

ASPECTS OF
THE ECOLOGY OF LEOPARDS
(*PANTHERA PARDUS*)
IN THE LITTLE KAROO,
SOUTH AFRICA

A THESIS SUBMITTED IN FULFILMENT OF THE REQUIREMENTS OF
DOCTOR OF PHILOSOPHY OF
RHODES UNIVERSITY
DEPARTMENT OF ZOOLOGY AND ENTOMOLOGY

BY
GARETH MANN

FEBRUARY 2014

ABSTRACT

ABSTRACT

Leopards (*Panthera pardus*) are the most common large predators, free roaming outside of protected areas across most of South Africa. Leopard persistence is attributed to their tolerance of rugged terrain that is subject to less development pressure, as well as their cryptic behaviour. Nevertheless, existing leopard populations are threatened indirectly by ongoing transformation of natural habitat and directly through hunting and conflict with livestock farmers. Together these threats may further isolate leopards to fragmented areas of core natural habitat. I studied leopard habitat preferences, population density, diet and the attitudes of landowners towards leopards in the Little Karoo, Western Cape, South Africa, an area of mixed land-use that contains elements of three overlapping global biodiversity hotspots. Data were gathered between 2010 and 2012 using camera traps set up at 141 sites over an area of $\sim 3100\text{km}^2$, GPS tracking collars fitted to three male leopards, scat samples ($n=76$), interviews with landowners ($n=53$) analysed in combination with geographical information system (GIS) layers. My results reveal that leopards preferred rugged, mountainous terrain of intermediate elevation, avoiding low-lying, open areas where human disturbance was generally greater. Despite relatively un-fragmented habitat within my study area, the leopard population density ($0.75\text{ leopards}/100\text{km}^2$) was one of the lowest yet recorded in South Africa. This may reflect low prey densities in mountain refuges in addition to historical human persecution in the area. Currently local landowners are more tolerant of leopards than other wildlife species with incidents of conflict involving leopards being rare relative to black-backed jackals (*Canis mesomelas*), baboons (*Papio hamadryas*), caracals (*Caracal caracal*) and porcupine (*Hystrix africaeaustralis*). Although current levels of conflict between leopards and stock farmers are low, leopards do depredate livestock, which constitute 10-15% of their diet. Improved livestock husbandry measures and co-operation between conservation authorities and farmers are necessary to mitigate such conflict and balance economic security with biodiversity conservation in the region.

ABSTRACT

Leopards are the only remaining top predators throughout much of the Little Karoo and the Western Cape and as such are predicted to play a critical role in ecosystem structure and the survival of other species. Current high levels of connectivity between areas of suitable leopard habitat bode well for the conservation status of leopards within this region and future conservation efforts need to ensure that narrow corridors linking such habitat are preserved. The potential for leopards to serve as both an umbrella and a flagship species for biodiversity conservation suggests that long term monitoring of this population would be a conservation priority for the Little Karoo.

ACKNOWLEDGMENTS

ACKNOWLEDGMENTS

Doing this project has been a privilege, and I've been fortunate to not only have been able to spend three years roaming one of the world's truly unique places, but also to have had incredible support from a wide variety of people while doing so. It is my pleasure to thank the following individuals and organisations who made this project possible:

- I am extremely grateful to my supervisors, Dr. Daniel Parker and Prof. Justin O'Riain for their help, advice, and constructive criticism throughout the development, analyses and writing of my thesis, as well as providing equipment and funding. Their help in dealing with the various non-scientific problems that arose at various times over the past four years is particularly appreciated!
- The financial and logistical assistance from the Cape Leopard Trust Scholarship towards this research is hereby gratefully acknowledged. Opinions expressed and conclusions arrived at, are those of the author and are not necessarily to be attributed to the Cape Leopard Trust. I would especially like to thank Dr. Quinton Martins for his assistance in setting up the project and his advice on all things leopard and conflict-related.
- The Nedbank WWF Green Trust provided substantial funding (grant no. GT1616 to Gareth Mann) that allowed me to do the camera trap survey and generally broaden the scope of the project, as well as covering most of the project running costs from 2011 onwards.
- This research was also supported by the International Foundation for Science, Stockholm, Sweden, through a grant to me (Gareth Mann), for which I am very grateful.
- Rhodes University provided funding to attend the Zoological Society of South Africa conference in 2011, the International Wildlife Management Congress in 2012 and the South African Wildlife Management Association symposium in 2013, as well as providing me with funding via a discretionary bursary from the Director of Research in 2013.
- Blackie & Associates for their generous donations to the project.

ACKNOWLEDGMENTS

- The Bateleurs for sponsoring a tracking flight in 2012.
- C.P. Nel Motors in Mossel Bay for sponsoring much-needed services of the project vehicle.
- CapeNature provided me with extensive support throughout my project, including provision of accommodation for the duration of my fieldwork, a permit for camera trapping and leopard capture (permit no. AAA-004-00592-0035), and access to GIS data. Ivan Donian, Dr. Alan Wheeler, Theresa van der Westhuizen, Meijer Julies, Jan Coetzee, Martin Botha and Erika Swanepoel all assisted me by providing administrative support, advice and information. Thanks also to Theo Taute for assistance with the camera trap survey and for introducing me to various landowners. Martin Botha of Gamkaskloof Nature Reserve helped to maintain cameras, and assisted me with identifying camera trap locations in that area
- Tom Barry and his superb team of rangers and conservation assistants at Gamkaberg Nature Reserve: Willem Goemas, Cornelius Julies, Abraham Lottering, Jan Oransie, Skhumbuzo Tembe, Willem Wagenaar, Joemat Delpont, Tom Horne and Morris Van Wyngard were incredibly supportive throughout my three years in the field in a wide variety of ways. This included (but was not limited to) maintaining the water supply to my house despite frequent blockages, breakages due to baboons, and the occasional flood, helping to carry heavy cage traps to trapping sites, giving me access to their workshop, assisting with checking camera traps, collecting scats and rescuing me when my project vehicle broke down. I owe them all a huge debt of gratitude for so often going beyond simply 'doing their job' to assist me. Tom Barry's enthusiasm for the project, vast local knowledge and love for nature were a constant source of inspiration to me, and a major contributing factor to the success of this project.
- The South African Weather Service provided me with weather data for my study area.
- Dairen Simpson trained me in the art of footloop trapping, and taught me a huge amount during his stint on the project in 2010. Thanks for all your help and being willing to go beyond the call of duty, Big D!

ACKNOWLEDGMENTS

- Much of my work was done on private land, and would not have been possible without the support provided by the various landowners who allowed me access to their land and were willing to let me set up my camera traps and/or search for leopard kills on their property. I am especially grateful to those landowners who showed great patience in sitting through lengthy interviews!
- Chris Steer, and by extension Ian and Rosheen Kriegler, provided me with (amongst other things) accommodation and also loaned me a vehicle when the project vehicle broke down, without which I would not have captured one of the leopards. Chris also assisted by monitoring a cage trap on my behalf. I am most grateful for their constant support, enthusiasm for the project, and for all the coffee, beers and braais that we shared, all of which helped to make my time in the field that much more enjoyable.
- Joan and Peter Berning allowed me unrestricted access to their property throughout the project, as well as taking me on a tracking flight in 2011.
- Louis Smit assisted in monitoring cage traps in 2011.
- Valerie Enzer and Pierre de Klerk for their generosity in providing me with accommodation on their properties when I was working in the surrounding areas.
- Dr. Willem Burger volunteered his considerable expertise in assisting with leopard captures in 2011 and 2012, for which I am particularly thankful.
- Aneri Vlok, Brenda Jonck and Sandile Ndoko assisted with fieldwork, data capture and fundraising during their Nature Conservation diploma practical year.
- I was also assisted by several volunteers during my three years of fieldwork; Sonja Schmidt, Heather DeYoung, Ty Hall, James Mainwaring, Huw Vaughan-Jackson, Luc Germonpre and Pennie Ginn all provided considerable assistance with fieldwork and data capture. Luc, James, Heather and Ty also assisted the project through donations, either of money or equipment. Thanks to all of my assistants and volunteers for your hard work, often under very tough conditions!

ACKNOWLEDGMENTS

- The Calitzdorp and Volmoed Agri organisations and the organisers of the Calitzdorp Port Festival provided me with regular opportunities to present my findings to the broader public.
- CONNEXIO Calitzdorp,, Erika Calitz, Heather DeYoung, Valerie Enzer, Mavis Gash, Jane and Rod Green, Ty Hall, Laurance Huckstep, Pieter Nel, and Bob Sowden sponsored cameras for the project, and all those landowners who bought their own cameras and sent me the pictures – those data made a big difference, particularly in the early stages of the project when cameras were in short supply.
- Dr Charlene Bissett and Armand Kok for their advice on matters statistical and GIS-related.
- Brendan Whittington-Jones for his assistance in the design of the landowner questionnaire.
- Dr. Beatrice Conradie for her insight and advice on analyzing questionnaire data.
- Colleen Beeming was very tolerant of me being away in the field for long periods, and provided encouragement and support throughout.
- My family has always provided me with amazing support, and it is thanks to them that I have had the immense privilege of taking on a project such as this. I can never thank my parents enough for all the love that they have shown me down the years.
- Finally, although this project presented many difficulties that needed to be overcome, I was also fortunate in many ways. I spent three years out in the field in beautiful, but remote areas, mostly alone, often off paths, with only a satellite phone to help me if things went wrong. Fortunately, they seldom did, and I thank the Lord for keeping me safe during all those long days of fieldwork and for keeping the leopards safe during the long waits for veterinary assistance!

CONTENTS

Table of contents

ABSTRACT	i
ACKNOWLEDGMENTS	iii
CHAPTER 1: INTRODUCTION	1
1.1 The ecological importance of apex predators	1
1.2 Leopards in the Western Cape: conservation status and threats	2
1.3 The biology of leopards in the Western Cape	3
1.4 Leopard biology: gaps in knowledge and research priorities	4
1.5 Research rationale	5
CHAPTER 2: GENERAL DESCRIPTION OF THE STUDY AREA	8
2.1 Location	8
2.2 General topography and geology	9
2.3 Climate	12
2.4 Vegetation	14
2.4.1 Vegetation diversity	14
2.4.2 Habitat types	15
2.5 History	17
CHAPTER 3: A LEOPARD'S FAVOURITE SPOTS: MAPPING LEOPARD HABITAT IN THE LITTLE KAROO..	21
3.1. Abstract	21
3.2 Introduction	22
3.3 Methods	25
3.3.1 Camera trap and scat data	25
3.3.2 GPS collar data	25
3.3.3 Environmental data	25
3.3.4 Test data	26
3.3.5 Sampling bias	26
3.3.7 Mapping model output	29
3.3.8 Model refinement	29
3.4 Results	31
3.4.1 Comparison of collar and camera trap/scat datasets	31
3.4.2 Full study area models	33
3.5 Discussion	38
3.6 Conclusion	42

CONTENTS

3.8 Appendices	43
CHAPTER 4: ESTIMATING AND MONITORING LEOPARD POPULATION DENSITY IN THE LITTLE KAROO	46
4.1 Abstract	46
4.2 Introduction.....	48
4.3 Methods	54
4.3.1 Overall study design and camera placement	54
4.3.2 Leopard identification	57
4.3.3 Data analysis	58
4.3.4 Monitoring framework.....	62
4.4 Results.....	65
4.4.1 Descriptive statistics.....	65
4.4.2 SECR models	68
4.4.3 CAPTURE models.....	71
4.4.4 Monitoring array design.....	74
4.5 Discussion.....	77
4.5.1 Population density estimates	77
4.5.2 Monitoring.....	82
4.6 Conclusion	85
4.8 Appendix 4A – Leopard identikits.....	86
CHAPTER 5: LEOPARD DIET AND PREY PREFERENCES	100
5.1 Abstract	100
5.2 Introduction.....	102
5.3 Methods	113
5.3.1 Scat analysis.....	113
5.3.2 Kill-site analysis.....	115
5.3.3 Data analysis	117
5.3.4 Prey abundance	121
5.4 Results.....	123
5.4.1 Scat analysis.....	123
5.4.2 Kill-site prey composition	128
5.4.3 Prey abundances and preference	134
5.4.4 Similarity of kill site and scat data.....	139
5.5 Discussion.....	143

CONTENTS

5.6 Conclusion	153
5.8 Appendix 5A - Trapping and collaring of leopards.....	154
CHAPTER 6: SPOTTING TROUBLE: ATTITUDES TOWARDS WILDLIFE AND CONSERVATION IN THE LITTLE KAROO.....	163
6.1 Abstract	163
6.2 Introduction.....	165
6.3 Methods	170
6.3.1 Data collection	170
6.3.2 Wildlife damage	173
6.3.3 Predictive models.....	174
6.3.4 Wildlife tolerance.....	181
6.3.5 Livestock husbandry	182
6.3.6 Perceptions regarding CapeNature.....	185
6.3.7 Conservation index	186
6.3.8 Knowledge index.....	186
6.4 Results.....	188
6.4.1 Demographic characteristics.....	188
6.4.2 Damage causing animals	190
6.4.3 Predictors of total stock value (%) lost to predators	194
6.4.4 Total damage.....	195
6.4.5 Wildlife tolerance.....	196
6.4.6 Livestock husbandry	199
6.4.7 Perceptions of CapeNature	201
6.4.8 Conservation index	203
6.4.9 Knowledge index.....	204
6.5 Discussion.....	205
6.5.1 Damage-causing wildlife.....	205
6.5.2 Livestock husbandry practices	211
6.5.3 Formal conservation perceptions	216
6.6 Conclusion	221
APPENDIX 6A – QUESTIONNAIRE	223
LITTLE KAROO LANDOWNER SURVEY.....	223
CHAPTER 7: SYNTHESIS.....	229
7.1 Introduction.....	229

CONTENTS

7.2 Conservation status of leopards in the Little Karoo	230
7.3 Camera trapping: time for a sex-specific approach?	233
7.4 Conclusion	237
CHAPTER 8: REFERENCES	239

CHAPTER 1: INTRODUCTION

1.1 The ecological importance of apex predators

Predation has a profound structuring influence on ecosystems (Terborgh 1988; Miller et al. 2001; Estes et al. 2011), and the loss of top predators such as leopards (*Panthera pardus*, Linnaeus 1758) can have important consequences for ecosystem structure and the survival of other species within the predator's habitat (Terborgh 1992; Ripple & Beschta 2004; Creel & Christianson 2009). However, apex predators are often among the most vulnerable elements of biodiversity, particularly due to anthropogenic factors such as habitat fragmentation (Terborgh 1992) and human persecution (Balme & Hunter 2004; Ray et al. 2005). Throughout many parts of southern Africa, leopards are the sole surviving large predator species outside of protected areas as they can persist in fragmented habitats and areas close to human settlements better than other large African felids (Ray et al. 2005; Swanepoel et al. 2013).

Leopards have the widest habitat tolerance of any African felid, occupying habitats ranging from tropical rainforests to deserts (Ray et al. 2005), and can live wherever there is sufficient prey and cover to allow them to ambush prey (Stander et al. 1997; Hayward et al. 2006). Leopards are also cryptic, solitary predators (Bailey 1993; Stander et al. 1997), characteristics which may contribute to their ability to survive in human-disturbed areas. In arid areas, leopards generally prefer rugged, broken terrain to more open areas, as these areas typically provide better cover for hunting and refuge from humans and other predators (Khorozyan & Malkhasyan 2002; McCarthy et al. 2005; Gavashelishvili & Lukarevskiy 2008). Together, these adaptations have allowed leopards to have the widest distribution of all large carnivores in Africa, being present throughout sub-Saharan Africa, as well as in the Middle East, southern Asia and the Russian Far East (Henschel et al. 2009).

Habitats of top predators are often biodiversity hotspots (Gavashelishvili & Lukarevskiy 2008) and these predators may thus be useful in identifying areas that offer prime opportunities for biodiversity conservation (Ray et al. 2005). The relatively large home ranges of leopards, which can

CHAPTER 1: INTRODUCTION

extend up to several hundred square kilometres (Stander et al. 1997; Martins & Harris 2013), may also make them a suitable 'umbrella species' (Simberloff 1998), whose conservation may protect numerous other local species. Leopards can also be viewed as a 'flagship species', one that could be used as a symbol and central element for broader conservation actions (Simberloff 1998). While the concept of using a single species as a surrogate for broader conservation measures has drawn criticism (Andelman & Fagan 2000; Roberge & Angelstam 2004), large carnivores may be seen as indicators of greater species richness (Sergio et al. 2006, 2008; Gavashelishvili & Lukarevskiy 2008).

Leopards are widely distributed throughout South Africa, although their range has been highly fragmented by anthropogenic land-use change (Skead 2011; Swanepoel et al. 2013). Nevertheless, the conservation status of leopards in South Africa is currently 'Least Concern', largely due to their wide distribution rather than empirical data on the size and status of the leopard population (Friedmann & Daly 2004; Balme et al. 2010a). Actual population data for leopards in South Africa remains sparse, and largely confined to protected areas (Balme et al. 2013). A population estimate of 23 000 leopards in South Africa (Martin & de Meulenaar 1988) is regarded as being fundamentally flawed (Norton 1990; Henschel et al. 2009), and the leopard population in South Africa is generally thought to be in decline (Henschel et al. 2009; Swanepoel 2012).

1.2 Leopards in the Western Cape: conservation status and threats

Globally, leopards are threatened by habitat loss and fragmentation, as well as hunting, both for trade in their pelts and in retaliation for livestock losses (Henschel et al. 2009). Leopards remain an important species for trophy hunting in South Africa, although this is regulated by the Convention for the International Trade in Endangered Species (CITES) and is restricted to the northern regions of the country (Balme et al. 2010a, 2012). Leopard populations in the remainder of the country (including the Western Cape province) are thought to be too small for sustainable hunting (Swanepoel 2012). However, retaliatory killing of leopards throughout South Africa is a greater source of mortality than trophy hunting, and thus poses a far greater threat to the leopard population (Swanepoel 2012). Leopards have been listed on CITES Appendix I since 1975, but were

CHAPTER 1: INTRODUCTION

recently (2008) upgraded on the IUCN Red list from a species of Least Concern to Near Threatened (Henschel et al. 2009). In South Africa, leopards are classified as 'Vulnerable' under the National Environmental Management: Biodiversity Act (NEMBA) (Government Regulation 151 of 2007), but in the Western Cape they have been listed as a 'Protected' species since the promulgation of Nature Conservation Ordinance No. 19 in 1974.

The leopards of the south-western Cape of South Africa tend to be restricted to mountainous areas that are unsuitable for intensive agriculture (Norton & Henley 1987; Ray et al. 2005; Martins & Martins 2006). The Cape Fold Mountains cover large parts of the Western Cape, and consequently such refuges have allowed leopards to persist in close proximity to both farmlands and urban areas throughout the province (Norton 1986; Martins & Martins 2006). Leopards were classified as vermin in the Cape Province until 1957 due to their perceived impact on livestock farming in the region. This meant that landowners were legally obliged to kill any leopards on their property (Ray et al. 2005). This status changed with the introduction of the Cape Problem Animal Control Ordinance (No. 26 of 1957), which required prospective leopard hunters to obtain a permit. Although they were officially 'protected' from late 1975 (when Nature Conservation Ordinance 19 of 1974 came into effect), leopards continued to suffer high levels of persecution, with as many as 110 leopards killed legally between 1977 and 1980 (Stuart et al. 1985). Despite a dramatic reduction in the number of permits issued for leopard hunting (Theresa van der Westhuizen, CapeNature, pers. comm.), the illegal killing of leopards, both by hunting and trapping, remains widespread (Ray et al. 2005; Martins & Martins 2006).

1.3 The biology of leopards in the Western Cape

Carnivore densities are typically related to the density of available prey (Carbone & Gittleman 2002) and the low prey densities in the Western Cape may explain both the low leopard population density (Norton & Henley 1987; Stander et al. 1997; Martins & Martins 2006; Martins 2010) and smaller body size of leopards relative to leopards in savannah regions (Bailey 1993; Martins 2010). Research in the Cederberg Mountains of the south-western Cape, South Africa has revealed home ranges of

CHAPTER 1: INTRODUCTION

several hundred square kilometres (Martins & Harris 2013), which is similar in size to home ranges recorded in arid areas such as the southern Kalahari (Bothma *et al.* 1997a) and north-eastern Namibia (Stander *et al.* 1997) but considerably larger than those of leopards in more productive areas such as the north-eastern parts of South Africa (le Roux & Skinner 1989; Bailey 1993) and Kenya (Mizutani & Jewell 1998). Low prey density in the Western Cape is considered to be a consequence of the poor nutritional quality of the indigenous vegetation (Boshoff *et al.* 2001; Radloff 2008) together with the loss of more productive low-lying regions to agriculture (Radloff 2008; Lombard *et al.* 2010).

The large spatial requirements of leopards in the Western Cape may also contribute to their frequent encounters with diverse land use types, particularly when they are dispersing from one mountainous area to another through lower lying transformed habitat. Such areas are typically associated with reduced cover and a higher probability of encountering people, dogs (*Canis lupus familiaris*), vehicles and illegal snares or traps, all of which pose a threat to leopards and increase the risk of mortality (McCarthy *et al.* 2005).

1.4 Leopard biology: gaps in knowledge and research priorities

While leopards are generally well-studied elsewhere in Africa (Ray *et al.* 2005), research in South Africa has been heavily biased towards the northern parts of the country (Balme *et al.* 2013). There have been relatively few studies of the leopards of the Western Cape, although these have resulted in a fair number of publications (Stuart 1981; Stuart *et al.* 1985; Norton & Lawson 1985; Norton 1986; Norton *et al.* 1986; Norton & Henley 1987; Stuart & Stuart 1991; Martins & Martins 2006; Martins 2010; Rautenbach 2010; Martins *et al.* 2011; Martins & Harris 2013). Martins and Martins (2006) suggest that many of the earlier studies suffered due to small sample sizes (e.g. Norton & Henley 1987) or technological limitations (e.g. Stuart & Stuart 1991). In addition, a disproportionate amount of this research has taken place within the Cederberg Mountains (Norton & Henley 1987; Stuart & Stuart 1991; Martins & Martins 2006; Martins 2010; Martins *et al.* 2011; Martins & Harris 2013), and recent research in other areas has focused on leopard diet (Rautenbach 2010) and

CHAPTER 1: INTRODUCTION

human-wildlife conflict (Minnie 2009), while topics such as habitat preferences, population size and density, dispersal routes and the identification of movement corridors have received little attention.

As leopards and other wildlife species come under increasing pressure from human development, it is important to conduct research that can inform future management and conservation actions, particularly in areas of high biodiversity value (Knight et al. 2008; Laurance et al. 2012). Leopard research in South Africa has, in general, failed to do this, focusing largely on purely ecological studies within protected areas (Balme et al. 2013). However, protected areas only account for approximately 32% of available leopard habitat within South Africa (Swanepoel et al. 2013), and conflict is likely to be greater outside of these areas, suggesting an incongruity between research effort and leopard conservation requirements (Balme et al. 2013).

Furthermore, as so little leopard research has been geared towards generating useful management recommendations, there is an even greater lack of research that empirically tests the efficacy of management interventions (Balme et al. 2013). There is thus an urgent need to develop baseline estimates of population densities, and to establish monitoring programmes to track future population changes, particularly outside of protected areas (Balme et al. 2013).

1.5 Research rationale

The Gamkaberg, Rooiberg and Swartberg Mountains are approximately 300km-south east of the Cederberg Mountains and fall within the Little Karoo, an area that contains elements of three global biodiversity hotspots; the Cape Floral Region, Succulent Karoo and Maputoland-Pondoland-Albany Thicket (Myers 1990; Myers et al. 2000; Mittermeier et al. 2005). The leopard population of this area is thought to be broadly similar to that of the relatively well-studied Cederberg with a similar terrain and climatic conditions. Possible differences may reflect adaptations to different habitat composition that includes subtropical thicket and succulent Karoo vegetation, and fine-scale variation in vegetation types in the Little Karoo (Mucina & Rutherford 2006). The Little Karoo is thus an ideal study site to test the generality of the findings of studies of the Cederberg leopard

CHAPTER 1: INTRODUCTION

population to the mountainous areas of the Western Cape, being geographically distinct, but with similar abiotic conditions. An ad-hoc camera trap survey of the area ran from September 2007 to January 2011, and the data gathered during this period appeared to confirm this assumption, with relatively few leopards ($n=18$) recorded over a large area of approximately 1000 km² (Cape Leopard Trust/this author, unpublished data).

As in much of the Western Cape, leopards are presumably able to persist in the Little Karoo due to the large tracts of undeveloped, mountainous land (Norton 1986; Ray et al. 2005; Martins & Martins 2006; Skead 2011). The main type of farming in such areas is low-density, free-ranging livestock farming, usually of cattle (*Bos taurus*) and goats (*Capra hircus*). The spatial overlap of leopard and livestock does bring the former into occasional conflict with farmers (Stuart et al. 1985; Martins & Martins 2006). In general, the mountainous areas provide leopards with relatively undisturbed corridors to move through the mosaic of farmland and formally conserved areas, such as the Gamkaberg Nature Reserve, Groenefontein Nature Reserve and the Swartberg Nature Reserve (see Chapter 2). Sub-adult leopards are known to travel large distances when dispersing (Fattebert et al. 2013), and are predicted to disperse between the various mountain ranges in and around the Little Karoo.

Other than two dietary studies (Norton et al. 1986; Rautenbach 2010), no other research has been published on the Little Karoo leopard population and thus we know little of their habitat preferences and movement corridors in this ecologically important region. Historic development trends in the Cape suggest that low-lying areas are particularly vulnerable to anthropogenic land-use change (Rouget et al. 2006; Lombard et al. 2010; Skead 2011), and the identification of any movement corridors and the implementation of management interventions through these areas should therefore be a high priority for future leopard conservation. Furthermore, the size and density of the Little Karoo leopard population remains unknown, which hinders the objective evaluation of any future conservation management interventions.

CHAPTER 1: INTRODUCTION

My research aims to address these shortcomings by assessing the likely drivers of leopard presence and density, diet, habitat use and conflict with livestock farmers. My study area thus includes a matrix of both privately-owned and conserved lands. Furthermore, as a highly-biodiverse area, the Little Karoo is ideally suited for the implementation of landscape-level conservation initiatives that will not only contribute to leopard conservation, but also help to preserve the unique floral biodiversity of the area in the long-term. My research will also contribute to the existing literature on the management of free-roaming large carnivores in mixed-use landscapes with high potential for human-wildlife conflict situations to develop. Conflict between mammalian carnivores and humans is a global phenomenon (Graham et al. 2005; Inskip & Zimmerman 2009), and my project will thus provide outputs relevant to other areas where conflict situations result in the persecution of carnivores. Similarly, the population density estimates and habitat preference outputs may inform carnivore management in other arid areas, and will help to determine the overall population status of leopards in the Western Cape and South Africa as a whole.

CHAPTER 2: GENERAL DESCRIPTION OF THE STUDY AREA

2.1 Location

The Little Karoo is located in South Africa's Western Cape Province. It covers an area of approximately 23 500 km², stretching from the town of Uniondale in the east to Barrydale in the west with the Swartberg Mountains forming the northern boundary and the Langeberg and Outeniqua Mountains the southern boundary (Vlok & Schutte-Vlok 2010) (see Figure 2-1). The Little Karoo is thus completely land-locked, and is geographically distinct from the Great Karoo, which covers a larger portion of South Africa's interior.

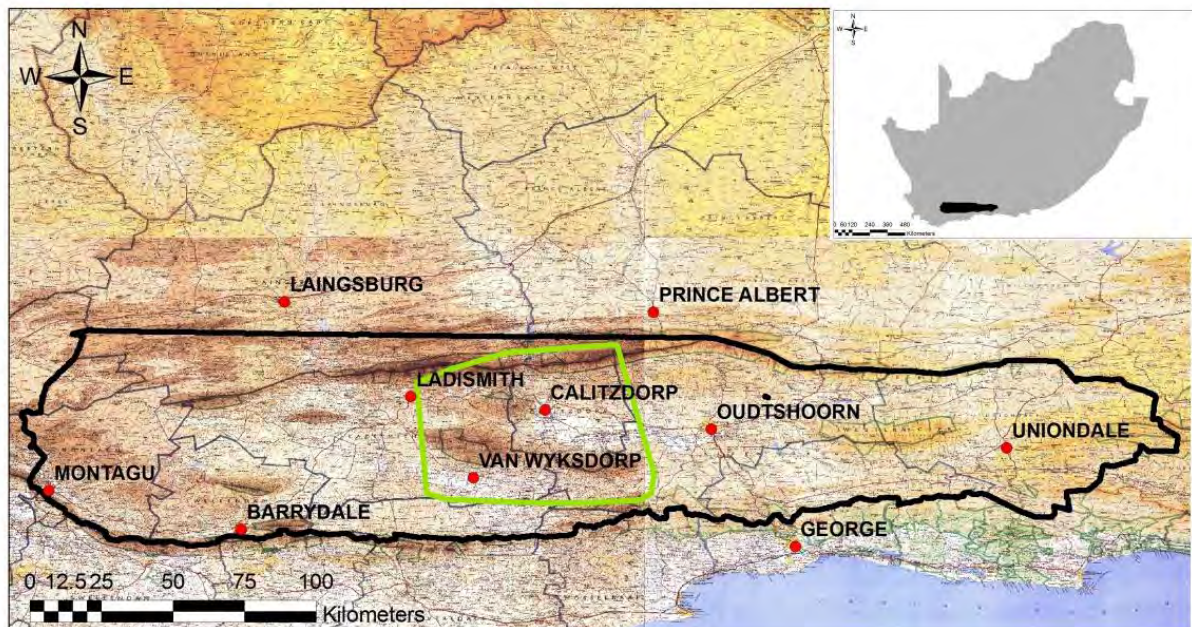


Figure 2-1. The location of the Little Karoo in South Africa (insert, and black polygon) and my study area within the Little Karoo (green polygon).

