2012). This threshold is determined by comparing the actual and expected distribution of distances between individuals, using statistical tools such as a non-parametric test of interaction (Doncaster 1990) and proximity analyses (Bertrand et al. 1996). Between species, however, this concept is only really applicable in homogenous environments, as it assumes that the animals are always equally aware of and reacting to one another, and that there are predictable detection rates. Detectability in heterogeneous environments depends on the immediate habitat, and can be up to hundreds of metres in open areas, but down to only a few metres in riparian vegetation, where it is further reduced by uneven topography.

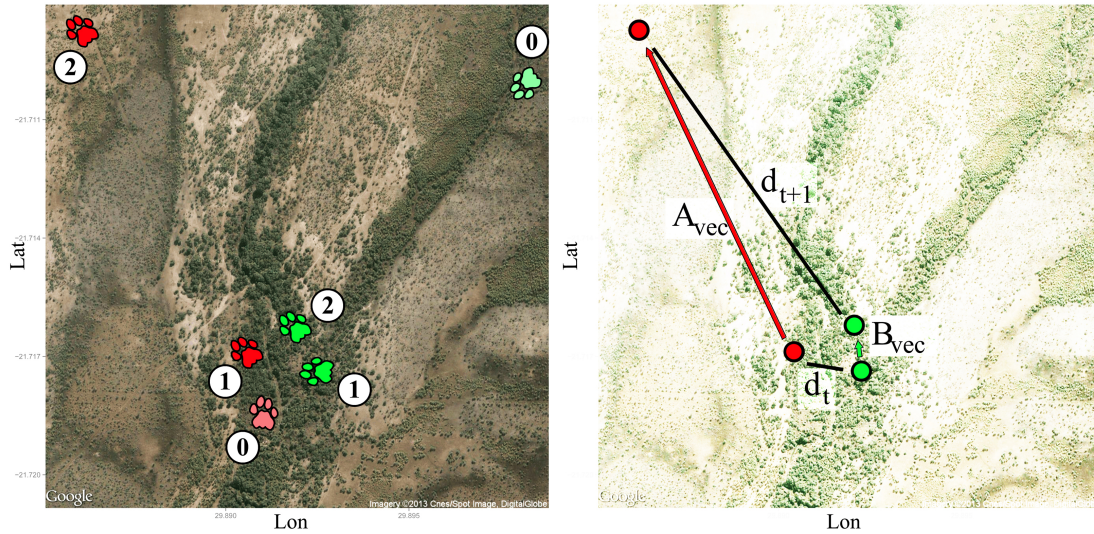


Figure 4.1: (i & ii). *Interaction-Reaction map plots of an observed interaction between cats A (leopardess [red]) and B (lion [green]). The image on the left (Fig. 4.1i) shows the actual unfolding of the encounter, with the position of the individuals ‘before’ (0), ‘during’ (1) and ‘after’ (2) interaction. The image on the right (Fig. 4.1ii) shows the vectors (A_{vec} and B_{vec}) and the spatial proximities (d_t and d_{t+1}) that are considered in calculation of the reaction indices. The relevant distances are: $A_{vec} = 1149$ m; $B_{vec} = 121$ m; $d_t = 108$ m; $d_{t+1} = 1044$ m. The Orientation-Index (Δd) for this interaction is -8.667 . This large negative number indicates a large degree of repulsion between individuals A and B, which is reflected in Fig. 4.1i, and confirmed by the Reaction-Index for animal A (Δa) of -1.705 , which is a large repulsion from (or ‘evasion’ of) animal B. Animal B has a Reaction-Index (Δb) of $+0.080$, which indicates slight attraction to A (or short ‘chase’, given A’s large negative Reaction-Index). The Action-Indices (ΔA and ΔB) for individuals A and B are -14.775 and $+0.692$ respectively. If d_t and d_{t+1} were increased by 1000 m each, the Action-Indices would be reduced to -0.526 and $+0.025$ respectively, reflecting that the reactions of A and B are less influenced by one another at greater separation distances. The Action-Indices are directly comparable between interactions and pairs of individuals.*

A single threshold distance in heterogeneous environments is therefore impossible to define. To account for this, the Reaction-Index takes into account the distance between individuals, so that the effects on the respective movement of animals at greater distances from one another are therefore relatively smaller. This reflects the

reduced effect of one animal on another at greater distances from one another – the larger the distance separation between animals, the less they are able to influence one another, and the closer to zero their Action-Indices will be. This scaling effect on the index is a function of the denominator (d_t), which nullifies the need to define an *ad hoc* critical or threshold distance. This incorporated distance function is an advantage of this interaction model as it allows the same index to be applied to different ecosystems and species combinations, without needing to define a different threshold distance for each system.

We wrapped the AI function in a loop in *R* [see *Appendix 4.8.6*] to facilitate the efficient processing of the large amount of track-data we recorded. This AI loop-function automatically calculates the Action-Indices for each synchronous pair combination. The resulting data frame created by the loop function could then be categorised by additional variables relevant to the study; for example, we included the species and sex of animal *A*, species and sex of animal *B*, and the habitat type in which each fix was recorded. The resulting Action-Indices could then be sorted between those not equal to zero, indicating actual interaction, and those approximating zero, which were physically too far apart to directly influence one another. This was achieved by rounding the resultant AI values to one decimal place, and all those that are subsequently reduced to zero values (where the animals did not interact) can be discarded, leaving just the values that describe interactions. The mean AI for each species/sex combination could then be calculated, with a positive value indicating overall attraction, and a negative value indicating overall repulsion.

4.3.7 *Additional variable attributes of interactions – habitat density*

du Preez et al. (*in press*) showed that leopard alter behaviour and habitat occupancy based on risk, and the Action-Indices for inter- and intra-specific pair combinations were therefore considered depending on the habitat type in which each interaction occurred. A satellite image of BVC was digitised in ArcGIS 10.1 (ESRI 2011) and classified into three simple classes of vegetation density. Riparian vegetation was classified as ‘*closed*’ habitat, grassland classified as ‘*open*’, and mixed mopane scrubland habitat was classified as ‘*meso*’ habitat (in-between closed riparian and open grassland). These habitat attributes were then extracted for each datum of collar GPS fix so that the influence of location on the outcome of interactions between individuals could be investigated.

4.4 RESULTS

4.4.1 *Static interaction between leopards and lions*

The UDOI and UD’s of the leopard-leopard and leopard-lion species/sex combinations (*Cat A – Cat B*) at both the 95% and 50% kernel levels, which indicate their probabilistic spatial distribution, were less than 1 for all combinations (Table 4.1). The individual UD’s are at least a decimal place larger than the UDOI’s for all pairs at both isopleth levels (50% and 95% kernels), which indicates strong avoidance of the overlapping area of use by one or both of the individuals.

Table 4.1: Mean utilisation distribution indices and overlap between pair combinations of various types of individuals ‘A’ and ‘B’ identified in the first and second columns respectively

Cat A	Cat B	UD 95% (Cat A)	UD 95% (Cat B)	UDOI 95%	UD 50% (Cat A)	UD 50% (Cat B)	UDOI 50%
Leopardess	<i>Leopardess</i>	1.288 ± 0.031	<i>1.950 ± 0.228</i>	0.016 ± NA	0.264 ± NA	<i>0.277 ± NA</i>	NA
Leopardess	<i>Leopard</i>	1.750 ± 0.128	<i>1.536 ± 0.071</i>	0.110 ± 0.079	0.276 ± 0.009	<i>0.271 ± 0.005</i>	0.021 ± 0.021
Leopardess	<i>Lioness</i>	1.714 ± 0.075	<i>1.658 ± 0.116</i>	0.072 ± 0.065	0.272 ± 0.006	<i>0.266 ± 0.007</i>	<0.001 ± NA
Leopardess	<i>Lion</i>	1.847 ± 0.103	<i>1.694 ± 0.065</i>	0.056 ± 0.033	0.272 ± 0.006	<i>0.278 ± 0.007</i>	NA
Leopard	<i>Leopardess</i>	1.536 ± 0.071	<i>1.750 ± 0.128</i>	0.110 ± 0.079	0.271 ± 0.005	<i>0.276 ± 0.009</i>	0.021 ± 0.021
Leopard	<i>Leopard</i>	1.414 ± 0.041	<i>1.524 ± 0.143</i>	0.179 ± 0.175	0.270 ± 0.010	<i>0.266 ± 0.006</i>	NA
Leopard	<i>Lioness</i>	1.465 ± 0.058	<i>1.616 ± 0.091</i>	0.212 ± 0.089	0.265 ± 0.007	<i>0.262 ± 0.007</i>	0.028 ± 0.011
Leopard	<i>Lion</i>	1.419 ± 0.041	<i>1.605 ± 0.046</i>	0.212 ± 0.079	0.263 ± 0.003	<i>0.264 ± 0.004</i>	0.025 ± 0.017

Bold numbers = combined values for individuals *A* and *B*; Normal numbers and text = Cat *A*; Italic numbers and text = Cat *B*

Female leopards have the smallest UDOI at the home range level (95% isopleth) with other females, and the greatest with male leopards. The core areas of female home ranges (50% isopleth) are especially exclusive, with minimal overlap of male core areas, and none with those of lions. Male leopards range over areas of similar size to those of lioness [*leopard* = $154 \pm 21 \text{ km}^2$; *lioness* = $151 \pm 27 \text{ km}^2$], and therefore have greater overlap with other individuals at both the 95% and 50% range isopleths. There was however no male leopard core area overlap at the 50% isopleth. The UDOI at the 50% isopleth between leopards with both sexes of lions is relatively small (Table 4.1; and see Appendix 4.8.7).

4.4.2 *Spatiotemporal avoidance of lions by leopards*

The distribution of real separation distances between leopards and lions is negatively skewed in shape, while the simulated separation distances approximate a normal distribution, with more fixes at closer distances to ‘lions’ than were present in the actual data (Figure 4.2). The difference between the real and simulated separation data was significant (ANOVA: $F_{1,398} = \sim 15.23$, $P < 0.001$), which indicates that leopard fixes were located at greater distances from lions than would occur randomly. This non-random spatiotemporal separation strongly suggests that leopards actively avoid lions.

4.4.3 *Dynamic interaction between leopards and lions*

Between 2010 and 2013 there were a total of eight *leopard-leopard*, 29 *leopard-lion*, and 55 *lion-lion* interacting pair combinations. Investigation of the track data for all species simultaneously tagged revealed 187 *leopard-leopard*, 241 *leopard-lion*, and 3,752 *lion-lion* interactions [only lion interactions between individuals associated with different social groups were considered in the dynamic interaction analysis]. The AI values presented for each pair combination type were calculated using the mean values of each individual to avoid pseudoreplication. The AI values between pair combinations of the different species indicated universal repulsion between individuals [Appendix 4.8.2]. The level of repulsion however is asymmetrical between the individuals of each pair, and is influenced by the habitat type in which the interaction occurs (Figure 4.3).

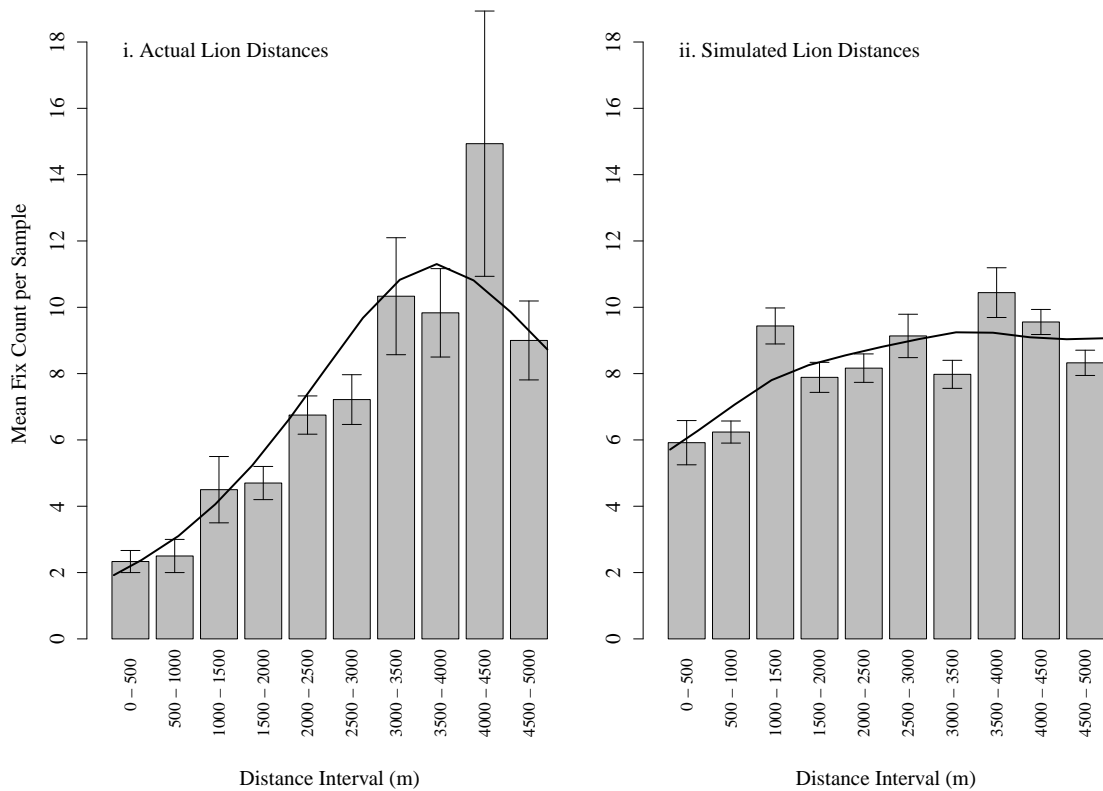


Figure 4.2: *Leopard density probability distribution in relation to actual lion distribution, which shows that leopard avoid lions (Fig. 4.2i), and leopard density probability distribution in relation to the simulated ‘lion’ distribution that would occur if both species moved independently of each other (Fig. 4.2ii).*

Leopards exhibited significantly greater reaction to lions in open habitat compared to that of meso (ANOVA: $F_{1,8} = 5.417$, $P = 0.048$) and closed habitats (ANOVA: $F_{1,8} = 5.775$, $P = 0.043$).

4.5 DISCUSSION

Here we’ve presented a new model, the *Action-Index*, for determining the individual outcomes of dynamic interaction between two animals. The significant improvement of this method over existing models is that it takes into account the

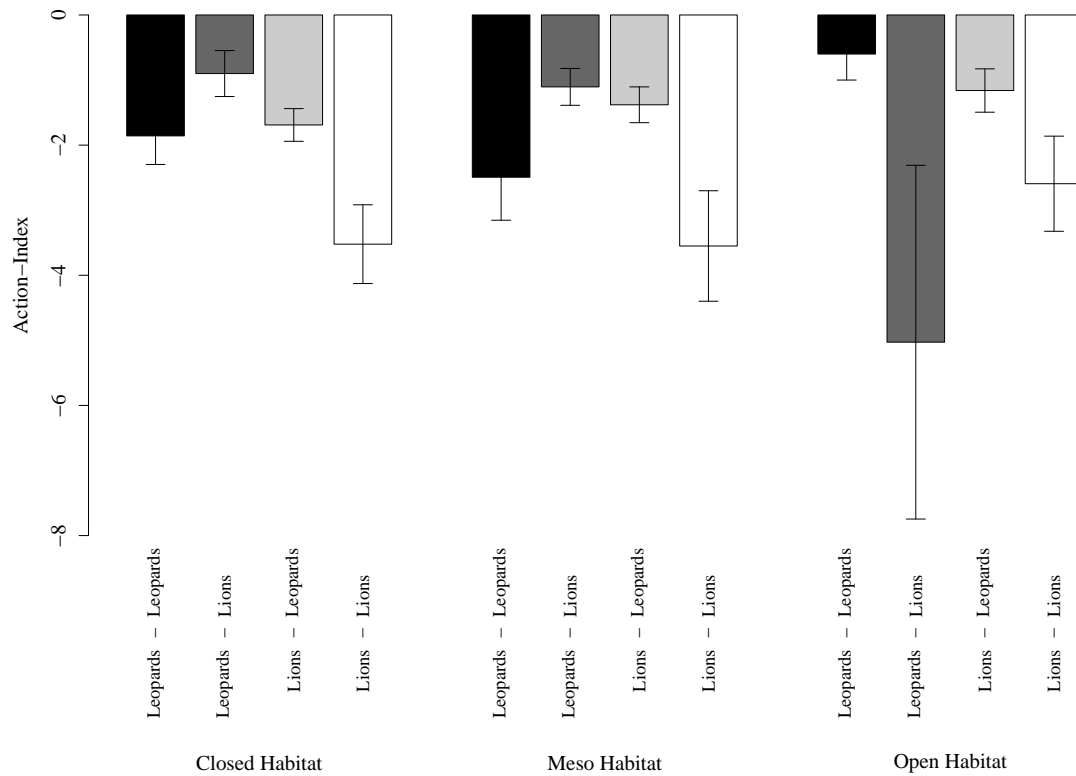


Figure 4.3: *Mean Action-Indices of the pairwise inter- and intraspecies combinations. The length of the bar indicates the strength of the reaction of individual A towards individual B in the Cat A–Cat B pair indicated on the x-axis. Lion intraspecies [i.e. Lions–Lions] Action-Indices considered only individuals belonging to different groups.*

proximity of the individuals to one another during and after interaction, precluding the need for *ad hoc* assignment of a ‘critical distance’ that does not take into account differential detectability and risk in heterogeneous landscapes. We tested the Action-Index on a large set of track-data from a sample of free-living leopard and lion and found significant avoidance of lion by leopard in open habitat types, which is to be expected given the aggressive nature of carnivore guild interaction. That there was relatively low avoidance of lion by leopard in closed and meso habitat types is not contradictory to our understanding of their competitive relationship;

Balme et al. (2007) showed that areas of meso habitat provided optimum cover for leopards whilst hunting, and it is likely that where cover is available leopard may also use cryptic behaviour as their primary strategy to avoid detection by lion. Indeed, this may explain why the mean AI avoidance between any pair combination was lowest for leopard toward lion in closed and meso habitat, as cryptic behaviour implies minimal movement of an individual that is hiding.