My study covered an area of approximately 3 100 km² within the Little Karoo (see Figure 2-1). To the north, I included the southern half of the Swartberg Mountains, including the Gamkaskloof valley (also known as 'Die Hel') which runs down the middle of the Swartberg Mountains on an east-west axis. The southern boundary of my study area extended to the foothills of the Outeniqua Mountains to the east, and approximately half-way between the Rooiberg and Langeberg Mountains on the

CHAPTER 2: STUDY AREA

western side. My study area was centered on the Gamkaberg/Rooiberg inselberg, which was included in its entirety.

This study area was chosen primarily to identify potentially important leopard dispersal corridors linking the large tracts of natural land in the northern (Swartberg) and southern (Outeniqua/Langeberg) mountain ranges. The study area includes large tracts of low-lying land (both open and rugged terrain) with diverse land uses including rural urban activities. Logistical considerations also played a part; I was based at Groenefontein Nature Reserve, which is relatively centrally located within the area described above (see Figure 2-7).

2.2 General topography and geology

The Little Karoo a mixture of rugged, mountainous terrain and broad valleys that can be up to 50 km wide and 200 km long (Watkeys 1999). The Swartberg Mountains rise sharply from low foothills to form two distinct lines of peaks that run on an east-west axis along the northern boundary of the study area, reaching a maximum elevation of 2308 m above sea level. The upper slopes of the Swartberg Mountains (above approximately 800 m) are extremely steep, with slope angles in excess of 65° (http://www2.jpl.nasa.gov/srtm/africa_radar_images.htm, accessed on 04/04/2013). In between the two ridges of the Swartberg lies the Gamkaskloof valley, a narrow gorge in which the lowest elevation is approximately 300 m. In contrast, the Gamkaberg and Rooiberg Mountains reach a maximum elevation of 1496 m, forming a relatively flat plateau at approximately 800 m. Although generally less steep than the Swartberg Mountains, the Rooiberg and Gamkaberg are characterised by deeply incised, narrow gorges, lined by near-vertical rocky cliffs. A belt of mountainous terrain extends north from the Rooiberg Mountains to the southern slopes of the Swartberg through the Huisrivier Pass. Other than this rugged strip, the remainder of the area between the Swartberg and Gamkaberg/Rooiberg Mountains is relatively flat and open, characterised by low ridges on the western side. The area east of Calitzdorp is a relatively low-lying (between 200 and 300 m elevation) broad, flat basin surrounded by mountains. The terrain to the south of the Gamkaberg and Rooiberg

CHAPTER 2: STUDY AREA

is fairly rugged, characterised by low hills and gullies, with numerous non-perennial rivers and streams (see Figure 2-2).

The mountains within the study area consist predominantly of sedimentary rocks of the Cape Supergroup, of which all three elements (Witteberg Group, Bokkeveld Group and Table Mountain Group) are present (Visser 1986; Watkeys 1999; Thamm & Johnson 2006). The sediments that make up the Cape Supergroup were deposited during the period from the Early Ordovician (~500 Ma) to the Early Carboniferous (~330 Ma). During this period, the Little Karoo formed part of a shallow marine shelf, which allowed for extensive deposition of fossil-rich sandstone, mudstone and shale sediments (Thamm & Johnson 2006). These deposits were subsequently folded to form the Cape Fold Mountains, a mountain range approximately 1000 km in length, during Permo-Triassic period (~300 to ~200 Ma), as part of the continental collision that accompanied the formation of the Pangean super-continent (Watkeys 1999; Newton et al. 2006; Thamm & Johnson 2006). The sedimentary mountains of the Little Karoo overlay the Cape Granite Suite, a massive granitic extrusion that is thought to be between ~555 and ~510 Ma (Scheepers & Schoch 2006). Soils in these mountainous areas are typically thin, with high limestone content, and are formed by the *in-situ* weathering of rock (Ellis & Lambrechts 1986).

The flat, low-lying valley between the Swartberg and Gamkaberg/Rooiberg Mountains is a part of the Oudtshoorn Basin, an area that gained sediment during the uplift and folding of the Cape Fold Mountains (Newton et al. 2006). The Oudtshoorn Basin is part of the Uitenhage Group of Mesozoic sedimentary deposits, which are equivalent in composition to the Enon and Kirkwood Formations (Shone 2006). The Enon-type sediments are a conglomerate of reddish, rounded pebbles of quartzite and slate, while the Kirkwood Formation strata are comprised of fluvial red and white siltstone and sandstone beds (Visser 1986; Shone 2006). Soil in these low-lying areas tends to be red in colour, highly basic, loosely structured and freely-drained (Ellis & Lambrechts 1986). Soils in riverine areas

CHAPTER 2: STUDY AREA

differ, being relatively deep (in excess of one metre), unconsolidated deposits, which range from being stratified to weakly structured (Ellis & Lambrechts 1986).

The Gamka-Olifants-Gouritz river system is the major perennial water source within the study area. The Gamka emerges from the Swartberg Mountains at Matjiesvlei, and flows south through the foothills of the Swartberg and Huisrivier Pass, where it is joined by the Huisrivier. The Gamka retains its name after this confluence and flows to the west of the town of Calitzdorp, before continuing its journey southwards. The Olifants River flows in a westerly direction to the north of the Gamkaberg Mountains and joins with the Gamka to form the Gouritz River in the valley that separates the Gamkaberg and Rooiberg Mountains. Another perennial river, the Groot River, lies south of the Rooiberg and flows westward, joining the Gouritz south of my study area.

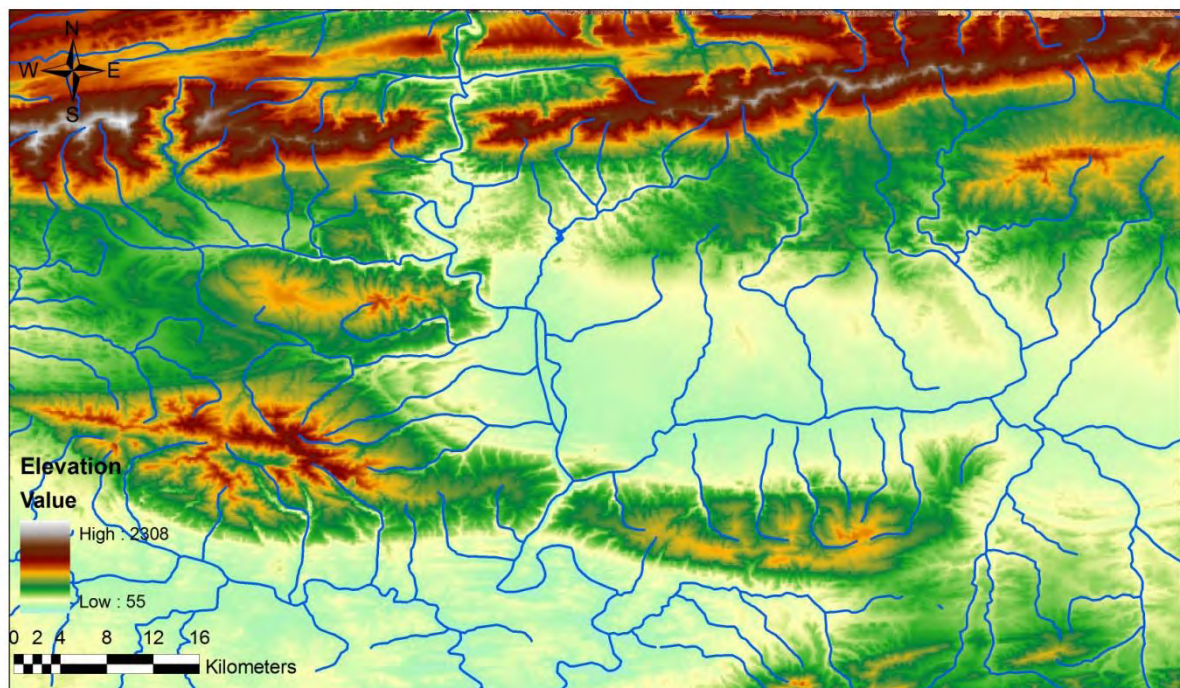


Figure 2-2. Elevation and drainage map of the study area, obtained from the Shuttle Radar Topography Mission (http://www2.jpl.nasa.gov/srtm/africa_radar_images.htm) accessed on 04/04/2013 (90 m resolution). All elevations are in metres above sea-level.

CHAPTER 2: STUDY AREA

2.3 Climate

The Little Karoo's climate is influenced by four main factors; the degree of latitude, distance from the sea, elevation and topography (Venter et al. 1986). Temperatures show strong seasonal and daily variation due to the low relative humidity and typically low cloud cover (Desmet & Cowling 1999). In summer, average monthly maximum temperatures often exceed 30°C (see Figure 2-3), while in winter average maximum temperatures are typically below 20°C. The highest maximum temperature recorded during my study was 45.2°C (9 February 2010 in Oudtshoorn). Unless otherwise stated, all climatic data were obtained from the South African Weather Service, and are based on data recorded at the Ladismith and Oudtshoorn weather stations. Suitable data were not available for the Calitzdorp area.

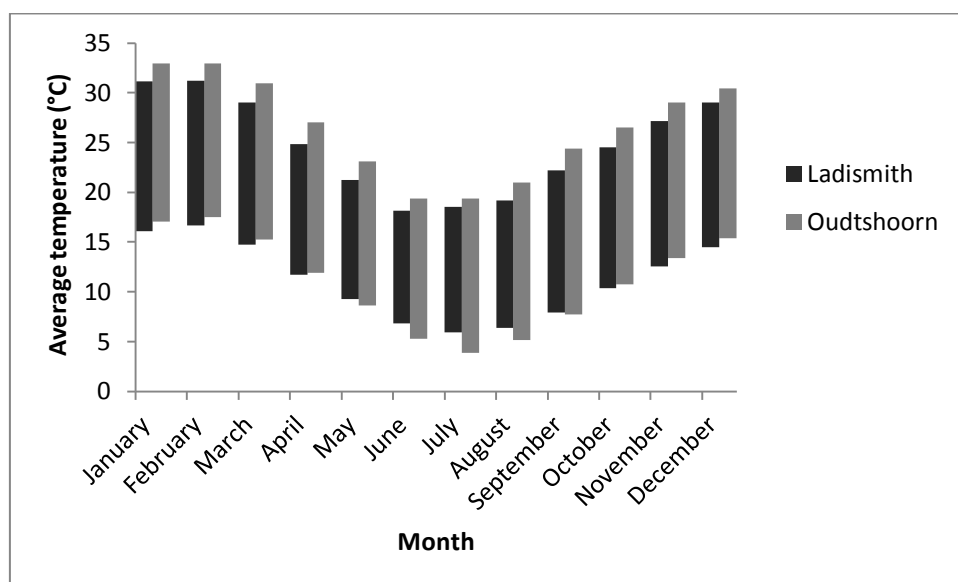


Figure 2-3. The average temperature range (in °Celsius) for Ladismith and Oudtshoorn over a ten-year period (2003-2012). Each bar represents the range between the average minimum and maximum temperatures for each month

Average minimum temperatures show similar variation (see Figure 2-3), ranging from 17.1°C in January (summer) to 3.9°C in July (winter), and the lowest recorded temperature was -0.9°C (13 July 2010 in Oudtshoorn). Both weather stations were situated at relatively low elevations (328 m in Oudtshoorn, 538 m in Ladismith), and it is thus likely that temperatures were generally cooler in the higher mountainous areas.

CHAPTER 2: STUDY AREA

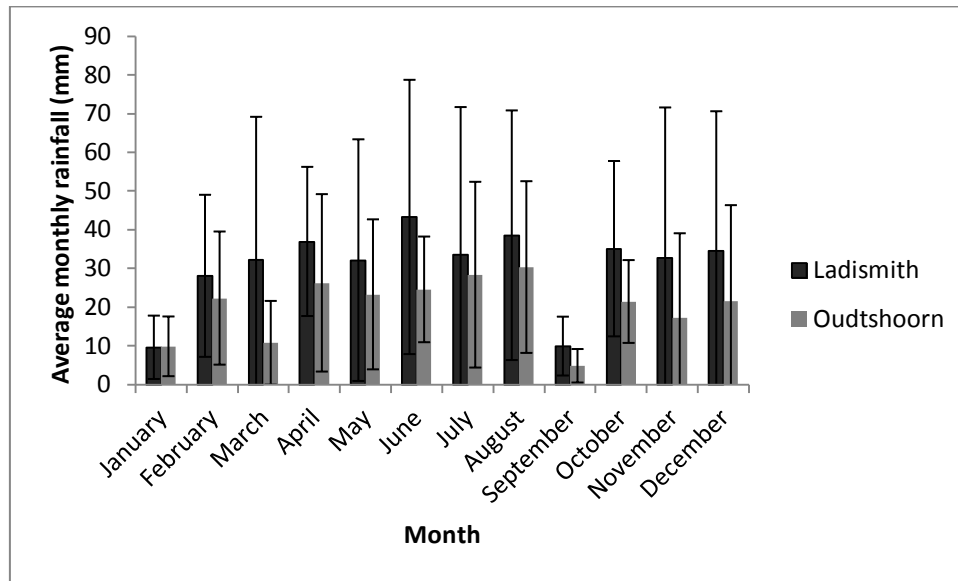


Figure 2-4. Average monthly rainfall ($\pm$ standard deviation) for Ladismith and Oudtshoorn over a ten-year period from 2003-2012.

The Little Karoo is generally considered to be an arid region with a mean annual rainfall from 2003-2012 of 366.1 (± 73.0) mm at Ladismith and 231.2 (± 60.7) mm in Oudtshoorn. The higher rainfall in Ladismith is attributed to its higher elevation and more westerly position (winter frontal systems approach from the west) (Desmet & Cowling 1999). The Little Karoo falls within the winter rainfall region of South Africa where mid-latitude cyclone systems bring cold, rainy weather that may persist for several days. Summer rainfall is mostly received in the form of unpredictable cloudbursts associated with convective storms. Thus, the Little Karoo differs from the majority of the Karoo areas of South Africa (located to the north and west of the Little Karoo), which receive the bulk of their annual rainfall from summer thundershowers (Venter et al. 1986; Desmet & Cowling 1999).

CHAPTER 2: STUDY AREA

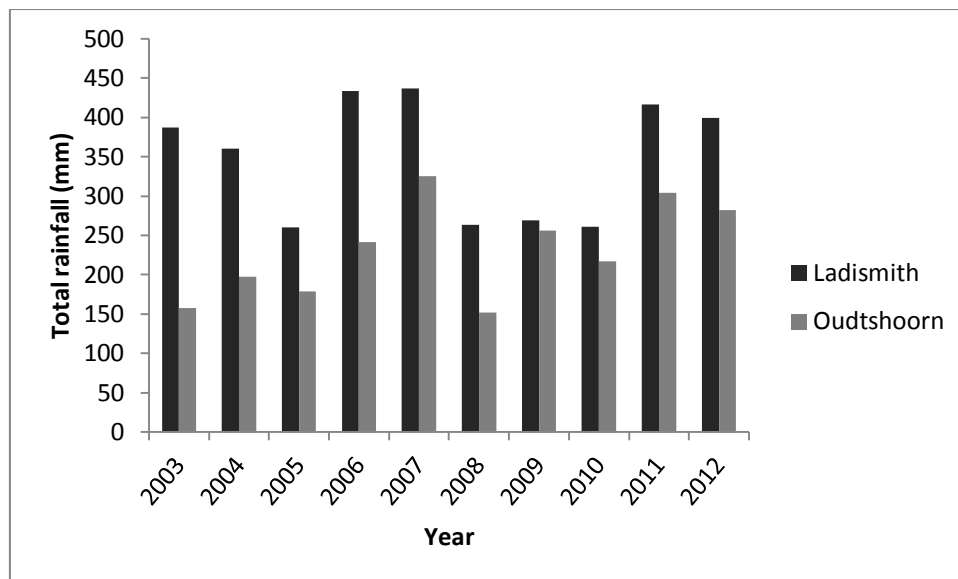


Figure 2-5. Total annual rainfall (mm) in Ladismith and Oudtshoorn from 2003 to 2012.

Rainfall within the study area is likely to vary substantially as mountainous areas are known to receive substantially more orographic rainfall than low-lying areas (Venter et al. 1986; Desmet & Cowling 1999), sometimes in excess of 1000 mm/year (Vlok & Schutte-Vlok 2010). Snow fell on the upper elevations of the Swartberg Mountains on several occasions during each winter of my study period (2010 to 2012), but snow was seldom observed on the lower Rooiberg and Gamkaberg Mountains.

2.4 Vegetation

2.4.1 Vegetation diversity

The most recent vegetation map of the Little Karoo was developed by Vlok et al. (2005), and is considerably more detailed than broader-scale vegetation maps that include the area (e.g. Mucina & Rutherford 2006). The Little Karoo has extremely high floral diversity, and contains elements of three global biodiversity hotspots; Cape Floral Region, Succulent Karoo and Maputoland-Pondoland-Albany Thicket (Myers et al. 2000; Mittermeier et al. 2005; Vlok et al. 2005). Vlok et al. (2005) identified 56 different habitat types in the area, belonging to six distinct biomes; perennial stream, river and floodplain, subtropical thicket, succulent Karoo, renosterveld and fynbos (see Table 2-1 for the proportional abundance of each vegetation type). Vegetation patterns in the Little Karoo are

CHAPTER 2: STUDY AREA

largely driven by rainfall, which is in turn strongly influenced by topography (Desmet & Cowling 1999). The spatial complexity of habitat type distribution is thus greatest in and around mountains (Vlok et al. 2005).

Table 2-1. Percentage of vegetation cover of the six different biomes for the Little Karoo and my study area, based on the map produced by Vlok et al. (2005). Figures are shown as the percentage of total vegetation cover.

Biome	Little Karoo	Study area
River and floodplain	5.5%	11.1%
Perennial stream	3.4%	2.9%
Subtropical thicket	35.3%	39.2%
Succulent Karoo	17.4%	12.0%
Renosterveld	12.6%	4.6%
Fynbos	25.9%	30.1%

2.4.2 Habitat types

River and floodplain habitats (hereafter referred to as 'riverine') are found in and around drainage lines at relatively low elevations within the study area (see Figure 2-6). Plants found in these areas are water-dependent, and tolerant of the relatively brackish water that characterises the Little Karoo (Vlok et al. 2005). Woody trees such as *Acacia karroo*, *Acacia caffra* and *Rhus lancea* are common in riverine areas, as are reeds (*Phragmites australis*) and bulrushes (*Typha capensis*) (Vlok et al. 2005; Vlok & Schutte-Vlok 2010). While riverine vegetation is largely restricted to low-lying areas with relatively deep soils, perennial stream vegetation is also found in rocky, mountainous areas in and around streams and seeps, where some sub-surface water is always available (Vlok et al. 2005). Plant species commonly associated with perennial stream habitats include shrub species such as *Empleurum uncapulare*, *Psoralea affinis*, *Psoralea imminens* and *Psoralea nubicola*, while flood-resistant trees and shrubs, including *Cliffortia strobilifera*, *Freylinia lanceolata*, *Rhus laevigata* and *Salix mucronata* may be found at lower elevations within the catchment (Vlok et al. 2005; Vlok & Schutte-Vlok 2010). Both riverine and perennial stream vegetation can form dense, impenetrable stands if left undisturbed for long periods.

CHAPTER 2: STUDY AREA

Subtropical thicket vegetation tends to occur at intermediate elevations within the study area, where fire and frost are infrequent (see Figure 2-6). Thicket vegetation is typically associated with summer rainfall areas, and requires a minimum of 100 mm of summer rainfall to survive in the Little Karoo (Vlok et al. 2005). Spekboom (*Portulacaria afra*) is one of the more easily recognisable plant species found in thicket habitats, which also contain woody trees (e.g. *Euclea undulata*, *Gloveria integrifolia*, *Gymnosporia szyszylowiczii*, *Rhus glauca*, *Rhus longispina*, *Rhus undulata*, *Pappea capensis*, *Lachnostylos bilocularis*, *Maytenus oleoides* and *Pterocelastrus tricuspidatus*), shrubs (*Carissa haematocarpa*, *Lycium cinereum*, *Lycium ferocissimum*, *Nymannia capensis*, *Putterlickia pyracantha* and *Rhigozum obovatum*) and spinescent vines such as *Asparagus burchellii*, *Asparagus densiflorus*, *Asparagus retrofractus* (Vlok et al. 2005; Vlok & Schutte-Vlok 2010). Many of the plant species found in thicket habitats are highly vulnerable to degradation through overgrazing (Vlok et al. 2005).

Succulent Karoo vegetation occurs on low hills and valleys (see Figure 2-6) with nutrient-rich soils and low annual rainfall (<350 mm) (Desmet & Cowling 1999; Vlok et al. 2005). There are no trees within this habitat type, which tends to be dominated by leaf-and-stem succulents and low (<1 m) shrubs belonging to the Aizoaceae, Amaranthaceae and Asteraceae families. While grasses are absent, a wide variety of mosses and lichens form a crust over the ground that helps to reduce runoff and erosion, but is vulnerable to trampling by domestic stock (Vlok et al. 2005).

Renosterveld vegetation occurs in hilly areas that are exposed to fire, and is typically dominated by a single species (usually one of either *Elytropappus rhinocerotis*, *Dodonaea angustifolia*, *Pteronia incana* or *Pteronia fascicularis*) (Vlok et al. 2005; Vlok & Schutte-Vlok 2010). Renosterveld may contain a large grass component (*Ehrharta* spp., *Pentameris* spp., *Pentaschistis* spp. and *Themeda triandra*), but overgrazing can lead to this being completely replaced by unpalatable renosterbos (*Elytropappus rhinocerotis*) (Roux & Theron 1986; Vlok et al. 2005).

CHAPTER 2: STUDY AREA

Mountain fynbos vegetation occurs on shallow, acidic, nutrient-poor sandy soils at higher elevations (Vlok et al. 2005). All three of the characteristic fynbos families (Proteaceae (*Protea* spp., *Leucospermum* spp. and *Leucadendron* spp.), Ericaceae (*Erica* spp.) and Restionaceae (*Cannamois* spp., *Hypodiscus* spp. and *Restio* spp.)) are present within this habitat type in the Little Karoo. Despite these areas receiving substantially more rainfall than the low-lying areas, fire is an important disturbance element in fynbos habitats (Vlok et al. 2005).

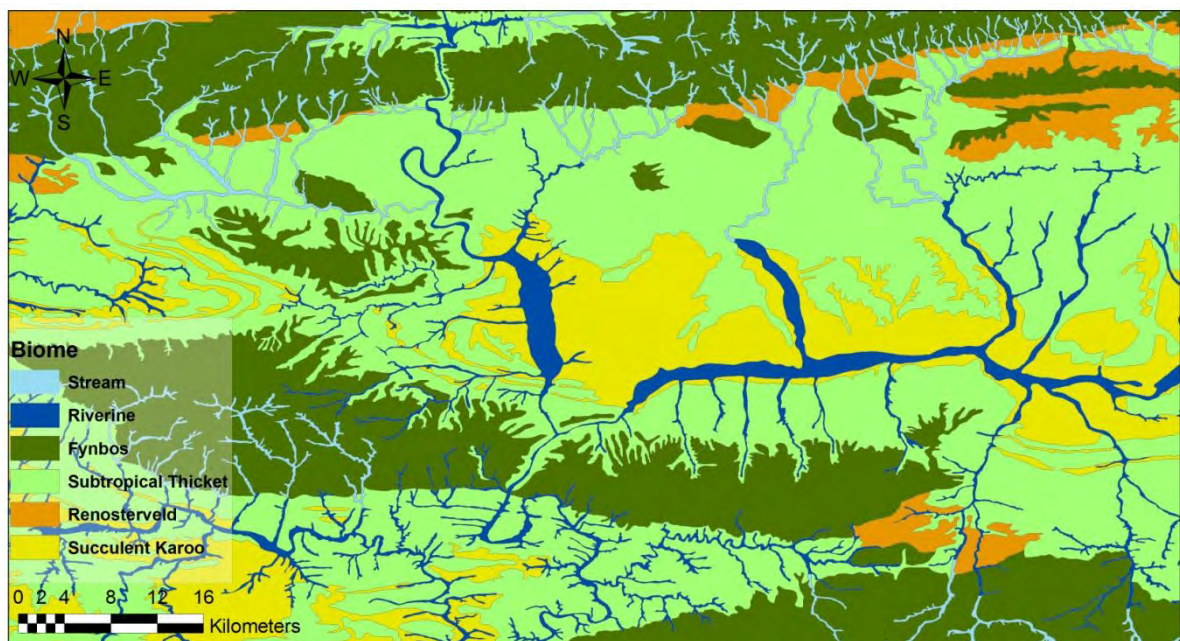


Figure 2-6. The distribution of the six different biomes within my study area

2.5 History

The Karoo is thought to have been inhabited continuously by humans for approximately three million years, from the early Stone Age (Smith 1999). The earliest human inhabitants (*Homo erectus*) are thought to have been supplanted by *Homo sapiens* approximately 250 000 years ago (Smith 1999). Agricultural activity in the Karoo is thought to date back 2000 years, with the emergence of the Khoi and San people (colloquially known as ‘Bushmen’) (Smith 1999). These groups were typically mobile pastoralists or hunter-gatherers, who would move frequently to take advantage of the patchily-distributed resources in the ephemeral Karoo landscape (Smith 1999). While these aboriginal groups hunted most of the wildlife species present in the area at the time, their impact

CHAPTER 2: STUDY AREA

upon wildlife populations is thought to have been minimal due to their low numbers, subsistence lifestyle and primitive hunting tools (Skead 2011). By contrast, the Khoi kept large herds of cattle (*Bos taurus africanus*) and indigenous sheep (*Ovis aries*), which would have competed for grazing with wildlife and may have caused erosion in more frequently-used areas (Sampson 1986). However, these activities are not thought to have significantly altered the distribution patterns of most mammal species, with the exception of the extinct blue antelope (*Hippotragus leucophaeus*), which is thought to have become critically endangered prior to the arrival of European settlers in the area (Skead 2011).

The arrival of European settlers in the Cape in 1652 had a far greater impact on ecosystems and wildlife populations (Beinart 2008; Skead 2011). The first European farming in the Little Karoo dates back to 1730, and was based predominantly on tobacco and fruit (Anonymous 1999). The domestication of ostriches (*Struthio camelus*) in the mid-19th century was followed by two booms in ostrich feather exports (1875-1886 and 1987-1914), which spurred massive economic growth in the region (Van Tonder & Van Horsten 1998; Beinart 2008). Ostriches became the dominant livestock in the area, while lucerne (*Medicago sativa*), which is used as ostrich feed, was the most widely-grown crop. This pattern persists to the present day (Cupido 2005; Beinart 2008) with the Little Karoo accounting for approximately 75% of current ostrich farming within South Africa (Van Helden et al. 2012). Vineyards were first established in the Calitzdorp area in the late 19th century, and wine and fruit farming remains an important activity in the immediate vicinity of Calitzdorp (Van Tonder & Van Horsten 1998, www.calitzdorp.co.za - accessed on 26/12/2013).

Agriculture remains one of the largest economic activities in the Little Karoo (Cupido 2005). Results of the most recent census in South Africa, which occurred in 2011 (<http://www.statssa.gov.za/Census2011/Products.asp> accessed on 26/12/2013), suggest that apartheid-era land ownership patterns remain largely intact, with the vast majority of farmland being owned by farmers of European descent. This racial group makes up only approximately 12% of

CHAPTER 2: STUDY AREA

the total population, which is predominantly (79%) of the 'coloured' racial group; a heterogeneous group composed of persons of mixed race, including descendants of slaves introduced from the Dutch East Indies and indigenous Xhosa and Khoi-San people (Bickford-Smith 1995; Smith 1999). Poverty levels are high amongst non-white population groups; 82% of the coloured population earn less than \$US 188 per month (the typical farm worker wage), while 40% of the coloured population have no income. Similar trends exist amongst the small black African population in the area. While approximately 34% of white people have no income (many of whom are likely to be retirees), over half (55%) of the white population earn more than \$US 188 per month. Afrikaans is the dominant language amongst both white and coloured population groups, and is spoken by almost 90% of the population of the Little Karoo.