Our analysis of spatiotemporal association is also a novel method of comparing the predicted and actual distributions of one individual in relation to another. In concurrence with what was shown by the Action-Index, this analysis showed that leopards significantly avoided spatiotemporal association with lion. Lions actively use auditory and olfactory communication as a means of territorial defence, as well as advertising group size (McComb et al. 1994; Schaller 1972). Because direct contact between rival groups can result in serious injury (e.g. West et al. 2006), spatial avoidance through such remote communication may help facilitate avoidance of unnecessary and potentially harmful aggression (Benhamou et al. 2014). It is conceivable that leopards also utilise these cues to aid in avoidance behaviour at the landscape level, resulting in the observed spatiotemporal separation, which was apparent even up to considerable distance from lions. Investigation of the level of static interaction between leopard and lion from the UD and UDOI values also indicated a large degree of avoidance by leopards towards areas favoured by lion, and confirms what was shown by our spatiotemporal association analysis.

Understanding the nature of interspecies interactions provides insight into the ecological constraints within which each individual species exists, such as avoidance

of risky habitat (e.g. Valeix et al. 2009b) or general areas of concentrated competitor use (e.g. Benhamou et al. 2014). The implications of intraguild competition during the Late Cretaceous period are even guiding the century-long debate as to whether the *Tyrannosaurus rex*, one of the largest terrestrial carnivores ever, was primarily a scavenger or an active predator (e.g. Carbone et al. 2011). Whilst intraguild killing is commonplace in extant carnivore communities (Caro and Stoner 2003; Palomares and Caro 1999), the fundamental behavioural ecology behind it often remains unclear.

Umbrella species such as the lion contribute to the protection of many less conspicuous plant and animal species when large areas are dedicated to their conservation [*115,000 km² in Zimbabwe*; (Lindsey et al. 2007)]. However, lions are apex predators, and capable of reducing the fitness and survival of subordinate species, which could ultimately also affect their conservation status (Cozzi et al. 2012; Harihar et al. 2011). In terms of holistic conservation management, understanding competitive interactions is therefore vital to ensuring the preservation of intact carnivore guilds (Linnell and Strand 2000), which, as a function of their position at the top of the food chain, regulate the entire ecosystem (Paine 1966).

4.6 CONCLUSION

Here we demonstrate both direct and indirect avoidance of a superior carnivore by a smaller competitor, and present a new index for describing dynamic interaction, as well as a novel method for determining the level of spatiotemporal association between individuals. Avoidance of lion core areas by leopards goes a long way to

limiting the amount of interaction between them, but does not prevent it entirely. Direct interaction between individuals occurs when the animals are close enough that they are aware of and can directly react to one another. Calculating an index of dynamic interaction that doesn't take into account the distance between individuals, even when they are several kilometres apart, and therefore unlikely to be affecting one another directly, is therefore misleading. Benhamou et al. (2014) created a dynamic interaction function, using data of similar resolution, to analyse lion intergroup interactions in shared ranges; and they identified the inclusion of proximity into interaction models as necessary to advancing the method.

The Action-Index that we present here builds on the original concepts of competition defined by Macdonald et al. (1980), and incorporates functions of proximity and movement, which are situation-specific as defined by the focal individual. The Action-Index function in R is able to analyse large datasets to determine interactions; automatically finding every simultaneous fix between all individuals, and comparing their concurrent vectors of movement whilst taking into account the distance between them. Specifying the level of decimal rounding simply but effectively separates the actual interactions from random movement. By defining simple rules that describe interaction as non-random change in speed and direction upon detection of another individual, we have created a novel interaction function that may also be applied to different species in other systems.

4.7 Acknowledgements

We would like to thank the BVC Management for allowing us to conduct the research, Blondie Leathem for his support, and Paul Trethowan for help in the

field. This project was funded by The Darwin Initiative for Biodiversity Grant 17-031. D.W.M. acknowledges the Robertson and Recanati-Kaplan Foundations. B.dP. would like to thank The Beit Trust for scholarship funding and support.

4.8 APPENDICES

4.8.1 *Direct interaction between a leopardess and a lioness*



Figure 4.4: (i & ii). Paired passive camera-trap photos of a leopardess (Fig. 4.4i) being chased by a lioness (Fig. 4.4ii) in a dry riverbed in the Buby Valley Conservancy (this study). This pair of cameras constituted 1 of 25 sites in a camera-trap survey of leopards in the study area to estimate their abundance. The camera-trap pair was set up at a road/river junction, with each camera on opposite sides of the road, but the same side of the river. The cameras were turned roughly 45° towards one another, so that the focal point of their fields of view intersected in the middle of the junction, and would record animals using both the riverbed and road as paths, and therefore increase the capture probability of the site.

4.8.2 *Capture and GPS radio-telemetry tagging of the study animals*

Between 2010 and 2013, 21 lions (9 female and 12 male) and 15 leopards (7 female and 8 male) were fitted with GPS radio-telemetry collars (Africa Wildlife Tracking, Pretoria, South Africa). All animals were handled only by project staff who were qualified through attendance of Zimbabwe's Physical and Chemical Capture of Wild Animals Course, and held valid drugs licences [*B. du Preez; Dangerous Drugs Licence No. 600131*]. Animal handling followed the ASAB/ABS recommendations for the Use of Animals in Research. Study animals were captured under permit from the Zimbabwe Parks and Wildlife Management Authority (23(1)(C) (ii) 13/2008) and with permission from the BVC landowner and conservancy management.

Adult lions were remotely darted with a Dan-Inject (DAN-INJECT ApS, Sellerup Skovvej 116, Børkop, Denmark, DK 7080) CO₂ propelled 1.5 ml dart that dispensed drugs intramuscularly to either the rump or shoulder of the animal. Lions were strictly captured only during the coolest part of the day; early morning or late afternoon. Leopards are elusive and difficult to free-dart, and were therefore trapped in cages measuring 1.500 × 0.750 × 0.600 m, with a 2 × 2 cm wire mesh that prevented their limbs and teeth from getting stuck. A door-stopper, combined with a lock, halted complete closure of the trap door to prevent injury to the animal's tail. Leopards were trapped during the night, and attended at dawn. The cages were covered before the leopard was darted, and the animal was then left in the trap until completely immobilised. Subadult leopards that were caught were darted in the trap so that they could be safely removed without causing injury, and were measured but not fitted with a collar. Small cubs were unable to trigger the trap door mechanism. Trapping was undertaken strictly in conjunction with camera-traps, which allowed specific animals to be targeted, preventing capture of heavily pregnant females or those with dependent cubs.

The capture drugs used to immobilise the animals included a combination of a dissociative anaesthetic [Zoletil; lion dosage: 1.445 ± 0.157 (range: 1.042 – 1.786) mg/kg; leopard dosage: 2.752 ± 0.181 (range: 2.400 – 3.000) mg/kg; manufactured by Virback RSA, Halfway house, South Africa], and a sedative [Xylazine; lion dosage: 0.578 ± 0.063 (range: 0.417 – 0.714) mg/kg; leopard dosage: 1.310 ± 0.156 (range: 1.000 – 1.500) mg/kg; manufactured by CP Pharma, Germany], which was reversed with an alpha-2 antagonist [Atipamezole; lion dosage: 0.058 ± 0.006 (range: 0.042 – 0.071) mg/kg; leopard dosage: 0.131 ± 0.016 (range: 0.100 – 0.150) mg/kg; manufactured by Novartis, Isando, South Africa] administered intramuscularly within one hour of immobilization. Doses were calculated for each

species and sex separately, and animals were monitored until they'd made a full recovery and had left the area [*up to 5 hours, but usually less than 3*]. Animals were monitored via radio-tracking for 48 hours following capture to ensure that there were no lingering effects. We observed no adverse effects from the drugs, and none have been reported in the literature.

Captured animals were under complete chemical immobilization/anaesthesia throughout all stages of handling. Ear-muffs were used to reduce external stimuli, and their eyes were covered with a blind-fold to protect them from light. The animal's front legs were lightly bound with rope in case of unexpected arousal, which did not once occur. Lion collars weighed 1.100 kg, and the leopard collars 0.650 kg, which represent 0.688% and 1.300% of the body weight respectively of the smallest individual collared of each species. Collars were replaced when their batteries began to lose power to allow long-term population monitoring. Only adult animals of both species were collared. Animals in late stage pregnancy were not captured, and although impossible to detect early pregnancy, the drugs are extensively used by veterinarians, and have no known effects on foetuses.

4.8.3 *R script – calculating the level of spatiotemporal association between individuals*

```

# IMPORT CAT INTERACTION DATA
CollarData <- read.csv("/Users/byrondupreez/Documents/CatCollarData.csv", header =
TRUE, sep = ",")

## MATCH SYNCHRONOUS PAIRS:
CollarData$RowNumber <- c(1:length(CollarData[,1]))
Interaction <- merge(CollarData[1,],CollarData[1,],by="RowNumber",all.x=T)
for(i in 1:length(CollarData[,1])){
  Alphacat <- CollarData[i,]
  Betacats <- CollarData[(CollarData$Realtime==Alphacat$Realtime),]
  Alphacat[(1:length(Betacats[,1])),] <- Alphacat[1,]
  Alphacat$RowNumber <- c((1:length(Betacats[,1])))
  Betacats$RowNumber <- c((1:length(Betacats[,1])))
  AlphaBeta <- cbind(Alphacat,Betacats)
  AlphaBeta <- merge(Alphacat,Betacats,by="RowNumber",all.x=T)
  Interaction <- rbind(Interaction,AlphaBeta)
  print(i)
  print(length(CollarData[,1])-i)
}

## DISTANCE CALCULATION:
library(trip)
for(j in 1:length(Interaction[,1])){
  locmatrix <- matrix(nrow=2,ncol=2)
  locmatrix[1,1] <- (Interaction[j,"X.x"])
  locmatrix[1,2] <- (Interaction[j,"Y.x"])
  locmatrix[2,1] <- (Interaction[j,"X.y"])
  locmatrix[2,2] <- (Interaction[j,"Y.y"])
  Interaction[j,"InteractionDist"]<-((trackDistance(locmatrix,longlat=TRUE))*1000)#For
spatial data in latlong format
#Interaction[j,"InteractionDist"]<-((trackDistance(locmatrix,longlat=FALSE))*1000)#For
spatial data in UTM format
  print(j)
  print(length(Interaction[,1])-j)
}

# SAVE
write.table(Interaction, file = paste("~/CatInteractions.", Sys.Date(), ".csv", sep =
""), row.names = FALSE, sep = ",")

```

4.8.4 *The Orientation, Reaction, and Action-Indices of dynamic interaction*

We first created a loop function in *R* [Appendix 4.8.5] that matches every fix for each individual with the simultaneously recorded fixes from each of the other collared animals; creating a paired data frame of every temporally synchronous pair combination. The relevant orthodromic (*great circle*) distances between each of these paired spatiotemporal data could then be calculated. The AI [Appendix 4.8.6] then uses the exact distance between all pairs of individuals at each date-time stamp t , as well as their subsequent location and separation at t_{+1} , to describe each individual's reaction to the other; with the threshold distance defined by the animal itself. This animal-defined threshold is based on the distance moved by each animal relative to the distance separating them, and removes the need to define a critical distance of interaction.

The AI considers the reaction of a pair of individuals to one another as the spatial displacement of each animal in terms of both distance and direction, and describes either a mutual attraction/repulsion or a *chase-and-evade* type dynamic. Consider two animals, A and B , of either sex or species, and at time t 'during' interaction and t_{+1} 'after' interaction. The spatial attributes during interaction are labelled A_t and B_t , and after interaction are $A_{t_{+1}}$ and $B_{t_{+1}}$ respectively. In order to define the AI for each individual, the length of the vectors from A_t to $A_{t_{+1}}$ (A_{vec}) and B_t to $B_{t_{+1}}$ (B_{vec}), and the distances between A_t and B_t (d_t) and $A_{t_{+1}}$ and $B_{t_{+1}}$ ($d_{t_{+1}}$) were calculated. Two separate formulae were then created to describe different aspects of the interaction reaction: the Orientation-Index describes the relative spatial convergence or divergence between the animals from A_t to t_{+1} ; and the Reaction-Index determines the level of attraction or repulsion for each individual towards the other. When combined, the result is scaled and directly comparable to subsequent interactions, or those between different pairs.

The Orientation-Index (Δd) determines the relative attraction or repulsion between the pair by comparing their distance from one another during and then after interaction:

$$\Delta d = \frac{d_t - d_{t_{+1}}}{d_t} \quad (4.3)$$

This index (Δd) describes the overall affinity of the pair for one another in

terms of attraction (*positive*) or repulsion (*negative*), with the size function of the denominator determining the magnitude of the result, and indicating the strength of the reaction; the further apart the animals are from one another *during* interaction, the larger the denominator, resulting in a smaller index.

The Reaction-Indices (Δa and Δb) are calculated separately for each animal, and determine separately each individual's level of attraction or repulsion toward the other animal:

$$\Delta a = \frac{(B_{\text{vec}} - A_{\text{vec}}) + (d_t - d_{t+1})}{(d_t + d_{t+1})} \quad (4.4)$$

$$\Delta a = \frac{(A_{\text{vec}} - B_{\text{vec}}) + (d_t - d_{t+1})}{(d_t + d_{t+1})} \quad (4.5)$$

The Reaction-Index for animal A (Δa) is a measure of the length and direction of its reaction vector from A_t to A_{t+1} with regard to that of animal B . It is calculated as the difference in the vector lengths of animals A and B , added to the difference in distance at interaction (t) compared with after interaction ($t+1$). Similarly to the Orientation-Index, the denominator acts to scale the magnitude of the result. The sign of the resulting index indicates whether animal A displayed attraction or repulsion towards animal B . The Reaction-Index for animal B (Δb) is calculated the same way. The sign preceding the index indicates either attraction or repulsion towards the other animal, and its magnitude indicates the level of the reaction.

4.8.5 *R* script – loop function to match synchronous data from simultaneously collared animals and calculate the distance between them:

```

CollarData <- BehavTrans
CollarData$RowNumber <- c(1)
Interaction <- merge(CollarData[1,],CollarData[1,],by="RowNumber",all.x=T)

# DISTANCE LOOP
for(i in 1:length(CollarData[,1])){
  Alphacat <- CollarData[i,]
  Betacats <- CollarData[(CollarData$Realtime==Alphacat$Realtime),]
  Alphacat[(1:length(Betacats[,1])),] <- Alphacat[1,]
  Alphacat$RowNumber <- c((1:length(Betacats[,1])))
  Betacats$RowNumber <- c((1:length(Betacats[,1])))
  AlphaBeta <- cbind(Alphacat,Betacats)
  AlphaBeta <- merge(Alphacat,Betacats,by="RowNumber",all.x=T)
  Interaction <- rbind(Interaction,AlphaBeta)
  print(i)
  print(length(CollarData[,1])-i)
  print(CollarData[1,"Year"])
}

# UTM DISTANCE CALCULATION
Interactions$CatDistUTM <- sqrt( (((Interactions$UTM.E.x) - (Interactions$UTM.E.y))^2) +
(((Interactions$UTM.N.x) - (Interactions$UTM.N.y))^2) )

# REMOVE ALL ZEROS
Interactions <- Interactions[Interactions[,"CatDistUTM"]!=0,]
Interactions$Row <- c(1:length(Interactions[,1]))

# CLOSEST LION TO LEOPARD
LEOPsvLIONS <- Interactions[order(Interactions$Realtime.x),]
MIN <- data.frame()
MINLEOPvLION <- data.frame()
for(i in 1:length(levels(LEOPsvLIONS$CatName.x))){
  LEOP <- LEOPsvLIONS[(LEOPsvLIONS$CatName.x==unique(unlist(LEOPsvLIONS$CatName.x))[i]),]
  for(j in 1:length(LEOP[,1])){
    MOMENT <- LEOP[(LEOP$Realtime.x==unique(unlist(LEOP$Realtime.x))[j]),]
    MIN <- MOMENT[which.min(MOMENT[,"CatDistUTM"]),]
    MINLEOPvLION <- rbind(MINLEOPvLION,MIN)
    print(j)
    print(length(LEOP[,1])-j)
    print(unique(unlist(LEOPsvLIONS$CatName.x))[i])
    print("Min distance to lions Loop")
  }
}

```

4.8.6 R script – Action-Index function loop:

```

# IMPORT CAT INTERACTION DATA
CollarData <- read.csv("~/CatInteractions.YYYY-MM-DD.csv", header = TRUE, sep = ",")

## SORT DATA FRAME
CatACatB <- CollarData
CatACatB <- CatACatB[order(CatACatB$CatName.y),]
CatACatB <- CatACatB[order(CatACatB$CatName.x),]

### LOOP THE ACTION-INDEX
for(i in 1:length(CatACatB[,1])){
  # VECTORS
  t <- CatACatB[CatACatB[,1],] # T
  t1 <- CatACatB[CatACatB[(i+1),1],] # T+1 !INTERVAL.x == 1
  CatABcontact <- do.call("rbind", list(t,t1))
  #DISTANCE A - B DURING: dt0
  A0B0 <- sqrt(((CatABcontact[1,"UTM.E.x"])-
(CatABcontact[1,"UTM.E.y"]))^2+((CatABcontact[1,"UTM.N.x"])-
(CatABcontact[1,"UTM.N.y"]))^2))
  CatACatB[i,"A0B0"] <- A0B0
  #DISTANCE A - B AFTER: dt1
  A1B1 <- sqrt(((CatABcontact[2,"UTM.E.x"])-
(CatABcontact[2,"UTM.E.y"]))^2+((CatABcontact[2,"UTM.N.x"])-
(CatABcontact[2,"UTM.N.y"]))^2))
  CatACatB[i,"A1B1"] <- A1B1
  #DISTANCE A DURING - A AFTER: AVec
  A0A1 <- sqrt(((CatABcontact[2,"UTM.E.x"])-
(CatABcontact[1,"UTM.E.x"]))^2+((CatABcontact[2,"UTM.N.x"])-
(CatABcontact[1,"UTM.N.x"]))^2))
  CatACatB[i,"A0A1"] <- A0A1
  #DISTANCE B DURING - B AFTER: BVec
  B0B1 <- sqrt(((CatABcontact[2,"UTM.E.y"])-
(CatABcontact[1,"UTM.E.y"]))^2+((CatABcontact[2,"UTM.N.y"])-
(CatABcontact[1,"UTM.N.y"]))^2))
  CatACatB[i,"B0B1"] <- B0B1
  ##ORIENTATION INDEX
  OrientationAB <- (A0B0-A1B1)/(A0B0)
  CatACatB[i,"OrientationAB"] <- OrientationAB
  ##REACTION INDEX A
  ReactionA <- ((B0B1-A0A1)+(A0B0-A1B1))/(A0B0+A1B1)
  CatACatB[i,"ReactionA"] <- ReactionA
  ##REACTION INDEX B
  ReactionB <- ((A0A1-B0B1)+(A0B0-A1B1))/(A0B0+A1B1)
  CatACatB[i,"ReactionB"] <- ReactionB
  ##INTERACTION REACTION INDEX A
  ActionA <- (((B0B1-A0A1)+(A0B0-A1B1))/(A0B0+A1B1))*(sqrt(((A0B0-A1B1)/(A0B0))^2))
  CatACatB[i,"ActionA"] <- ActionA
  ##INTERACTION REACTION INDEX B
  ActionB <- (((A0A1-B0B1)+(A0B0-A1B1))/(A0B0+A1B1))*(sqrt(((A0B0-A1B1)/(A0B0))^2))
  CatACatB[i,"ActionB"] <- ActionB
  print(length(CatACatB[,1])-i)
  print(i)
}

## REMOVE THE LAST ROW OF EACH PAIR ^
for (i in 1:length(CatACatB[,1])){
  if(CatACatB[i,"CatName.y"]!=CatACatB[i+1,"CatName.y"]){
  CatACatB[i,c("A0B0","A1B1","A0A1","B0B1","OrientationAB","ReactionA","ReactionB","Acti
ona","ActionB")]<-NA
  }
  print(length(CatACatB[,1])-i)
  print(i)
}

CatACatB$action <- as.numeric(as.character(CatACatB$actionA))
CatACatB$action <- specify_decimal(CatACatB$action, 2)
CatACatB$action <- as.numeric(as.character(CatACatB$action))
CatACatBinteraction <- subset(CatACatB, Interval.x == 1) # Consecutive fixes
CatACatBaction <- subset(CatACatBinteraction, Action != 0) # Remove all zero actions

# SAVE
write.table(CatACatBaction, file = paste("~/CatActionIndices.", Sys.Date(), ".csv", sep
= ""), row.names = FALSE, sep = ",")

```

4.8.7 *Static overlap at the 95% ('home range') and 50% ('core area') isopleths*

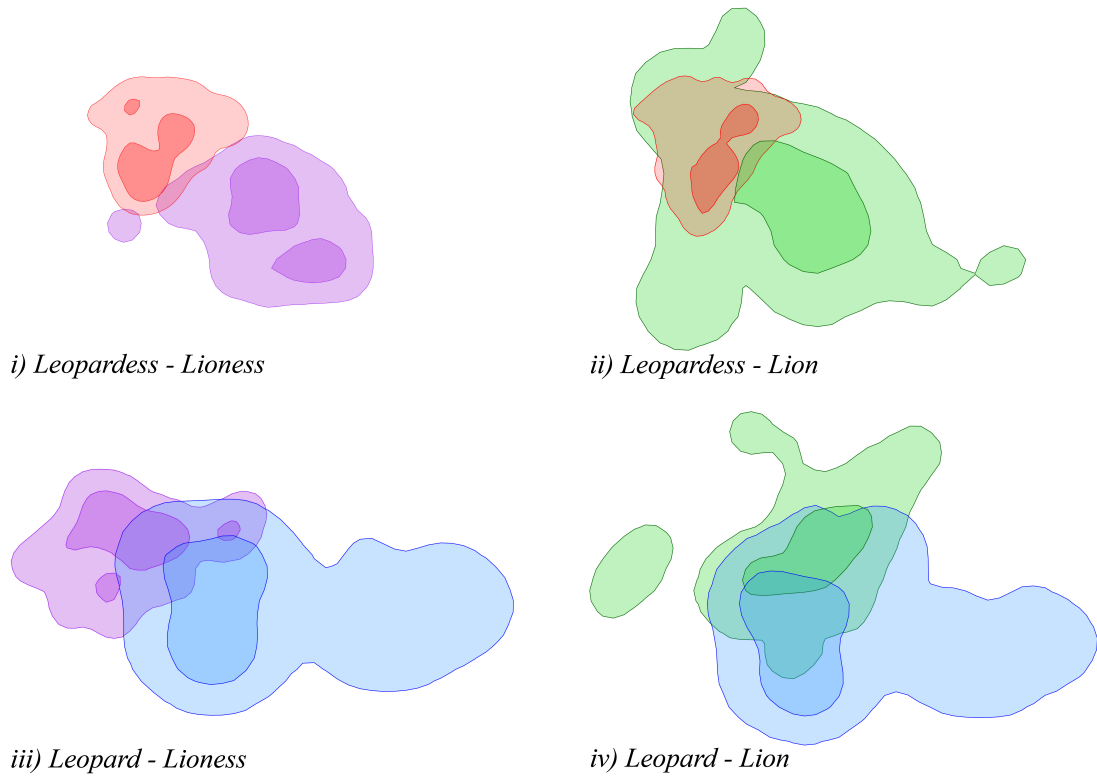


Figure 4.5: (i – iv). Scale amoeboid plots of the 95% (light) and 50% (dark) home-range kernels for pair combinations of a leopardess (Figs. 4.5i & 4.5ii; red) and a leopard (Figs. 4.5iii & 4.5iv; blue) each with a lioness (purple) and a lion (green), displaying large overlap at the 95% kernel level, but little overlap at the 50% core areas [see Table 4.1].

4.8.8 *Action-Indices calculated for each species-sex combination*

Table 4.2: *Interspecific Action-Indices*

Cat A	Cat B	Action-Index (Cat A)
Leopardess	Leopardess	NA
Leopardess	Leopard	-1.970 ± 0.567
Leopardess	Lioness	-0.600 ± 0.306
Leopardess	Lion	-0.181 ± 0.211
Leopard	Leopardess	-1.950 ± 0.784
Leopard	Leopard	-4.588 ± 1.905
Leopard	Lioness	-1.504 ± 0.386
Leopard	Lion	-1.590 ± 0.567
Lioness	Leopardess	-3.132 ± 0.921
Lioness	Leopard	-0.743 ± 0.286
Lioness	Lioness	-1.451 ± 0.712
Lioness	Lion	-2.216 ± 0.552
Lion	Leopardess	-1.325 ± 0.236
Lion	Leopard	-1.298 ± 0.212
Lion	Lioness	-3.842 ± 0.726
Lion	Lion	-3.000 ± 1.639

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Chapter 5

Dietary niche differentiation facilitates coexistence of two large carnivores

Byron du Preez, Jean Purdon, Paul Trethowan, David W. Macdonald and Andrew J. Loveridge

IN REVIEW: *Journal of Zoology*

Authorship: Collected the scats: BdP and PT. Processed the scats: JP. Conducted the sighted-transects: PT. Analysed the data: BdP. Produced first manuscript: BdP. Contributed to revisions: BdP, JP, PT, AJL and DWM. Oversaw the project: AJL and DWM

5.1 ABSTRACT

An animal's diet is an important attribute of its niche, and affects the role that it plays in the ecosystem. Comparing the diets of sympatric species reveals the level of dietary niche overlap between them, which can be used to gauge the potential for competition, as well as each species' vulnerability to competitive exclusion. Because of a morphology adapted to predation, sympatric carnivores have particularly aggressive competitive interactions; the scale of which may be directly related to the amount of overlap in the prey species that they both consume.

Here we analyse and compare the diets of sympatric populations of lion and leopard to test for possible mechanisms of competitive avoidance between them. After controlling for prey handling ability, we show that there was still a significant difference in mean prey body size preference between the carnivores, despite a relatively high level of dietary niche overlap. Where intraguild competitors overlap spatiotemporally, dietary niche segregation such as this may be a mechanism through which competition is avoided and, in the case of carnivores, could reduce the frequency of potentially costly interactions.

5.2 INTRODUCTION

The average carnivore in Africa overlaps in range and habitat with 26 other members of the order Carnivora, and feeds on the same prey as 22 of them (Caro and Stoner 2003). The leopard *Panthera pardus* has the largest natural range of any wild felid (Henschel et al. 2008; Nowell and Jackson 1996), and overlap with more intraguild competitors ($N = 66$) than any other predator (Caro and Stoner 2003). Comparable to their relationship with the larger tiger *Panthera tigris* in Asia (Harihar et al. 2011), leopard are competitively subordinate to lion *Panthera leo* in Africa (Macdonald et al. 2010; Palomares and Caro 1999). Competition between sympatric species may be reduced through temporal, spatial and dietary niche segregation (Pianka 1973). Here we investigate whether the level of dietary overlap could influence the competitive relationship between leopard and lion.

Among the large carnivores, the leopard consumes the widest range of prey, with 92 species reported in Africa (Hayward et al. 2006), from mice *Rhabdomys pumilio* (Braczkowski et al. 2012) up to the size of adult eland *Tragelaphus oryx* (Bailey 1993). This dietary breadth, and prey size variation, could in part reflect the level of intraguild competition that leopard are exposed to throughout their range, and may be a means by which to relieve the potential effects of this competition. Caro and Stoner (2003) report that the leopard is the most vulnerable carnivore to exploitative competition; with 13 potential kleptoparasitic competitors in Africa, and as many as 10% of their kills are lost just to lion (Bertram 1979). In India, leopard were shown to switch from a diet dominated by rodents to consumption of larger prey following extirpation of the local tiger population (Mondal et al. 2011).

This suggests that leopard alter their behavioural ecology in relation to the level of intraguild competition they face.

Competition within the predator guild may force species into niches within which they may be less efficient and impact on their survival. This niche deviation may include habitat restricted hunting behaviour and limited prey species accessibility (Harihar et al. 2011). The available prey within the ecosystem may be largely responsible for determining the carnivore guild component densities (Andheria et al. 2007; Karanth and Sunquist 1995), and the selective killing of different prey species could potentially facilitate their coexistence through ecological separation (Karanth and Sunquist 2000). It has even been suggested that prey selection is more dependent on the level of intraguild competition than on the relationship between predator and prey body size (Radloff and Du Toit 2004). Knowledge of carnivore diet may therefore provide insight into the potential level of exploitative competition between sympatric carnivores, and the mechanisms of mitigating this, by comparing relative intake versus availability of prey (e.g. Klare et al. 2011).

Here we compare the diets of sympatric lion and leopard, in terms of prey species biomass and relative consumption, to investigate the level of dietary niche overlap between the two large carnivore species. By considering only the prey species accessible to direct predation by both carnivores in our analyses, we test for the mechanisms by which the level of dietary competition (as a proxy for general competitive potential) between lion and leopard may be alleviated. Specifically, we investigate the patterns of prey group size and prey body size utilisation between the carnivores to test for differences that may facilitate reduction in competition.

The lion in this study exist at one of the highest densities in Africa [~ 19 lions 100 km^{-2}], and were shown to be having a negative impact on leopard density, age and demographic structure, recruitment and survival (du Preez et al. *in review*). Knowledge of the dietary overlap between sympatric carnivores may be particularly important in this situation where there is the risk of the competitive exclusion of a species (e.g. Harihar et al. 2011).

Prey group size may be related to its level of vigilance, and therefore indicate the relative difficulty in hunting it; where the differences in hunting strategy between leopard and lion may lead to different levels of predation on species with different social systems living in different group sizes (e.g. Radloff and Du Toit 2004). Prey body size may be used as a proxy indication of energetic reward, and therefore also the potential risk of kleptoparasitism (e.g. Hayward and Slotow 2009; van der Meer et al. 2011). Instances of opportunistic predation, which deviate from the patterns of prey group size or body size selection for each carnivore, are unlikely to mask any trends in prey selection that are due to actual niche segregation.

We aimed to establish whether individual characteristics of prey selection, as a proxy for intraguild competition, potentially facilitate coexistence or exacerbate conflict between sympatric lion and leopard. We therefore hypothesize, firstly, that the differing social organisation and intraspecies cooperation between leopard and lion would lead to different patterns in prey group size utilisation; and, secondly, that to reduce dietary competition between leopard and lion there would be a difference in prey body size selection after controlling for differences in each predator's prey handling ability.

5.3 METHODS

5.3.1 *Study site*

Between August 2010 and November 2012, a total of 64 leopard and 89 lion scats were collected opportunistically on the 3,743 km² Buby Valley Conservancy (BVC) in the Matabeleland South province of Zimbabwe (geographically centred at 30°7'E, 21°30'S; approximate elevation of 550 m). BVC is a wildlife conservancy boasting the full complement of historically endemic species. The mean annual rainfall at BVC between 2007 and 2012 was 351 ± 76 mm, which fell mostly during November through March with May through August being the driest months. Artificial water points are abundantly available throughout the conservancy, and help to sustain the wildlife in drought years. The vegetation on BVC is dominated by mopane *Colophospermum mopane* and acacia *Acacia* spp. scrub and woodland, which is traversed by seasonal drainage-lines and the associated riparian vegetation. Patches of open grassland are dispersed throughout the conservancy.

5.3.2 *Lion and leopard dietary data*

Direct observations of feeding behaviour are difficult to obtain from secretive species such as the leopard, and due to the biases associated with observational data (e.g. Hayward et al. 2006; Radloff and Du Toit 2004) it is not possible to use these data to predict prey selection. However, even non-experimental investigation of diet can provide indications of predation patterns (Karanth and Sunquist 1995). The

most commonly used technique employed to determine predator dietary composition is identification and analysis of the undigested prey matter detected in a sample of their scats (Andheria et al. 2007; Klare et al. 2011). Scat analyses produce a more complete picture of carnivore diets than do observations or encounters with conspicuous kills (Bodendorfer et al. 2006), which are biased towards larger prey (Karanth and Sunquist 1995). An additional and attractive aspect of the scat analysis method is its non-invasive nature (Andheria et al. 2007).

The volume, mass and frequency of each prey type detected in scats may be modelled in various ways to define a species' diet, and allow determination of dietary overlap and niche partitioning between species (Klare et al. 2011). If a prey species is consumed in a greater proportion than it naturally occurs relative to other species, then this indicates that it is preferentially taken (Hayward et al. 2006), possibly because it is easier to kill (Schaller 1972). Klare et al. (2011) review and describe several of the most common methods of modelling carnivore diets from scat analyses, and conclude that biomass calculations tend to produce the most accurate depiction of actual predation and consumption.

Here we used samples of sympatric leopard and lion scats to determine and compare their diets; only fresh scats that were identifiable by the visible spoor of the carnivore that left them were collected. Big cats use scats as social communicators and therefore deposit them in areas of high traffic where they will be detected by conspecifics (Karanth and Nichols 2002; Smith et al. 1989), such as along roads and game trails (e.g. Figure 5.1), and which was where we collected most of our samples (e.g. Andheria et al. 2007; Bodendorfer et al. 2006).