There is an extensive network of Provincial nature reserves within the study area (see Figure 2-7). In the north, the Swartberg, Gamkapoort and Towerkop Nature Reserves cover most of the Swartberg Mountains, with a total extent of approximately 180 000 hectares. The Gamkaberg and Rooiberg Mountains contain a number of relatively small, non-adjacent nature reserves. The oldest of these is the Gamkaberg Nature Reserve (9600 ha), which was proclaimed in 1974 to protect endangered Cape Mountain Zebra (*Equus zebra zebra*). This reserve has subsequently been expanded to form the Gamkaberg Reserve Cluster, which includes Rooiberg Nature Reserve (12 800 ha), Groenefontein Nature Reserve (5200 ha), Paardenberg Nature Reserve (1500ha) and Vaalhoek Nature Reserve (1200 ha), all of which are situated in and around the Gamkaberg and Rooiberg Mountains. In addition to these Provincial reserves there are a number of private nature reserves and conservancies; the two biggest of which are the Rooiberg and Groenefontein conservancies. Conservancies are voluntary landowners associations that manage their natural resources co-operatively in a sustainable manner, without necessarily changing the land-use of their individual properties (i.e. conservancies can include productive farmland) (National Association of Conservancies and Stewardship South Africa, www.nacsa.org.za, accessed 28/12/2013).

CHAPTER 2: STUDY AREA

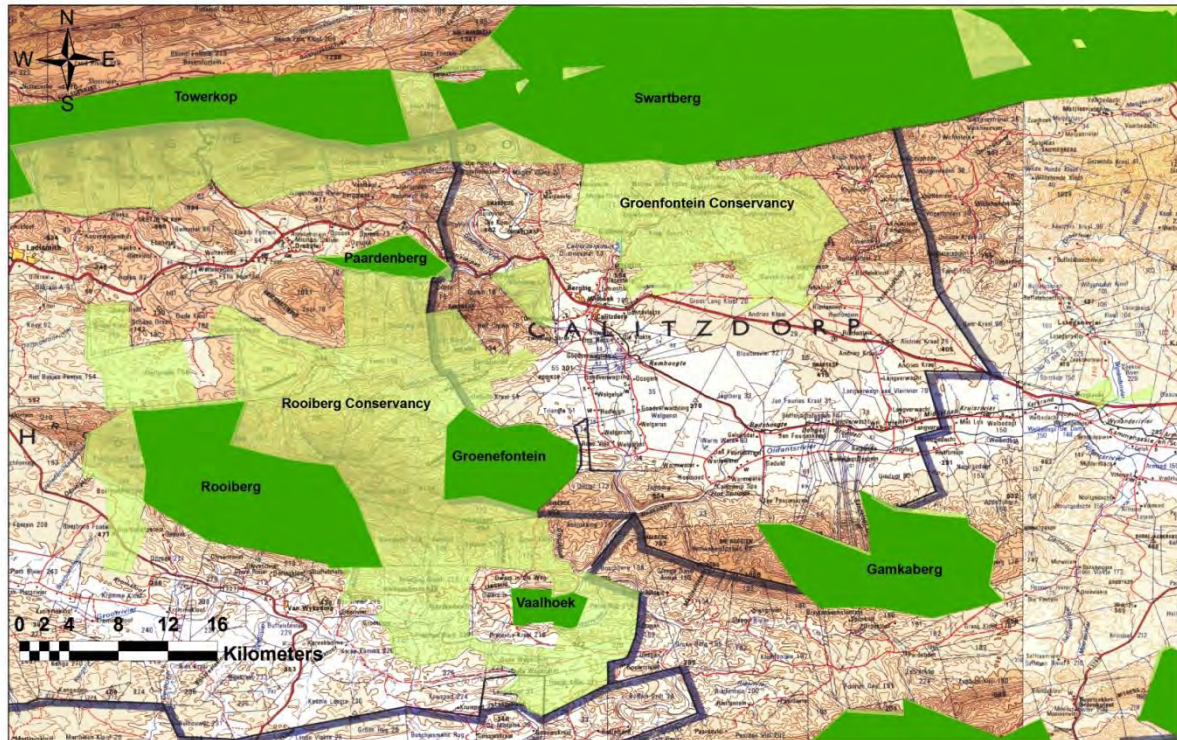


Figure 2-7. Nature reserves within my study area. Dark-green shaded areas are formal conservation areas, while light-green areas show privately owned land that is either part of a conservancy or a privately-owned nature reserve.

CHAPTER 3: A LEOPARD'S FAVOURITE SPOTS: MAPPING LEOPARD HABITAT IN THE LITTLE KAROO

3.1. Abstract

Large carnivores are vulnerable to anthropogenic land-use change and habitat fragmentation. Leopards are the only large predator to still occur naturally throughout the Western Cape, South Africa. Their behavioural plasticity and broad dietary niche allow them to occupy diverse habitat types including the remote Cape Fold Mountains that have endured with minimal human impact. I used the programme Maxent to map potential leopard habitat in the Little Karoo based on two independent data sources; leopard presence data based camera trap and scat location records, and GPS tracking data from three collared leopards. Leopard habitat was modelled using seven variables that encompass landscape, vegetation and human disturbance categories. Models based upon a combination of camera trap and scat location data performed better than those using GPS collar data, despite having a smaller dataset. Distance to rivers was the most important predictor variable of leopard presence, as leopards showed a strong preference for drainage lines and riverine areas. Leopards were also strongly associated with mountainous terrain of intermediate elevation and high slope angle. The best-performing model classified 26.33% or 46.85% of the study area as suitable leopard habitat, depending on the threshold used to convert the continuous model output to a binary presence/absence map. My results suggest that tracking collars may be inappropriate sources of data for Maxent modelling, and that better results can be obtained from non-invasive techniques such as camera-trapping. Leopard habitat in the Little Karoo is largely restricted to mountainous areas, which are near-contiguous in the study area. Current high levels of connectivity between areas of suitable leopard habitat bode well for the conservation status of leopards within this region and future conservation efforts need to ensure that narrow corridors linking such habitat are preserved.

CHAPTER 3: LEOPARD HABITAT

3.2 Introduction

Land transformation for urban and agricultural use has arguably been the single biggest contributor to the extinction of terrestrial fauna on a global scale (Crooks et al. 2011). Large mammalian predators are particularly vulnerable to habitat loss and degradation because of the impact of land transformation on prey and the direct and indirect threat that these predators pose to humans and their livestock (Terborgh 1992; Estes et al. 2011). Extirpation of large predators has been demonstrated to have broader ecosystem impacts through processes such as meso-predator release and changes in the behaviour of prey species, both of which can ultimately alter plant communities (Ripple & Beschta 2004, 2008; Elmhagen & Rushton 2007; Allen et al. 2012). Large predators have consequently been recognised as a conservation priority due to this combination of sensitivity and disproportionate ecosystem impact (Ray et al. 2005; Estes et al. 2011; Ripple et al. 2014).

In the Western Cape, South Africa, leopards are the sole remaining large predators outside of formally conserved areas. Leopards have also suffered range constriction due to anthropogenic disturbance in the Western Cape province (Norton 1986; Skead 2011) and are presently largely restricted to the Cape Fold Mountain range that extends in a broad belt across the province. The Western Cape contains 20% of the suitable leopard habitat in South Africa, but 29% of this habitat has been degraded by human activities (Swanepoel et al. 2013). Thus while leopards are widely distributed in this province, they are particularly vulnerable to further loss of more productive low-lying habitat and further fragmentation of the mountain refugia they currently use. It is therefore important to identify and conserve areas of habitat suitable for leopards including potential movement corridors between such habitats.

Species distribution models seek to find common patterns between the presence of a species and various ecological variables, which are expected to influence the suitability of an area for that particular species (Hirzel et al. 2002). Historically, many distribution models were reliant on having records of both the presence and absence of a species to compare those areas where the species was present to areas of unsuitable habitat. However, the absence of a species from a particular area is difficult to reliably quantify (Hirzel et al. 2002). Species may be classified as absent when they were present but not detected, while areas of suitable habitat may be incorrectly classified as being unsuitable due to the absence of a species for historical reasons, such as human persecution (Hirzel et al. 2002). Only absence that is a result of a lack of suitable habitat is relevant to formulating species distribution models, and false absences can bias analyses by incorrectly classifying potentially suitable habitat as unsuitable (Hirzel et al. 2002; Elith et al. 2011). The recent emergence of models that are reliant on presence-only data such as BIOCLIM (Busby 1991), boosted regression

CHAPTER 3: LEOPARD HABITAT

trees (Friedman et al. 2000), the Genetic Algorithm for Rule-set production (GARP) (Stockwell 1999) and MAXENT (Phillips et al. 2006; Phillips & Dudik 2008) has thus been a boon for biologists.

Elith et al. (2006) reviewed a variety of presence-only models and used independent presence-absence datasets to verify the results. Their findings suggest that models based exclusively on presence data can usefully model species distributions, and that these models can be sufficiently accurate for use in conservation planning (Elith et al. 2006). Presence-only data are often more appropriate for modelling highly mobile species, when true absence of the species from an area can be difficult to measure (Guisan & Thuiller 2005). The program Maxent (Phillips et al. 2006) was found to be among the best-performing of the presence-only models (Elith et al. 2006). Although Li et al. (2011) found that Maxent performed poorly in relation to a novel PBL (presence background learning) and presence-absence models (Li et al. 2011), the ecological assumptions implicit to their PBL approach have been heavily criticized (Phillips 2012).

The PBL approach (Li et al. 2011) assumes that the target species is always present in areas with the ideal combination of environmental variables, an unrealistic assumption as the species may be absent from these areas due to a myriad of factors such as dispersal limitation, historical incidents (fire, disease, human persecution, etc.) and the presence of predators or competitors (Phillips 2012). In their comparison of the PBL approach and Maxent, Li et al. (2011) did not adjust the presence probability parameter in Maxent, which is set at 0.5, to a value closer to one, which would have been appropriate given the assumption of presence under ideal conditions (Phillips 2012). This poor parameterisation resulted in Maxent producing lower probabilities of presence than the PBL method at suitable sites, explaining Maxent's poor performance relative to the PBL method (Phillips 2012).

In addition, the recent finding that Maxent is equivalent to a Poisson point process model allows for further improvement of Maxent as a modeling technique, such as choosing an appropriate spatial resolution and number of background points against which to test presence data, as well as an appropriate regularisation parameter for Maxent models (Renner & Warton 2013). There have also been several studies on the interpretation of Maxent results, such as the influence of sampling bias (Veloz 2009; Bean et al. 2012; Syfert et al. 2013), model evaluation (Warren & Seifert 2011; Golicher et al. 2012; Jiménez-Valverde 2012) and selecting appropriate probability thresholds to convert the continuous probability output generated by Maxent into binary presence-absence maps (Liu et al. 2005, 2013; Bean et al. 2012)

Maxent is based upon the theory of maximum entropy, which characterises associations from incomplete information (Jaynes 1957). In a species distribution modelling context, Maxent finds the

CHAPTER 3: LEOPARD HABITAT

least-constrained distribution of a species that conforms to the range of environmental variables at which presence of the species was recorded (Phillips et al. 2006). In addition, Maxent has been shown to perform well when relatively few presence data are available (Hernandez et al. 2006; Pearson et al. 2007) and has been used to produce a wide range of species distribution models, including plants (Raes et al. 2009), geckos (*Uroplatus* spp.) (Pearson et al. 2007), vultures (*Gyps fulvus*) (Mateo-Tomás & Olea 2010), jaguars (*Panthera onca*) (Ferraz et al. 2012) and leopards (Mondal et al. 2013; Swanepoel et al. 2013).

This chapter aims to compare maximum entropy habitat models for leopards constructed using two independent datasets; presence data recorded by a camera trap survey combined with opportunistic scat collections, and more detailed movement data recorded from only three adult male leopards fitted with GPS tracking collars. GPS tracking collars are widely used for both wildlife research and monitoring purposes, but their efficacy as a research tool has been questioned due to factors such as high costs and small sample sizes (Hebblewhite & Haydon 2010). The use of tracking collars also necessitates the live capture of study animals, which can be time-consuming and expensive, as well as potentially harmful (Tuytens et al. 2002; Dennis & Shah 2012). In contrast, detecting leopard presence using camera traps and scat locations is non-invasive, relatively inexpensive and can cover a broader area. However, these latter two methods do not gather detailed data on animal movement patterns and can be influenced by uneven sampling effort. By comparing these two methods, I hope to identify the most effective way of gathering data for generating species distribution models for leopards and wide-ranging felids in general. I also aimed to test the null hypothesis that leopards would be evenly distributed across the landscape compared with the alternative hypothesis that leopard distribution would be strongly influenced by terrain and human disturbance.

CHAPTER 3: LEOPARD HABITAT

3.3 Methods

3.3.1 Camera trap and scat data

Leopard presence data were collected from 141 camera trap sites distributed throughout the study area (see Chapter 4). All independent leopard photographs were included in the analysis. Photographs were classified as being independent if they occurred more than 12 hours after the previous leopard photograph (*sensu* Yasuda 2004). Multiple samples from the same location were included, as sites with greater numbers of independent leopard photographs were likely to represent better quality habitat than those with only one capture (Bowkett et al. 2007). Samples from the same location had their GPS co-ordinates changed slightly (at the fifth decimal point, resulting in a change in accuracy of approximately 1.5 m) to ensure that they were recognised as distinct sample locations.

Leopard scat samples were collected opportunistically over a three-year period between November 2009 and November 2012. A combined database of camera trap-recorded presence and scat sample locations was produced.

3.3.2 GPS collar data

Three male leopards were captured in 2010 and fitted with Vectronics GPS-Plus tracking collars (Vectronics Aerospace GmbH; see Chapter 5). I originally intended to capture and collar six individuals, but logistical difficulties hindered trapping activities for much of 2011, and I decided not to attempt capturing any 'new' individuals in 2012, as this was my final year of fieldwork and I did not consider it ethical to capture and collar leopards for a relatively short period before the collars would have to be removed. Fixes were recorded at four-hour intervals. All 2-D and 'unverified' 3-D fixes were excluded from the analysis to avoid bias due to low GPS fix accuracy. It was not possible to calculate the actual spatial error caused by this lack of accuracy (R. Schulte, Vectronics Aerospace GmbH, pers. comm.). Maxent is known to be susceptible to spatially auto-correlated sampling (Veloz 2009). To reduce auto-correlation, I sub-sampled collar data by only using every 6th data point, thus ensuring that there was a minimum period of 24 hours between successive data points used in the analyses.

3.3.3 Environmental data

Eight environmental variables were used as predictors of leopard habitat suitability (see Appendix 3A, Table 3-4). These were largely based on the variables used in previous studies of leopard distribution (Gavashelishvili & Lukarevskiy 2008; Swanepoel et al. 2013).

Four topographical variables were assessed; elevation (°), slope (°), Euclidean distance to water (m) and a terrain ruggedness index (TRI) calculated using the Riley method (Riley et al. 1999). Two

CHAPTER 3: LEOPARD HABITAT

vegetation variables were included; vegetation type (categorical) and a normalised difference vegetation index (NDVI). The Little Karoo has a wide variety of vegetation types, comprising three distinct biomes (fynbos, succulent Karoo and subtropical thicket) and transitional shrublands, rivers and floodplains, and freshwater streams (Vlok & Schutte-Vlok 2010). NDVI was used as a measure of productivity to provide an assessment of herbivore food availability within the study area (Box et al. 1989; Pettorelli et al. 2011). Finally, a habitat condition variable was used as a measure of human disturbance within the area (Kirkwood 2010). This measures ecosystem degradation based on MODIS satellite imagery combined with a variety of data including the National Land Cover 2000 assessment, presence of agricultural fields, dams and infestation by invasive alien plants (Kirkwood 2010). The Euclidean distance (m) to the nearest town was also included as a measure of potential disturbance.

All variables were tested for co-linearity using the program ENMTools 1.4 (Warren et al. 2010). The TRI variable was found to be strongly correlated with both elevation ($r=0.819$) and slope ($r=0.889$). Highly correlated variables can introduce bias (Guisan & Thuiller 2005; Mateo-Tomás & Olea 2010; Lahoz-Monfort et al. 2010) and TRI was thus excluded from any Maxent analysis. The slope and elevation variables had weaker correlations and were retained on the basis that both were likely to be biologically significant (*sensu* Freckleton 2011). Maxent assumes that all grid cells are of equal size (Elith et al. 2011) and thus all data were projected using the Africa Albers Equal Area Conic projection in ArcGIS 9.3 (ESRI, Redlands, California, USA). The data were also projected at the 90 metre raster grid cell resolution.

3.3.4 Test data

Maxent allows for the inclusion of independent test data, which can improve the predictive quality of the output (Elith et al. 2006). I used the locations of 79 scats collected from 2007 to early 2009 during a previous study on the diet of leopards in the Little Karoo (Rautenbach 2010). As these scats were collected shortly before the commencement of my study, it was unlikely that there would have been any significant changes in leopard distribution patterns during the intervening period.

In addition to using independent test data, each dataset was also analysed using the subsample tool available in Maxent. For these models, 70% of the presence data were used for model training, and the remaining 30% used as test data (Swanepoel et al. 2013).

3.3.5 Sampling bias

In order to reduce sampling bias, I divided the study area into 50 km² grid cells following the recommendation of Karanth & Nichols (1998). Two camera sites were set up within each grid cell. The spatial distribution of camera sites was random, and within each grid cell I attempted to locate

CHAPTER 3: LEOPARD HABITAT

one camera on a road or jeep track and one on a less obvious game trail. Sites were chosen based on the presence of leopard sign, or where there was sign of frequent use by other animals (Karanth & Nichols 1998; Balme et al. 2009; Chapman & Balme 2010). However, sampling was also done across large tracts of low-lying, disturbed habitat where leopard presence was considered to be highly unlikely (Boshoff et al. 2001). Sampling effort was thus relatively evenly distributed across the study area.

Uneven sampling effort can result in biased samples and hence model results (Phillips et al. 2006) and correcting for this has been shown to improve Maxent performance (Syfert et al. 2013). Failure to correct for this can result in models that do not adequately reflect the true range of habitats used by the study animal. This is likely to be particularly true in mountainous regions where certain areas are inaccessible and thus inadequately sampled. A further constraint was the necessity of attempting to avoid camera theft on publically-accessible land. I quantified sampling effort by mapping all sample locations, including sites where camera traps did not record leopard presence. The Euclidean distance (m) to each sampling location was calculated and mapped as a continuous raster layer using the Spatial Analyst extension of ArcGIS 9.3. These distances were inverted using the following equation:

$$(([\text{'distance'}] - Z_Max) \times (-1)) + Z_Min,$$

where 'distance' is the distance of that particular grid cell to the nearest sample point, Z_Max is the largest distance value recorded, and Z_Min is the minimum distance from a cell to the nearest sample point.

This calculation was made using the Single Output Map Algebra function in ArcGIS 9.3. The output map was a raster layer where sample points had the highest values, representing the greatest sampling effort. Sampling effort thus decreased inversely to distance from the sample points. Separate bias layers were calculated for each of the datasets used in Maxent. This provided a map of relative survey effort across the landscape (Elith et al. 2011).

3.3.6 Model selection

The camera trap survey covered an area of 3219.55 km², far greater than the territories of the three collared leopards (1115.28 km²). As the three leopards had adjoining territories, I combined the collar data from all three individuals and used this to produce a minimum convex polygon (MCP) for all three using Hawth's Analysis Tools (Beyer 2004) in ArcGIS 9.3. All environmental variable layers were clipped to the extent of this polygon. I used two independent leopard presence datasets to model leopard habitat in this area. The first dataset consisted of locations where I had recorded

CHAPTER 3: LEOPARD HABITAT

leopard presence through both camera trap photographs and scats. Many of these locations fell outside of the collar data MCP, and these data were clipped so that only locations falling within the MCP were used in the analysis. The second dataset was the GPS locations from the three collared leopards. All of these locations fell within the collar data MCP. These two datasets were pooled to produce a third dataset, which contained all presence records (GPS collar, camera trap and scat) from within the collar MCP area.

All models were presented using Maxent software version 3.3.3k (<http://www.cs.princeton.edu/~schapire/maxent/>). Each dataset was used in two Maxent models constructed with each type of test sample data (independently collected scat locations and subsampling). This resulted in a total of six models being developed. I used the default Maxent settings, with the exception of the maximum number of iterations, which I increased from 500 to 5000 to ensure model convergence. The convergence threshold was set to 0.0001 and 10 000 background points were used. The regularisation parameter was set to 1, as this has been found to be suitable for a wide range of presence-only data (Phillips & Dudik 2008). Maxent performed jackknife calculations of variable importance, and data were outputted in the 'raw' format.

Although Phillips & Dudik (2008) suggest using the area under the Receiver Operating Curve (AUC) as a measure of model performance, subsequent research has found that Akaike's Information Criterion (AIC) yields more accurate results (Warren & Seifert 2011). The model selection function in the programme ENMTools version 1.4 (Warren et al. 2010) was used to calculate AIC and small-sample AIC (AIC_c) scores for each model (Akaike 1974; Burnham & Anderson 2002). Due to the relatively small sample sizes used to produce the models, AIC_c was used to determine the best-performing model following the guidelines suggested by Symonds and Moussalli (2011). The models were sorted according to AIC_c score, and the difference between the lowest-scoring model and the other models (ΔAIC_c) was calculated. AIC_c weight was calculated using the following equation:

$$AIC_c \text{ weight} = \exp(-\Delta AIC_c/2) / (\text{the sum of all of these values for all models})$$

To compare the performance of the different datasets across the full study area, a second set of models were built. The same GPS collar data were used, but these were compared to the full camera trap and scat location dataset, which covered the entire study area. These two datasets were again pooled to produce a third, combined dataset of collar and camera/scat data. The resulting models were analysed using the process described above.

The final phase of the model selection process involved optimising the best-performing model. This was done by manipulating the regularisation parameter in Maxent, as suggested by Warren & Seifert

CHAPTER 3: LEOPARD HABITAT

(2011). Regularisation parameters were selected on an ad-hoc basis according to model performance. AIC and AIC_c scores were generated for each model in ENMTools.

To increase the accuracy of the final model, 20 replicates were run using the independent test data. Jackknife estimators of variable importance were calculated using Maxent's Jackknife and heuristic test. This calculates the training gain of the model based solely on each variable, and the loss of gain in the absence of each variable.

3.3.7 Mapping model output

The standard Maxent output is a map layer of continuous probabilities across the study area, which represent the probability of the study species occurring in a given area (Phillips et al. 2006; Phillips & Dudik 2008). This necessitates converting the continuous probability distribution generated by Maxent into a binary presence-absence distribution. I used the sensitivity-specificity equality approach (Cantor et al. 1999), which is effective at minimising both false positives and false negatives (Liu et al. 2005; Lobo et al. 2008). I also calculated the maximum sum of sensitivity and specificity threshold, which has been shown to perform well when true absence data is lacking (Liu et al. 2013). To further investigate the influence of threshold, I produced a second map using the 10 percentile model training presence as a threshold, which has been used as a threshold in other Maxent-based felid distribution maps (Ferraz et al. 2012; Swanepoel et al. 2013). This approach uses the suitability of the presence record below which 10% of the presence records fall to determine the 'presence' probability threshold.

3.3.8 Model refinement

When developing species distribution models it is important to take the ecological requirements of the target species into account (Guisan & Thuiller 2005). This is particularly true of leopards, which are known to have large home ranges in the Western Cape (Martins & Harris 2013). The smallest reported home range for leopards in the Western Cape is 40 km² (Norton & Henley 1987), however this study was based purely on VHF tracking of three leopards in the Cederberg Mountains. Martins (2006) argued that these estimates are likely to be inaccurate due to the small sample size and inherent difficulties involved in radio-tracking leopards in rugged terrain. Martins & Harris (2013) reported a minimum home range of 74 km² for female (n=4), and 100 km² for male leopards (n=7) in the Cederberg Mountains, based on data obtained from leopards fitted with GPS tracking collars. Therefore, I assumed that an area of less than 50 km² would be too small to support a resident leopard, and excluded these areas from the habitat model. Leopards in the Cederberg travel an average of 1.7 km per day, and therefore 'holes' within areas of continuous leopard habitat which are less than 1.7 km in diameter were reclassified as areas in which leopards were present. This is a

CHAPTER 3: LEOPARD HABITAT

conservative estimate, as leopards are known to move up to 13 km in a single day (Bailey 1993), and snow leopards (*Panthera uncia*) have been known to move rapidly across 30 km of unsuitable habitat in a single day (McCarthy et al. 2005).

Using these guidelines, the map output from Maxent was reclassified into a binary presence-absence map, which was converted to a polygon feature layer. Polygons covering an area greater than or equal to 50 km² were then selected and aggregated if they were located within 1.7 km of one another to produce the final habitat map.

As a final test of specificity, model outputs were assessed on their ability to predict leopard habitat based on the relatively fine-scale and specific data obtained from the three leopards fitted with GPS tracking collars by assessing how many of the collar GPS points fell within the predicted habitat areas.

CHAPTER 3: LEOPARD HABITAT

3.4 Results

3.4.1 Comparison of collar and camera trap/scat datasets

The MCP of the combined leopard GPS collar data covered an area of 1 115.28 km². This area contained 91 presence records from the camera trap and scat dataset and 589 presence records from the GPS collar dataset. The third, combined dataset consisted of 664 presence points. The test dataset contained 51 presence points that fell within the collar MCP area. The output models are summarized in Table 3-1, together with the AIC_c scores calculated using ENMTools.

Table 3-1. Results of Maxent model selection on six models using three datasets: Locations where leopard presence was recorded by camera traps or scat collection ('Camera/scats'), locations subsampled from GPS collar data ('Collar'), and a combination of the two datasets ('Combined'). Test samples were either independently-collected scat samples (Scat locations), or subsampled from the dataset

Dataset	Test sample	AUC _{test}	AIC _c	AIC _c weight
Camera/scats	Scat locations	0.775±0.029	3146.490	1
Camera/scats	Subsample	0.734 ± 0.053	3185.789	2.93 x 10 ⁻⁹
Collar	Subsample	0.732± 0.018	14854.310	0
Collar	Scat locations	0.566 ± 0.017	14863,670	0
Combined	Subsample	0.726 ± 0.017	17941.950	0
Combined	Scat locations	0.624 ± 0.035	17945.01	0

The models showed little difference in AUC_{test} scores between the three best-performing models (Table 3-1). However, there were larger differences between the AIC_c weight, suggesting that the models based on the camera trap and scat data performed best (Table 3-1). These models also performed better when tested using independent test data rather than subsampled data. Mapping the probability distributions generated by Maxent revealed similar trends between the different datasets. However, models that included collar data appeared to predict far greater use of low-lying areas than those using the camera and scat data (Figure 3-1).

CHAPTER 3: LEOPARD HABITAT

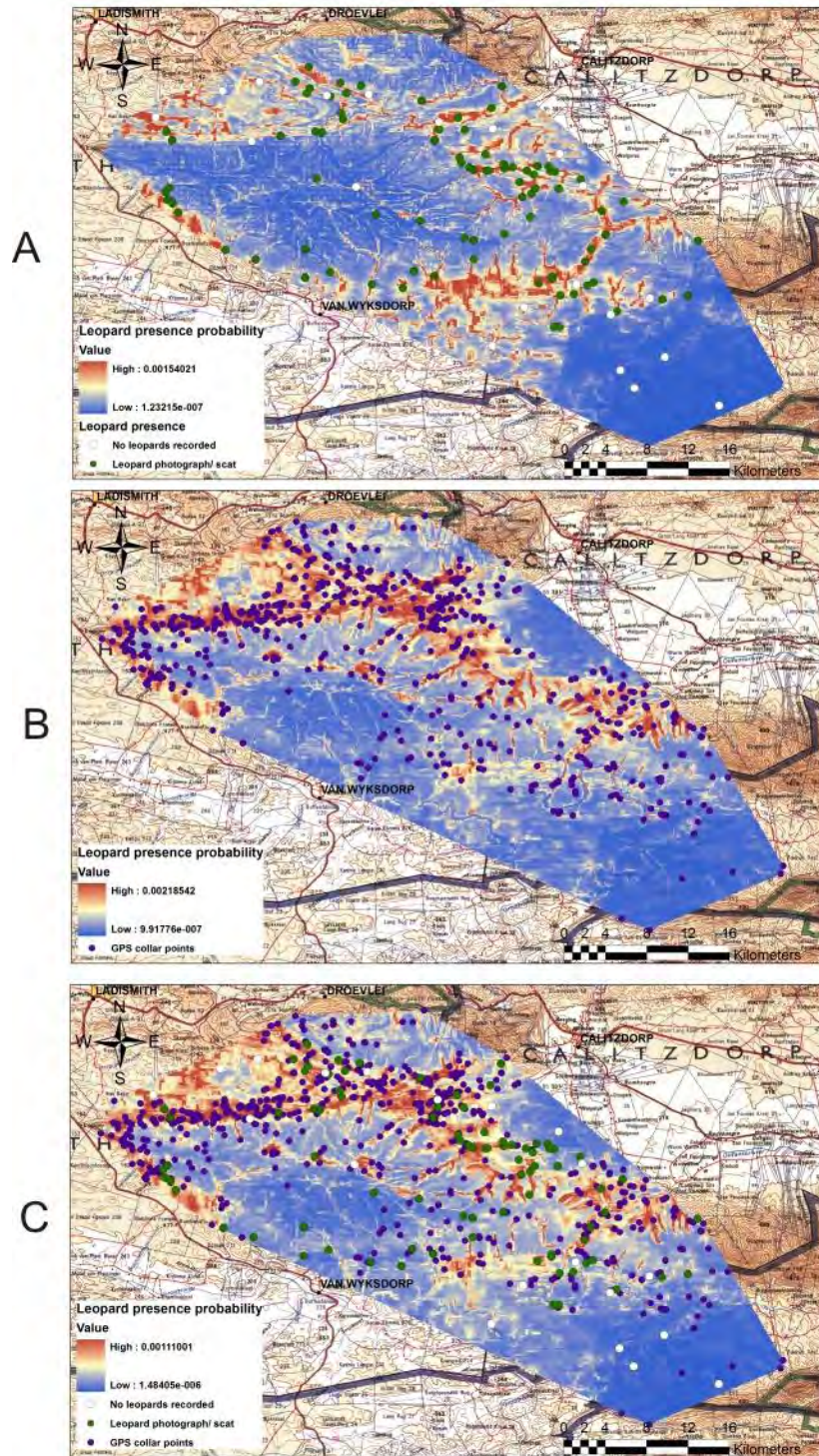


Figure 3-1. Maxent output maps of models restricted to the area used by GPS-collared leopards. Two datasets were used: camera and scat data (A) and GPS tracking collar data (B). Map C was generated using all presence data from both datasets. Green dots show the locations of leopard records from camera traps and scats, while purple dots indicate GPS points collected from the collar data. White dots indicate camera sites at which no leopards were recorded; these sites were not included in the Maxent model but were used to produce the bias layer (see Section 3.3.5). All models were tested using independent scat location data collected by Rautenbach (2010).