Figure 5.1: *Camera-trap image of a leopard and recently deposited scat on a high-traffic game trail in the Buby Valley Conservancy.*

Trites and Joy (2005) used Fisher's exact test on Monte Carlo simulations of frequency of occurrence methods to investigate the effect of sample size in scat analyses, and they calculated that a minimum of 59 scats are required to broadly describe a site specific species' diet (but see Mukherjee et al. 1994). Braczkowski et al. (2012) determined leopard diet in an area of relatively low ungulate abundance from a total of just 50 scats.

5.3.3 *Scat component identification and analysis*

As with Bodendorfer et al. (2006), identification of consumed prey was done almost solely on identification of hairs present in the scats [*see Appendix 5.8.1*]. Hair is indigestible by mammals (Gamberg and Atkinson 1988) and therefore passes through the digestive tract and into the scats in the same proportion as ingested. We classified scat prey remains to the highest taxonomic level possible (e.g. Klare et al. 2011) based on prey hair length, width, colour, cross-sectional shape and structure (Keogh 1985), as well as microscopy of their external scale patterns (Demarinis and Agnelli 1993; Mukherjee et al. 1994).

To avoid problems associated with regional variation, hair identification was based on a reference sample of 29 mammal species' collected from carcasses opportunistically encountered at the study site. Hair was collected from various parts of the body, including the spinal ridge, flank, and belly. Non-mammalian prey was identified to as high a level as possible using whatever undigested matter remained detectable in the scat, such as scales, feathers and claws.

While scat analyses are inherently biased, this affects equally the results for both lion and leopard, and is not a confounding factor in their comparison [*for a brief summary of the common scat analysis methods, see Appendix 5.8.2*]. Increased sample sizes would probably reveal additional prey species (e.g. Bodendorfer et al. 2006; Trites and Joy 2005), however the aim of this research was not to categorically list each predator's menu, but to investigate the dietary niche overlap between them. For comparative purposes, categorising species by body size and social grouping

behaviour was therefore sufficient.

5.3.4 *Statistical analyses*

All statistical analyses were done in *R* (*R* 3.0.1, *R* Core Team 2013).

5.3.5 *Dietary analysis*

Prey biomass consumption was calculated using Ackerman's equation, $Y = 1.980 + 0.035X$ [where X is the prey species' mean female weight (kg), and Y is the weight of prey consumed per scat (kg); Ackerman et al. 1984]. This equation was derived from feeding trials of captive cougars (see Ackerman et al. 1984). Comparative studies on leopard and lion digestion are not available, but assumed equivalent (e.g. Andheria et al. 2007; Henschel et al. 2005; Karanth and Sunquist 1995).

Prey species' body weights were taken from Kingdon and Hoffmann (2013a) and Kingdon and Hoffmann (2013b). There were breaks in the distribution of the mean female body mass of prey consumed (e.g. Packer 1983; Caro and Stoner 2003), and prey was therefore divided into the body size classes 'small' (<5 kg), 'medium' (5 – 100 kg), 'large' (101 – 500 kg) and 'mega' (>501 kg) based on these breaks (Figure 5.2).

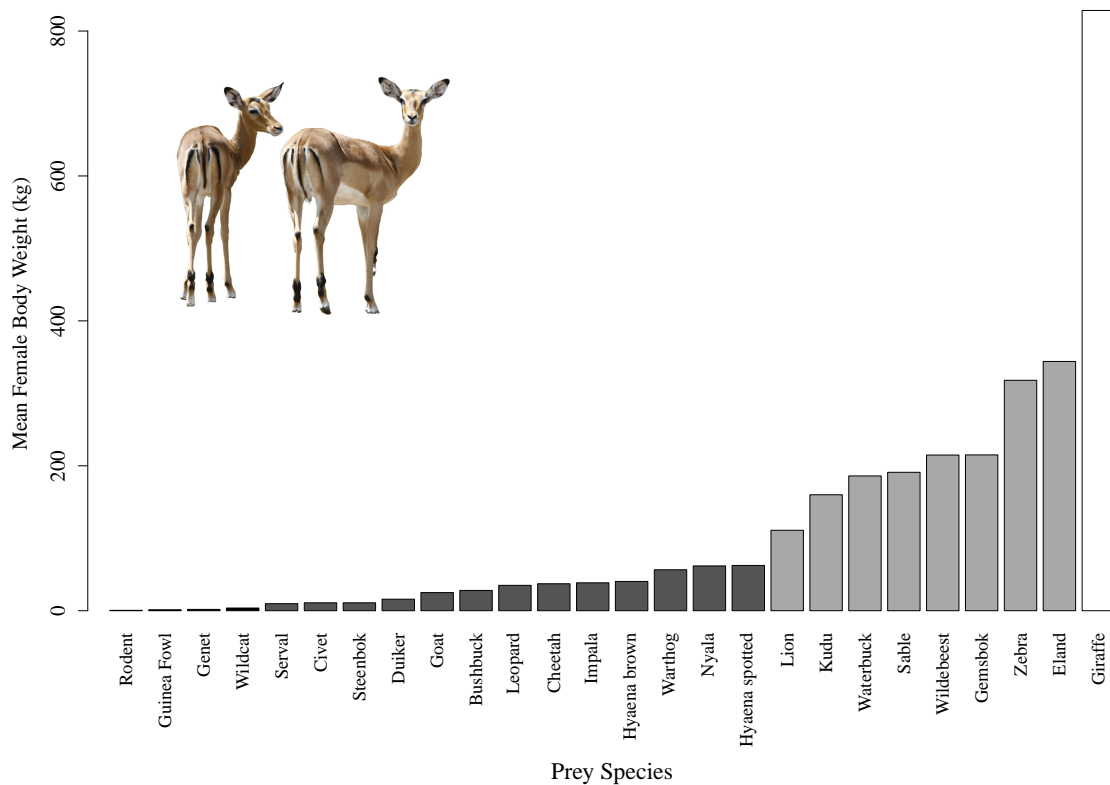


Figure 5.2: *Distribution of the mean female body mass of prey species recorded in the scat samples of lion and leopard in this survey. Colour of the bars indicates the body size classification of each species (black = ‘small’, dark grey = ‘medium’, light grey = ‘large’, white = ‘mega’). Only prey in the mega body size class was inaccessible to leopard, and all prey in the small, medium and large body classes were considered available for consumption by both leopard and lion.* [Inset top left: impala *Aepyceros melampus* ewes. Mean impala ewe body mass lies approximately at the median position in the body mass spectrum of the prey consumed by leopard and lion].

Although the actual size of the animals killed cannot readily be determined from scat samples, it is likely that larger prey species detected in the leopard diet were juveniles (e.g. Radloff and Du Toit 2004); and we therefore recognise the potential limitation of direct prey body size inference due to the uncertainty of the actual size of prey consumed. However, intraspecific prey size variation is not important with respect to investigating niche segregation between the carnivores, as juveniles

and adults of the same prey species are likely to associate spatiotemporally (see Estes 1991; Kingdon and Hoffmann 2013b). Therefore, even though there may be separation in the age/size class selection of the same prey species by each carnivore, there may be little spatial separation in actual predation behaviour and events when consuming the same prey species. Hunting different body size classes of the same prey species could therefore still lead to incidents of interaction and conflict; and the potential ecological separation between the carnivores to reduce competition may still be tested without including data on the size of individuals consumed.

A diverse range of life history traits and ecological niches characterised each prey body size class (except *mega*). Importantly, within each body size class there was no overrepresentation of any particular niche, such as either by browsers or grazers, that might bias any analysis of predator size preference where the predator itself selects, or is limited to, any specific habitat type.

5.3.6 *Ungulate abundance estimation*

Sighted line-transects were used to determine ungulate density (e.g. Karanth and Sunquist 1995; Karanth et al. 2002; Ramesh et al. 2009). The extensive road network on BVC allowed long, straight transect roads ($N = 30$) that cut perpendicularly across drainage lines to be chosen within the study site, independent of vegetation type to reduce habitat-associated bias (e.g. Stander 1998), and were driven at a constant speed of 15 km hour^{-1} , while every animal visually detected was recorded (e.g. Karanth et al. 2002). Examination of the transects overlaid on satellite imagery confirms that habitat types were represented fairly according to

their abundance.

The perpendicular distance (x) of an animal from the transect was then calculated using a rangefinder (Scout DX 1000 ARC, Bushnell, Kansas, USA) to determine the radial distance (r), and a compass to determine the sighting angle (Θ); and via the equation $x = r\sin\Theta$ (Thomas and Karanth 2002). Not every animal will be detected during sighted transects, but the fundamental assumption of this method is that every animal on the transect path will be detected [*all assumptions specified by Thomas and Karanth (2002) were met by this survey*]; animal detection probability is therefore a declining function of perpendicular distance from the transects, as vegetation and cryptic colouration increasingly obscure the animals (Thomas and Karanth 2002; but see O’Kane et al. 2014). A detection metric is then fitted to the data to estimate the proportion of the population detected, and which can then be used to estimate species population abundance with the standard estimator of the form: $N = AC/2wLp$ [*where N is abundance, A is the total survey area, C is the number of animals counted, w is the approximate distance view on each side of the transect, L is the length of the transect, and p is the detection probability of each animal*]. We used the statistical software package *DISTANCE* (Thomas et al. 2001) to fit the models and estimate species abundance as it employs the models briefly described here, and also takes into account size bias associated with the increased probability of detecting larger animal groups. Akaike’s Information Criterion (AIC) was used to select the model of best fit (Buckland et al. 1993; Burnham and Anderson 2002). The surveys were repeated in both the wet and dry seasons, to account for seasonal variation in abundance, and the results were averaged as carnivore scats were collected throughout the year.

The social organisation and group size of a prey species may be used a proxy for the potential level of predator detection (Hayward and Kerley 2005; Pays et al. 2012), and the differing social organisation of predators themselves may lead to distinct foraging strategies that cope with varying prey group sizes differently (Periquet et al. 2012). The maximum group size of each species detected during the line-transects was used to categorise prey into the group size classes; ‘*single*’ (1), ‘*small*’ (2 – 10), ‘*medium*’ (11 – 40) and ‘*large*’ (>40). Including the group sizes preyed on by both leopard and lion in the analysis helped control for potential bias regarding a relationship between prey group size and catchability by each carnivore species.

5.3.7 *Predator prey preference*

Prey selection preference was determined by comparing the proportional abundance of each species recorded in the scat samples to the proportional density of the species in the study site (e.g. Karanth and Sunquist 1995; Ramesh et al. 2009), using Jacobs’ index (Jacobs 1974), $D = r-p/((r+p)-(2rp))$ [where r is the proportion of total kills containing a particular prey species, and p is the proportional abundance of that species detected in the ecosystem’s prey population].

To compare the similarity of the diet between lion and leopard, and their overlapping consumption of the same species, we used Pianka’s multiplicative measure of niche overlap (Pianka 1973), $P = \sum_i^n p_{ij}p_{ik}/\sqrt{(\sum_i^n p_{ij}^2\sum_i^n p_{ik}^2)}$ [where p_{ij} is the percentage of prey i of predator j , and p_{ik} is the percentage of prey i of predator k]. This index is a value between 0, indicating no dietary overlap between

competitors, and 1, suggesting complete overlap.

5.3.8 *Potential for dietary niche segregation between leopard and lion*

The potential for dietary segregation between leopard and lion was considered separately in two different respects: *prey group size*, and *prey body size*.

The effect of prey group and body size on predation by each carnivore was first investigated with all prey detection data for both species included. However, the group and body size differences between the predators themselves means that lion are able to kill prey larger than is possible for leopard. Therefore, if a significant difference was detected either in group or body size selection, the data would be reanalysed including only those prey species accessible to both carnivores. By considering only those species available to predation by both leopard and lion means that any differences in the patterns of predation between them may be directly due to dietary niche segregation.

5.4 RESULTS

5.4.1 *Jacobs' Indices of individual prey species*

In total, 19 prey species were identified from 64 leopard scats, and 18 species from 89 lion scats. A Jacobs' Index value was calculated for each prey species to

determine its comparative preference (relative to abundance) by each carnivore species [see Appendix 5.8.3 for the comprehensive list of calculated Jacobs' Indices]. Prey was first converted to biomass based on mean female body weight using Ackerman's equation, and the proportions of remains detected in the scats were then compared to the proportion of that prey species' biomass abundance in the study site. The conversion from frequency into biomass reduces the bias associated with overrepresentation of smaller species in scat analyses (Ackerman et al. 1984).

5.4.2 *Pianka's Index of niche overlap*

In total there were 11 prey species common to the scats of both leopard and lion, while eight species were preyed on exclusively by leopard, and seven by lion see Appendix 5.8.4 for the list of common prey species]. The Pianka Index of dietary overlap was calculated as 0.717 between the two carnivore species.

5.4.3 *Prey group size preference*

A linear model was used to regress the Jacobs' Index values of prey selection preference against prey group size, and was compared between the carnivore species. This analysis revealed no significant difference in prey group size utilisation between lion and leopard (model: $lm(formula = JacobsIndex \sim GroupSize * CarnivoreSpecies)$, $F_{3,48} = 0.793$, $P = 0.504$, $R^2 = 0.047$), which suggests that the carnivores both have similar preferences for the group size of the prey they hunt.

The mean Jacobs' Index values for each prey group size class were plotted to compare the influence of group size on carnivore selection (Figure 5.3). Leopard and lion both displayed a decreasing trend of prey selection preference with increased group size; and although there was no significant difference in the trend of group size preference between the carnivores, this trend was more exaggerated for leopard than lion.

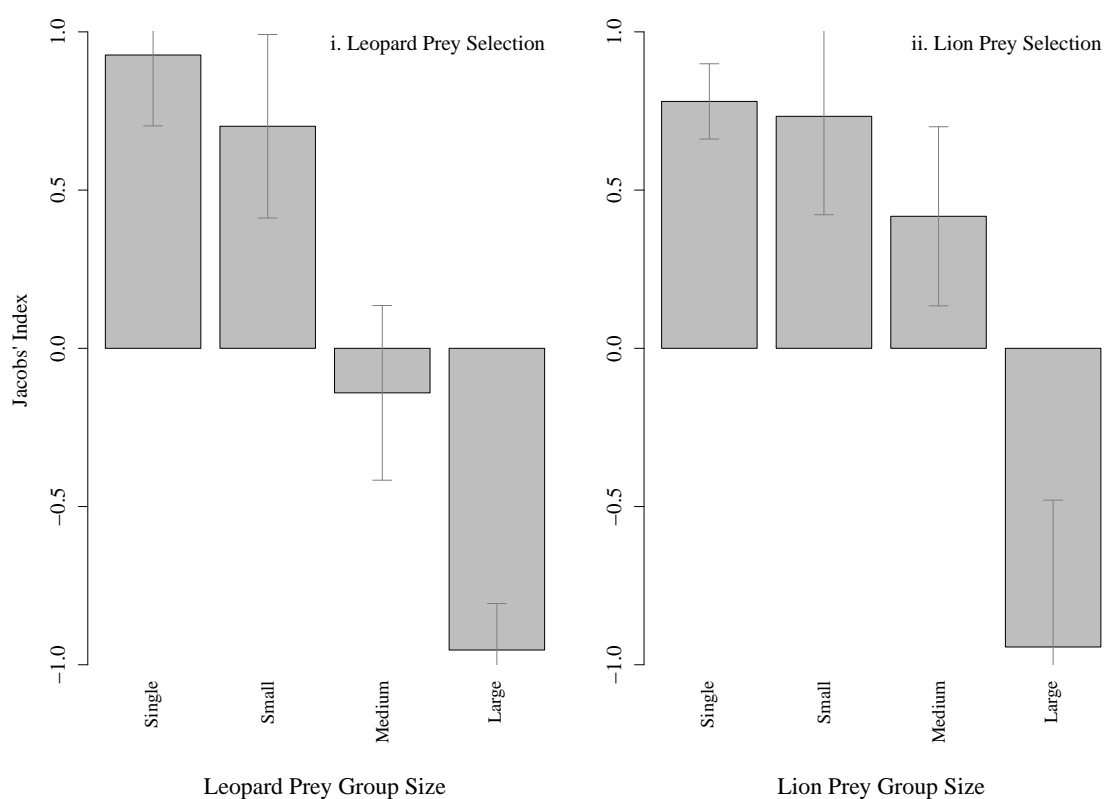


Figure 5.3: (i & ii). *Jacobs' Indices indicating the mean and standard error leopard (Fig. 5.3i) and lion (Fig. 5.3ii) prey group size class preference.*

Both carnivores avoided prey species that tend to associate in larger group sizes (Figure 5.3) (e.g. Funston et al. 2001; Hayward and Kerley 2005). Leopard avoided prey in medium sized groups and preferred prey that were either solitary or form

small groups. In contrast, whilst lion also preferred single animals or those in small groups, they did not avoid preying on species that form medium sized groups.

5.4.4 *Prey body size preference*

A linear model was also used to regress the Jacobs' Index values of lion and leopard prey selection preference against prey body weight, and compared between the carnivore species. This analysis revealed a significant difference in prey body size utilisation between lion and leopard (model: $lm(formula = JacobsIndex \sim PreyMass * CarnivoreSpecies)$, $F_{3,48} = 4.126$, $P = 0.011$, $R^2 = 0.205$), indicating that leopard and lion select for different prey body size classes.

The mean Jacobs' Index values for each prey body size class were plotted to compare the influence of prey body size on selection by each carnivore (Figure 5.4). Leopard and lion had distinctly different patterns of prey preference based on body size; there was a strong trend of decreasing preference with increasing prey size for leopard, whilst lion showed a trend of increasing preference with increasing prey size.

The negative relationship between mean prey body weight and its occurrence in leopard diet indicates strong preference for smaller prey, and avoidance of large species. In comparison lion avoided small prey, preferring larger bodied animals (Figure 5.4).

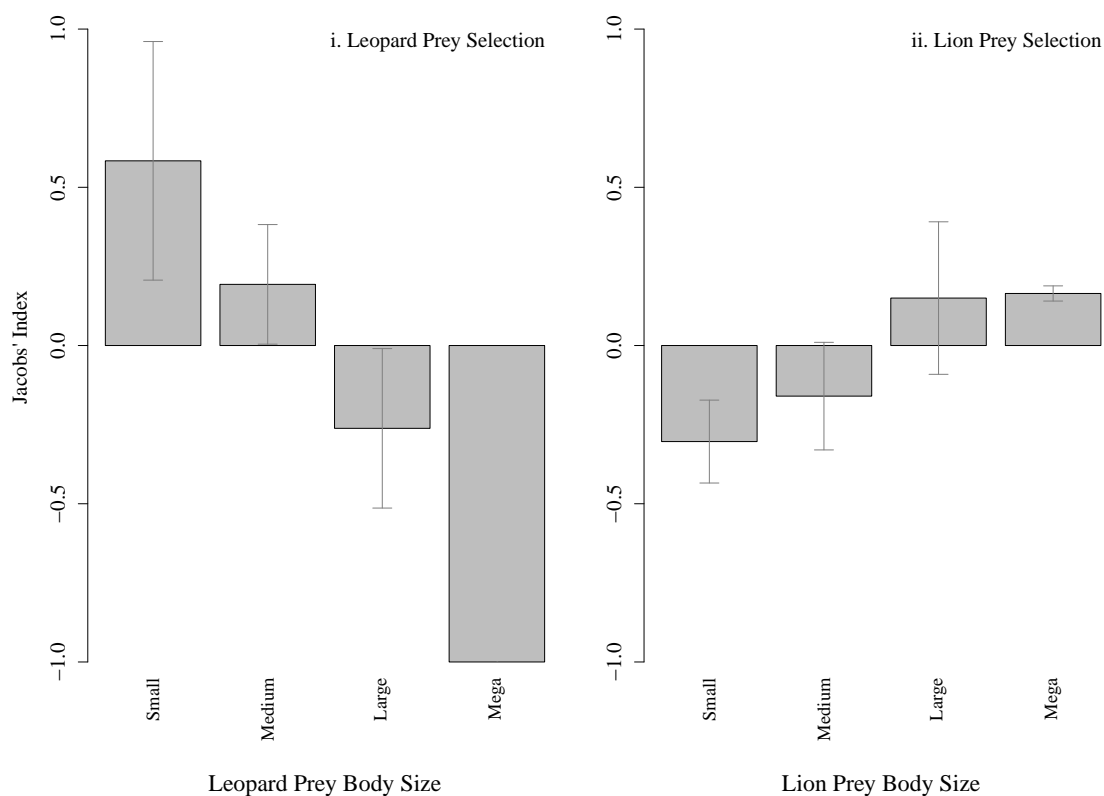


Figure 5.4: (i & ii). *Jacobs' Indices* indicating the mean and standard error leopard (Fig. 5.4i) and lion (Fig. 5.4ii) prey body size class selection preferences.

5.4.5 *Potential dietary niche segregation between leopard and lion*

Prey characterised by each group size (*'single'*, *'small'*, *'medium'* and *'large'*) were represented in the scat samples of both leopard and lion, and there was no significant difference in the selection patterns of any of the classes between the carnivore species. It is therefore unlikely that selecting for different prey group sizes is important in reducing competition by facilitating dietary niche segregation between leopard and lion.

Prey of all the body size classes (*‘small’*, *‘medium’*, *‘large’* and *‘mega’*) were detected in the lion scat samples; however, only three prey body size classes (*‘small’*, *‘medium’* and *‘large’*) were detected in the leopard diet. Notably, there was no detection of any prey belonging to the *‘mega’* body size class in the leopard scat samples. The overall comparison between leopard and lion diet revealed a significant difference in prey body size preference when all prey was included; however this analysis alone was not enough to determine whether this difference was due to dietary niche segregation, or whether it was just because of the physical disparity between the carnivores in terms of the maximum size of prey they could each handle.

Therefore, to test whether the difference in the prey body size utilisation between leopard and lion was due to carnivore selection, as opposed to differential ability to subdue large prey species, only those prey within the body size range consumed by both carnivores in this study were compared. This analysis revealed that there was a significant difference in prey body size selection preference between the carnivores – despite the exclusion of prey accessible to only lion (model: $lm(formula = JacobsIndex \sim PreyMass * CarnivoreSpecies)$, $F_{3,46} = 2.794$, $P = 0.050$, $R^2 = 0.099$). All of the prey considered in this analysis, including those preferentially selected for by lion, were within the body size range accessible to predation by leopard.

5.5 DISCUSSION

The difference in the body sizes of leopard and lion may largely be the result of long-term evolutionary adaptation, by one or both species, to reduce competition by allowing each carnivore to maximise the cost-benefit trade-off of preying on different sized animals. However, here we show that leopard and lion further reduce dietary competition with each other in the short-term by still selecting for different prey within the size range accessible to predation by both carnivore species.

Whilst leopard preferentially killed smaller prey species, this may be less due to their ability to kill large prey than their ability to defend it from kleptoparasitism. Smaller prey items may either be instantly consumed, or are easier to cache; both of which may have contributed to their preferential selection by leopard. If lion density was reduced, and hence the level of kleptoparasitism lowered, the balance of predation risk/reward would be different, and under less competitive conditions leopard may select for larger prey, as has been found for cheetah (McVittie 1979), wild dog (Carbone et al. 1997), and even insectivorous mammals (Dickman 1988).

The Pianka Index of dietary overlap between leopard and lion calculated here, at 0.717, was lower than reported between sympatric leopard and tiger, of 0.840 by Andheria et al. (2007) and 0.777 – 0.897 by Harihar et al. (2011), which suggests that the level of dietary competition between leopard and lion is relatively low. Where the dietary niches of two sympatric competitors are identical, the species that can survive at the lowest resource density will outcompete and exclude the other (Odden et al. 2010). Preying on the same species therefore increases the

level of competition between carnivores; but the ability to hunt a wider variety of prey may allow for dietary niche partitioning, and reduce the chance of encounters between carnivores (Andheria et al. 2007; Karanth and Sunquist 1995).

That there was no significant difference in the prey group size utilisation between leopard and lion is not really surprising. Despite any differences in leopard and lion social organisation that may result in different hunting strategies (e.g. Hayward et al. 2006), the success of the hunt may still depend on the predator being able to approach undetected to within a critical distance of the prey to begin the chase. Both carnivores favoured preying on smaller group sizes, which is likely due to a reduced level of vigilance and a greater chance of hunt success than there is in larger groups with higher levels of vigilance (e.g. Pays et al. 2012; Periquet et al. 2012).

Sympatric carnivores, with similar predatory morphology, and that utilise the same prey resources, have the potential for both exploitative and interference competition (Caro and Stoner 2003; Durant 2000), which may include intraguild predation. In fact, more than a third of the prey species identified in this study were other carnivores (9/26); which included detection of both lion and leopard remains in each other's scats. These incidents may have been the result of direct predation, and highlight the potential cost of carnivore competition.

5.6 CONCLUSION

The abundance and diversity of prey within an ecosystem limits predator density (Carbone et al. 2011; Hayward and Slotow 2009); and, via the competitive hierarchy, influences the component densities of the local carnivore guild (Harihar et al. 2011). Competitive release by the removal of dominant carnivores could lead to a broader range in the prey available to mesocarnivores (Hayward et al. 2006; Johnson et al. 1993; Mondal et al. 2011), and the level of competition between carnivores is therefore likely to have a direct relationship to the level of overlap in prey species consumed (Karanth and Sunquist 2000). Increased competition for prey may in turn lead to increased incidents of direct interaction and a greater level of interference competition between predators (Harihar et al. 2011).

Here we found that differential prey selection may facilitate the sympatry of lion and leopard by reducing the potential for competition between them. Future work may include a comparison of the trend in both leopard and lion density and how this affects the level of dietary competition between them.

5.7 Acknowledgements

We would like to thank the BVC Management for allowing us to conduct the research, Blondie Leathem for his support, Matt Trisos for helping collect scats, and Dennis du Preez for servicing the microscope and keeping it functional. This project was funded by The Darwin Initiative for Biodiversity Grant 17-031. D.W.M. gratefully acknowledges the support of the Robertson and Recanati-Kaplan Foundations. B.dP. would like to thank The Beit Trust for scholarship funding and support.

5.8 APPENDICES

5.8.1 *Prey species identification from undigested matter detected in the scat*

The hair of carnivore prey is largely undamaged by the digestive process and is a good way to identify prey species (Ramakrishnan et al. 1999). Each scat was given a unique individual number and then placed in a paper bag. Before analysis, each scat with its number was put into a stocking and soaked in water with sodium hypochlorite to remove any potentially hazardous pathogens. Once the scats had softened, they were placed over a sieve (1 mm), and running water was used over it to remove all other organic material from hairs, bones and other prey particles (Breuer 2005). These components were then dried out and placed into bags along with their individual numbers ready for macroscopic and microscopic analysis. For each scat the percentage of hair was recorded along with the percentage of any other organic material that was not washed away. A photograph of each dried scat was taken in order to help with the identification process. The colour and length of hair was noted and used in the overall identification of the scat along with the microscopic analysis of the hairs.

In preparation for the microscopic analysis between six to ten hairs were picked randomly from the scat. These were then placed on a couple of slides that had a thin layer of wood glue over it. The hairs were placed in the wood glue on the slide and once the wood glue had dried the hair was removed leaving behind their cuticular scale pattern. These unique scale patterns can then be used in the identification of the prey species using a microscope. A cross section was also done to aid the identification process. Ten randomly picked hairs were placed in a plastic pipette, which then was filled with melted beeswax. Once the beeswax had solidified, a number of small thin slices were cut using a very sharp razor blade. These slices were then placed under the microscope and then analysed.

A reference collection of prey hairs was made using hairs collected from poached, hunted or from animals that died of natural causes. The scale patterns, cross sections and overall colour, length and texture of the hairs were then compared to this reference collection as well as the literature from (Keogh 1979).

5.8.2 *Scat analysis methods*

The different scat analysis methods can be broadly classified into three categories: *qualitative*, in which the frequency of prey species occurrence is determined; *composition*, which uses either the mass or volume of undigested matter of each species; or *biomass calculations*, that take into account the mass of the prey consumed. Klare et al. (2011) reviewed 11 different methods of describing diet, and concluded that using the wrong method for the species and data could lead to inaccurate biological conclusions. Scat analysis is an indirect method of describing diet and is therefore inherently biased (Klare et al. 2011), so this limitation was kept in mind when interpreting the results.

Frequency of occurrence methods over represent smaller prey species in the diet (Ackerman et al. 1984), as smaller bodied animals have relatively larger, hairy, surface areas (Floyd et al. 1978). To overcome this bias, these relative frequencies of occurrence may be converted into estimates of biomass consumption, which was originally calculated for a large felid by Ackerman et al. (1984) via feeding experiments with cougars *Puma concolor*, and has subsequently been applied to other large felids, including leopard (e.g. Henschel et al. 2005). This method is not without errors (Bodendorfer et al. 2006), but generally considered more accurate and representative of actual consumption.

Quantitative scat analysis methods (e.g. biomass calculations) are preferred over qualitative methods (e.g. frequency of occurrence) when describing a carnivore's diet, determination of niche, and for comparison with other carnivores (Klare et al. 2011). When biomass calculation models are unavailable, the volume or mass composition of different food categories may be used. Volumetric methods consider the components of all scats as adding up to 100%, while the mass method assigns larger scats more importance (Klare et al. 2011). These methods may be affected by variable density and digestibility between different food categories, but this is more likely to affect omnivores than obligate carnivores (Reynolds and Aebischer 1991).

5.8.3 *Jacobs' Indices for individual prey species*

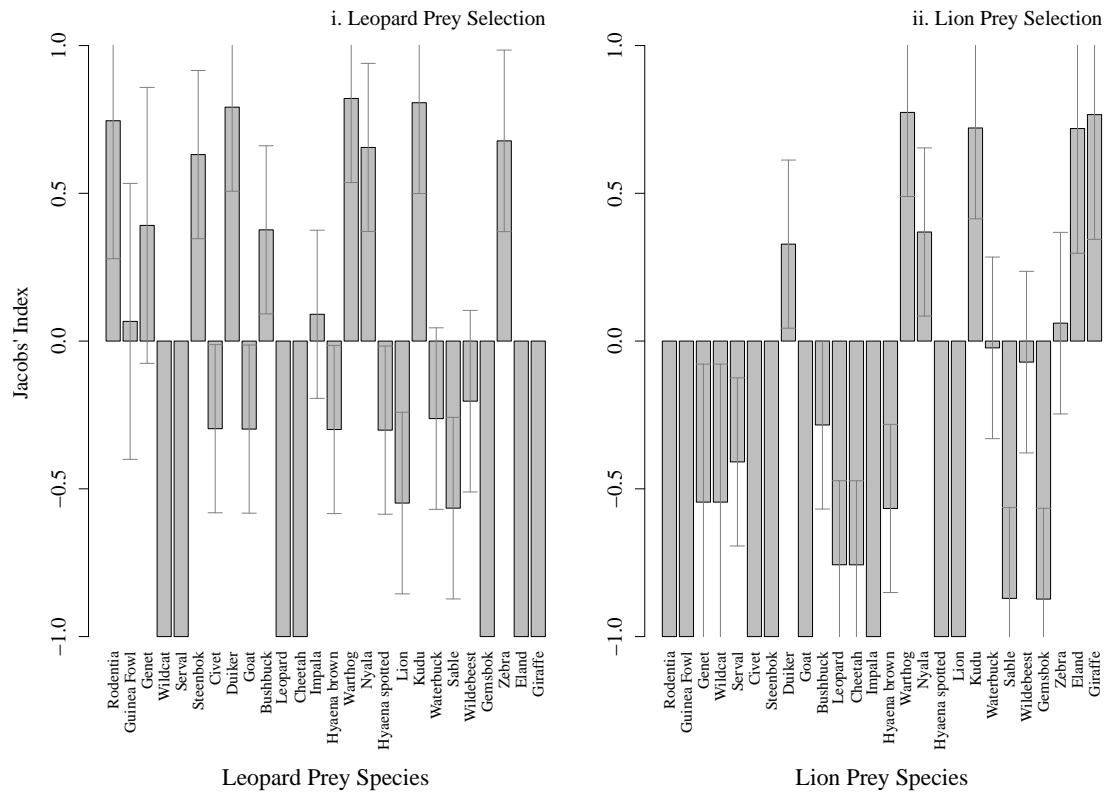


Figure 5.5: (i & ii). *Jacobs' Indices* indicating leopard (Fig. 5.5i) and lion (Fig. 5.5ii) prey preference based on the proportion of the biomass of the individual prey species detected in the scats and compared to relative abundance of that species' biomass in the environment. The prey species indicated along the x-axis are arranged by increasing body weight. The Jacobs' Index values lie within a continuum, with those approaching +1 indicating strong preference, whilst values towards -1 indicate prey that is not particularly favoured. Standard error was derived from the population abundance calculation. The species with values of -1 on the each plot were not consumed by that carnivore, but were detected in the diet of the other.

5.8.4 *Prey common to both leopard and lion*

Table 5.1: *Total scat detections of prey species common to both lion and leopard*

Prey Species	Carnivore Species	
	Leopard	Lion
Bushbuck	4	4
Duiker	15	14
Genet	2	1
Hyaena (<i>brown</i>)	1	2
Kudu	3	8
Nyala	8	15
Sable	1	1
Warthog	1	3
Waterbuck	2	12
Wildebeest	1	5
Zebra	5	6

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Chapter 6

Experimentally testing an intraguild hostility hypothesis: the impact of lions *Panthera leo* on leopards *Panthera pardus*

Byron du Preez, Andrew J. Loveridge and David W. Macdonald

IN REVIEW: *The American Naturalist*

Authorship: Collected the data: BdP. Analysed the data: BdP. Produced first manuscript: BdP. Contributed to revisions: BdP, AJL and DWM. Oversaw the project: AJL and DWM

6.1 ABSTRACT

Lions and leopards are sympatric intraguild competitors that are both facing extensive habitat fragmentation and declining population sizes throughout their natural range in Africa. Habitat fragmentation increases the extinction probability of small populations, as they are more susceptible to threats; and while many current conservation efforts are single-mindedly focused on increasing apex predator density, few measure the impact that this has on the conservation of less conspicuous species, including both competitors and prey species.