CHAPTER 3: LEOPARD HABITAT

3.4.2 Full study area models

The scat and camera trap dataset contained 259 presence points, while the subsampled GPS dataset contained 598 presence points. The combined dataset contained 728 presence points. The output models are summarised in Table 3-2, together with the AIC_c scores calculated using ENMTools.

Table 3-2. Results of Maxent model selection on six models using three datasets: Locations where leopard presence was recorded by camera traps or scat collection ('Camera/scats'), locations subsampled from GPS collar data ('Collar'), and a combination of the two datasets ('Combined'). Test samples were either independently-collected scat samples (Scat locations), or subsampled from the dataset.

Dataset	Test sample	AUC_{test}	AIC_c	AIC_c weight
Camera/scats	Scat locations	0.831 ± 0.021	6467.817	1
Camera/scats	Subsample	0.758 ± 0.037	6537.728	1.18×10^{-15}
Collar	Subsample	0.827 ± 0.015	16586.480	0
Collar	Scat locations	0.669 ± 0.024	16616.73	0
Combined	Subsample	0.809 ± 0.014	23310.770	0
Combined	Scat locations	0.723 ± 0.022	23303.420	0

Although the AUC_{test} scores for the six models were similar, the AIC_c scores show that the models using the camera trap and scat data performed best, and that using independent, rather than subsampled test data improved model performance (Table 3-2). This pattern was reversed in the other two datasets, as the subsampled models achieved better AUC_{test} and AIC_c scores (Table 3-2).

AIC_c may be considered a more reliable predictor of model performance than AUC_{test} (Warren & Seifert 2011). The model using camera and scat data, with the independent test data was thus selected as the best-performing model, and subsequently optimised using the regularisation parameter in Maxent. The results of this analysis are displayed in Table 3-3.

CHAPTER 3: LEOPARD HABITAT

Table 3-3. Results of a comparison of Maxent models using 12 regularisation parameters. All models were based on the camera trap/scat dataset, with independently-collected scat sample locations used as the test data.

Regularisation parameter	AUC _{test}	AIC _c	AIC _c weight
1.5	0.813 ± 0.023	6344.102	1.00
2	0.804 ± 0.024	6385.191	1.02 × 10 ⁻⁹
3	0.791 ± 0.023	6399.565	9.05 × 10 ⁻¹³
2.5	0.797 ± 0.023	6403.001	1.62 × 10 ⁻¹³
5	0.785 ± 0.022	6435.741	1.26 × 10 ⁻²⁰
1	0.831 ± 0.021	6467.817	1.37 × 10 ⁻²⁷
0.5	0.821 ± 0.025	6468.864	8.10 × 10 ⁻²⁸
1.75	0.804 ± 0.022	6486.290	1.33 × 10 ⁻³¹
1.25	0.811 ± 0.022	6491.915	8.00 × 10 ⁻³³
10	0.748 ± 0.022	6510.302	8.13 × 10 ⁻³⁷
15	0.744 ± 0.023	6555.735	1.11 × 10 ⁻⁴⁶
20	0.729 ± 0.024	6610.938	1.14 × 10 ⁻⁵⁸

When using only the camera and scat data, but changing the regularisation parameters, there were far greater discrepancies between the AIC_c model rankings and the AUC_{test} scores of the models than were obtained in the analysis involving different datasets (*cf.* Table 3-2 and Table 3-3). While the model with a regularisation parameter of 1.5 had the best AIC_c ranking, it had the second-lowest AUC_{test} score (Table 3-3). AUC_{test} scores increased in inverse proportion to the magnitude of the regularisation parameter (Table 3-3). Following Warren & Seifert (2011), the model with the best AIC_c ranking was accepted as the best-performing model, particularly as AUC scores have been shown to become less reliable when the regularisation parameter is low.

The Jackknife estimators of variable importance revealed that distance from rivers is the most important determinant of leopard presence (see Figure 3-2). Removing this variable resulted in the largest loss of training gain, suggesting that this variable had the most unique information relative to the other variables used in the model.

CHAPTER 3: LEOPARD HABITAT

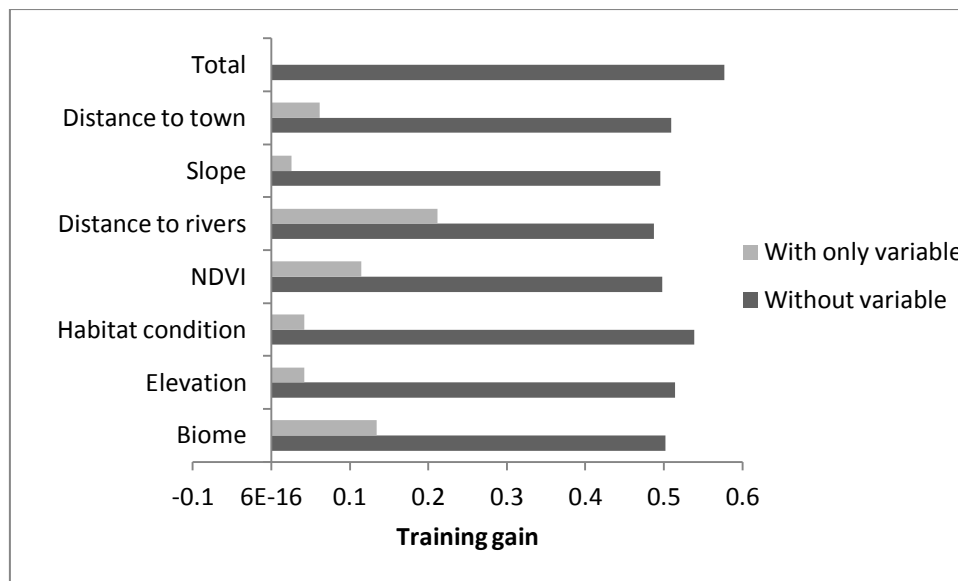


Figure 3-2. The contribution of each predictor variable to model training. The grey bar shows the contribution of each variable in isolation. The black bar indicates the total training gain of the model if that variable were omitted. The 'Total' bar shows the overall regularised training gain of the model.

The equal test sensitivity and specificity threshold averaged across the 20 replicates of the final model was 0.4032 and identified 28.91 percent of the study area as suitable leopard habitat. Similar figures were obtained for the maximum sum of sensitivity and specificity threshold, which was 0.4062 and identified 27.90 percent of the area as leopard habitat. The tenth percentile logistic training threshold was 0.2695 and identified 46.85 percent of the study area as suitable leopard habitat. The equal test sensitivity and specificity and tenth percentile logistic training thresholds were applied to the continuous study area probability output to produce the final binary presence-absence maps (Figure 3-3 and Figure 3-4).

There are obvious visual differences between the model outputs based on the 'presence' threshold used (Figure 3-3 and Figure 3-4). A presence threshold based on the equal model sensitivity and specificity predicted 2559 of the 3942 leopard presence points obtained from the tracking collars (64.92%). The aggregated polygon based on this threshold overlapped with 2304 of the tracking collar points. The tenth percentile training present logistic threshold model included 3265 of the tracking collar points (82.83%). The aggregated polygon based on this threshold performed better, as it overlapped with 3309 of the 3942 collar data points (83.94%). The model outputs were compared using a Chi-square (χ^2) goodness-of-fit test to test their relative ability to predict collar data points. The tenth percentile logistic threshold included significantly more of the collar data points ($\chi^2 = 888.90$, $df=1$, $p<0.01$) as did the aggregated polygon based on this threshold ($\chi^2 = 1900.85$, $df=1$, $p<0.01$).

CHAPTER 3: LEOPARD HABITAT

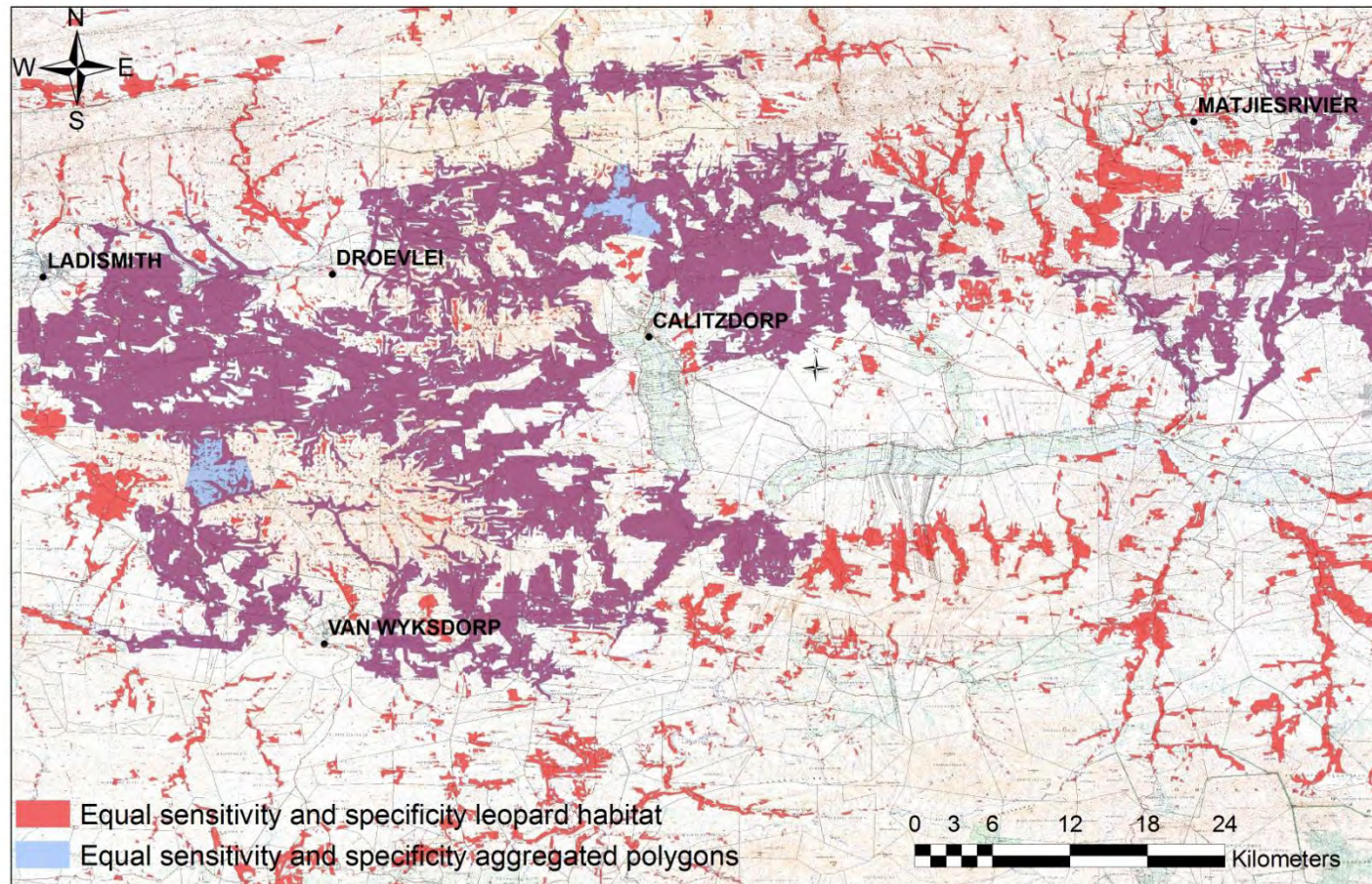


Figure 3-3. Leopard habitat map for the study area based on an equal model sensitivity and specificity threshold. Red-shaded areas represent areas with a high probability of leopard presence based on the Maxent model without additional processing. Areas were classified as leopard habitat when the probability of leopard occurrence exceeded 0.4032. The areas shaded in purple show overlap of the aggregated polygons (blue) and leopard habitat (red) identified using the equal sensitivity and specificity threshold.

CHAPTER 3: LEOPARD HABITAT

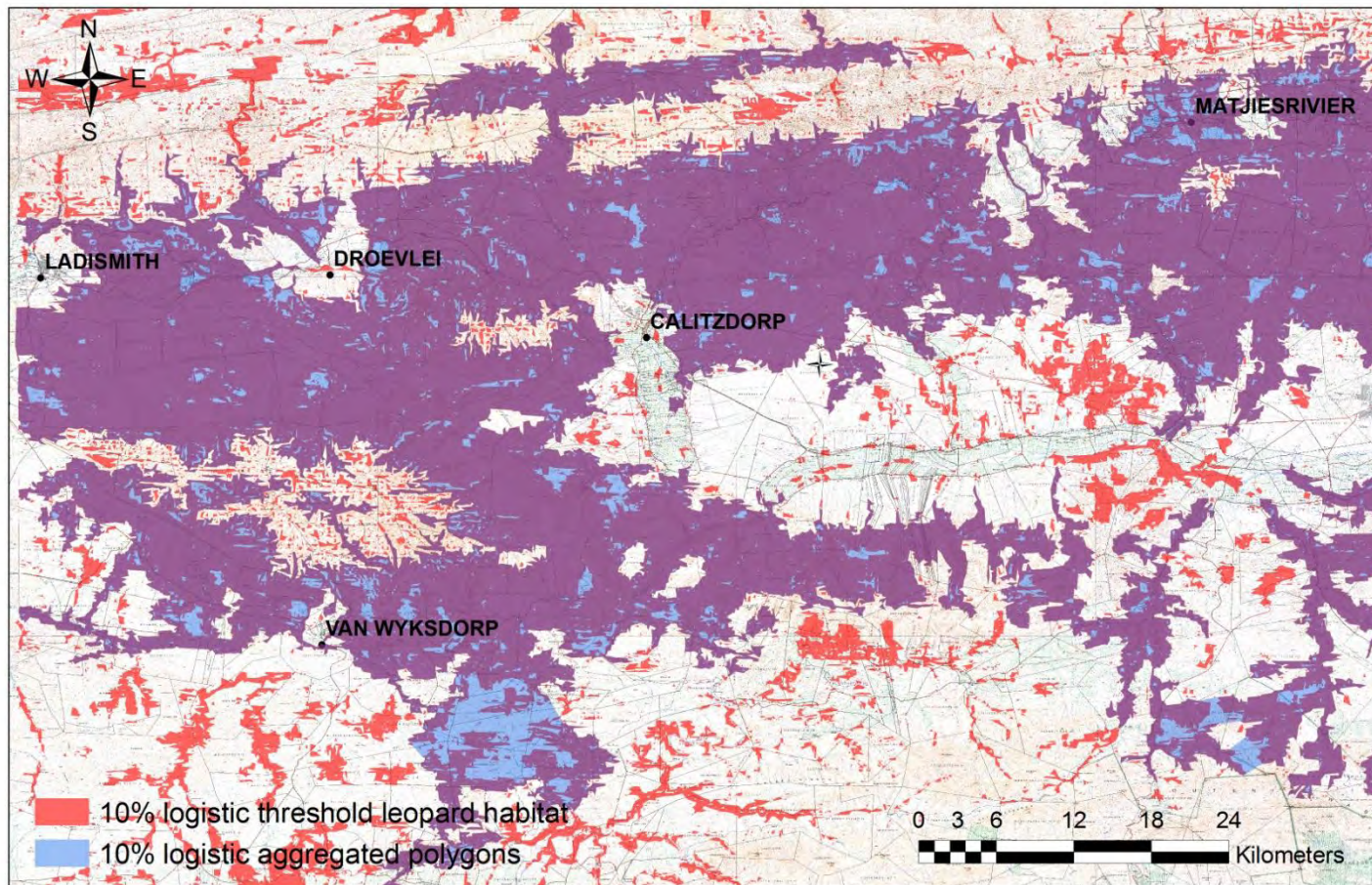


Figure 3-4. Leopard habitat map for the study area based on the tenth percentile training presence logistic threshold. Red-shaded areas represent areas with a high probability of leopard presence based on the Maxent model without additional processing. Areas were classified as leopard habitat when the probability of leopard occurrence exceeded 0.2695. The areas shaded in purple show the overlap between the aggregated polygons (blue) overlap with the areas identified as leopard habitat (red).

CHAPTER 3: LEOPARD HABITAT

3.5 Discussion

Leopard distribution across the study area was strongly influenced by topography and, to a lesser extent, human disturbance. I therefore rejected the null hypothesis that leopards are evenly distributed across the study area. Models based on camera trap and scat data performed significantly better than those that used GPS collar data, despite the latter having a larger sample size. These results support the findings of Bean et al. (2012), who suggested that models based on data sampled over a larger extent of the study area with fewer records are likely to be superior to those based on many records obtained from spatially biased sampling. The three collared leopards occupied adjoining territories that together made up approximately one third of the total study area. Data from the GPS collars were thus a relatively dense cluster of presence points which were not necessarily representative of environmental conditions found across the entire study area. In contrast, data from camera traps and scats were collected at lower densities, but were far more evenly distributed over the study area. The broader spatial coverage and range of environmental conditions sampled within the camera/scat dataset is likely to have contributed to the superior performance of models based on these data. Models that included all three data sources (camera/scat/GPS collar) performed worse than any three of these methods analysed alone supporting the suggestion by Warton and Aarts (2013) that movement data from the collars and static data from the cameras and scats should ideally be evaluated separately.

GPS collar data provided more data on leopard presence than either camera traps or scat, even after correcting for autocorrelation. However, these data were derived from only three individuals, all of which were male and hence these data are biased, both by sex and spatially within the study area. It goes without saying that the inclusion of more individuals and the inclusion of females would have greatly increased the ability of this type of data to predict leopard presence within the region. However, the logistics were such that after 1048 trap nights and eight captures, only data from three adult males was obtained.

I attempted to control for this lack of GPS location data by developing a preliminary set of models that only covered the area within a minimum convex polygon based on combined GPS collar data from the three leopards. The collar data were far more evenly distributed within this reduced area, and comprised a much larger number of presence points than the camera and scat dataset. Despite this, the camera and scat dataset still produced better results. One possible explanation for this trend is that the collar data only reflected the movements of adult male leopards. Female and sub-adult male leopards are also likely to have used the area, but may have exhibited different movement patterns to the collared adult males (Bailey 1993; Mizutani & Jewell 1998; Odden & Wegge 2005). These demographic groups, unrepresented in the collar dataset, were detected by

CHAPTER 3: LEOPARD HABITAT

camera traps and could also have been represented amongst the scat samples collected for both the model-training and testing datasets. Despite a general bias towards adult male leopards (see Chapter 4), it is possible that the broader demographic spread of the camera and scat database contributed to the superior performance of these models, especially when tested against a similarly demographically indiscriminate test dataset. Furthermore, the independent data set against which models were tested consisted of locations of leopard scats that were collected in a similar manner to how scats were collected in this study (i.e. opportunistically, with a bias towards roads and paths). This may have caused similar bias in both the camera/scat and test datasets, resulting in the camera and scat dataset performing better simply because it was tested against similar data. Unfortunately, without independent collar data, it is not possible to empirically test this assumption, and all models tested by subsampling performed substantially worse than those tested against the independent test data.

The relatively poor performance of all models in this restricted area may also have been influenced by the manner in which Maxent selects background points, or pseudo-absences. Maxent selects 10 000 of these points, which are compared to the presence data to produce the model (Phillips et al. 2006). In an area mostly comprised of suitable leopard habitat, it is difficult to construct an accurate model, as many of these background points would have been drawn from areas that are actually used by leopards.

Tracking data from more leopards, covering a larger area, may have reduced spatial bias and improved the performance of the models based on the collar data alone. However, it is seldom possible to fit tracking collars on all individuals of the target species within a study area. Furthermore, unless tracking collars are fitted to a representative sample of the study population, including females and sub-adults, the resulting models are unlikely to be accurate for the entire population. Capturing and collaring a representative sample of the study population is difficult, particularly in arid areas where population densities are low (Stander et al. 1997; Martins 2010). The value of tracking collars as a tool for predicting leopard presence on a landscape level is thus questionable, especially given the effort required to capture leopards, the invasive nature of collaring, and the difficulty of retrieving collars, even with drop-off devices.

When assessing models covering the full study area, AUC_{test} showed little difference between the model based on camera trap and scat location data, which was tested with independently-collected scat location data and the model based on collar data, tested by subsampling. The AUC_{test} scores of these two models were within one standard deviation of one another, suggesting little difference between the models. However, the AIC_c scores strongly suggested that the camera trap/scat location

CHAPTER 3: LEOPARD HABITAT

model was superior. The nature of the test data used in these two models provides further evidence for preferring the camera trap/scat location model, as independent test data are less likely to provide over-optimistic measures of model performance than subsampled data (Fielding & Bell 1997).

The test of different regularisation parameters also emphasises the importance of optimising the regularisation parameter in Maxent. The default value of one has been found to be most appropriate for a wide range of species and ecosystems (Phillips & Dudik 2008). My study found that five of the alternative regularisation parameters tested provided better model performance than the default setting when AIC_c was used as a measure of model performance (Warren & Seifert 2011). These parameter values were all greater than one, suggesting that the default parameter of one over-fitted the data and thus limited the predictive capacity of the model. The greater the value of the regularisation parameter used, the 'smoother' the model fit becomes, with greater tolerance of deviance from the environmental variables associated with presence points (Phillips & Dudik 2008; Warren & Seifert 2011). A regularisation parameter of zero will thus fit the model precisely to the combination of environmental variables associated with the presence points entered into the model. A regularisation parameter of greater than one may improve the predictive ability of the model, but can also result in a loss of specificity. This can be useful when modeling range-shifting or invasive species, where regularisation parameters as high as 10 have been used (Elith et al. 2010).

The Jackknife parameters of variable performance in the final model identified the variable 'distance to rivers' as the most important in model training. Leopards in the Karoo portion of the Cederberg Mountains have been shown to preferentially select areas close to rivers based on GPS tracking collar data (Martins 2010). This would provide more cover to leopards and potentially improve hunting success. Leopards hunt in areas where they have a greater chance of catching prey (Balme et al. 2007), which could partially explain a preference for drainage lines, where dense vegetation is likely to provide more cover.

Higher elevation sites and steeper slopes were also important predictors of leopard presence, suggesting that leopards prefer mountainous terrain. Similar trends have been observed for leopards in both the Cederberg (Martins & Martins 2006) and in central Asia (Gavashelishvili & Lukarevskiy 2008), indicating that mountains have provided leopards with an important refuge within an otherwise largely human transformed landscape. Interestingly, very high elevations had a low probability of leopard presence (Figure 3-3 and Figure 3-4), suggesting that leopards prefer steep slopes at lower altitudes, typical of foothills and the deeply incised valleys common in the Little Karoo. Martins (2010) found that leopards in the Karoo region of the Cederberg Mountains avoided

CHAPTER 3: LEOPARD HABITAT

elevations over 800 m, preferring the deep gorges where there was more cover available. In this study, the majority of collar locations points were recorded at lower altitudes and only 20 percent of all locations were recorded at altitudes above 764 m. While there is no evidence to suggest that leopards are incapable of using high altitude habitats, these data indicate that they prefer the lower altitudes. It is also important to note that from a conservation perspective, the exclusion of high altitude areas is largely irrelevant for two reasons. Firstly, high altitude areas are generally well-conserved in the Western Cape (Lombard et al. 2010), and most of the excluded areas fall within the Swartberg Nature Reserve. Secondly, the rugged terrain and general inaccessibility of these areas means that they are highly unlikely to be subjected to human development in the foreseeable future.

However, leopards also occupy non-mountainous habitat elsewhere in South Africa (Henschel et al 2009). Balme et al. (2007) found that leopards avoided open areas where there was little cover and my results show a similar trend for the Little Karoo, where low-lying, flat areas do not comprise suitable leopard habitat. The succulent Karoo vegetation which characterises these low-lying areas would provide little or no cover to leopards, while both the rugged topography and denser vegetation found in mountainous areas would provide cover and improve hunting success.

The choice of threshold used to reclassify continuous probability Maxent output maps into binary presence/absence maps can have a major influence on the manner in which the model is interpreted (Liu et al. 2005; Bean et al. 2012). The equal sensitivity and specificity (ESS) threshold-based map produced in my study had a much higher threshold than the alternative map, which used a tenth percentile training presence logistic threshold (TenPT). This resulted in the ESS map output identifying a much smaller area as potential leopard habitat; an area which was further reduced with the aggregation of the map into minimum habitat size areas of at least 50 km². Even without this additional processing, the ESS threshold excluded more than one third of the location points recorded by the collared leopards. Recent research has shown that using the maximum sum of sensitivity and specificity (Max SSS) produces similar thresholds for presence-only data as for presence-absence data (Liu et al. 2013). My results showed that the Max SSS threshold (0.4062) was similar to the ESS threshold (0.4032) in the final model. The ESS and Max SSS thresholds are based on the assumption that errors of omission (the model falsely excludes areas of suitable habitat) and commission (the model includes areas of unsuitable habitat) are equally costly (Lobo et al. 2008). In this situation, errors of omission are far more costly than errors of commission, and the threshold should be adjusted accordingly (Lobo et al. 2008). My results suggest that both the ESS and Max SSS thresholds are too stringent and can exclude large areas of actual leopard habitat.

CHAPTER 3: LEOPARD HABITAT

The TenPT model showed the opposite trend, where the aggregation of polygons actually resulted in a larger proportion of the collar data being included in the model. While the TenPT model may have overestimated the amount of available leopard habitat in the area, the precautionary principle suggests that this is the more appropriate threshold upon which to base future planning and management for leopards in the Western Cape. This threshold has also been used to model leopard presence in South Africa on a national scale (Swanepoel et al. 2013) and for leopards in India (Mondal et al. 2013)

Leopard habitat within the study area appears to be relatively unfragmented, and largely falls within previously identified biodiversity corridors (Lombard et al. 2010). This suggests that leopard conservation goals could easily be incorporated into existing conservation plans (see Figure 3-5, Appendix 3B). Top predators have been shown to be associated with relatively high biodiversity (Sergio et al. 2006, 2008), and the congruence between leopard conservation and landscape-level conservation plans is thus to be expected. As large, charismatic predators, leopards could be used as a flagship species to raise public awareness and support for broader conservation initiatives.

3.6 Conclusion

Topography, vegetation and human disturbance variables all influenced leopard distribution within the study area. Between 28.91 and 46.85% of the total study area was identified as being suitable leopard habitat with high levels of connectivity, courtesy of mountain chains and river corridors. Leopard presence within the study area was highest along drainage lines and the steep slopes of intermediate elevation, typical of mountainous areas and lowest at low altitudes characterized by a lack of cover and strong human presence. Future conservation management should focus on maintaining the lowland corridor areas identified in this study, as these form potential links between core mountain habitat areas. In addition, detailed and accurate habitat models can be produced without resorting to the live capture and collaring of leopards, which should guide future research efforts (Balme et al. 2013).

CHAPTER 3: LEOPARD HABITAT

3.8 Appendices

Appendix 3A

Table 3-4. Summary of data used to generate environmental predictors of leopard habitat suitability in the Little Karoo

Variable	Resolution of original layer	Units or categories	Source
Elevation	90 metre	Continuous, ranging from 55 to 2308 metres	Shuttle Radar Topography Mission (http://www2.jpl.nasa.gov/srtm/africa_radar_images.htm) accessed on 04/04/2013
Slope	90 metre	Continuous, ranging from 0° to 69.2702°	Calculated from the Elevation data using the Slope function in the Spatial Analyst extension of ArcGIS 9.3
TRI	90 metre	Continuous index values ranging from 0 to 1209.86	Calculated from Elevation data using the Map Algebra function in ArcGIS 9.3
Distance to river	100 metre	Continuous, ranging from 0 to 0.0368632 decimal degrees	Calculated using the Euclidean Distance function in ArcGIS 9.3 from river data obtained from the Western Cape Nature Conservation Board Integrated Biodiversity Layer – Rivers (Garden Route and Little Karoo and Central Karoo areas)
Vegetation	Vector	6 vegetation categories: fynbos, renosterveld, succulent karoo, thicket, drainage and source	Little Karoo Vegetation Map Planning Domain, accessed via the South African National Biodiversity Institute Biodiversity GIS
NDVI	500 m	Continuous index values ranging from 1369 to 8111	Moderate Resolution Imaging Spectroradiometer (MODIS) (http://reverb.echo.nasa.gov/reverb/), accessed on 01/04/2013

CHAPTER 3: LEOPARD HABITAT

Variable	Resolution of original layer	Units or categories	Source
Habitat condition	Vector	5 categories: natural, near natural, degraded, no natural habitat and unknown	Obtained from the Western Cape Biodiversity Framework habitat layer produced in 2010 for the Western Cape Nature Conservation Board.
Distance to town	90 metre	Continuous, ranging from 0 to 0.412186 decimal degrees	Polygons of all towns and villages within the study area were drawn by tracing the outline of the settlement in Google Earth. ArcGIS 9.3 was used to convert these to a shapefile and to calculate the Euclidean distance between towns.