We investigated the impact of lions on leopard density and age class structure through monitoring populations at both a control site and a neighbouring impact site where lions were originally absent but later introduced. Leopard density was calculated using spatially explicit capture-recapture models, and was compared between sites and seasons using a *Before-After-Control-Impact-Pairs* experimental design to measure the impact of lions on the leopard population. Here we show that lions negatively impact on leopard population density, cub survival and recruitment rates. This impact suggests that some leopard populations in competition for resources with lions are not self-sustaining.

Whilst leopards are still thought to be abundant throughout their current range, the impacts of lions on other endangered carnivores, such as cheetah and wild dog, may be of great concern.

6.2 INTRODUCTION

The intensity of interspecific competition increases with trophic level, as energy resources necessarily become scarcer and harder-won; and in carnivores, intraguild interactions can result in direct aggression, and even mortality (Bonesi and Macdonald 2004; Caro and Stoner 2003). Intraguild killing may affect not just the individuals involved, but the entire population (Palomares and Caro 1999); and because predators exert a top-down control over other species, this may impact the local ecosystem (Crooks and Soule 1999). Although intraguild killing is common among mammalian carnivores on five continents (Caro and Stoner 2003), the ecological effect that it has is not fully understood; particularly with regard to species conservation and population management (Palomares and Caro 1999).

What we do know, however, is that competitively dominant carnivores can enhance the extinction probabilities of lesser guild members through both direct and indirect means (Berger and Gese 2007; Creel 2001). For example, population densities of cheetah *Acinonyx jubatus* and wild dogs *Lycaon pictus* are negatively related to those of lions *Panthera leo* (Creel and Creel 1996; Durant 2000); and wild dogs are even susceptible to local extinction where lion densities are high (Vucetich and Creel 1999). By the same token, a reduction in dominant carnivore abundance may allow subordinate carnivore populations to expand beyond their sustainable carrying capacity; which may in turn cause similar detriment to the ecosystem, including the extinction of vulnerable species [*'mesopredator release'*; (Crooks and Soule 1999)].

Large carnivores are atypical prey for other predators, and are rarely consumed (Palomares and Caro 1999), but yet they are still killed. It has been suggested therefore that intraguild killing may serve to reduce a potential source of mortality for the killer or its offspring (Eaton 1979; op. cit. Palomares and Caro 1999), or simply to reduce competition for resources (Polis et al. 1989).

Palomares and Caro (1999) undertook a comprehensive literature review of carnivore guild interactions, and recorded nearly 100 pairs of sympatric species in which one may kill the other. Amongst the Carnivora, the Felidae were the only Family with more killers than victims, indicating their predilection for aggression. Leopard *Panthera pardus* and lion were specifically identified as being the top two most important carnivore killers by their killing of more species than any other member of the guild.

Caro and Stoner (2003) identify five forms of intraguild competition between carnivores that both separately and combined may significantly reduce the density of the subordinate species. Age, size and social behaviour are the important determinants of which is the killer and which is the victim between carnivores; for example, lions can kill all age classes of leopards, whilst leopards are only able kill lion cubs (Palomares and Caro 1999).

Populations of endangered species such as wild dog and cheetah may suffer by the over protection of dominant carnivores such as lion (Palomares and Caro 1999). With the imminent decision on whether or not to ban the import of lion trophies into the United States (see: http://www.fws.gov/endangered/what-we-do/african_-lion.html [accessed 2014-08-15]), knowledge on intraguild killing is more important

than ever. For better or worse, a ban on lion trophy imports into the United States (55.3% of the lion trophy market between 2003 and 2013; <http://trade.cites.org> [accessed 2014-08-15]) would significantly affect lion conservation practices in Africa; and while some lion populations may increase as a result, some will decrease. Both positive and negative changes in lion abundance could have far reaching impacts on the ecosystem; and as such, data on the direct effect that lions have on other species is particularly relevant forthwith to both wildlife managers and conservationists.

Although several studies of intraguild competition have shown an inverse relationship between lion and smaller carnivore densities (e.g. Creel and Creel 1996; Durant 2000; Vucetich and Creel 1999), none have previously been experimentally tested. To investigate the impact of intraguild killing on a subordinate carnivore, we took advantage of a large-scale environmental management change that created the opportunity to conduct a natural experiment. This experiment allowed us to test an intraguild hostility hypothesis (e.g. Maran et al. 1998) regarding the impact of lion on leopard population ecology.

Here we investigated two leopard sub-populations that were initially divided by an electrified fence that excluded lion from one side, and which were therefore exposed to different levels of risk (Figure 6.1). The subsequent removal of the fence at the end of the first study season allowed us to employ a simple *Before-After-Control-Impact-Pairs* (BACIP) design (e.g. Bonesi and Macdonald 2004; Stewart-Oaten et al. 1992) to experimentally test the impact of lion on leopard population dynamics by comparing the subpopulation attributes (*demographics; recruitment; survival; density; behaviour*) both *with* and *without* lion, and *before*

and *after* their introduction.

We predicted that lion would negatively impact on all leopard population attributes and behavioural ecology, and therefore hypothesise:

H₁ – leopard population demographics would differ between areas with and without lions

H₂ – leopard population recruitment and survival rates would be lower in the presence of lion

H₃ – leopard density would be higher in the absence of lion

H₄ – leopard behaviour would differ between areas with and without lions

The advantage of experimental manipulations over comparative and descriptive studies is that because they include proper controls they can be conclusive (Bonesi and Macdonald 2004). The rarity of such studies on large mammals, particularly carnivores, indicates the gravity, and often irreversibility, of such ecological changes (Bonesi and Macdonald 2004), and makes this study uniquely important.

6.3 METHODS

6.3.1 *Study site*

The Buby Valley Conservancy (BVC) is a wildlife conservancy of 3,743 km² located in the Matabeleland South province of Zimbabwe, centred at 30°7'E, 21°30'S, and about 550 m above sea level. The mean annual rainfall between 2007 and 2012 was 351 ± 76 mm, which falls mostly during November through March.

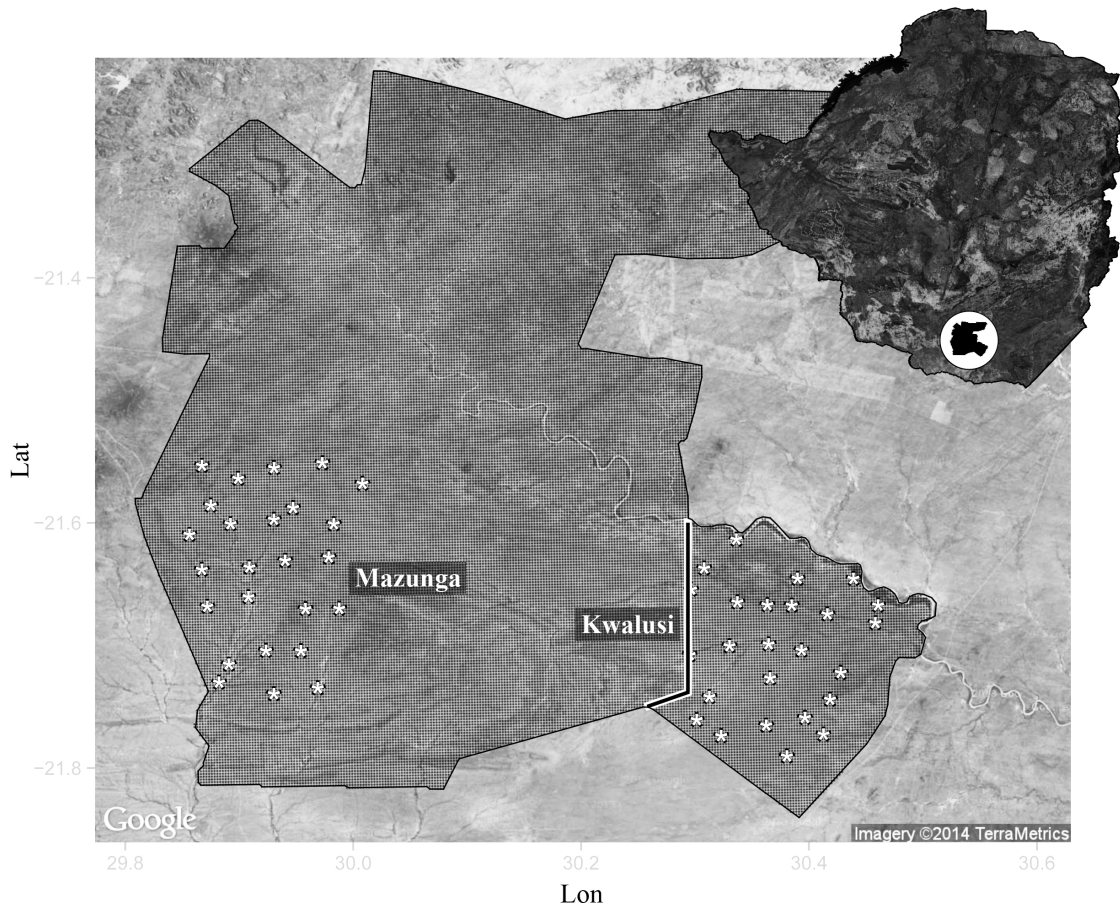


Figure 6.1: Map of the Buby Valley Conservancy (stippled), and its relative size and position within Zimbabwe (inset top right). White stars indicate the location of the camera-sites at both the ‘control’ site (Mazunga; west) and the ‘impact’ site (Kwalusi; east). The bold line (black-and-white) indicates the position of the electrified fence that separated the impact site from the control site.

May through August are the driest months of the year. The vegetation consists largely of mopane *Colophospermum mopane* and acacia *Acacia* spp. scrub and woodland, traversed by seasonal river-lines and the associated riparian vegetation, with scattered open grassland areas in between.

BVC was formed in 1994 when neighbouring cattle ranches were merged and converted into a continuous wildlife area [*catalysed by the drought of 1992*; see Cane

et al. (1994)]. Lions were reintroduced to BVC in 1999 having been exterminated by cattle ranchers prior to 1994 [*local area management records indicate that resident lions had been exterminated by 1960*]. The lion-free enclosure ('*Kwalusi*'; hereafter '*the experiment site*') was a former cattle ranch adjacent to BVC and that was also converted to a wildlife area in 1994 (K. Leathem, pers. comm.). However, this site remained separated from the main body of BVC until the 25th of August 2011, when the electrified fence dividing the areas was removed (Figure 6.1). The fence removal allowed lions previously confined within the main conservancy ('*Mazunga*'; hereafter '*the control site*') to move into and colonise the experiment site. Monitoring of lion spoor along the length of the fence's original position and within Kwalusi itself indicated that lion immigration was immediate after its removal.

The exponentially increasing BVC lion population exists at one of the greatest densities in Africa (~ 0.190 lions km^{-2} ; Figure 6.2), greater than that of the Serengeti, Tanzania (0.100 lions km^{-2} : Pusey and Packer 1987; Spong 2002), Selous, Tanzania (0.080 – 0.130 lions km^{-2} : Creel and Creel 1996, 1997), Kruger National Park (KNP), South Africa (0.096 – 0.112 lions km^{-2} : Mills 1995), and Hwange National Park, Zimbabwe (0.027 lions km^{-2} : Loveridge et al. 2007).

6.3.2 *Study design*

We based this study on the BACIP design (e.g. Baker et al. 2007; Bonesi and Macdonald 2004; Stewart-Oaten et al. 1992) to test the hypotheses that lion negatively impact on leopard population demographics, density and behaviour. In natural experiments, differences between locations and sampling periods are

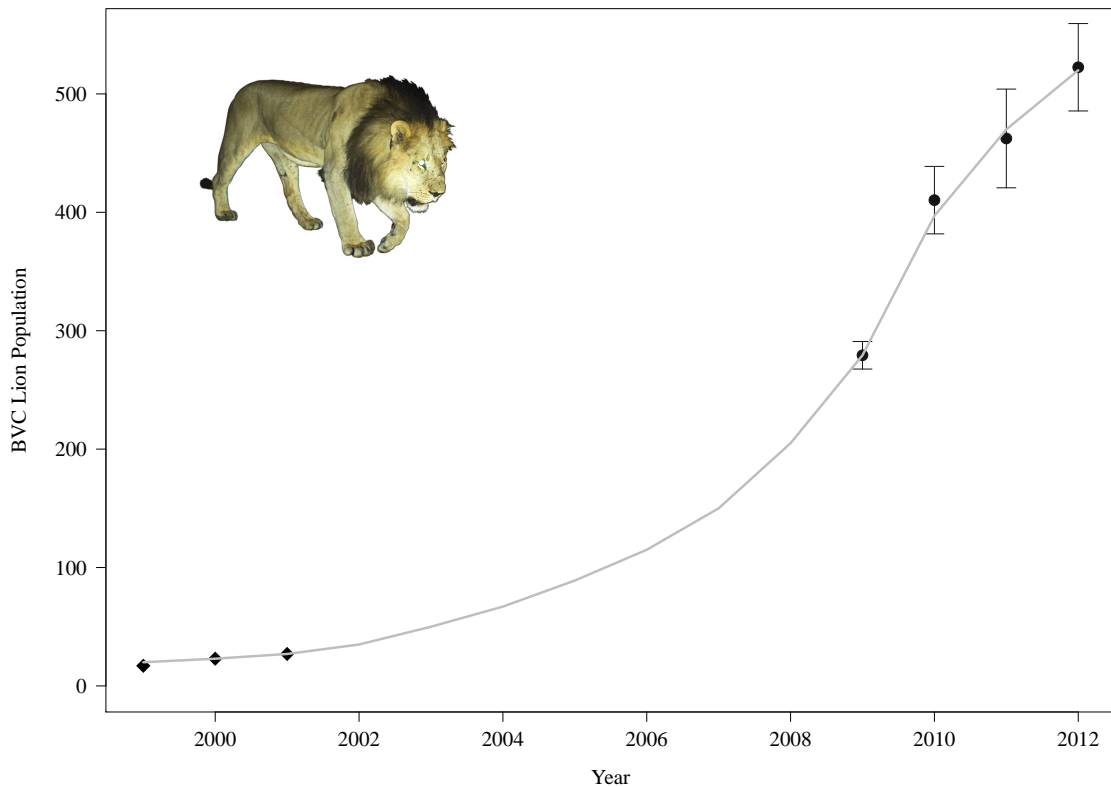


Figure 6.2: *The BVC lion population growth. Diamonds represent the known lion population abundance from monitoring of the original individuals introduced; Points indicate lion abundance calculated from spoor transect analyses, and error bars represent the standard error of the mean.*

expected, and these are allowed for in BACIP design given that any external influences not measured (e.g. weather) affect both sites similarly (Stewart-Oaten et al. 1992).

BACIP is a paired sampling design, where the control and experiment sites are surveyed simultaneously, as far as possible, and replication is achieved by taking measurements over several discrete sampling occasions both before and after the perturbation (Stewart-Oaten et al. 1992). The difference between the mean measurements at each site, before the perturbation, is taken as the expected

difference that would occur during the after period if there were no perturbation. The differences between the experiment and control measurements approximate a time-series, and a change in the mean difference between the control and impact site measurements when compared before and after the perturbation indicates that the experiment site system has been affected by the perturbation (Stewart-Oaten et al. 1992).

Testing for the effects of perturbation experimentally using a BACIP design requires at least two system observations: firstly before, and then after introduction of the lions (the ‘*impact*’, or perturbation), while all other conditions remain unchanged. It also requires simultaneous sampling of the control and experiment sites (Bonesi and Macdonald 2004; Stewart-Oaten et al. 1992). Both of these conditions were met by this study.

Before-After-Control-Impact-Pairs

Baited camera-trap surveys (see du Preez et al. 2014) were undertaken to compare leopard population density, demographics, and behaviour at two study sites (‘*control*’ and ‘*experiment*’ sites) on each side of the fence before its removal. The surveys were subsequently repeated at both sites after removal of the electrified fence and the subsequent immigration of lion (the ‘*perturbation*’) to the experiment site. The leopard population attributes at each site could therefore be compared both with and without and before and after the introduction of lion.

Lion density was determined annually at both sites via spoor transects (e.g.

Funston et al. 2010; Stander 1998). Individual lion identifications were not made via the camera-trap surveys, and the exact numbers of lions present on each occasion was difficult to determine accurately, due to the fission-fusion nature of lion society (Mosser and Packer 2009; Pusey and Packer 1987), and so was not attempted here.

A notable point is that leopard were being ‘impacted’ by lion at the control site continuously throughout this study, and we would therefore expect to detect the effect of this on leopard population attributes in our results.

Replication and randomisation is not always possible, particularly with regard to landscape level perturbations that cannot be reversed (e.g. Bonesi and Macdonald 2004; Stewart-Oaten et al. 1992), and due to the nature of our study, this was the case.

6.3.3 *Lion population surveys*

Spoor transects are commonly used for calculating relative carnivore population densities (Balme et al. 2009a; Beier and Cunningham 1996; Funston et al. 2010; Hayward et al. 2002; Smallwood and Fitzhugh 1995; Stander 1998). Stander (1998), and subsequently Funston et al. (2010), showed that there is a strong positive correlation between spoor frequency and actual population size, which means that spoor detection data can be used to monitor fluctuations in population abundances.

Spoor transects are ideal for calculating relative densities of predator populations, because the method is relatively simple, inexpensive, and the results are comparable

over time and between similar habitats in relatively close proximity (Funston et al. 2010). Some carnivore spoor will inevitably be missed during the surveys, as carnivore spoor is lighter than that of hoofed animals and so more likely to be obliterated by wind and other animals (B. du Preez, pers. obs.), and carnivores often travel alone, making the spoor harder to detect. However, insofar as these factors are constant over time and between areas, they will not affect relative density estimates (Balme et al. 2009b).

Variation in the trackability of different road surface substrates is the single largest factor limiting the accuracy of spoor transects and their use in comparisons between different survey areas (Funston et al. 2010). However, annual comparisons in the same study area, where detection probabilities remain constant (Funston et al. 2010), will reflect changes in species' abundance.

The BVC survey area road networks were assessed using a digital management map of the conservancy, and roads running west to east [*because of the position of the sun and improved spoor definition due to the shadow cast*] were identified and scouted. Spoor transects were selected, independent of habitat, along prominent roads which were most likely to offer a suitable tracking surface over the entire transect. We attempted to cover the survey area as uniformly as possible in order to eliminate habitat related bias.

The area penetration ratio [*survey area (km²)/total transect length (km)*; see Stander (1998)] is a measure of sampling effort related to adequate coverage of the survey area. Provided that this penetration ratio is ≤ 6.5 , the transects may be covered as many times as necessary to improve the precision of the density

estimation.

Selected roads were driven at a uniform speed of 10 km hour⁻¹ with a professional tracker positioned on the front of the vehicle in such a way that he could easily detect any spoor on the road. All fresh (<24 hours) lion spoor was recorded, and the spoor encounter frequency per kilometre driven was determined for each.

Lion spoor survey data analysis

We conducted a bootstrap analysis to establish whether the results obtained were representative for the area surveyed. This involved artificially augmenting the data obtained over the distance driven, for a known area, to determine that no further increase in survey effort (here, *distance driven*) would be likely to increase the encounter rate of spoor.

Spoor density was then converted to lion density, based on the known direct relationship $d = 0.303s + 0.097$ [where d is lion density, and s is spoor density (adapted from Funston et al. 2010)]. This relationship is linear ($R^2 = 0.97$), and has been shown to apply in different survey areas with differing environmental features (Funston et al. 2010), owing to the robust universal assumptions underpinning the method. The habitat, altitude and rainfall of BVC are similar to several areas that Funston et al. (2010) incorporated in their model, which is therefore applicable to our study.

6.3.4 *Prey surveys*

The tracks of prey species at both sites were also recorded during the lion spoor surveys in 2011. Although spoor transects are not ideal calculating the density of herbivores, for which sighted line transects are much better suited (e.g. O’Kane et al. 2014; Thomas and Karanth 2002), they may be used to compare the encounter rate of species (*spoor km⁻¹*) between areas, as a proxy for density. We selected five common species of herbivore (warthog *Phacochoerus africanus*, impala *Aepyceros melampus*, kudu *Tragelaphus strepsiceros*, wildebeest *Connochaetes taurinus* and zebra *Equus quagga*) in the body size range accessible to predation by both leopard and lion (<200 kg), and that have previously been detected in the diets of both species (Hayward et al. 2006; Hayward and Kerley 2005; du Preez et al. in review), and compared the prey encounter rates between the control and experiment sites to determine whether there was a notable difference that might explain any difference in leopard density between the sites.

6.3.5 *Leopard population surveys*

Camera-trapping surveys were conducted from the 5th of May to the 26th of June 2011 at the experiment site, and from the 4th of July to the 22nd of August 2011 at the control site. Lions were then able to enter the experiment site from the 25th of August 2011 with the removal of the electrified fence, and the camera-trap surveys were repeated the subsequent year during the same season, from the 11th of May to the 29th of June 2012 at the experiment site, and from the 10th of July

to the 28th of August 2012 at the control site.

The area of the minimum camera-trap perimeter was measured in ArcMap 10.1 (ESRI) using a 100% polygon with the periphery camera-traps. This resulted in a similar area between sites: 281 km² for the experiment site, and 284 km² for the control site.

Equipment

The camera-trap units that were used in this study were either Cuddeback Capture or Cuddeback Attack models (Cuddeback, WI, USA). The Attack model was placed at odd camera-trap site numbers, and the Capture model at even site numbers, so that there was approximately equal distribution of each model within each survey area.

Baited camera-trap setup

Baited camera-trapping has advantages over unbaited camera-trapping as the baits attract leopards to the cameras, which increased both capture probability (by 138% – 147%) and capture frequency (by 478% – 617%) over unbaited surveys (du Preez et al. 2014).

GPS data from tagged leopards in BVC indicated home-range sizes for females (N = 7) of 61 ± 13 km² and males (N = 8) of 154 ± 21 km². Camera spacing was thus based on a modest home-range size of 40 km², and cameras were set at a

maximum of 5 km apart based on one camera per 20 km².

Baits, weighing approximately 25 kg each, were hung from trees at the camera-trap sites so that the lowest part of the bait was at least 2 m off the ground. A wooden pole, on which leopards could stand while they fed, was leant against the tree under the bait (Figure 6.3). The camera-trap was placed perpendicular to the right hand side of the pole, approximately 3 m away, which ensured that the right hand flank of each leopard visiting the trap site would be photographed as it used the pole to access the bait. The baits were fixed in place with nylon rope so that they could not be removed and consumed out of sight of the camera. The baits were checked at least every second day, and replaced before they were finished.



Figure 6.3: *Camera-trap photos of a collared male leopard (ID: 11K05M04), a female leopard (ID: 11K11F08) and one of her two small cubs (neither of which survived until the 2012 survey) at the experiment site camera-trap number 11 in the 2011 survey. Note the side-on position of the leopard, facilitated by the leaning pole used to guide the animal's access to the bait. This camera-trap setup ensured broad side photographs of the right flank of each individual and allowed straightforward comparison between photographs for accurate identification.*

6.3.6 *Leopard population demographics*

From the resulting photographs recorded at each camera-trap station (e.g. Figure 6.3), individual leopards were identified based on the unique patterns of their pelage. The baited camera-trap setup facilitated accurate sexing of individuals as their genitals were always visible in some of the images recorded. However, aging of leopards from photographs is notoriously inaccurate (e.g. Balme et al. 2012), and therefore all independent leopards were considered as ‘*adult*’, whilst cubs were defined as either ‘*small*’ (<1 yr old) or ‘*large*’ (>1 yr old).

6.3.7 *Leopard population recruitment and survival*

The local recruitment rate was defined as the proportion of large cubs [i.e. *older than 1 year in 2011*] that survived to independence and remained within the study site, being detected again as independent adults in 2012.

The local survival rate was calculated as the proportion of the 2011 population that were subsequently detected in 2012. Missing individuals may have died or emigrated.

Unfortunately, the lack of surveys before and after this study prevents the recruitment and survival rates from being calculated for the 2011 and 2012 seasons respectively.

6.3.8 *Leopard population density*

The camera-trap data were analysed in *R* (*R 3.0.1*, *R Core Team 2013*), using the spatially explicit capture-recapture (SCR) packages *secr* version 2.5 (Efford 2013) and *SPACECAP* version 1.0.6 (Gopalaswamy et al. 2013) to calculate the leopard population densities.

SCR submodels used to analyse felid capture-recapture data (see Royle et al. 2014) often allow for heterogeneity resulting from differential capture probabilities arising from the territorial nature and behavioural variability of individual carnivores, as well as a varying number of camera-traps between home ranges (Karanth and Nichols 1998). Baited survey analyses should also consider trap-response in terms of whether or not there is a positive reaction towards the trap sites (Karanth et al. 2011a; Karanth et al. 2011b). Whilst *SPACECAP* offers only ‘*trap response present*’ or ‘*trap response absent*’ submodels, we were able to test several *secr* submodels, including the ‘*base*’ (submodel: $g0 \sim 1$), ‘*site*’ (submodel: $g0 \sim k$), ‘*sex*’ (submodel: $g0 \sim Sex$, $\sigma \sim Sex$), ‘*time*’ (submodel: $g0 \sim T$), ‘*behaviour*’ (submodel: $g0 \sim h2$) and ‘*trap response*’ (submodels: $g0 \sim bk$ and $g0 \sim Bk$) models.

SCR submodels

The *secr* submodels were compared using Akaike’s Information Criterion (AIC) and Akaike’s Information Criterion corrected for finite sample size (AICc) (Burnham and Anderson 2002; Karanth et al. 2011b), which showed that the *site behavioural*

response submodel ($g0\sim bk$) fitted the independent adult data best, followed by the *site transient response* submodel ($g0\sim Bk$) (see Royle et al. 2014). Both of these submodels relate to leopard behaviour, and indicate a positive response towards the survey sites (e.g. Royle et al. 2011). This concurs with incorporating individual behavioural heterogeneity and trap-response, as suggested by Karanth et al. (2011a). *SPACECAP* offers only trap response present and trap response absent submodel options, and given both the AIC results of the *secr* submodel comparison, and the logical assumption that the baits would elicit some form of response from the leopards, we used the *SPACECAP* trap response present submodel definition in calculating the densities. The *secr* site behavioural response and *SPACECAP* response present submodels are also the most comparable models between the SCR packages in terms of the parameters used (Efford 2013; Gopalaswamy et al. 2013; Royle et al. 2014).

6.3.9 *Leopard population behaviour*

Because of the unreplicable nature of the study (e.g. Bonesi and Macdonald 2004; Stewart-Oaten et al. 1992), the SCR density calculations cannot be directly compared for statistical differences between areas or seasons. However, feeding at baits effectively represents scavenging or kleptoparasitic behaviour, which both lion and leopard naturally exhibit. This potentially exposes leopard to risk, as lion are similarly attracted to the same sites, and leopard are thus likely to be wary of lion whilst at a bait, and avoid the bait altogether if lion are in the vicinity. We therefore used individual detections at each camera-trap station as a proxy for

leopard behaviour in the presence and absence of lion. To this end, we determined the mean number of individual leopards detected per sampling occasion for each survey (50 × 24 hour sampling occasions), for which we calculated the mean differences between the control and experiment sites both before and after the introduction of lions to the experiment site. Any difference in leopard density per site and season was controlled for by dividing the number of individuals detected at each sampling occasion by the total number of individuals detected for that survey, which was effectively a calculation of daily detection rate [i.e. *the proportion of the population detected per day*].

Due to the relatively short total duration and unrepeatability of this study, the effect size and direction may be more practically indicative of the relationship than the *P*-value (Nakagawa and Cuthill 2007; Stewart-Oaten et al. 1992), and we therefore calculated both. We examined the difference in leopard behaviour *with* and *without*, and *before* and *after* lion risk, using the *t.test* function in *R*. We calculated the effect size, in terms of Cohen’s *d* and Pearson’s *r* (Nakagawa and Cuthill 2007), using the *tes* function in the *R* package *compute.es* (Del Re 2014).

6.4 RESULTS

6.4.1 *Prey encounter rates*

The encounter rates of prey species were generally quite similar between the control and experiment sites in 2011 (Table 6.1). Slightly more warthog spoor was detected, but less zebra and wildebeest spoor, was detected at the experiment site

than at the control site.

Table 6.1: *Encounter rates of prey species (spoor km⁻¹) at both the control and experiment sites in 2011*

Prey species	Encounter rate (Spoor km ⁻¹)	
	Control Site	Experiment Site
Warthog	0.606	1.373
Impala	10.057	10.805
Kudu	2.291	3.098
Wildebeest	14.648	8.135
Zebra	15.537	13.737

6.4.2 *Leopard population demographics*

A total of 94 individual leopards were photographed on 1,905 separate occasions between 2011 (*‘before’*) and 2012 (*‘after’*) at both the control and experiment sites (24 individuals were observed in both 2011 and 2012). The demographics recorded for each leopard population during each survey are presented in Table 6.2. No lion were detected at the experiment site in 2011. However, lion were detected at the experiment site in 2012, and at the control site in both 2011 and 2012.

In 2011, dependent cubs made up 37.1% of the leopard population at the experiment site when lion were absent, but only 12.0% of the population at the control site where lion were present. Additionally, in 2012 after the introduction of lion, the proportion of cubs at the experiment site had reduced from 37.1% to only 12.1% of the population, which was comparable to the control site in 2012 of still

only 12.0%, none of which had remained from the previous year.

Table 6.2: *Leopard demographic summary for each survey*

Site		Leopards	Captures	Male (Adult)	Female (Adult)	Large (Cub)	Small (Cub)	Recruited †	Survived §	Lions
Impact	2011	35	645	7	15	8	5	–	54.3%	Absent
Impact	2012	33	530	8	21	0	4	75.0%	–	<i>Present</i>
Control	2011	25	329	8	14	0	3	–	44.0%	<i>Present</i>
Control	2012	25	401	10	12	0	3	0.0%	–	<i>Present</i>

† Recruitment refers to the proportion of large cubs (i.e. older than 1 year in 2011) that survived to independence and remained within the study site.

§ Local survival refers to the proportion of the 2011 leopard population that were still present in 2012.

Despite all of the mothers being detected in both seasons at both sites, no small cubs that were recorded at both the control and experiment sites during the 2011 surveys were detected (as large cubs) during the 2012 surveys. The only leopard population in which large cubs were detected (i.e. small cubs had survived from the previous season) was at the experiment site before the presence of lion. No large cubs were detected after lion were present at the experiment site, and no large cubs were detected in either season at the control site where lion were always present (since 1994).

6.4.3 *Leopard population recruitment and survival*

At the control site, where lion were always present, there was no local population recruitment from the 2011 leopard population into the 2012 population, due to the

absence of large cubs in 2011. In comparison, six of the eight large cubs recorded at the experiment site in 2011 without lion were recruited into the 2012 population as independent adults. None of the five small cubs recorded in 2011 were subsequently recorded in 2012 after the introduction of lion however, despite all mothers being recorded in both surveys.

There was a lower survival rate of only 44.0% at the control population exposed to lion in 2011, compared to 54.3% survival in the experiment population absent lion, despite the similar numbers of individuals captured at each site each year.

6.4.4 *Leopard population density*

The leopard population density at the experiment site, calculated with both the SPACECAP and secr SCR models, was reduced between 2011 and 2012, after the introduction of lion. There was also a reduction in leopard population density at the control site between 2011 and 2012, however this was expected, as lions were always present at this site (Table 6.3).

Table 6.3: SPACECAP and secr model resultant population density calculations for each site and season, comparing the results using independent adult data with that of all leopard demographics

Site		Leopard density (leopards km ⁻²)		Lion [lions km ⁻²]
		SPACECAP	secr	[Spoor]
Impact	2011	0.085 ± 0.012	0.082 ± 0.014	0.000 ± 0.000
Impact	2012	0.071 ± 0.010	0.072 ± 0.013	0.202 ± 0.020
Control	2011	0.054 ± 0.010	0.045 ± 0.009	0.202 ± 0.018
Control	2012	0.040 ± 0.007	0.039 ± 0.008	0.187 ± 0.012

Lion density was similar between the experiment site in 2012 and the control site in 2011 and 2012. No lions were detected at the experiment site in 2011.

6.4.5 Leopard population behaviour

In 2011, the mean daily detection rate of leopards was 10.2% higher at the experiment site, where there were no lions present. However, in 2012, when lions were present at both sites, there was only a difference of 0.1% leopard day⁻¹ detected between sites (Figure 6.4).

There was a significant reduction in the mean detection rate difference between the control and experiment sites before and after lions were present at the experiment site (Paired *t*-test: $t_{97.214} = 3.774$, $P < 0.001$, $d = 0.75$, $r = 0.36$) indicating that lions impacted on leopard detection rates.