CHAPTER 3: LEOPARD HABITAT

Appendix 3B

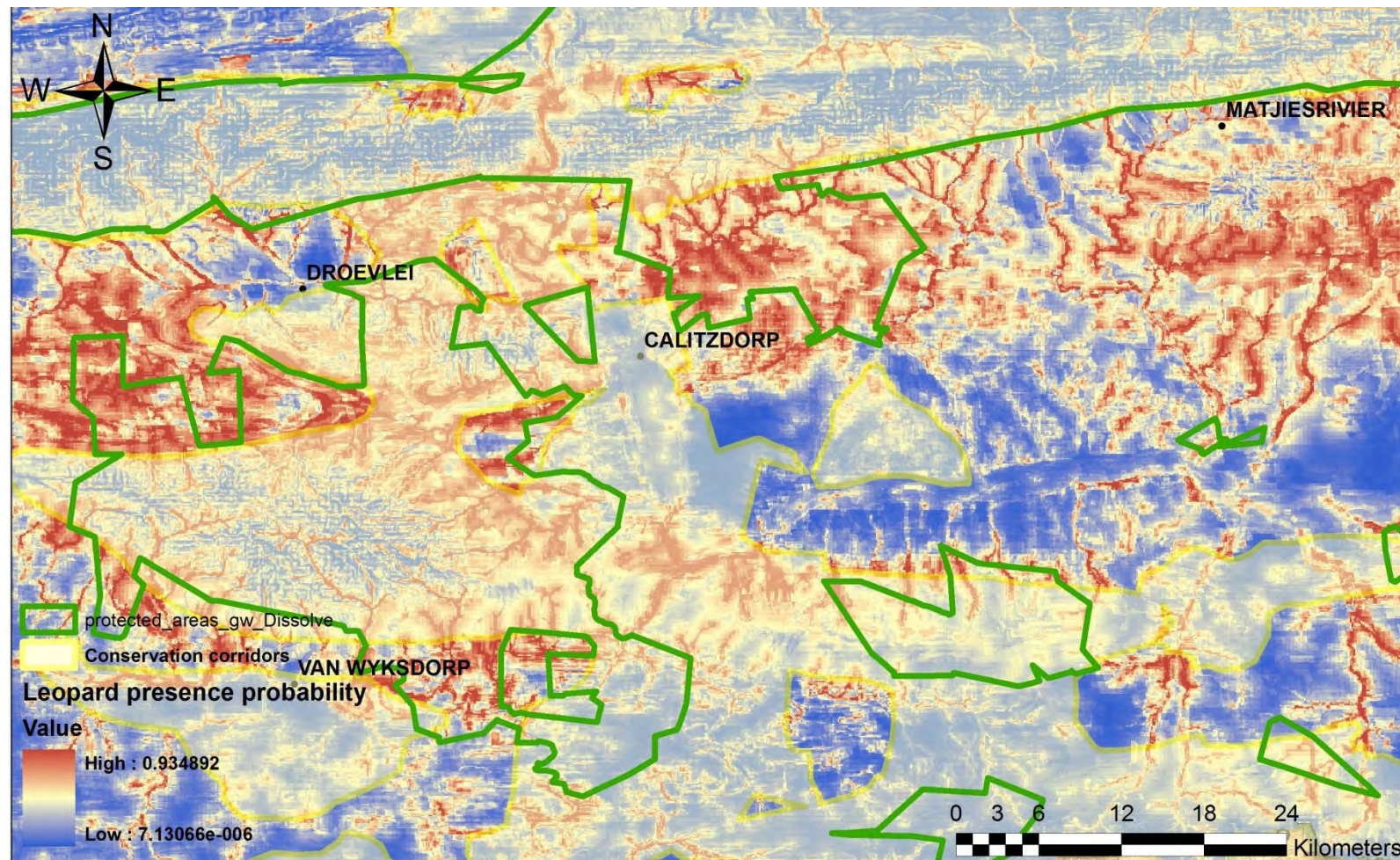


Figure 3-5. Continuous leopard habitat probability map of the Little Karoo, ranging from blue (low probability) to red (high probability). Yellow shaded areas are corridors identified by Lombard et al. (2010). Existing conservation areas (both state and private nature reserves) are shown with green borders.

CHAPTER 4: ESTIMATING AND MONITORING LEOPARD POPULATION DENSITY IN THE LITTLE KAROO

4.1 Abstract

Reliable estimates of population size and density are critical for the effective conservation management of ecologically important species. This chapter presents the first assessment of the population density of leopards in the Little Karoo, South Africa, using both conventional capture-recapture and spatially explicit capture-recapture methods. Camera traps were set up at 141 sites, covering an area of 3219 km². Camera sites were active for an average of 93 days, and the entire survey took 520 days to complete. Data were analysed using the program DENSITY for spatially explicit capture-recapture (SECR) analysis, and CAPTURE for non-spatial abundance estimation. A total of 150 usable leopard photographs were recorded of 13 male leopards, 6 females and 10 sub-adults of unknown sex. SECR methods estimated population density as 1.184 (± 0.224) leopards/100 km² for the whole population, and 0.756 (± 0.176) leopards/100 km² when sub-adults were excluded. Non-spatial capture-recapture population density estimates were lower, ranging from 0.469 (± 0.025) to 0.8574 (± 0.142) leopards/100 km² for the whole population and from 0.383 (± 0.083) to 0.6076 (± 0.1309) adult leopards/100 km². These population densities are amongst the lowest ever recorded in South Africa. Spatially explicit capture-recapture methods appear to offer more reliable population density estimates as they are more robust to the size of the buffer strip around the camera grid. An array of 22 sites was selected for long-term monitoring of the leopard population using camera traps. The ability of these sites to detect leopard population declines was tested by randomly removing individual capture histories from the dataset. The monitoring array obtained similar density estimates to the full survey, and was able to detect population density declines greater than or equal to 12 percent of the original density estimate. Although the proposed monitoring array offers a relatively low-cost method of monitoring the leopard population in future, surveys of a similar scale to that done for this study should be repeated at five to 10 year intervals to

CHAPTER 4: LEOPARD POPULATION DENSITY

allow for finer scale understanding of population changes in different land use areas and to identify potential new threats.

CHAPTER 4: LEOPARD POPULATION DENSITY

4.2 Introduction

Robust population size and density estimates are crucial data for any conservation project (Gusset & Burgener 2005; Sharma et al. 2010). Although acquiring this information is often difficult, time-consuming and expensive, it is necessary to guide strategic, science-based conservation planning, while the absence of such data hampers conservation planning and consequently impedes effective conservation (Blake & Hedges 2004; Linkie et al. 2006). This is particularly true of large carnivores, which are often more vulnerable to extirpation than other ecosystem components and have a disproportionate ecological importance (Woodroffe & Ginsberg 1998; Estes et al. 2011; Ripple et al. 2014).

Studying large carnivores is difficult due to their relatively low population densities, large home ranges and the general difficulties in capturing or observing them (Terborgh 1988; Mills et al. 2000). Direct counts of these predators are thus seldom possible and consequently abundance has been estimated through data gathered by indirect means such as spoor or animal sign counts (Stander 1998; Gusset & Burgener 2005; McCarthy et al. 2008; Balme et al. 2009), transects (Silveira et al. 2003) and camera trap surveys (Karanth 1995; Karanth & Nichols 1998).

Sign-based methods have been criticised as having too much observer bias (McCarthy et al. 2008), and uneven detection ability due to environmental conditions (Karanth et al. 2003; Funston et al. 2010). Karanth et al. (2003) criticised sign-based census methods for annual population estimates of tigers (*Panthera tigris*) in India citing the inability of observers to reliably distinguish between tracks left by different individuals.

However, camera trap surveys have been found to perform well in comparison to other abundance estimation methods for individually recognizable carnivores (Silveira et al. 2003; McCarthy et al. 2008; Balme et al. 2009). The first abundance estimates from camera trap surveys were produced for tiger populations in India (Karanth 1995; Karanth & Nichols 1998) and were based on a mark-recapture framework (Otis et al. 1978). As camera traps do not physically mark passing animals, the

CHAPTER 4: LEOPARD POPULATION DENSITY

method assumes that all individuals of the target species are individually identifiable (Karanth 1995). Despite this limitation, camera trap surveys using the methods pioneered by Karanth (1995) have been used to estimate the abundance of a wide variety of species including tigers (Karanth & Nichols 1998; Mohd. Azlan & Sharma 2003; O'Brien et al. 2003; Kawanishi & Sunquist 2004; Linkie et al. 2006; Lynam et al. 2009), ocelots (*Leopardus pardalis*) (Trolle & Kery 2003; Dillon & Kelly 2008), jaguars (*Panthera onca*) (Silver et al. 2004; Soisalo & Cavalcanti 2006; Núñez-Pérez 2011), Andean bears (*Tremarctos ornatus*) (Ríos-Uzeda et al. 2007), cheetahs (*Acinonyx jubatus*) (Marnewick et al. 2008), European wildcats (*Felis silvestris silvestris*) (Anile et al. 2012), Geoffroy's cats (*Oncifelis geoffroyi*) (Cuellar et al. 2006), pumas (*Puma concolor*) (Negrões et al. 2010), common genets (*Genetta genetta*) (Sarmiento et al. 2010) and maned wolves (*Chrysocyon brachyurus*) (Trolle et al. 2006).

Camera traps have also been used to survey leopard (*Panthera pardus*) populations in a variety of different habitat types including Asian tropical forests (Harihar et al. 2011; Gray & Prum 2012; Mondal et al. 2012a), African forests (Henschel 2008), bushveld and savannah (Steyn 2007; Balme et al. 2009; Chapman & Balme 2010; Stein et al. 2011; Grant 2012) and semi-arid mountains (Martins 2010). In Africa, camera trap-derived leopard densities have been estimated to range from approximately 0.25 leopards per 100 km² in more arid areas (Martins 2010; Stein et al. 2011) to over 12/100 km² in tropical forests (Henschel 2008).

One of the major flaws of traditional (non-spatially-explicit) capture-recapture analyses of camera trap data is that it is difficult to calculate the area that has been effectively sampled during the survey (Efford 2004; Borchers 2010). The method used to determine the effectively sampled area can have a major impact on density estimates, potentially biasing results (Pereira et al. 2011; Foster & Harmsen 2012). Individuals whose home range is not completely contained within the sample grid will make use of an area outside the grid, and failure to incorporate this area will result in inflated density estimates (Karanth 1995). In an attempt to negate this problem, researchers have routinely

CHAPTER 4: LEOPARD POPULATION DENSITY

calculated the mean maximum distance that animals move between camera stations (MMDM) and then added a buffer of either half or the full MMDM to the perimeter of the sample grid to approximate the effective sample area (Karanth 1995; Karanth & Nichols 1998; Silveira et al. 2003; Silver 2004; Soisalo & Cavalcanti 2006; Balme et al. 2009). However, this approach is problematic because the observed MMDM is likely to be heavily influenced by camera spacing and is generally truncated at the edge of the sampled area (Efford 2004; Maffei & Noss 2008; Foster & Harmsen 2012). Thus, other studies have used a maximum distance moved (MaxDM) based on telemetry data of collared individuals to calculate the buffer zone (Mccarthy et al. 2008; Martins 2010; Grant 2012). This is generally considered to be a more reliable method of determining the buffer zone. The MMDM derived from camera traps can underestimate true home range size and result in inflated population density estimates as individuals are likely to have home ranges that extend beyond the two furthest points at which they are recorded (Soisalo & Cavalcanti 2006).

Recently, a more robust statistical framework has been developed for analysing capture-recapture data. Spatially explicit capture-recapture (SECR) methods (Efford 2004; Borchers & Efford 2008; Royle et al. 2009a) differ from traditional capture-recapture methods by specifically incorporating the spatial location of camera traps into the analysis. SECR models combine a 'state' model (based upon potential activity centres for individuals within the study area) with a spatial detection function to estimate density (Foster & Harmsen 2012). By incorporating the spatial locations of camera traps, SECR models are able to calculate the effectively sampled area based on the capture-recapture data, reducing the reliance on ad-hoc buffer estimates to calculate density (Borchers 2010). SECR methods have been applied to a range of species including birds (Dawson & Efford 2009), minke whales (*Balaenoptera acutorostrata*) (Marques et al. 2010), black bears (*Ursus americanus*) (Obbard et al. 2010) in addition to camera trap surveys of large felids (Royle et al. 2009a; Sollmann et al. 2011; Kalle et al. 2011; Grant 2012; Mondal et al. 2012b; Noss et al. 2012; Gray & Prum 2012; Tobler et al. 2013).

CHAPTER 4: LEOPARD POPULATION DENSITY

Little is known of the status of the leopard population in the Western Cape, largely due to the inherent difficulties of studying such a wide-roaming, cryptic species. To date, the only published capture-recapture-based population estimate of Western Cape leopards is for the semi-arid Cederberg Mountains (Martins 2010). Here substantial variation in leopard population density was reported between the fynbos (1.8 to 2.3 leopards/100 km²) and Karoo biomes (0.25 to 0.99 leopards/100 km²). The aim of my study is thus to explore the generality of the findings in the Cederberg region (Martins 2010) by applying capture-recapture population size and density methods to the extreme eastern extent of the Western Cape's Cape fold mountain chain. As Martins (2010) used non-spatial capture-recapture estimators to calculate the density of the leopard population in the Cederberg Mountains, it was necessary to employ these methods as well as the spatially explicit capture-recapture methods to allow for a direct comparison between the two areas.

Finally, I will attempt to develop a smaller camera trap array to enable local conservation authorities (CapeNature) with less time and resources than were available to me, to perform long-term monitoring of this leopard population. Such monitoring is essential to identifying both current and future threats and the impacts of interventions on the conservation status of this important species within this global biodiversity hotspot (Myers et al. 2000; Lombard et al. 2010).

Despite the large body of literature on applying capture-recapture methods to estimate felid population densities, there has been little attention given to modifying these methods to monitor long-term population trends. To date, monitoring frameworks have largely been applied to spoor counts as a measure of abundance (Stander 1998; Hayward et al. 2002). While these have been found to correspond to absolute population in some cases (e.g. Stander 1998), spoor counts have also been strongly criticised as a monitoring technique (Karanth et al. 2003). An important consideration in the Little Karoo is that spoor counts could only be applied across a small proportion of the habitat available to leopards where the substrate is suitable for spoor identification. These areas generally only occur in river valleys and along roads, which are likely to introduce a strong

CHAPTER 4: LEOPARD POPULATION DENSITY

spatial bias to the survey. Furthermore, if leopards occur at low densities in this area then the probability of detecting spoor in the few areas where leopard spoor could be reliably identified will be very low (McCarthy et al. 2012). There is also a strong possibility that leopard spoor would be obscured by rain, wind or the spoor from other animals (e.g. baboons (*Papio hamadryas*)) before being observed.

An alternative approach is to use occupancy modelling based on presence/absence data to monitor population trends (MacKenzie et al. 2002; Mackenzie & Royle 2005). Occupancy models have been used successfully to monitor tiger populations in India (Hines et al. 2010; Karanth et al. 2011). In the Little Karoo, where occupancy is likely to be relatively low, occupancy modelling would require that a large number of sites be surveyed (Mackenzie & Royle 2005). Occupancy modelling can be done at the level of specific sites (in this case, camera stations) or within grid cells (MacKenzie et al. 2005). While grid cells were used to guide camera location in this study, these were large relative to the study area (50 km²), and therefore any occupancy estimates derived from the camera survey data would have low spatial resolution. More importantly, occupancy-based monitoring has been heavily reliant on being able to reliably detect animal sign, such as spoor and scats (Hines et al. 2010; Karanth et al. 2011). As discussed above, this is problematic in the Little Karoo. Interview data has also been used to model carnivore occupancy (Zeller et al. 2011). This approach is also difficult to apply in the Little Karoo, as human encounters of leopards (or even leopard sign) are rare due to the leopard's low population densities and preference for rugged, remote areas (see Chapter 3).

Camera traps are thus likely to be the most reliable means of gathering leopard population data in the Little Karoo, and have the additional advantage of allowing for the identification of individuals. This additional information allows monitoring to utilise a spatially explicit capture-recapture framework (Efford 2004; Borchers & Efford 2008; Efford et al. 2009), which is generally considered to be the most reliable of the current methods available for estimating population density of

CHAPTER 4: LEOPARD POPULATION DENSITY

individually recognizable species (Sollmann et al. 2011; Foster & Harmsen 2012; Tobler & Powell 2013).

There are currently no published studies that have adopted this framework for long-term monitoring using camera traps (Noss et al. 2013), and my study thus represents a novel application of capture-recapture theory.

CHAPTER 4: LEOPARD POPULATION DENSITY

4.3 Methods

4.3.1 Overall study design and camera placement

A pilot camera trapping study was carried out by the Cape Leopard Trust in the Little Karoo between September 2007 and January 2011 (unpublished data). During this period, approximately 10 camera traps were set up at 35 relatively accessible sites where leopards were thought to be active. Camera traps were typically deployed on likely leopard travel routes (i.e. along game trails and dirt roads); sites remained active for periods varying from 14 days to over three years. During the pilot study, between 27 and 33 unique leopards were photographed. A more precise estimate is not possible as most sites were set up with a single camera, and thus simultaneous photographs of both flanks of most individuals were not recorded. This impeded reliable identification and the development of complete capture histories of individuals. Although none of these data were used in the analysis presented in this chapter, the pilot study did provide important information on likely capture rates and leopard habitat preference, which I used to optimize my study design.

Capture-recapture studies assume that all individuals can potentially be captured (Otis et al. 1978; White et al. 1982). Cameras were thus systematically arranged in a grid superimposed over the entire study area (see Figure 4-1) to ensure even coverage (Karanth 1995; Karanth & Nichols 1998). Cameras were set in 71 grid cells, each of which covered an area of 50 km², an area smaller than the minimum home range size (74 km²) recorded for leopards in the Western Cape (Martins & Harris 2013). Two camera sites were located within each grid cell. This ensured that all leopards living within the study area were likely to have some portion of their home range include at least one camera station, satisfying the assumption that all animals could be detected (Karanth & Nichols 1998; O'Connell et al. 2011). Cuddeback Capture camera traps (Non-Typical Inc. Wisconsin, USA) were used at all sites, occasionally in combination with Cuddeback Attack (12 sites) and Cuddeback Expert (9 sites).

Within each grid cell, camera stations were set up at sites where leopards were likely to be photographed in order to maximise capture probability and the proportion of the total population

CHAPTER 4: LEOPARD POPULATION DENSITY

sampled (Karanth & Nichols 1998; O'Connell et al. 2011). Each station consisted of two camera traps set up on opposite sides of a trail to allow for simultaneous photographs of both sides of any passing leopards (Karanth & Nichols 1998; Silver 2004). Although using two cameras per station reduces the number of active stations, this approach has been shown to increase survey efficiency as it increases photographic capture rate (i.e. detection failure is reduced) and it allows for more individuals of the target species to be identified (Negroes et al. 2012).

Large felids are often reported to habitually move along roads (Karanth 1995; Mohd. Azlan & Sharma 2003; Soisalo & Cavalcanti 2006; Balme et al. 2009). However, setting cameras on roads has been shown to introduce bias into population density estimates (Negrões et al. 2010; Sollmann et al. 2011). I thus attempted to set at least one camera site in each grid cell on less obvious pathways such as hiking or game trails, dry riverbeds, or in narrow gorges. Sites were selected based on the presence of leopard sign (including prior records of leopard activity during the pilot survey and previous observations by landowners), my own knowledge of the area and topographical features, such as along the bottom of steep gorges and along other drainage lines (Karanth & Nichols 1998; Martins 2010; Gutierrez-Gonzalez et al. 2012). If no leopard sign was evident, the cameras were set at game trails identified by the presence of other animal tracks, in the expectation that any leopards in the area would also use these trails.

Capture-recapture analysis assumes that the study population is demographically and geographically closed for the duration of the survey period (Otis et al. 1978; White et al. 1982). The assumption of population closure is particularly troublesome and can easily be violated (Soisalo & Cavalcanti 2006; Grant 2012). A general trend is to restrict the length of the survey period to reduce the risk of this assumption being violated (Karanth & Nichols 1998; Silver et al. 2004). However, leopards were expected to occur at low densities within the study area based on the pilot study (unpublished data). It was thus necessary to run the survey over a period of approximately 18 months (520 days), with each camera station active for an average of 93 days (± 6.90), to ensure that sufficient leopard

CHAPTER 4: LEOPARD POPULATION DENSITY

photographs were obtained and adequate sampling at each site. This is a longer period than most other studies, however some studies have been conducted over similar periods without the assumption of population closure being violated (Kawanishi & Sunquist 2004; Simcharoen et al. 2007; Mazzolli 2010). In general, the data gathered through an extended survey period is likely to outweigh the risk of violating the assumption of population closure (Tobler & Powell 2013).

The survey was carried out in five phases of approximately 90 days each. The first phase covered the westernmost side of the study area, and the cameras were shifted eastwards with each successive phase. The full north-south extent of the study area was sampled during each phase, and I used all available cameras to cover the maximum number of grid cells during each phase. This sampling scheme was adopted partially for logistical reasons, but also to reduce the influence of rainfall gradients and other climatic factors on results (Foster & Harmsen 2012). Rainfall in the Little Karoo is extremely variable, and is influenced by both season and topography (Vlok & Schutte-Vlok 2010). Although seasonal variation was unavoidable due to the extended duration of the survey, constant sampling along the full latitudinal extent of the study area ensured that I had constant representation of most habitat types throughout.

At the end of each phase, cameras were collected and deployed to their new locations as quickly as possible. Due to the size of the study area and the difficulties involved in gaining access to some sites, this process usually took approximately three weeks to complete. While the grid cells were used to guide broad-scale camera distribution, cameras were occasionally located just outside of the 'target' grid cell if no suitable site was identified. This was a rare occurrence and only affected four percent of sites. In some areas, it was necessary to position the cameras in sub-optimal locations to reduce the risk of flooding or theft. The latter is an unfortunate consequence of working on land with public-access, particularly in riverine corridors where there was abundant leopard sign, but also frequent use by subsistence fishermen and hikers. These considerations also prevented me from setting up cameras on public roads such as the Seweweekspoort Pass, despite relatively frequent

CHAPTER 4: LEOPARD POPULATION DENSITY

sightings of leopards by motorists. These factors may have negatively influenced the leopard population estimate derived from this survey but represent genuine limitations of camera trap surveys in landscapes with high human presence.

Sites were classified as active if at least one of the two cameras was operational. Camera failure occurred for a variety of reasons, including destruction or removal of the cameras by flooding, fire, theft or physical damage from animals such as baboons. Premature battery failure was also a common cause of camera failure. If both cameras failed more than 10 days before the site was visited to service or rotate the cameras, the site was kept active for an additional equivalent period to ensure even sampling effort. Heavy floods in June 2011, near the end of the first phase, resulted in the loss of 10 camera traps that were either washed away or rendered inoperable by water damage. Due to the risk of further flooding in these areas, I decided not to do further sampling at these sites. As a result, six sites had relatively short sample periods of less than 80 days, of which three were active for less than 60 days. Although uneven sampling effort can compromise survey results, the total number of trap days lost was relatively low (164 trap days) when compared to the overall sample effort (13 085 trap days). The habitat types in which these sites were located were also well-sampled over the remainder of the survey.

4.3.2 Leopard identification

The time, date, camera location and species present in each photograph were recorded using the program Camerabase version 1.4 (Tobler 2007). Individual leopards were identified by their unique spot and rosette patterns (Balme et al. 2009; Martins 2010; Grant 2012) and sexed based on their external appearance (Balme et al. 2012). Males tended to be heavier-set, with a thick neck and an obvious orange scrotal sac. It was often difficult to distinguish between female and sub-adult male leopards, and this was typically only done when I obtained repeated observations of specific individuals allowing for greater confidence in the final decision (Martins 2010). Leopard identikit developed during the pilot study were also used to assist the identification process (see Appendix 4A).

CHAPTER 4: LEOPARD POPULATION DENSITY

4.3.3 Data analysis

Two distinct methods have emerged for SECR analysis; the inverse prediction/maximum likelihood approach (Efford 2004; Borchers & Efford 2008; Efford et al. 2009) and the Bayesian approach (Royle et al. 2009b, 2009a). A number of studies have found that the two methods produce similar results (Marques et al. 2010; Kalle et al. 2011; Noss et al. 2012), but that the likelihood approach requires substantially less computation time and is also less sensitive to the size of the buffer zone around the camera grid (Kalle et al. 2011). I therefore used the program DENSITY (version 5.1, Efford et al. 2004), which does SECR analysis using the maximum likelihood approach, as this was expected to require less computation time and be less sensitive to buffer width than the Bayesian approach.

DENSITY requires two input files; one containing the camera trap locations and the other the capture histories of individual leopards. The trap location file contained the co-ordinates of each camera site (these were projected to the Albers Equal Area Conic projection using ArcGIS 9.3). I defined a trapping occasion as one day. As a maximum of 38 of the 141 sites were active at any time, I pooled the data so that all camera site histories were synchronised, in effect analysing the data as though all sites were active simultaneously (*sensu* Karanth & Nichols 1998; O'Brien et al. 2003; Trolle & Kery 2003; Soisalo & Cavalcanti 2006; Wang & Macdonald 2009a). I also included a record of when the camera trap was active in a binary format, where a '1' indicated that the trap was active on a particular trapping occasion, and a '0' inactive. This allowed for the individual activity history of each camera site to be taken into account during the analysis. Roads have been identified as a potential source of bias in camera trap surveys (Sollmann et al. 2011; Tobler & Powell 2013), and I thus included a binary covariate to differentiate between sites located on roads and those set on game paths or trails.

The capture history file consisted of a list of all leopard captures recorded during the survey. Each entry included the identity number assigned to the individual leopard, the site(s) at which the leopard was recorded, the occasion on which the capture took place, and the sex of the leopard. All individuals whose sex could not be reliably determined were classified as 'unknown'. These

CHAPTER 4: LEOPARD POPULATION DENSITY

unknown individuals were likely to be either adult females or sub-adults of either sex, as adult males were the most easily identifiable group. There are marked behavioural differences between females and sub-adult males in particular. Females are territorial, and tend to have significantly smaller home ranges than adult male leopards (Bailey 1993; Mizutani & Jewell 1998; Martins & Harris 2013). In contrast, sub-adult males are seldom able to hold a territory, but may remain within an area for several months (Bailey 1993; Stander et al. 1997), and can disperse over large distances (Bothma et al. 1997a; Stander et al. 1997).

The possible misidentification of females and sub-adults was a potential source of error in this study. I did three separate analyses in an attempt to control for this. In the first set of models, I treated 'unknown' individuals as sub-adults, and modeled three-way heterogeneity in capture probability. In the second set, I classified all 'unknown' individuals as female, with a two-way heterogeneity in capture probability. Stander (1997) reported that sub-adult males spent several months within their natal range before dispersing. Sub-adult females have also been known to remain within their natal range (Bailey 1993). This suggests that non-dispersing sub-adults may live within similar-sized territories to adult females, and are thus likely to have had similar capture probability during the period when that area was being surveyed. In the final set of models, I excluded these individuals and restricted the analysis to a two-way heterogeneity model of adult individuals that I could confidently identify as either male or female.

I used *DENSITY* to produce full maximum likelihood and conditional likelihood SECR population density estimates. I assumed a half-normal spatial detection function and a Poisson distribution of home range centres, following Gray and Prum (2011). To assess the influence of buffer size on the SECR density estimates I applied three different buffer zones to each model; the HMMDM (5968 m), MMDM (11936 m) and the MaxDM, based on the maximum distance between points recorded by any of the three GPS-collared leopards (45 000 m). To test the influence of the road covariate, I ran one model without the road covariate with the MMDM buffer zone. Spatially-explicit models were

CHAPTER 4: LEOPARD POPULATION DENSITY

evaluated using Akaike's Information Criterion (Akaike 1974). Models that included sub-adults (either as a separate group or grouped with females) were analysed separately to those which excluded sub-adults completely.

The camera trap survey included large areas of low-lying, open habitat that was unlikely to be used by leopards (see Chapter 3). DENSITY allows users to identify areas of suitable habitat using a mask that can be superimposed on the sample area. I used a habitat mask generated using the program Maxent (Phillips et al. 2006; Phillips & Dudik 2008) to identify likely leopard habitat within the study area. The modelling process is described in detail in Chapter 3. Areas falling outside the mask can be classified as either 'habitat' or 'non-habitat'. I felt that neither classification was suitable due to the heterogeneous landscape surrounding my study area. I thus extended the mask to cover a buffer zone of 45 km from the outer perimeter of the study area. Due to the limited spatial extent of the vegetation layer (Vlok et al. 2005) used to produce the original Maxent model (see Chapter 3), I used the less detailed South African vegetation map (Mucina & Rutherford 2006) to produce a habitat mask covering a 45 km buffer around the trapping grid. All other data and parameters used to produce this extended map were identical to those used to produce the best-performing Maxent model in Chapter 3. The larger map was clipped to the edges of the original habitat map (see Chapter 3), thus ensuring that the more accurate habitat map within the study area was retained. Despite the reduced quality of the habitat map in the buffer zone, this was probably a more accurate representation of habitat availability than classifying the entire area around the study area as 'habitat' or 'non-habitat'.

Non-spatial capture-recapture assessments were done using the CAPTURE program (White et al. 1982). CAPTURE is an old program, and has limited capacity to handle large datasets. To reduce the number of trapping occasions to fall within the limits imposed by CAPTURE, I classified two days as one capture occasion. This effectively reduced the maximum number of capture occasions from 107 to 54. I calculated two abundance estimates; one for all leopards recorded during the study, and a

CHAPTER 4: LEOPARD POPULATION DENSITY

second estimate that excluded all sub-adult or unknown individuals, a similar approach to that used by Martins (2010).

A number of closed population estimators are available in CAPTURE. These include the M_0 estimator (Otis et al. 1978) as a null model. This estimator assumes equal capture probability across all sampling occasions and all individuals, and has been found to perform well in some studies (Trolle & Kery 2003; Jackson et al. 2006). I tested this against the M_h jackknife (Burnham & Overton 1978) closed population estimator, which assumes heterogeneous capture probabilities amongst individuals. These have been widely used in camera trap capture-recapture studies and are generally considered to be the most biologically realistic and robust of the closed population estimators (Karanth 1995; Karanth & Nichols 1998; Balme et al. 2009; Martins 2010; Anile et al. 2012; Foster & Harmsen 2012; Mondal et al. 2012a; Tobler & Powell 2013). In addition, a number of other estimators were tested, including M_b which assumes a behavioural response to capture that influences the chances of recapture, and M_t which assumes that capture probability varies between occasions (Otis et al. 1978; White et al. 1982). CAPTURE also calculates estimates for models that permit three sources of variation, M_{bh} (individual heterogeneity and a capture response), M_{th} (individual heterogeneity and variation between occasions) and M_{tb} (variation between occasions and a response to being captured). The eight different models were evaluated using CAPTURE's model evaluation function.

The effective trapping area was calculated by adding buffers to the edge of trapping grid. Three buffers were used; two of these, the half mean maximum distance moved (HMMDM) and full MMDM, were calculated from the camera trap data. The third buffer, the MAXDM was calculated based on the maximum distance between two GPS fixes recorded overall by any of the three collared leopards. The amount of habitat falling within a particular buffer zone was considered to be the amount of available habitat within the area. Non-spatial density estimates were calculated by

CHAPTER 4: LEOPARD POPULATION DENSITY

dividing the estimated population size by the amount of available habitat. The assumption of population closure was also tested using CAPTURE's closed population test (Otis et al. 1978).

4.3.4 Monitoring framework

The number and locations of sites to be used for the purposes of long-term monitoring of the leopard population with a subset of the total trap sites was determined from data gathered during the population survey described above. All sites at which no leopards were recorded were considered unsuitable for population monitoring, and were not considered for monitoring purposes (Nichols & Williams 2006). The survey design was based on the presence of adult leopards only, as sub-adults were more likely to be transient through a particular site, and their inclusion may have reduced the stability of the model. This may have led to the exclusion of some adult females that were misidentified as sub-adults. Continued monitoring at these sites should reduce these errors in future, as improved photographic capture histories of individuals of unknown sex will aid in accurately discriminating between females and sub-adults. Adults are more likely to have stable home ranges, and were thus more likely to be regularly detectable (Bailey 1993; Stander et al. 1997; Martins 2010). Adults were detected at 55 of the camera sites during the survey.

In order to maximise detection probabilities, preference was given to sites where more than one leopard 'capture' had occurred during the survey, which reduced the number of candidate sites to 31. Selecting sites at which leopards were more common implied that the most efficient monitoring design would be to sample a few sites more frequently (Steidl et al. 2013), a sampling regime for which camera traps are well suited as a data gathering tool. If two of the remaining sites fell within the same grid cell, only one was selected. This selection was based primarily on the accessibility of the site, as these sites would need to be visited regularly as part of a monitoring programme. The number of photographs recorded and the number of different individuals recorded at each site was used to choose between two equally accessible sites. This further reduced the number of candidate sites to 24. At this stage, the positions of the remaining sites were plotted on a map using ArcGIS 9.3. When two sites were in close proximity to one another (e.g. close to the shared border of two

CHAPTER 4: LEOPARD POPULATION DENSITY

adjacent grid cells), one was removed, using the criteria detailed above. To ensure relatively even sampling effort across the landscape, additional sites were selected from the previously discarded sites, based on leopard presence and accessibility. This helped to ensure that all adult male leopards within the study area had the possibility of being recorded by the monitoring array.

The final camera trap array was then tested in three ways. Firstly, a conditional likelihood SECR analysis was done using only the sites identified for the putative monitoring array and the capture data gathered during the full survey. The survey period was restricted to 90 days, even though some of the cameras may have been active for longer than this. The resulting density estimate and standard errors were compared to those of the full survey (Goldsmith 1991). I attempted to identify the most parsimonious monitoring array configuration that would provide similar density estimates to that of the main survey, with minimal loss of precision as measured by the magnitude of the standard error.

Monitoring must be able to reliably detect changes in the target population (Goldsmith 1991; Steidl et al. 2013). Once the final configuration of camera traps had been selected, it was thus tested for sensitivity using two distinct methods. The power of the reduced number of sites to detect change was assessed using a Chi-Square test in the program MONITOR (Gibbs & Ene 2010). Chi-Square tests can be applied to monitoring schemes involving multiple identical plots in which changes in presence/absence frequency are the focus of trend tests (Gibbs & Ene 2010). A sampling period of 90 days was assumed for each survey. The monitoring array was expected to have 80% power to detect a 10% annual change in the population, with a 20% chance of a Type 1 error (following Hayward et al. 2002) The power of the monitoring array was assessed over four sampling periods (one year), as it is envisaged that the monitoring stations will remain permanently active.

An additional sensitivity test was done using a jackknife approach to conditional likelihood SECR methods. The ability of the monitoring array to detect population decline was tested by removing the capture histories of individual leopards from the data gathered during the full survey. Different

CHAPTER 4: LEOPARD POPULATION DENSITY

levels of decline were simulated by removing the histories of two (12.5% decline), four (25% decline) and eight (50% decline) randomly selected leopards from an adult population of 16 individuals recorded at the sites used in the monitoring array. Ten replicates were done of each simulated level of decline. For each replicate the appropriate number of randomly selected individuals was removed, and population density estimates calculated using maximum likelihood SECR. These density estimates were compared to those generated for the full sample (16 capture histories), using the Mann-Whitney U-Test in STATISTICA 11 (Stat Soft Inc., Tulsa, Oklahoma). This provides a comparison of the simulated decline against the null hypothesis of a stable population, an important component of robust population monitoring (Nichols & Williams 2006).

CHAPTER 4: LEOPARD POPULATION DENSITY

4.4 Results

4.4.1 Descriptive statistics

In total, 141 sites were used in the camera trap survey; covering an area of 3219 km² with a mean inter-site distance of 2768 m (see Figure 4-1). The camera trap survey ran over a 520-day period for a total of 13 085 trap days, during which 12 335 photographs were recorded. These included 44 mammal species, excluding domestic species and livestock. In total, 189 leopard photographs were recorded, of which 162 were independent capture events. Overall, leopard capture probability was thus 0.012 captures/trap/day. Of the 155 leopard captures recorded when both camera traps at a site were active, only 89 were recorded by both cameras, indicating a maximum possible detection failure rate of 42.58%. As there was no independent means of determining the number of occasions when a leopard passed between the two cameras, it was not possible to calculate an absolute detection failure rate for the cameras.

It was not possible to identify the individual leopard in 12 (7.4%) of the photographs, and these capture events were thus not used in the analysis. A total of 31 unique leopards were identified (see Appendix 4A). Simultaneous photographs of both flanks were recorded for 23 individuals, while photographs of the right flank only were obtained for six individuals. A further two individuals were only recorded from the left side. To avoid inflating population estimates, the two individuals that were only identifiable from the left side were excluded from the analysis. This left a total of 146 independent captures that were analysed in DENSITY. When capture occasions were aggregated from one day/occasion to two days/occasion for analysis in CAPTURE, the number of captures was reduced to 136.

Male leopards accounted for 76.02% of all leopard captures recorded in the survey (see Table 4-1) and were significantly more likely to be photographed than females, assuming an even sex ratio ($\chi^2 = 60.9$, $df=1$, $p<0.01$). However, one would expect female leopards to occur at a higher density than males due to their smaller home range size (Bailey 1993; Mizutani & Jewell 1998; Martins 2010),

CHAPTER 4: LEOPARD POPULATION DENSITY

suggesting that the true difference in capture probability is even more significant than presented here.

Table 4-1: Summary of leopard photographic captures recorded during the camera trap survey

Sex	Individuals	Captures	Captures on roads (%)
Male	13	111	42.34
Female	6	22	9.091
Sub-adult/unknown	10	13	30.77
Total	29	146	36.30

In total, 59 of the 141 sites (41.84%) were located on roads or jeep tracks (hereafter referred to as roads). Males (Fisher's exact test, $p=1.00$) and sub-adults (Fisher's exact test, $p=0.56$) showed no significant preference for roads, but sites on roads had significantly lower female capture probability (Fisher's exact test, $p=0.0036$) suggesting that females avoided the roads.

CHAPTER 4: LEOPARD POPULATION DENSITY

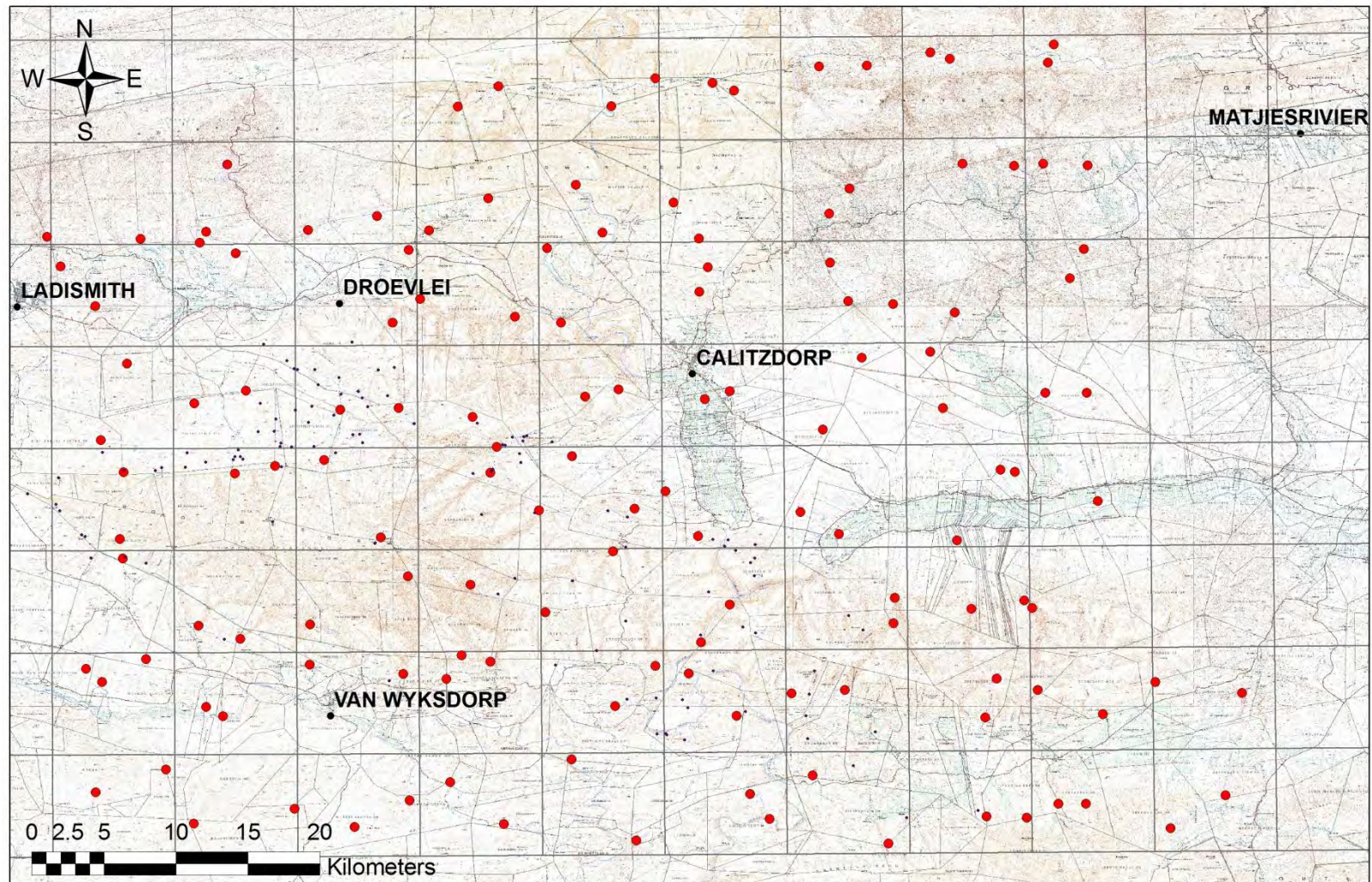


Figure 4-1: Map showing the locations of the 141 camera stations used in the leopard population survey (red points) and the grid cells used to guide site location

CHAPTER 4: LEOPARD POPULATION DENSITY

4.4.2 SECR models

Density estimates were robust with respect to variation of buffer size used, and only increased slightly as buffer size was reduced (see Table 4-2 and Table 4-3). Models were ranked according to Akaike's Information Criterion score, adjusted for small sample size (AIC_c) (Burnham & Anderson 2002). Conditional likelihood models that used sex as a covariate were the best-performing models. Maximum likelihood models that grouped sub-adult individuals with females performed better than those that analysed sub-adult leopards as a separate group using three-way heterogeneity. However, density estimates were similar for all models. Inclusion of the road covariate had little influence on density estimates, but improved performance of two-way heterogeneity models (see Table 4-2). There was relatively little difference between the AIC_c scores of the conditional likelihood models, suggesting that all of these models fit the data similarly (Symonds & Moussalli 2011).

Excluding sub-adult leopards lowered density estimates by an average of 0.438 leopards per 100 km² (see Table 4-2 and Table 4-3). Conditional likelihood models were ranked higher than maximum likelihood models, although the density estimates produced remained consistent for all models. Exclusion of the road covariate appeared to slightly improve model performance, but the low ΔAIC_c difference between all four models suggests that there is very little difference between them (Symonds & Moussalli 2011).

All models required substantial computation time. Conditional likelihood models had a mean processing time of 17.57 hours (± 6.23 hours, $n=6$). The maximum likelihood three-way heterogeneity models had a mean computation time of 35.58 hours (± 20.72 hours, $n=4$), while the two-way heterogeneity models required an average of 7.85 hours (± 7.13 hours, $n=8$).

CHAPTER 4: LEOPARD POPULATION DENSITY

Table 4-2. Results of the conditional and maximum likelihood SECR analyses which included sub-adult individuals. Three buffer zones were considered; MaxDM (45 000 m), MMDM (11 936 m) and HMMDM (5968 m). Sub-adult individuals were either grouped with females ('female'), or analysed as a third heterogeneous group ('separate'). The 'Road covariate' column denotes which models included a covariate indicating which sites were located on roads. Density is expressed as number of leopards per 100 km². The ΔAIC_c shows the difference between the AIC_c scores between each model and the highest ranked model. AIC_c weight gives the probability of each model being the best-approximating model (Symonds & Moussalli 2011).

Model	Likelihood	Buffer	Sub-adults	Road covariate	Density (/100 km ²)	Standard error	Parameters	AIC_c	ΔAIC_c	AIC_c weight
19	Conditional	MMDM	separate	excluded	1.184	0.224	4	1972.834	0	0.658
15	Conditional	MaxDM	separate	included	1.117	0.222	6	1975.855	3.021	0.145
20	Conditional	MaxDM	female	included	1.117	0.222	6	1975.855	3.012	0.145
8	Maximum	MaxDM	female	included	1.169	0.219	8	1979.193	6.559	0.025
7	Maximum	MaxDM	female	excluded	1.166	0.219	6	1980.346	7.512	0.015
13	Maximum	HMMDM	female	included	1.203	0.226	8	1982.720	3.3268	0.005
9	Maximum	MMDM	female	included	1.186	0.223	8	1982.877	3.4837	0.004
6	Maximum	MMDM	female	excluded	1.183	0.222	6	1985.013	5.6196	0.001
1	Maximum	MaxDM	separate	included	1.169	0.073	11	1991.381	11.9876	6.18×10^{-5}
5	Maximum	MMDM	separate	excluded	1.184	0.308	9	1994.538	15.1452	1.27×10^{-5}
3	Maximum	HMMDM	separate	included	1.223	0.077	11	1996.481	17.0875	4.83×10^{-6}
2	Maximum	MMDM	separate	included	1.351	0.660	11	2003.482	24.0886	1.46×10^{-7}

CHAPTER 4: LEOPARD POPULATION DENSITY

Table 4-3: Results of the conditional and maximum likelihood SECR analyses which excluded sub-adult individuals. Three buffer zones were considered: Maximum distance moved (MaxDM - 45 000 m), mean maximum distance moved (MMDM - 13 475 m) and half of mean maximum distance moved (HMMDM - 6 737 m). The 'Road covariate' column denotes which models included a covariate indicating which sites were located on roads. Density is expressed as number of leopards per 100 km². The ΔAIC_c shows the difference between the AIC_c scores between each model and the highest-ranked model. AIC_c weight gives the probability of each model being the best-approximating model (Symonds & Moussalli 2011)

Model	Likelihood	Buffer	Road covariate	Density (/100 km ²)	Standard error	Parameters	AIC_c	ΔAIC_c	AIC_c weight
18	Conditional	MMDM	excluded	0.756	0.176	4	1741.588	0	0.892
16	Conditional	MaxDM	included	0.746	0.174	6	1746.188	4.600	0.089
17	Conditional	MMDM	included	0.756	0.176	6	1749.730	8.143	0.015
14	Maximum	MMDM	excluded	0.756	0.176	6	1753.52	11.932	0.002
10	Maximum	MaxDM	included	0.746	0.174	8	1756.237	14.650	0.588×10^{-3}
11	Maximum	MMDM	included	0.754	0.176	8	1758.897	17.309	0.156×10^{-3}
12	Maximum	HMMDM	included	0.764	0.178	8	1759.104	17.516	0.140×10^{-3}

CHAPTER 4: LEOPARD POPULATION DENSITY

4.4.3 CAPTURE models

A capture probability of 0.0223 leopards/capture occasion was recorded. The population closure test (Otis et al. 1978) showed that the population was not closed for the duration of the survey when all leopards were included in the analyses ($z=-1.82$, $p=0.035$). When sub-adults were excluded from the analysis, the test suggested that the population was closed ($z=-1.02$, $p=0.13$). The model selection criterion scores in CAPTURE were similar for M_h jackknife (1.00) and M_0 models (0.97), suggesting that both of these models fit the data well (see Table 4-4).

Table 4-4. Leopard abundance estimates from non-spatial capture-recapture models in CAPTURE. The 'Model' column shows which mark-recapture estimator was used in the analysis, with the population size estimate, standard error and 95% confidence intervals. The final column shows the model selection criterion score generated by CAPTURE, where a score close to one represents good model fit.

Model	Abundance estimate	Standard error	95% CI range	Model selection criterion score
M_h	25	4.1522	22 – 42	1.00
M_0	22	1.1577	21 – 28	0.97
M_b	21	0.3144	$\pm <1$	0.86
M_{bh}	21	0.3144	$\pm <1$	0.71
M_t	21	0.6155	21 – 24	0.00
M_t Chao	24	2.9525	22 – 36	0.25
M_h Chao	25	4.0485	22 – 41	0.77

When sub-adults were excluded from the analysis, abundance estimates decreased. CAPTURE identified the M_h jackknife model as the only appropriate estimator (see Table 4-5).

CHAPTER 4: LEOPARD POPULATION DENSITY

Table 4-5. Abundance of adult leopards as estimated by non-spatial capture-recapture models in CAPTURE. The 'Model' column shows which mark-recapture estimator was used in the analysis, with the population size estimate, standard error and 95% confidence intervals. The final column shows the model selection criterion score generated by CAPTURE, where a score close to one represents good model fit.

Model	Abundance estimate	Standard error	95% CI range	Model selection criterion score
M_h	18	3.8477	18 - 43	1.0
M_0	17	0.7619	17 - 17	0.95
M_b	17	0.1658	17 – 17	0.77
M_{bh}	17	0.1658	17 – 17	0.71
M_t	17	0.0065	17 – 17	0.00
M_t Chao	18	1.9082	18 – 25	0.38
M_h Chao	19	2.1615	18 - 28	0.75

Population density estimates for non-spatially explicit models showed large variation according to the size of buffer zone used (see Table 4-6). When all individuals were included in the analysis, M_h and M_0 estimators produced lower density estimates than the best-performing SECR model, although SECR density estimates fell within the 95% confidence intervals of the M_h models with buffer zones of the HMMDM and MMDM (see Table 4-6).

CHAPTER 4: LEOPARD POPULATION DENSITY

Table 4-6. Density of the leopard population as derived from non-spatial capture-recapture models. Only the two models selected as appropriate by CAPTURE (M_h and M_0) were used to produce density estimates. The 'buffer' column shows the size of the boundary strip added to the perimeter of the camera grid; this ranged from the maximum distance moved by a collared leopard (MaxDM – 45 000 m), the mean maximum distance moved (MMDM – 11 940 m) and the half mean maximum distance moved (HMMDM – 5970 m). The effective trapping area (ETA) is the amount of habitat available to leopards within the camera grid and buffer zone. Density was calculated by dividing the abundance estimate of the appropriate model (see Table 4-4) by the effective trapping area. The 95% confidence intervals of the density estimate are based on those of the abundance estimate (see Table 4-4) and were calculated in the same manner as the density estimates. For comparative purposes, the best SECR model for this dataset is included in the final row.

Model	Buffer	ETA (km ²)	Density/100 km ² (± standard error)	95% confidence interval
M_h	HMMDM (5.97 km)	2915.64	0.8574 (±0.1424)	0.7546 – 1.441
M_h	MMDM (11.94 km)	3279.91	0.7622 (±0.1266)	0.6708 – 1.281
M_h	MaxDM (45 km)	4694.84	0.5325 (±0.0885)	0.4686 – 0.8946
M_0	HMMDM (5.97 km)	2915.64	0.7546 (±0.0397)	0.7203 – 0.9603
M_0	MMDM (11.94 km)	3279.91	0.6708 (±0.0353)	0.6403 – 0.8537
M_0	MaxDM (45 km)	4694.84	0.4686 (± 0.0247)	0.4473 – 0.5964
SECR (model 19)	MMDM(11.94 km)	NA	1.1840 (± 0.2240)	NA

When sub-adults were excluded from the analysis, density estimates declined (see Table 4-7). M_h was selected as the only appropriate model for this dataset, and produced lower population density estimates than the best maximum likelihood SECR model for the same data. The SECR density estimate fell within the 95% confidence intervals of the M_h density estimates when the effective trapping area was determined according to HMMDM and MMDM.

CHAPTER 4: LEOPARD POPULATION DENSITY

Table 4-7: Densities of adult leopards derived from non-spatial capture-recapture models. The M_h model was the only estimator that CAPTURE identified as appropriate for this dataset. The 'buffer' column shows the size of the boundary strip added to the perimeter of the camera grid; this ranged from the maximum distance moved by a collared leopard (MaxDM – 45 000 m), the mean maximum distance moved (MMDM – 11 940 m) and the half mean maximum distance moved (HMMDM – 5970 m). The effective trapping area (ETA) is the amount of habitat available to leopards within the camera grid and buffer zone. Density was calculated by dividing the abundance estimate of the appropriate model (see Table 4-5) by the effective trapping area. The 95% confidence intervals of the density estimate are based on those of the abundance estimate (see Table 4-5) and were calculated in the same manner as the density estimates. . For comparative purposes, the best SECR model for this dataset is included in the final row.

Model	Buffer	ETA (km ²)	Density /100 km ²	95% CI
M_h	HMMDM (6.74 km)	2962.59	0.6076 (± 0.1309)	0.6077 – 1.451
M_h	MMDM (13.48 km)	3370.23	0.5341 (± 0.1150)	0.5341 – 1.276
M_h	MaxDM (45 km)	4694.84	0.3834 (± 0.0826)	0.3834 – 0.9159
SECR (model 18)	MMDM (13.48 km)	NA	0.7560 (± 0.1760)	NA

4.4.4 Monitoring array design

A total of 22 sites were selected for use in the monitoring array (Figure 4-2). The sites selected for the monitoring array recorded captures of 16 adult leopards during the main survey. Only three adults were not recorded at these sites; two males and one female. One of these males was only recorded once during the survey, and may thus have been a non-resident individual. The greater distances between sites used in the monitoring array is likely to omit some females due to the smaller size of their territories. Only one potentially resident male was not recorded at the sites identified for the monitoring array. This individual was recorded at three sites at the north-eastern edge of the survey area, and it is thus likely that the majority of this individual's territory falls outside of the survey area.

Analysis in MONITOR suggested that an array of 22 cameras would have low power to detect changes in the population. Over four 90-day survey periods (one year), the array would only have 26.6% power to detect a 10% population decline with a 20% chance of a Type 1 error ($\alpha=0.2$), assuming an initial density of 0.79 leopards/100 km². This fell well below the threshold of 80% power to detect a 10% population decline ($\alpha=0.2$) suggested by Hayward et al. (2002). However, MONITOR

CHAPTER 4: LEOPARD POPULATION DENSITY

analysis suggested that even using the full survey array (141 camera sites) would only provide 58% power to detect a 10% population decline over one year ($\alpha=0.2$). Only an 18 month survey with all 141 sites would provide sufficient power to reliably detect a 10% population change (power = 89.6%, $\alpha=0.2$).

Extending the number of survey periods to eight (i.e. a two year period), substantially improved the power of the monitoring array to detect changes, but only three years of monitoring would provide the power to track a 10% population decline with the proposed 22 camera array (power = 0.8, $\alpha = 0.2$). This relatively low power should be balanced against the relative cost of the survey. Assuming an average battery life of 60 days (based on the typical battery performance observed during my study), three years of monitoring with 22 cameras would require 1142 batteries. In contrast, 18 months of monitoring with 141 cameras would require 5076 batteries. The latter is clearly not feasible due to the high cost of purchasing and maintaining such a large number of cameras.

Conditional likelihood SECR estimates from the 22 monitoring sites produced a density estimate of 0.792 adult leopards per 100 km², with a standard error of 0.22. This was similar to the estimate generated by the full survey (0.756 leopards/100 km² $\pm$ 0.176). When capture histories of two individuals were removed from the sample (to simulate a reduction in population size of 12.5%), the mean density estimate was 0.709 leopards/100 km² ($\pm$ 0.05, n=10). This represents a significant decline in density (Wilcoxon matched pairs test $Z = 2.60$, $p<0.05$). Removing a larger portion of the population resulted in a more noticeable drop in density estimates; when four individuals (25%) of the population were removed, the mean density estimate was 0.627 ($\pm$ 0.064, n=12) leopards per 100 km² ($Z=2.80$, $p<0.05$). A simulated 50% population decline resulted in a mean density estimate of 0.412 ($\pm$ 0.055, n=8). These density estimates were also significantly lower than the density estimate for the full population ($Z = 2.80$, $p<0.05$).