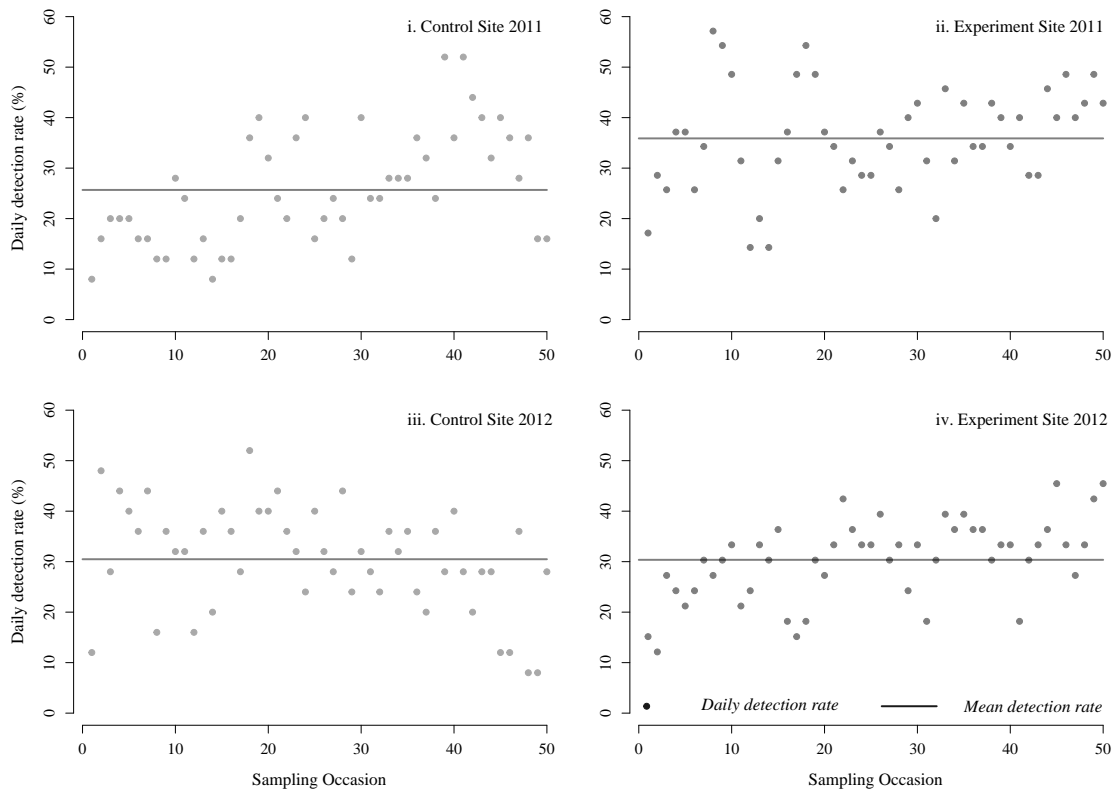


Figure 6.4: *Leopard detection rates* (Percentage of total leopard detected day⁻¹) per survey. Points represent the daily detection rate, the line represents the mean detection daily detection rate per survey. The mean daily detection rates were: i. control site 2011 = 25.7%; ii. experiment site 2011 = 35.9%; iii. control site 2012 = 30.5%; and iv. experiment site 2012 = 30.4%.

6.5 DISCUSSION

Opportunities for natural experiments on the scale that we have conducted here are very rare, almost unknown for large carnivores, and therefore the insight that they provide is precious. The lion exclosure fence and its subsequent removal provided us with a unique opportunity to experimentally test an intraguild hostility hypothesis between two competitively mismatched species. Apart from the immigration of lion, the removal of the electrified fence did not have a large effect

on the rest of the environment, with regard to leopard; because prey density within the experiment site was, if anything, slightly lower than it was at the control site while the fence was in place. Therefore, by comparing firstly leopard populations with and without lion present, and secondly a leopard population before and after the introduction of lion, we found that lion impacted on: i. *leopard population demographics*, ii. *recruitment and survival*, iii. *density* and iv. *behaviour*.

Field based studies of competition are the most conclusive (e.g. Baker et al. 2007; Stewart-Oaten et al. 1992). However, experimental tests necessarily require a control (Bonesi and Macdonald 2004), and this is rarely available for large mammalian species in their natural environment. Even rarer is the opportunity to monitor a population both before and after the introduction of a putative competitor, and the fact that we were simultaneously able to take advantage of both situations further improved our ability to make inference.

We estimate that as many as 77 lion (including cubs) entered the 464 km² experiment site within a year of the exclosure fence removal. In comparison, just 17 otters *Lutra lutra*, released over 1,353 km², were found to significantly reduce the population density of the invasive American mink *Mustela vison* (Bonesi and Macdonald 2004). Leopard density was lower where lions were present compared with where they were absent; and furthermore, leopard population density at the experiment site was reduced following the introduction of lion. Although leopard are sympatric with lion over a large portion of their natural range, the lion in BVC exist at a very high density, which may have exceeded the threshold that leopard can naturally cope with.

Despite the fact that the same number of leopard were recorded at the control site in both surveys, less than half of the original 2011 population were subsequently detected in 2012. The additional land area with the inclusion of the impact site (approximately 20% of the area of the control site) did little to reduce the density of the exponentially increasing lion population in BVC.

The low survival rate of the leopard in our study area is cause for concern, especially when compared to other systems where leopards are monitored. For example, on a private reserve adjacent to KNP, the survival rate of leopard cubs prior to independence is estimated at 37% (Balme et al. 2013), while within KNP [*less than 100 km as-the-crow-flies from BVC*], where lion density is only 0.096 – 0.112 lions km⁻², adult leopard survival is estimated at 81% for adults (Bailey 1993). In comparison, on BVC where the lion density is approximately 0.190 – 0.200 lions km⁻², we recorded a 0% survival rate of cubs in both leopard populations when lions were present, and a much lower adult survival rate of only 44%.

Lion scat samples collected at the study site have been found to contain leopard hair (B. du Preez, unpublished data). As large cubs were detected only in the leopard population where lion were absent (2011 experiment site), and not in any of the other three leopard populations in which lion were present (2012 experiment site, 2011 and 2012 control site), we therefore posit that the reduced cub survival in our study area was due to intraguild killing by lion.

6.6 CONCLUSION

The management of large carnivore populations could be necessary for the successful conservation of smaller guild members (Ray et al. 2005). This may be particularly relevant in closed or fenced systems where resource limitation may enhance interspecific competition (Cristescu et al. 2013), and where limited space increases interspecific encounter rates (Chesson 1985; Hanski 1994).

The combination of low cub survival and high adult turnover indicates that the high lion density in BVC may be leading to the creation of a leopard population sink that may soon require recruitment from a separate source population to remain extant (e.g. Delibes et al. 2001; Holt 1985).

Lion and leopard are both iconic carnivores that are facing extensive range contraction and population decline throughout Africa (Bauer et al. 2013; Henschel et al. 2008), and understanding the factors affecting their behavioural ecology is not only fundamentally interesting, but also practically important. Here we reveal the paradox that the successful conservation of one species is leading to local endangerment of another, and this study highlights the need for careful conservation through informed and holistic management.

6.7 Acknowledgements

We would like to thank the BVC shareholders and management for allowing us to conduct the research, Blondie Leathem for his support and enthusiasm, Paul Trethowan and Matt Trisos who helped in the field, Sandra Baker for a critical reading of the manuscript, and Tom Hart, Paul Funston and Alex Braczkowski for

discussions regarding the analyses. Dusty Joubert conceived of the baited camera-trap setup. This project was sponsored by The Darwin Initiative for Biodiversity Grant 17-031. D.W.M. gratefully acknowledges the support of the Robertson and Recanati-Kaplan Foundations. B.dP. would like to thank The Beit Trust for scholarship funding and support.

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Chapter 7

Discussion and Conclusion

7.1 DISCUSSION

Large carnivores receive more conservation attention than smaller and less conspicuous species; and while animals such as lion are undeniably valuable for both ecosystem services and as ‘flagship’ and ‘umbrella’ species (Macdonald et al. 2010), single-minded prioritisation of their conservation (e.g. Linnell and Strand 2000) could compromise the conservation status of smaller members of their guild through elevated levels of intraguild persecution (e.g. Harihar et al. 2011).

Historically, interference competition has been more difficult to measure and is therefore understudied compared to exploitative competition (Valeix et al. 2007). There is also a tendency to focus research on endangered species; which may in part be responsible for the lack of scientific attention leopards receive, being the most abundant large carnivore in Africa (Nowell and Jackson 1996). However, because of their range, and extensive overlap with so many other carnivores, leopards are the ideal model species on which to investigate the impacts of intraguild competition on behavioural ecology.

7.1.1 *Main findings*

This research aimed to comprehensively explore the sympatric relationship between two competitively mismatched large carnivores. Intraguild competition with lions was shown to impact on leopard density and demographics (Chapter 6; *this thesis*), and in response, leopards displayed: behavioural adjustment and

altered habitat transition probabilities due to predation risk (Chapter **3**; *this thesis*); significant avoidance of spatiotemporal overlap, static and dynamic interaction (Chapter **4**; *this thesis*); and a relatively low dietary niche overlap with lions (Chapter **5**; *this thesis*).

The ecological dynamics between these aggressive competitors is fairly intuitive, and may therefore be not that surprising to one familiar with large carnivore ecology (e.g. Caro and Stoner 2003; Harihar et al. 2011; Macdonald et al. 2010; Palomares and Caro 1999). While the interaction between lions and leopards has never been directly investigated before, some authors have alluded that it is either neutral (Mills 1991) or negative (Bailey 1993), without being able to collect data and experimentally test hypotheses. Most research on African carnivore interaction with lions has been limited to cheetah or wild dogs, largely due to a combination of their endangered status and largely diurnal activity (e.g. Broekhuis et al. 2013; Caro 1994; Cozzi et al. 2012; Creel 2001; Creel and Creel 1996; Creel et al. 2001; Durant 1998, 2000; Laurenson 1994, 1995; Vucetich and Creel 1999). However, this study took advantage of relatively common remote research tools (i.e. camera-traps and biotelemetry), but applied and analysed them specifically to determine the consequences of interspecies interaction and reveal the underlying rules of behaviour. Although observational data may allow a large amount of detail when it can be collected without bias, analysing remote monitoring data with powerful computer algorithms may be even more valuable; facilitating access to large samples of otherwise elusive species, while still producing high quality biological insight.

7.1.2 *The wider context*

A large number of studies indicate that extinction-risk is unevenly distributed in space, which impedes the application of blanket conservation initiatives to achieve conservation goals (Olea and Mateo-Tomas 2014). Heterogeneity of species-specific risk, and the requirement for situation specific approaches, is rarely recognised and implemented (Mateo-Tomas and Olea 2010). This is typified in the case of the lion in South Africa, where excess lions were translocated from one small fenced reserve to another until there was nowhere left send them (Miller and Funston 2014). The collective management expense of these populations is excessive, and their value to the species' genetic diversity is non-existent (Miller and Funston 2014). What's more is that very little published research was undertaken on these areas in assessing the impact of the overpopulated lions on mesopredator and prey populations; subsequently, some managers have reported noticeable declines in certain species (biased towards those that are generally easier to observe).

Lions are mainly limited by anthropogenic influence (Packer et al. 2013a) and local prey biomass (e.g. Valeix et al. 2010), and do not suffer the same intraguild predation and population suppression that they exert on lesser guild members (e.g. Creel and Creel 1996; Laurenson 1995; Palomares and Caro 1999). Larger carnivores benefit from physical superiority in competitive interactions, and may have relatively more important ecological influence. As the remaining land available to wildlife in Africa rapidly fills up with lions, mesocarnivore refuges dwindle. Spatial heterogeneity is considered key to carnivore coexistence (Berger and Gese 2007; Karanth and Sunquist 2000), and cheetahs have even been shown

to have higher densities outside of protected areas than within them; preferably eking out an existence amongst people rather than facing intraguild competition by lions (Caro and Laurenson 1994; Laurenson et al. 1995). Similarly, wild dogs avoid areas with high concentrations of impala (their main prey species) as these areas were associated with higher probability of encountering lions (Creel and Creel 1996). In certain areas wild dogs and cheetahs have even suffered greater intraguild persecution directly because of lion protection policies in those areas (Caro and Laurenson 1994; Creel and Creel 1996; Gorman et al. 1998; Kelly et al. 1998). With the potential for ecosystem level consequences, the negative effects of carnivores desperately need to be considered when planning conservation initiatives (e.g. Harihar et al. 2011; Wegge et al. 2009).

The question therefore – *addressing the elephant in the room both practically and ethically* – is what to do with excess lions? The options for lion translocation are limited by the available land area dedicated to wildlife; and as this becomes saturated, conservationists face contraception, euthanasia or commercial hunting with which to control lion populations (see Miller and Funston 2014). All these options have their pros and cons; however if wildlife is to persist in the long run, it has to be economically viable.

7.1.3 *Carnivore values: practical conservation in Africa*

Carnivore conservation outside of protected areas is boosted by revenue from safari hunting (Bauer and Van Der Merwe 2004; Brassine and Parker 2012; Child 2000; Treves 2009), and in Africa the land area conserved for trophy hunting exceeds

that conserved in national parks by nearly 25% (Lindsey et al. 2007). There is a general consensus among conservationists that Africa's national park network is not sufficient for maintaining biodiversity, and this creates a market for private wildlife areas (Lindsey et al. 2006). However, for these private conservancies to be successful, they have to be financially self-sustainable.

Big cats have the potential to generate significant income from both photographic tourism and trophy hunting operations (Funston et al. 2013). In Zimbabwe, trophy hunting is conducted on a total area of over 65,000 km² in size outside of national parks. As trophy hunting is the most profitable form of consumptive wildlife use (Child 2000), these areas are actively protected against illegal poaching, habitat destruction and alternative land use, such as agriculture (Lindsey et al. 2006); and as a consequence, they are therefore valuable to regional conservation. This is highlighted by the fact that in Zimbabwe, 16.6% of the total land area is actively protected by safari hunting operations, compared to only 12.7% of the country that lies within national parks (Lindsey et al. 2007).

On the Save Valley wildlife conservancy (SVC) in Zimbabwe, 17 male lions were hunted over a 5 year period, generating a gross income of US\$182,580 year⁻¹. In comparison, 144 leopards were hunted over the same period, resulting in earnings of US\$427,046 year⁻¹ (Funston et al. 2013). Funston et al. (2013) calculated that, in terms of predation, the cost of carrying lions at any density outweighed the value of hunting them. In contrast, leopards were profitable to the landowners (Balme et al. 2012; Funston et al. 2013). This cost of lions in an economical context highlights the need to carefully manage lion populations regarding the broader objectives of

each particular system; lion populations may require external control if wildlife conservation is to be successful outside of protected areas (Funston et al. 2013).

Leopards are probably only protected in about 10% of their current natural range (Martin and de Meulenaer 1988; Nowell and Jackson 1996; Ray et al. 2005) although this may be far less (Lindsey and Chikerema-Mandisodza 2012), and their current population status and trends with Zimbabwe are not known. Added to this, political instability (e.g. Dudley et al. 2002) and resultant land-use changes within the country since 2000 (particularly the conversion of many private wildlife conservancies into subsistence farms) have probably impacted on the national leopard population status (Lindsey and Chikerema-Mandisodza 2012). Bushmeat hunting is also a growing problem within Africa that threatens the persistence of wildlife in many areas (Lindsey et al. 2011a; Lindsey et al. 2011b), and is likely to have a devastating impact on local leopard populations (Henschel et al. 2011; Lindsey and Chikerema-Mandisodza 2012). The status of the leopard may therefore only be secure in safari hunting areas where offtake is limited, and wildlife and habitat actively protected from illegal destruction (Lindsey and Chikerema-Mandisodza 2012). Regionally increasing incentive for wildlife conservation outside of protected areas is considered crucial for its persistence (Brassine and Parker 2012; Marker and Dickman 2005); Zimbabwe remains one of the most popular hunting destinations in Africa, and leopards are the second most sought after trophy species (Lindsey et al. 2006) – which ironically might save them from anthropogenic persecution.

7.1.4 *What's next?*

There is an on-going theoretical debate amongst scientists as to the most important priorities and foci of contemporary research. Some theorists argue that research on endangered species is necessary for their future survival; others claim that endangered species are doomed to extinction anyway (e.g. Meyer 2006), and that we should concentrate on protecting species before they become endangered, saving more in the long-term (e.g. Possingham et al. 2002); still others contend that data on species even well on their way to extinction is useful to future conservation efforts of other species (see Trimble and Van Aarde 2010). Scientists often have the luxury of separation from the on-the-ground realities of practical management; and debates between them can continue *ad nauseam* in irrelevance – the so-called ‘academic point’. An example of this is the recent debate over the pros and cons of fences for conserving lions that has divided scientists (see in order: Packer et al. 2013a; Creel et al. 2013; Packer et al. 2013b; Woodroffe et al. 2014); while the reality is that each wildlife landowner faces situation-specific challenges to which the general opinions of academics make little difference, and government legislation that removes any choice. However, despite differences in opinions and approaches, what all do agree on is that the conservation of carnivores is vital for the role they play in ecosystem services – and that we need a greater understanding of their ecology within the context of a balanced and stable system.

With their superior ability among large carnivores to survive outside of protected areas, even thrive within human dominated landscapes (Harihar et al. 2011; Martin and de Meulenaer 1988; Myers 1976; Nowell and Jackson 1996; Seidensticker 1976),

leopards are surely secure in their conservation status; for the time being. However, by better understanding the natural impacts on such a resilient species, we also glean an insight to the greater holistic ecosystem; and reinforce the need for carefully considered management strategies.

7.2 CONCLUSION

There is great concern over absolute lion numbers in Africa (e.g. Bauer and van der Merwe 2004), despite their complete saturation of almost all of the remaining available habitat (e.g. Miller and Funston 2014). And while lions may be considered ‘umbrella’ species by the coincident protection of certain other biota (e.g. Williams et al. 2000), it is important to note that this cover does not necessarily extend to their subordinate intraguild competitors.

Despite their particularly resilient nature, leopards have already disappeared from a large proportion of their historical range (Nowell and Jackson 1996; Ray et al. 2005), and data on the threats they face are crucial to their conservation, as well as informing the conservation of even less accessible species.

The results of this research are not considered to be at odds with the data available for intraguild competition between carnivores. Rather, they further this knowledge. Indeed, what has been presented here regarding the leopard’s response to risk, and their fantastically generalist nature, may be considered a surrogate for large carnivore competition in the wider ecosystem framework; both regionally and globally.

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THE END.



“Conservation cannot be done on a tourist visa.”

– K. Ullas Karanth
(1st of May 2013, The University of Oxford)