CHAPTER 4: LEOPARD POPULATION DENSITY

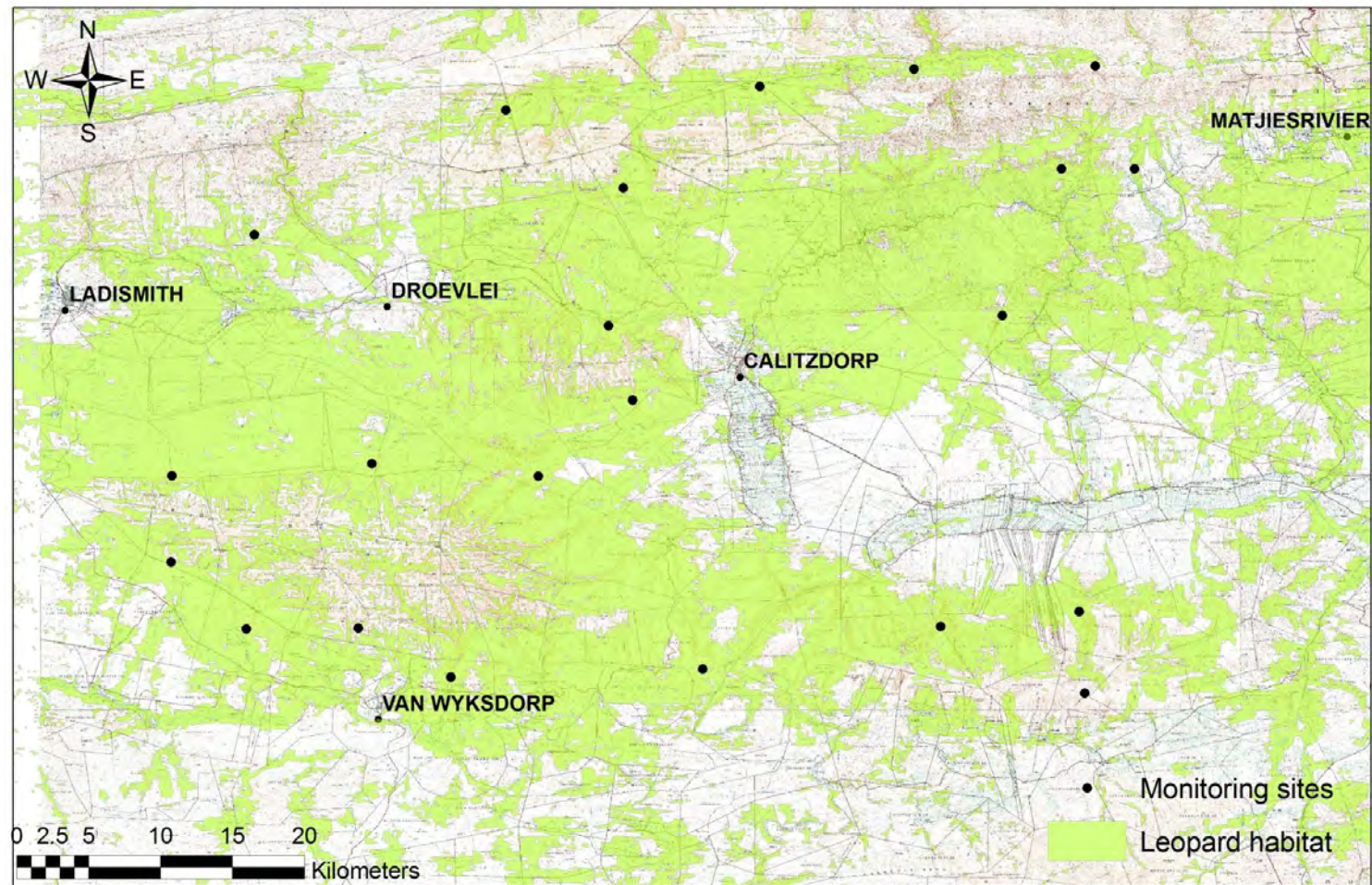


Figure 4-2: Proposed sites for long-term monitoring of the Little Karoo leopard population. Potential leopard habitat is shaded green, and black points show the sites identified as suitable for long-term monitoring.

CHAPTER 4: LEOPARD POPULATION DENSITY

4.5 Discussion

4.5.1 Population density estimates

Female leopards are likely to occur at higher densities than males (Bailey 1993; Mizutani & Jewell 1998; Balme & Hunter 2004; Martins & Harris 2013), and are thus likely to be far more numerous than the results of my survey would suggest. Density estimates based on my data should thus be treated as a minimum density (Larrucea et al. 2007). The bias towards males is a trend that is often observed in camera trap studies across a range of species (Karanth 1995; Wallace et al. 2003; Maffei et al. 2004; Silver et al. 2004; Soisalo & Cavalcanti 2006; Foster 2008). It is generally assumed that the greater home range size of males and their preference for moving along trails and roads contributes to their higher capture probability using camera traps (Foster & Harmsen 2012). I attempted to use sites where topographical features were likely to force both sexes to use the same routes (Spalton et al. 2006) but the finding that females avoided roads, similar to jaguars (Foster 2008; Harmsen et al. 2010a), and the fact that 41.84% of my traps were on roads or trails may in part explain the bias in male capture in this study. The low number of female leopards recorded here precluded the separate calculation of male and female leopard densities (as suggested by Foster 2008). This occurred despite attempts to avoid bias by locating the majority of camera traps away from the trails (Karanth 1995; Mohd. Azlan & Sharma 2003; Soisalo & Cavalcanti 2006; Foster 2008; Balme et al. 2009).

Capture-recapture models assume that the study population is both demographically and geographically closed during the survey period (Otis et al. 1978). The assumption of population closure is seldom realistic in natural populations (Karanth 1995; Soisalo & Cavalcanti 2006), and was violated in my study when all leopards were included in the analysis. However, when restricting the analyses to adults the leopard population was found to be demographically closed. Adult leopards usually hold stable territories and are less likely to disperse than sub-adults (Stander et al. 1997; Martins 2010), suggesting that adults would be less likely to violate the assumption of geographic closure. Mortality rates have also been reported to be higher amongst sub-adult leopards (Stander

CHAPTER 4: LEOPARD POPULATION DENSITY

et al. 1997; Balme & Hunter 2004), which further increases the risk of violating the assumption of demographic closure.

Of the closed population CAPTURE models, the M_h jackknife estimator performed best. The M_h jackknife estimator assumes heterogeneity in capture probabilities between individuals, and is therefore often found to be the best of the closed population estimators (Karanth 1995; Karanth & Nichols 1998; Soisalo & Cavalcanti 2006; Wang & Macdonald 2009a; Grant 2012). The densities derived from closed population estimators were low, and fluctuated substantially according to the size of the buffer strip applied to the sample area.

The main purpose of using non-spatial closed population estimators in my study was to allow a comparison with the leopard population densities obtained by Martins (2010) in the Cederberg Mountains. Leopards in the Cederberg had an overall density of 1.1 – 1.5 leopards/100 km² using the MMDM as a buffer (Martins 2010). Martins (2010) also observed substantial differences in leopard densities between the fynbos and the Karoo portions of the Cederberg. My study area contained a mosaic of Karoo, fynbos and subtropical thicket vegetation (Vlok et al. 2005; Vlok & Schutte-Vlok 2010), unlike the Cederberg, which is clearly split into fynbos and Karoo areas (Mucina & Rutherford 2006). Using the same estimator (M_h jackknife) and buffer zone (MMDM) as Martins (2010), my data suggest an adult leopard density of 0.5 leopards/100 km², which is lower than the Karoo portion of the Cederberg and much lower than the overall leopard density for the Cederberg (Martins 2010).

However, the results from both studies should be treated with some caution. Closed population estimators have been shown to be unreliable when applied to small populations (<50 individuals) with a capture probability of less than 0.1, especially when there is high heterogeneity in capture probability (Harmsen et al. 2010a). Martins (2010) had a capture probability of 0.038 leopards/capture occasion, while my study recorded a capture probability of 0.022 leopards/capture occasion, and both studies recorded fewer than 50 individuals. The closed population estimates for both my study and the study in the Cederberg (Martins 2010) are thus likely to lack both accuracy

CHAPTER 4: LEOPARD POPULATION DENSITY

and precision (Harmsen et al. 2010a). Harmsen et al. (2010a) found that in most cases, the 95% confidence intervals of closed population estimators did include the true population size, but in my study these confidence intervals are very wide, providing estimates of between 0.5341 and 1.276 adult leopards/100 km².

There are a number of factors that could have contributed to this result. Martins (2010) had 11 leopards fitted with GPS tracking collars, which may have contributed to better camera placement that improved capture probabilities. The Little Karoo is also more developed than the Cederberg area surveyed by Martins (2010), which did not include any large settlements. The Little Karoo study area has a larger human population (www.statssa.gov.za/Census2011, accessed on 19 July 2013) and a greater degree of human disturbance that could also have contributed to lower leopard population densities.

In contrast, all SECR models produced remarkably consistent density estimates, and were robust to changes in buffer width. This is similar to the findings of Kalle et al. (2011), who found that maximum likelihood SECR estimates were robust to changes in buffer size. Although inclusion of a road covariate has been found to improve SECR density estimates (Sollmann et al. 2011; Tobler & Powell 2013), my study found that conditional likelihood SECR models ranked higher when the road covariate was excluded. Inclusion of a road covariate had little influence on the actual density estimates. Male and sub-adult leopards did not appear to use roads with any greater frequency than would be expected by chance alone; in fact the percentage of male photographs recorded on roads (42.34%) almost exactly matched the percentage of camera traps that were located on roads (41.84%).

The ruggedness of large portions of the study area, with the consequent lack of roads, forces leopards to make use of other natural routes (e.g. dry river beds) through dense vegetation and rugged terrain. In these situations, topographical features can guide camera placement and improve capture probability at sites that are not located on roads. This improved 'off-road' success rate may

CHAPTER 4: LEOPARD POPULATION DENSITY

reduce the influence of roads on the density estimates. It is also likely that leopards use some public roads that have low levels of traffic. These roads were not sampled during this survey due to the unacceptably high risk of camera theft. All camera locations used in this study, both on and off roads, were selected to maximise the probability of capturing leopards; had I used a mixture of 'targeted' and purely randomly located sites, it is likely that a far greater effect would have been observed between the two groups of sites.

The potential misclassification of sub-adult individuals had little influence on density estimates; although models that treated sub-adults as female leopards generally ranked higher according to AIC_c , actual differences in the density estimates were minor. The removal of sub-adult individuals reduced population density estimates, an expected result as sub-adults comprised over one-third of the sampled population. SECR models that only included the adult leopards tended to be more precise than those that also included sub-adults, possibly due to greater demographic stability within the adult population.

The density estimates generated by the SECR models were substantially higher than those of the non-spatial capture-recapture methods. Similar incongruities between SECR and M_h jackknife estimates have been observed in other studies, although non-spatial capture-recapture estimates are typically higher than SECR derived densities (Sollmann et al. 2011; Kalle et al. 2011; Noss et al. 2012; Gray & Prum 2012; Mondal et al. 2012a). This suggests that comparisons of the SECR-derived density estimates with non-spatial capture-recapture estimates obtained for other populations in southern Africa should be treated with caution. Comparison of the non-spatial population density estimates suggests that the Little Karoo leopards have one of the lowest population densities in South Africa, comparable only to that of the Karoo portion of the Cederberg (Martins 2010). The only area where lower population densities have been recorded is in Kalahari Gemsbok National Park (now the Kgalagadi Transfrontier National Park) (Bothma et al. 1997a).

CHAPTER 4: LEOPARD POPULATION DENSITY

SECR methods hold a number of advantages over non-spatial capture-recapture methods. The incorporation of trap locations into the analysis allows for inferences to be drawn about the locations of individuals (Efford 2004; Borchers & Efford 2008; Efford et al. 2009), while the inclusion of trap and individual covariates can also improve density estimates (Sollmann et al. 2011; Foster & Harmsen 2012; Tobler & Powell 2013). Most importantly, while a buffer zone still needs to be specified, the influence of the buffer zone on population density estimates is greatly reduced in comparison to density estimates derived from non-spatial capture-recapture methods.

In a recent simulation study, Tobler et al. (2013) made a series of recommendations for jaguar population density studies, which are equally applicable to leopards. These were that the total survey area should exceed the size of one adult male's home range, that cameras should be spaced according to female home range size, that survey periods should exceed 60 days to maximise the amount of data available for analysis, that cameras should be positioned to maximise capture probabilities, and that SECR methods should be used to estimate population density. My study has a number of flaws, most notably the probable lack of true population closure, the aggregation of data from 520 days of sampling into a single sampling period, and the observational bias towards male leopards. Nevertheless, it conforms to the 'best practice' criteria specified by Tobler et al. (2013), and I thus conclude that the SECR density estimates derived from this study are as reliable as can be expected given the logistical challenges inherent to conducting a study of this magnitude on a cryptic predator across a large area of mixed land-uses.

CHAPTER 4: LEOPARD POPULATION DENSITY

4.5.2 Monitoring

Karanth et al. (2006) adapted capture-recapture data obtained from camera traps to monitor demographic changes in an Indian tiger population. This was done by developing an open population model that included factors such as migration in and out of the study area, transient individuals and mortality, within a robust design camera trapping framework (Karanth et al. 2006). However, this was based upon nine years of data collection, which allowed for capture histories to be developed for 74 individuals. This provided a wealth of demographic data that allowed for reasonable calculation of mortality rates, etc. Furthermore, the study by Karanth et al. (2006) was based on non-spatial capture-recapture methods. The approach used by Karanth et al. (2006) was therefore not well-suited to my study, which took place over a far shorter period and consequently could not draw upon sufficiently detailed demographic information to accurately determine the parameters required to produce an accurate open population model. My study also found SECR density estimation methods to be more consistent than the non-spatial capture-recapture methods employed by Karanth et al. (2006). For these reasons, I considered it preferable to base the monitoring framework on spatially-explicit closed-population models, repeated continuously, rather than an open population model. While open-population spatially explicit capture-recapture models have been developed (Gardner et al. 2010), I preferred to base this framework on an ongoing series of closed population models. The main reason for this was to allow for the monitoring programme to be managed by CapeNature in future, and the program DENSITY provides a relatively easy and accessible means of analysing the camera trap data compared to the more technical WINBugs programming needed to produce open population models (Gilks et al. 1994; Gardner et al. 2010).

Analysis with MONITOR suggested that the proposed monitoring array has low power to track changes in leopard population density on an annual basis. However, continuous monitoring over a three-year period would provide sufficient power to detect a 10% population change with 80% confidence. This power has been deemed sufficient for effective monitoring of rare Amur tigers (*Panthera tigris altaica*) (Hayward et al. 2002), albeit on an annual basis.

CHAPTER 4: LEOPARD POPULATION DENSITY

This result is contradicted by the results of the removal-resampling tests done using DENSITY, which produced significantly lower population density estimates when the population declined by anything more than 12%. Despite this, only when 50% of the population was removed did the mean population density estimate fall below the standard error of the baseline survey. This suggests that the power of any single survey using the monitoring array to detect changes in the leopard population is relatively low. However, if the monitoring array was kept active continuously, it would generate four independent population density estimates per year, substantially improving the probability of detecting a change in the leopard population density.

The proposed monitoring array design is based on one important assumption; that the capture frequencies observed during the current study will remain constant over time, and that a decline in capture frequency is due to a decline in density rather than any other factors. Reducing the number of sites surveyed from 141 to 22 greatly increases the risk of abnormal capture frequencies at one site disproportionately influencing the density estimates. Factors that cause capture probabilities to vary over time, such as seasonal variation in leopard movements, could thus bias density estimates.

Reducing the number of active sites necessitated either restricting the monitoring array to a smaller area or increasing the distance between camera sites. I opted for the latter option, with the result that camera spacing is based upon male home range, rather than the (smaller) female home range, as is usually recommended for camera trap studies (Foster & Harmsen 2012; Tobler & Powell 2013). Although the 'full' survey was designed around female home range size, females were rarely captured. Female capture success may be improved by drastically reducing grid cell size and intensively sampling a small area, but this is difficult to reconcile with the need for a camera survey to cover an area in excess of one male's home range (Tobler & Powell 2013). Consequently, the monitoring array was largely designed to monitor the male leopard population, which tends to be more reliably detectable. The greater spatial requirements of male leopards (Bailey 1993; Odden & Wegge 2005; Martins 2010; Martins & Harris 2013) are likely to render males more sensitive to edge

CHAPTER 4: LEOPARD POPULATION DENSITY

effects and land use change (Balme et al. 2010b). Adult male leopards are also more likely to be found closer to human habitation (Odden & Wegge 2005) and suffer more anthropogenic induced mortality than females (Balme et al. 2010b). Male felids have also been shown to be more frequent killers of livestock than females, increasing the risk of retaliatory killing (Odden et al. 2002). Given the greater risk of adult male mortality, I believe that focusing the monitoring programme on this demographic group is justifiable with the assumption that adult male population status provides a conservative proxy for adult female status, given that the latter face fewer anthropogenic threats.

The number of individuals within an area is often directly proportional to the proportion of the area occupied by a territorial species (MacKenzie et al. 2005). Given the monitoring array is currently restricted to sites at which leopards have previously been recorded, an increase in leopard abundance is likely to indicate that a greater proportion of the available habitat is being used by leopards. Thus, while the monitoring array may be able to detect increases in leopard abundance, this would only occur if increased abundance caused population density to increase, rather than leopards occupying currently vacant areas. The monitoring programme should thus be primarily viewed as a means of detecting declines in the leopard population.

Conducting more intensive surveys at greater time intervals has been shown to be more efficient than more frequent, but less intensive monitoring surveys (Danell & Andrén 2010). Repeating the full survey done for this study would have a cost of 1692 battery units, as well as involving extensive time and travel costs. The same number of batteries could power the 22 cameras used for the monitoring array for over 3 years. As accessibility has been an important consideration in choosing sites for the monitoring array, the time and travel costs involved in monitoring these cameras would be substantially less than would be required to repeat the main survey. Furthermore, there are additional benefits to maintaining a relatively low number of camera stations in the long term, such as being able to gather more detailed demographic information on the leopard population and tracking broader trends in faunal biodiversity (Lindenmayer et al. 2012). However, the monitoring

CHAPTER 4: LEOPARD POPULATION DENSITY

array should not be viewed as a replacement of the more detailed survey carried out during this survey. This should be repeated in future, both to provide a more rigorous estimate of leopard population densities, but also to allow for comparison with the population density derived from the monitoring array. For these reasons, and due to the relatively low costs involved in setting up and maintaining the monitoring array, this offers a viable means of tracking leopard population until sufficient resources are available to repeat the full survey.

4.6 Conclusion

This study successfully applied SECR density estimation methods to the leopard population of the Little Karoo. Unlike non-spatial capture-recapture methods, SECR-based density estimates were robust to buffer strip size and possible parameterisation errors. The results of this study suggest that leopards in the Little Karoo have one of the lowest population densities recorded in southern Africa. Females were almost certainly under-represented in this sample, and it is likely that the true population density is higher than these estimates suggest. Nevertheless, SECR methods appear to offer a more reliable means of estimating the densities of rare and cryptic species such as leopards. The extension of this method to the design of a parsimonious sub-set of camera sites for use in long-term monitoring of the leopard population is a novel application of the SECR framework. Simulated results suggest that this monitoring array has the potential to detect population declines of 12% or more. The monitoring framework presented here could thus offer a relatively inexpensive method of monitoring the leopard population until a survey of similar scope to that done in this project can be undertaken in future. Future 'full' surveys are vital to provide more rigorous estimates of the leopard population and to further validate the results of the monitoring survey.

CHAPTER 4: LEOPARD POPULATION DENSITY

4.8 Appendix 4A – Leopard identikits

All leopards were assigned an identity code using the following format. The letter 'G' denotes the Gouritz area, to prevent confusion with leopards identified in other Cape Leopard Trust project areas (the Cederberg and Boland Mountains). This was followed by an 'M' (male), 'F' (female) to denote the sex of the individual. Leopards for which the sex was unclear were given the temporary identifier 'L', which could change to 'M' or 'F' once the sex of the individual was determined. If only one flank of an individual had been recorded, an additional 'L' (left) or 'R' (right) was added to indicate which flank had been recorded. If both flanks of the individual had been recorded, the sex identifier was followed by an identifying number. These were allocated sequentially, but separately for males and females (i.e. GF1 and GM1 were the first male and female to be identified in the Gouritz area, respectively). Photographs of all the leopards identified during the camera trap survey are included below, and where available photographs of both sides of the individual are shown. I have selected the photographs in which spot patterns are best visible, rather than pairs of photographs that were recorded simultaneously.

CHAPTER 4: LEOPARD POPULATION DENSITY



GM1 - left



GM1 - right



GM2 - left



GM2 - right

CHAPTER 4: LEOPARD POPULATION DENSITY



GM5 - left



GM5 - right



GM6 - left



GM6 - right

CHAPTER 4: LEOPARD POPULATION DENSITY



GM8 - left



GM8 - right



GM10 - left



GM10 - right

CHAPTER 4: LEOPARD POPULATION DENSITY



GM11 - left



GM11 - right



GM16 - left



GM16 - right

CHAPTER 4: LEOPARD POPULATION DENSITY



GM17 - left



GM17 - right



GM18 - left



GM18 - right

CHAPTER 4: LEOPARD POPULATION DENSITY



GM22 - left



GM22 - right



GM23 - left



GM23 - right

CHAPTER 4: LEOPARD POPULATION DENSITY



GM24 - left



GM24 - right



GM25 - left



GM25 - right

CHAPTER 4: LEOPARD POPULATION DENSITY



GML32 - left



GMR3 - right



GMR33 - right

CHAPTER 4: LEOPARD POPULATION DENSITY



GFR1 - right



GFL19 - left



GF12 - left



GF12 - right

CHAPTER 4: LEOPARD POPULATION DENSITY



GF13 - left



GF13 - right



GF15 - left



GF15 - right

CHAPTER 4: LEOPARD POPULATION DENSITY



GF26 - left



GF26 - right



GF27 - left



GF27 - right

CHAPTER 4: LEOPARD POPULATION DENSITY



GL28 - left



GL28 - right



GLR29 - right



GLR30 - right

CHAPTER 4: LEOPARD POPULATION DENSITY



GLR31 - right



GLR34 - right

CHAPTER 5: LEOPARD DIET AND PREY PREFERENCES

5.1 Abstract

The diet of a carnivore defines its impact on prey populations, both in terms of the number of prey killed and the impact on prey behaviour. Leopards have the broadest range of prey species of any African felid, but tend to prey upon species weighing between 10 and 40 kg. In the Western Cape, South Africa, leopards have been shown to target relatively small prey species such as klipspringer (*Oreotragus oreotragus*) and rock hyrax (*Procavia capensis*). I used both hair samples obtained from 76 scats and the remains of prey found at 93 kills made by three male leopards fitted with GPS tracking collars, to assess the diet of leopards in the Little Karoo. SIMPER analysis was used to compare the two methods, as well as the results of the scat analysis to previous studies conducted in the Little Karoo. I identified 21 prey species from hair samples found in scats and 18 species from remains found at kill sites. Rock hyrax (*Procavia capensis*), kudu (*Tragelaphus strepsiceros*) and Karoo and bush rats (*Otomys* spp.) were the most frequently found items in scats, but kudu, eland (*Tragelaphus oryx*) and rock hyrax were the most important species in terms of biomass consumed. At kill sites, baboon (*Papio hamadryas*) remains were the most common, followed by donkeys (*Equus asinus*) and common duikers (*Sylvicapria grimmia*). There was high compositional dissimilarity between the two methods (49.8%), and SIMPER analysis indicated 94% dissimilarity between scat and kill site data. The high dissimilarity between scats and kill sites suggests that these two methods should be viewed as complementary techniques for dietary analysis, especially as scat analysis may detect small prey items that will not be represented at kill sites. Both methods suggest that large prey species (those exceeding 40 kg) are critical components of the diet of leopards in the Little Karoo. My scat analysis findings differ from a previous study which used similar methods. Given that leopards are opportunistic predators, this may reflect changes in the composition of prey in the region or indicate different prey abundances in the areas in which scats were collected. The introduction of large ungulates to game farms within the study area has increased the amount of

CHAPTER 5: LEOPARD DIET

large prey available to leopards, which may explain the shift towards larger prey items found in scats. Future scat sampling in the area should be done over a broad area to avoid biased results due to local variations in the availability of prey species. Ideally, future studies should use scat analysis and GPS kill site location techniques together to improve the accuracy of dietary analysis.

CHAPTER 5: LEOPARD DIET

5.2 Introduction

The diet of a carnivore determines its ecological role within an ecosystem, both in terms of the impact on prey populations and potential competition with other carnivores (Klare et al. 2011). Diet can be influenced by a range of factors, including prey availability (Bailey 1993; Hayward et al. 2006), whether the carnivore is solitary or group-living (Hayward & Kerley 2005), interactions with other carnivores (Karanth & Sunquist 2000; Linnell & Strand 2000) and the risk associated with catching and subduing particular prey items (Hayward et al. 2006).

Leopards have been recorded preying upon 92 species in Sub-Saharan Africa, the most varied prey base of any African felid (Bailey 1993; Mills & Harvey 2002; Ray et al. 2005; Hayward et al. 2006). Prey items can range from arthropods to eland (*Tragelaphus oryx*), which can weigh up to 900 kg (Bailey 1993), but the most commonly consumed prey are medium-sized ungulates weighing between 20 and 80 kg (Bailey 1993; Stander et al. 1997; Mills & Harvey 2002). Ungulates and other potential leopard prey species occur at low densities in the Western Cape Province of South Africa, particularly when compared to the savannah areas of the country (Bailey 1993; Boshoff et al. 2001; Radloff 2008). This is especially true of the mountainous regions of the Western Cape, where leopards occur (Radloff 2008). As carnivore population density is generally correlated with the amount of available prey biomass, one would expect leopard population densities in the Western Cape to be low as a result of the limited food availability (Carbone & Gittleman 2002).

Predators that exceed a threshold of between 15 and 21 kg body mass are expected to prey predominately upon relatively large prey species that approach or exceed their own body mass (Carbone et al. 1999, 2007). By contrast, smaller predators tend to be more reliant on small mammal and invertebrate prey species (Carbone et al. 1999, 2007). Leopards in the Western Cape, with a mean body mass of between 21 and 35 kg, are thus predicted to prey mainly upon relatively large species (weighing more than 10 kg) which are close to their own mass (Carbone et al. 1999; Martins 2010). Carbone et al. (2007) found that prey size tends to increase with predator size, and one would thus expect the relatively small leopards of the Western Cape to be more reliant on smaller prey

CHAPTER 5: LEOPARD DIET

species than the larger leopards that inhabit the savannah regions of Africa. The results of previous studies of leopard diet in southern Africa suggest that prey size does generally correspond to the size of leopards in the study area (see Table 5-1). The larger leopards in the northern regions of South Africa (Kruger National Park, Waterberg Mountains and Phinda Game Reserve) hunted larger prey items than the smaller leopards of the Western and Eastern Cape (Cederberg, Little Karoo/Gamkaberg, Jonkershoek, Wemmershoek, southern Cape and Baviaanskloof). Leopards in the Western Cape also show a preference for smaller prey, even when larger prey species are available (Martins et al. 2011).

CHAPTER 5: LEOPARD DIET

Table 5-1. Summarised results of leopard diet studies in southern Africa. Leopard mass indicates the average weight of adult male and female leopards at a study location. When not supplied in the reference, leopard size was inferred from the following studies; Bailey (1993)¹, Balme et al. (2010)², Grimbeek (1992)³, Stuart (1981)⁴, Martins (2010)⁵ and this study⁶. Major prey species shows species which comprised 10% or more of kills, or were found in 10% or more of scat samples. The prey mass shows the average weight of the major prey species (Skinner & Chimimba 2005), and the percent of diet gives the frequency of occurrence of the prey species, either at kill sites or in scats. The majority of studies did not apply a correction factor for the frequency of occurrence of prey items found in scats - those that did are marked (^c) Number of kills/scats gives the total number of samples (either kill sites or scats) used in the study, while the method column provides brief details on how data were collected.

Location	Leopard mass (kg)	Major prey species	Prey mass (kg)	Percent of diet	Number of kills/scats	Method	Reference
Kaudom National Park, Namibia	Male: 44.6 (±0.5)	common duiker (<i>Sylvicapria grimmia</i>)	16.1	32.8%	131	Spoor tracking/ direct observation	Stander (1997)
	Female: 25.0 (±2.2)	steenbok (<i>Raphicerus campestris</i>)	11.1	13.0%			
Kgalagadi Transfrontier National Park, Northern Cape, South Africa	Not reported	porcupine (<i>Hystrix africaeaustralis</i>)	12.2	20%	80	Spoor tracking/ direct observation	Bothma et al. (1997b)
		gemsbok (<i>Oryx gazella</i>)	158	18.8%			
		common duiker	16	10.0%			
Kgalagadi Transfrontier National Park, Northern Cape, South Africa	Not reported	springbok (<i>Antidorcas marsupialis</i>)	40	65.0%	80	Direct observation	Mills (1990)
Kruger National Park, Mpumalanga, South Africa	Male: 63.1 Female: 37.3 ¹	impala (<i>Aepyceros melampus</i>)	30	77.3%	5478	Direct observation/ inferred from carcass	Pienaar (1969)

CHAPTER 5: LEOPARD DIET

Location	Leopard mass (kg)	Major prey species	Prey mass (kg)	Percent of diet	Number of kills/scats	Method	Reference
Kruger National Park, Mpumalanga, South Africa	Male: 63.1 Female: 37.3 ¹	impala	30	87.3%/ 60%	55 kills /94 scats	Direct observation /scat analysis (macroscopic comparison)	Bailey (1993)
Sabi-Sand Game Reserve, Mpumalanga, South Africa	Male: 63.1 Female: 37.3 ¹	impala	30	83.4%	1135 kills	unknown	Graupner & Graupner (1971)
Sabi-Sand Game Reserve, Mpumalanga, South Africa	Male: 63.1 Female: 37.3 ¹	impala	30	83.0%	882	unknown	Crabtree (1973, 1974)
Timbavati Game Reserve, Mpumalanga, South Africa	Male: 63.1 Female: 37.3 ¹	impala	30	92.3%	168	unknown	Hirst (1969)
Phinda Game Reserve, KwaZulu-Natal, South Africa	Male: 64.5 Female: 35.0 ²	nyala (<i>Tragelaphus angasii</i>)	47	43.3%	217 kills	Direct observation	Balme et al. (2007)
		impala	30	15.7%			
		warthog (<i>Phacochoerus africanus</i>)	45	10.1%			
Waterberg mountains, Limpopo, South Africa	Male: 58.8 Female: 38	impala	30	26.3%	76 scats	Scat analysis (cross-sections)	Grimbeek (1992)

CHAPTER 5: LEOPARD DIET

Location	Leopard mass (kg)	Major prey species	Prey mass (kg)	Percent of diet	Number of kills/ scats	Method	Reference
Waterberg mountains, Limpopo, South Africa	Male: 58.8	kudu (<i>Tragelaphus strepsiceros</i>)	110.9	24.7%/14.1% ^c	89 kills/ 39 scats	GPS kill site location/ scat analysis using cross-sections and cuticle patterns	Swanepoel (2009)
	Female: 38 ³	warthog	31.83	21.3%/ 10.3% ^c			
		impala		12.4%/ 7.69% ^c			
		bushbuck (<i>Tragelaphus scriptus</i>)	34.85	7.9%/ 19.3% ^c			
			21.29				
Baviaanskloof, Eastern Cape, South Africa	Males: 36	mountain reedbuck (<i>Redunca fulvorufula</i>)	23	17.5%	40 scats	Macroscopic analysis of scats and cuticle patterns	Ott et al. (2007)
	Females: 21 ⁴	bushbuck	22.5	15.0%			
		vlei rat (<i>Otomys irroratus</i>)	0.2	12.5%			
		rock hyrax (<i>Procavia capensis</i>)	3.6	12.5%			
		grysbok (<i>Raphicerus melanotis</i>)	10.3	10.0%			
Southern Cape, Western Cape, South Africa	Males: 31.0	bushbuck	22.5	58.3% ^c	50 scats	Macroscopic analysis of scats and cuticle patterns	Brackowski et al. (2012)
	Females: 21.0 ⁴	vlei rat	0.2	13.3% ^c			

CHAPTER 5: LEOPARD DIET

Location	Leopard mass (kg)	Major prey species	Prey mass (kg)	Percent of diet	Number of kills/scats	Method	Reference
Cederberg mountains, Western Cape, South Africa	Males: 34.5	rock hyrax	3.6	79.1%	129 scats	Macroscopic analysis of scats	Norton et al. (1986)
	Females: 20.5 ⁵	klipspringer (<i>Oreotragus oreotragus</i>)		15.5%			
			11.9	12.4%			
		grey rhebok (<i>Pelea capreolus</i>)	20.0				
Cederberg mountains, Western Cape, South Africa	Males: 34.5	klipspringer	11.9	29.3%	98 scats	Macroscopic analysis of scats and cuticle patterns	Rautenbach (2010), Martins et al. (2011)
	Females: 20.5 ⁵	rock hyrax	3.6	25.0%			
Cederberg mountains, Western Cape, South Africa	Males: 34.5	klipspringer	11.9	39.6%	53 kills	GPS kill site location	Martins et al. (2011)
	Females: 20.5 ⁵	rock hyrax	3.6	30.2%			
Jonkershoek, Western Cape, South Africa	Males: 31.0	rock hyrax	3.6	41.6%	24 scats	Macroscopic analysis of scats	Norton et al. (1986)
	Females: 21.0 ⁴	grysbok	10.3	20.8%			
		vlei/ Karoo rat (<i>Otomys spp.</i>)	0.2	16.7%			
Wemmershoek, Western Cape, South Africa	Males: 31.0	Feral pig (<i>Sus scrofa domesticus.</i>)	>20	60.0%	25 scats	Macroscopic analysis of scats	Norton et al. (1986)
	Females: 21.0 ⁴	grysbok	10.3	32.0%			
		rock hyrax	3.6	20.0%			

CHAPTER 5: LEOPARD DIET

Location	Leopard mass (kg)	Major prey species	Prey mass (kg)	Percent of diet	Number of kills/scats	Method	Reference
Gamkaberg mountains, Western Cape, South Africa	Males: 41.0	rock hyrax	3.6	67.8%	59 scats	Macroscopic analysis of scats	Norton et al. (1986)
	Females: 21.0 ⁶	grysbok	10.3	25.4%			
		klipspringer		20.3%			
			11.9	10.2%			
Little Karoo, Western Cape, South Africa	Males: 41.0	rock hyrax	3.6	27.6%	77 scats	Macroscopic analysis of scats and cuticle patterns	Rautenbach (2010)
	Females: 21.0 ⁶	klipspringer	11.9	16.3%			

CHAPTER 5: LEOPARD DIET

A recent study on leopard diet in Cederberg and Little Karoo regions of the Western Cape found that klipspringers were the most important leopard prey species, followed by rock hyraxes and other small species, including rodents, lagomorphs, birds and reptiles (Rautenbach 2010). Leopard diet was similarly broad in both areas, with 22 prey types being recorded in both areas. However, the average size of prey was significantly smaller in the Gamkaberg (Little Karoo) area (6.6 kg, 123 prey items identified in 77 scats) than in the Cederberg (8.8 kg, 140 prey items identified in 98 scats) (Rautenbach 2010). Rautenbach (2010) suggested that there had been significant shifts in prey composition since the previous dietary analysis of leopards in the Cape, which included both the Cederberg and Gamkaberg areas (Norton et al. 1986), with small prey (rodents weighing less than 0.5 kg) forming a far greater proportion of the diet. This may have been due to reduced availability of larger prey items, such as rock hyraxes or increased rodent abundances allowing for more opportunistic predation by leopards, which has also been suggested in other studies where similar dietary shifts have been observed (Hayward et al. 2006; Ott et al. 2007; Rautenbach 2010). While livestock such as goats (*Capra hircus*), cattle (*Bos taurus*) and ostriches (*Struthio camelus*) are widely farmed in the Little Karoo, both studies of leopard diet in the area, as well as another study in the Baviaanskloof area to the east, suggested low levels of livestock predation (Norton et al. 1986; Ott et al. 2007; Rautenbach 2010).

Currently, two main methods exist for inferring carnivore diet in the absence of direct observation. While most dietary analysis has been done by identifying prey remains found in scats or stomachs, GPS tracking technology has allowed researchers to identify the sites of predator kills based on a cluster of GPS points. These clusters indicate that the study animal has remained in one area for an extended period of time (Anderson & Lindzey 2003; Sand et al. 2005) as is typically the case when a predator has successfully captured a medium to large sized prey species. The site of the potential kill can then be visited, and the area searched for prey remains. This method allows for more accurate estimation of predation rates on large prey species than can be obtained from scat or stomach analysis, and provides additional data such as the times at which kills occur and seasonal changes in

CHAPTER 5: LEOPARD DIET

hunting behaviour (Anderson & Lindzey 2003; Sand et al. 2005). Kill site analysis can also be used to study predation habits by identifying sites where predation is more likely to occur (Pitman et al. 2012). However, kills of small prey that can be eaten rapidly without leaving a signature 'cluster' of GPS points cannot be reliably detected using this method (Anderson & Lindzey 2003; Sand et al. 2005; Martins et al. 2011).

Scat analysis is a more established technique for assessing carnivore diet, and has been widely used, both in South Africa and abroad (Norton et al. 1986; Karanth & Sunquist 1995; Ramakrishnan et al. 1999; Ott et al. 2007; Aryal & Kreigenhofer 2009; Rautenbach 2010; Harihar et al. 2011; Braczkowski et al. 2012). Scat analysis is non-invasive, relatively inexpensive and can be an effective means of assessing the diet of cryptic carnivores such as leopards (Chame 2003). However, scat analysis is reliant on collecting a sufficiently large sample of scats, which can be difficult, particularly in rugged terrain (Reynolds & Aebischer 1991; Trites & Joy 2005; Williams et al. 2012). Identifying prey remains from scats can also be difficult, and is subject to observer bias (Verma et al. 2002). A variety of methods have been used to identify prey found in scats, including identification based on bone and tooth fragments (Norton et al. 1986), visual comparison of hairs found in scats to a reference collection (Bailey 1993), comparison of prey hair cuticle scale imprints to a reference collection (Keogh 1983; Ott et al. 2007; Rautenbach 2010) or comparison of prey hair cross-sections to a reference collection (Douglas 1989; Swanepoel 2009). Several studies have employed a combination of these methods, presumably to increase the probability of correctly identifying the prey species (Swanepoel 2009; Martins et al. 2011; Harihar et al. 2011). While correct identification of prey species is clearly of paramount importance, the different methods involved make comparisons among scat analysis studies difficult (Reynolds & Aebischer 1991). A further disadvantage of scat analysis is that it tends to overestimate the importance of small-bodied prey items unless a suitable correction factor can be applied (Ackerman et al. 1984; Karanth & Sunquist 1995). To date, no captive feeding trials have been conducted on leopards, and in the absence of a leopard-specific correction factor most studies have employed a correction factor developed for cougars (*Puma*

CHAPTER 5: LEOPARD DIET

concolor) (Karanth & Sunquist 1995; Swanepoel 2009; Brackowski et al. 2012) or simply presented uncorrected frequencies of occurrence (%) for prey species within scats (Norton et al. 1986; Ott et al. 2007; Rautenbach 2010; Martins et al. 2011).

A number of studies have used a combination of kills (located either opportunistically or through GPS tracking) and scat analysis to gather data on carnivore diet (Bailey 1993; Karanth & Sunquist 1995; Swanepoel 2009; Martins et al. 2011; Morehouse & Boyce 2011; Bacon et al. 2011; Tambling et al. 2012; Pitman et al. 2013). These studies have found that reliance on kill sites alone tends to bias results towards larger prey species, underestimating the role of smaller prey (Karanth & Sunquist 1995; Swanepoel 2009; Bacon et al. 2011; Tambling et al. 2012). In a study of cougars, Bacon et al. (2011) found that estimates of ungulate biomass consumed were almost identical for the two methods, although as ungulates are relatively large prey the bias inherent to using kill-site locations is likely to have had a reduced influence on their results. Two recent studies have compared the scat and kill-site methods for determining leopard diet in South Africa (Martins et al. 2011; Pitman et al. 2013). In the Cederberg Mountains of the Western Cape, Martins et al. (2011) found that the two methods produced very similar results, as the small species found exclusively in scat samples accounted for less than one percent of all biomass consumed. Similarly, in a study in the Waterberg Mountains in northern South Africa, Pitman et al. (2013) found that supplementing kill-site data with scat-derived data yielded no statistically significant results. Nevertheless, Pitman et al. (2013) suggested that the two methods be used in combination for future leopard research, if only to provide more data to improve the accuracy of diet assessments.

The previous studies in the Gamkaberg (Norton et al. 1986; Rautenbach 2010) and Baviaanskloof (Ott et al. 2007) areas were based upon analysing scats to identify the remains of prey. This chapter investigates leopard diet in the Little Karoo using scat analysis, but combined with kill sites located with GPS tracking collar clusters. In doing so, I hope to continue to track leopard dietary preferences to see whether the trend of increased reliance of small mammals continues, as well as quantifying

CHAPTER 5: LEOPARD DIET

the impact of leopard predation on livestock and game farms in the area. My study will also compare the two methods of assessing diet composition, and in so doing draw inferences about the reliability of the two approaches. The results of my study are thus likely to be the most robust estimates of leopard diet produced for the Little Karoo, despite the inherent limitations of only being able to identify kills from a sample of three adult male leopards, and will aid our understanding of leopard ecology in the area.

CHAPTER 5: LEOPARD DIET

5.3 Methods

5.3.1 Scat analysis

Scats were collected opportunistically in the field while I was either walking or driving through the study area (see Figure 5-1). Search effort was thus biased towards roads and trails, and it is thus likely that the majority of scats came from male leopards (see Chapter 4). Scats appeared to persist for approximately six months in the field before disintegrating (pers. obs.), and were collected from November 2009 to October 2012. The sampling period represented by the scats analysed in this study is thus likely to extend from ~May/June 2009 to October 2012, approximately 3.5 years. The location of the scat was recorded using a handheld GPS unit (Garmin eTrex H, Garmin International Inc. Olathe, Kansas, USA), and scats were stored in paper envelopes until they could be processed. Scats were identified as belonging to leopards based on shape (Norton et al. 1986) and diameter (Norton et al. 1986; Henschel 2008; Wang & Macdonald 2009b; Martins et al. 2011; Braczkowski et al. 2012). As leopard and caracal (*Caracal caracal*) scats can be difficult to distinguish from one another due to their similar, segmented appearance, only scats with a diameter exceeding 2cm were used (following Norton et al. 1986; Ott et al. 2007; Rautenbach 2010). In addition, because leopards may use scats to mark their territories (Bailey 1993; Chame 2003), approximately half of each scat was left *in situ* (following Rautenbach 2010; Martins et al. 2011). Due to the difficulty in finding scats, all available scats were collected, except if they were extremely decomposed and the hairs appeared to have disintegrated. Extremely decomposed scats were typically brittle, with little structural integrity and crumbled when handled. Scats considered to be sufficiently fresh were more robust to handling, probably due to hair binding the scat material together. Scats were stored for periods of up to one year before being cleaned and processed in the laboratory. There was no noticeable degradation of stored scats; presumably protection from the harsh Karoo climate dramatically slowed further decomposition.

Each scat sample was placed inside a stocking and soaked in hot water for 24 hours to allow it to soften (Rowe-Rowe 1983; Bissett 2004; Do Linh San et al. 2009; Forbes 2011). Each scat was then

CHAPTER 5: LEOPARD DIET

washed under running water while still in the stocking, and hairs and other macroscopic prey remains (bones, etc.) were collected. Hair samples were then placed in petri dishes and allowed to dry for approximately seven days. The dried hair samples were spread over a sorting tray, and a sample of hairs removed (Reynolds & Aebischer 1991; Ramakrishnan et al. 1999; Rautenbach 2010). For each sample, I ensured that all hair types present in the scat were represented in both the scale pattern and cross-section samples (Reynolds & Aebischer 1991). Twenty hairs from each sample were placed on glass microscope slides that had been dipped into 5% gelatine solution to allow negative cuticle impressions to be made (Keogh 1983; Bissett 2004; Forbes 2011). In addition, as many other hairs as possible (usually between 20 and 50) were prepared for cross-section analysis using the method proposed by Douglas (1989). Hairs were placed inside a disposable plastic pipette, and hot paraffin wax (Paraplast Plus, Sherwood Medical Co., St. Louis, Missouri, USA) sucked up into the pipette, which was then placed in a beaker full of ice to cool before being cut into two-millimetre sections and mounted onto glass slides using a drop of hot wax to attach the cross-section to the slide (Douglas 1989; Kaunda & Skinner 2003; Bissett 2004).

CHAPTER 5: LEOPARD DIET

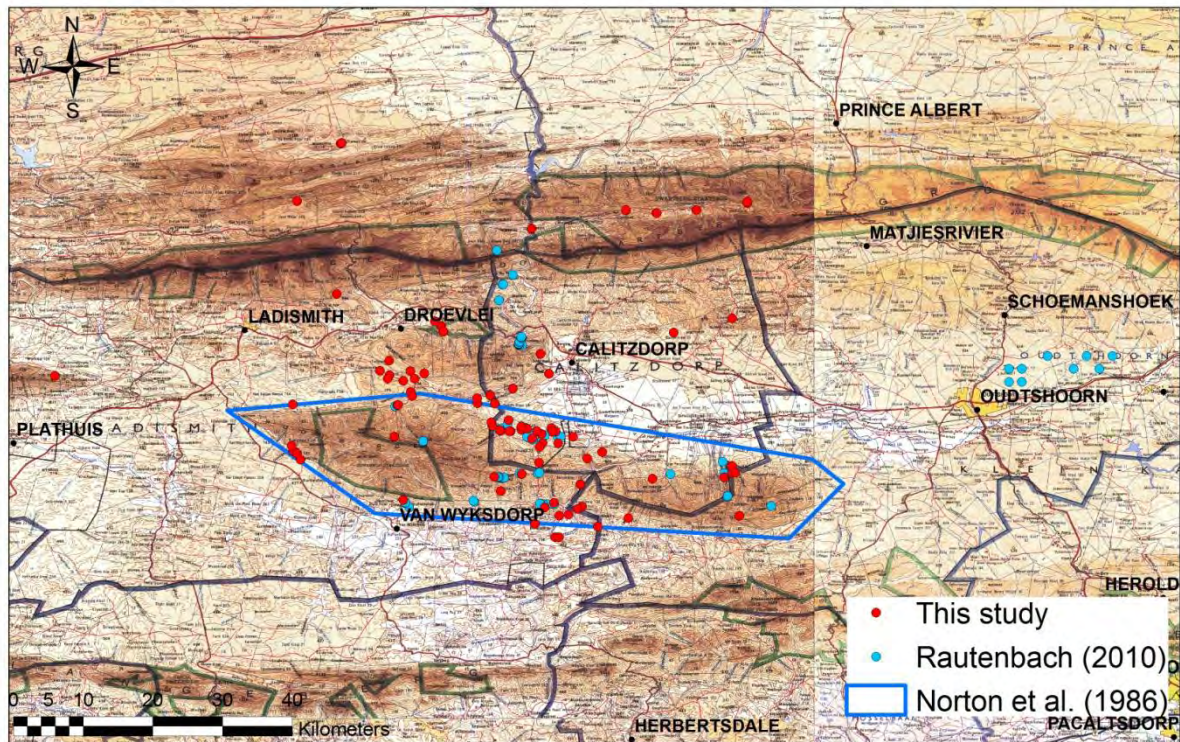


Figure 5-1. Map showing scat sample collection sites for this study (red dots), the Rautenbach (2010) study (blue dots) and the approximate area in which scats were collected by Norton et al. (1986) (blue line), as inferred by the study area description.

Hair samples were identified to species-level by comparing samples to the mammalian reference collection at Rhodes University, South Africa (sensu Keogh 1983; Bissett 2004; Forbes 2011; Tambling et al. 2012). Cross-sections were used as the primary means of identifying hairs, as these samples generally contained a larger sample of hairs and were usually easier to identify than the negative cuticle imprints. Cuticle imprints and macroscopic remains were used to aid identification when results from the cross-section analysis were ambiguous (Norton et al. 1986; Ott et al. 2007; Rautenbach 2010; Brackowski et al. 2012). All samples were examined under a Zeiss Primostar™ light microscope at 40x magnification, digitally photographed and measured using the AxioVision software package (Carl Zeiss MicroImaging GmbH, Jena, Germany).

5.3.2 Kill-site analysis

Three male leopards were captured and fitted with GPS Plus tracking collars (Vectronics Aerospace GmbH, Berlin, Germany). All trapping and collaring activities were done with the authorisation of the Rhodes University Ethical Standards Committee (ethical clearance number: ZOOL-02-2010)

CHAPTER 5: LEOPARD DIET

and CapeNature (permit number: AAA004005920035). Further details of leopard capture and immobilization methods are provided in Appendix 5A. The collars were programmed to record a GPS fix at four-hour intervals, starting at midnight (i.e. six fixes per day). Data were downloaded whenever possible, using a VECTRONICS Aerospace Handheld Terminal (VECTRONICS Aerospace GmbH, Berlin, Germany) (leopards GM2 and GM9) or via GSM network (leopard GM1) and systematically checked for clusters of points that could indicate the site of a kill (Anderson & Lindzey 2003; Sand et al. 2005; Martins et al. 2011; Tambling et al. 2012; Pitman et al. 2012, 2013). Points within 50 m of one another were considered to be part of the same cluster (following Martins et al. 2011; Pitman et al. 2012). The length of time between the first and final point of the cluster of GPS points has been identified as the most accurate predictor of a kill (Anderson & Lindzey 2003; Martins et al. 2011; Pitman et al. 2012). Martins et al. (2011) found that the probability of successfully locating a kill increased dramatically if the leopard spent more than 24 hours at a site. I investigated all clusters at which the leopard had spent more than 20 hours. Although this increased the risk of missing kills of smaller prey items, I was often only able to visit sites long after the potential kill had occurred due to difficulties in locating and downloading tracking data from the collared leopards. Rapid investigation of smaller kill sites has been identified as a key factor in the success rate of locating and identifying these kills (Pitman et al. 2012), and the lengthy delay in visiting smaller kill sites would have further reduced the probability of successfully locating these kills. Investigating clusters of a shorter duration would also have increased the risk of expending considerable time and effort to visit sites at which no kill had actually been made (Pitman et al. 2012). Furthermore, Pitman et al. (2012) found that kill-site analysis had an inherent bias against smaller prey items regardless of the threshold applied to determine whether a site would be investigated.

Once identified, potential kill sites were investigated on foot. A central GPS point from the cluster would be identified and the co-ordinates entered into a handheld GPS unit (Garmin Etrex). An area of up to a 50 m radius around the central point would be searched until remains were found. Search

CHAPTER 5: LEOPARD DIET

time was limited to a maximum of one hour, double the maximum search times of most similar studies (Martins et al. 2011; Jooste et al. 2012; Pitman et al. 2012).

5.3.3 Data analysis

Diet composition was determined by relative frequency of occurrence (%) of a food item (Lockie 1959). This was calculated by dividing the number of times that a prey item occurred by the total number of prey items found in all scats and converted to a percentage by multiplying by 100 (Lockie 1959). This method allowed comparison to previous studies of leopard diet in the Cape (Norton et al. 1986; Ott et al. 2007; Rautenbach 2010; Martins et al. 2011), and has been found to be correlated to other diet estimators based on relative frequency of prey items (Klare et al. 2011). However, frequency-based methods have been criticised for tending to overestimate the importance of smaller food items (Karanth & Sunquist 1995; Klare et al. 2011). Thus, when multiple food items were found in a scat, the items were assigned a weighting, calculated by dividing that species by the total number of species remains present in the scat to generate a corrected frequency of occurrence (Karanth & Sunquist 1995; Brackowski et al. 2012). For example, in scats containing remains of two prey species, each was assigned a weighting of 0.5, while prey species in scats containing remains of three species were each assigned a weighing of 0.33. For the majority of scats (68.4%, n=52), only one prey species was identified, and these were assigned a weighting of one. Twenty scats (26.3%) contained remains from two species, and the remains of three species were identified in four scats (5.3%). No more than three different prey species were identified in a single scat.

An alternative quantification approach is to measure the volume or mass of prey items found within scats and to model biomass intake using conversion factors or models (Loveridge & Macdonald 2003; Mcdonald & Fuller 2005; Forman 2005). However, accurate implementation of these methods is dependent upon conversion factors to convert the frequency of occurrence of prey items into prey biomass or the number of individual prey ingested (e.g. (Ackerman et al. 1984; Marker et al. 2003b). Two conversion factors have been developed for large felids (Ackerman et al. 1984; Marker et al. 2003b; Klare et al. 2011). One of these conversion factors is for cheetahs (*Acinonyx jubatus*) in

CHAPTER 5: LEOPARD DIET

Namibia, and is unlikely to be useful for estimating leopard biomass consumption as cheetahs typically only consume ~70% of the carcass of smaller prey species and ~16% of the carcass of large antelope species (Marker et al. 2003b). Although I did not weigh the carcasses found at leopard kill sites, leopards in the Little Karoo appeared to consume a far greater proportion of each kill than was recorded for cheetahs by Marker et al. (2003b), possibly due to the lack of interference from other predators (see Figure 5-2 for an example of a kill site). Estimating the actual percentage of carcass biomass consumed was not possible due to the lengthy delays in visiting kill sites, by which time carcasses had often partially decomposed or dried out. Species of comparable size to the 'small' species used by Marker et al. (2003b) were almost entirely consumed, with only hairs and some of the larger bones remaining.



Figure 5-2. The remains of a goat, *Capra hircus* (estimated weight ± 40 kg) killed by leopard GM1, seven days after the kill had taken place.

Ackerman et al. (1984) developed a conversion equation for correcting for the number of scats produced per animal consumed. This provided a better estimate of the numerical importance of the different species consumed than frequency of occurrence (Ackerman et al. 1984). The equation developed by Ackerman (1984) is $Y = 1.98 + 0.035X$, where Y is the weight of prey consumed per

CHAPTER 5: LEOPARD DIET

scat, and X is the overall biomass of the prey item. Following Ackerman (1984), I assumed that all species weighing less than two kilogrammes were consumed whole and accounted for a single scat. The correction factor was not applied to these species, and biomass consumed was calculated by simply multiplying the average biomass of the species by the number of scats in which its remains were found (Ackerman et al. 1984).

Species accumulation curves were plotted for both scat and kill site data using the program EstimateS 8.20 (Colwell 2006). Prey items were divided into four categories; small mammals (weighing < 1 kg), small-medium mammals weighing between one and 10 kg, medium-sized mammals weighing between 10 and 40 kg, and large mammals that weighed over 40 kg.

The average time between leopard kills (hereafter referred to as the 'kill rate') was calculated by dividing the total number of days of GPS tracking data for each leopard by the total number of confirmed kills (i.e. sites at which prey remains were found) for each leopard. A maximum kill rate was calculated in the same manner, except that all potential kill sites, including those at which no remains were found, were divided by the number of days for which each collar was active. The biomass consumed at leopard kills was calculated using the average weight of prey species (Burke 2004; Skinner & Chimimba 2005). When necessary, the biomass of some larger prey items (eland (*Tragelaphus oryx*), kudu (*Tragelaphus strepsiceros*) and cattle (*Bos taurus*) was adjusted to compensate for leopards preying upon juvenile and sub-adult individuals. In the case of juveniles, adult biomass was multiplied by 0.3, while for sub-adults, the adult biomass was multiplied by 0.7 (Radloff & du Toit 2004). When calculating the biomass of prey items found in scats I assumed that the trends observed at kill sites also held true for prey items found in scats and that larger prey items were juvenile or sub-adult individuals.

Leopard predation on baboons (*Papio hamadryas*) is a relatively unusual phenomenon (Hayward et al. 2006), which has only been recorded at low levels in the Western Cape (Norton et al. 1986; Rautenbach 2010; Martins et al. 2011; Brackowski et al. 2012) and baboon kills were therefore

CHAPTER 5: LEOPARD DIET

examined in greater detail than other kills. The time at which kills were made was inferred from the time at which the first GPS point of a kill site cluster was recorded (Jooste et al. 2012). The time of baboon kills was compared to that of other confirmed kills using a Kolmogorov-Smirnov two-sample test, as it has been hypothesised that leopards may employ specialised hunting strategies to overcome the group defences of baboon troops (Cowlishaw 1994; Jooste et al. 2012).

The degree of similarity of the two datasets (scats and kill sites) was explored by calculating relative compositional similarity (Colwell & Coddington 1994; Magurran 2004). Similarity and its inverse, complementarity, provide insight into how many prey species were common to both sample datasets. Compositional similarity can range from zero to one, where a score of zero indicates that no species are common to the two samples, while a score of one indicates that the two samples are composed of identical species (Colwell & Coddington 1994; Jost et al. 2011). This provides an indication of the value of employing both sampling methods, as opposed to relying solely on either scat or kill site sampling. However, in the absence of direct observational data it is not possible to definitively claim that one method was more accurate than the other. As species weighing less than 10 kg were unlikely to be detected at kill sites (Martins et al. 2011), a second compositional analysis was done where these species were excluded.

Further analysis of the differences between the two datasets was done using SIMPER analysis in the program PRIMER 6 (Clarke 1993; Clarke & Gorley 2006). SIMPER identifies the contribution of variables to the average dissimilarity between two or more groups of samples (Clarke 1993; Clarke & Gorley 2006). Bray-Curtis dissimilarity was calculated between the groups of samples, as this is more useful for analysing abundance data than Euclidean distance (Clarke & Gorley 2006). SIMPER analysis was used to compare the results of the scat analysis done during this study with those obtained by Rautenbach (2010), as well as to compare the results of scat and kill site analyses. Finally, SIMPER was also used to investigate dissimilarity between the diets of the three collared leopards at an individual level.

CHAPTER 5: LEOPARD DIET

5.3.4 Prey abundance

Prey abundances were estimated based on data gathered opportunistically during the camera trap survey designed to assess leopard population density in the study area (see Chapter 4 for a detailed description of camera trapping activities). The vast majority of potential prey species in the study area lacked distinctive features that allowed for identification to the level of individuals, and thus mark-recapture methods could not be used to accurately measure the absolute abundance of prey species in the area (Oliveira-Santos et al. 2010). Furthermore, the low prey densities, rugged terrain and cryptic nature of many prey species in the area rendered alternative means of estimating prey densities, such as game counts or transects, impractical (Funston et al. 2010). I thus calculated the relative abundance of prey species by dividing the number of photographs recorded of each species by the total number of useable photographs recorded (Martins et al. 2007; Stein et al. 2008; Rautenbach 2010; Brackowski et al. 2012). To avoid inflating relative abundance estimates by repeatedly counting the same individual, I only considered photographs of the same species that were more than one hour apart as independent photographic events (Yasuda 2004). This is likely to have resulted in underestimation of the relative abundance of group-living species such as baboons, which had troop sizes that varied from approximately 20 to 100 individuals within my study area (pers. obs.). All other (non-independent) events were excluded from the analysis, as were photographs of humans and vehicles. Horses and dogs were also excluded; despite being potential prey species these were all photographed in close proximity to humans, and I assumed that this dramatically reduced the risk of leopard predation. I restricted the analysis to sites that fell within areas identified as leopard habitat (see Chapter 3), when comparing relative abundance to the results of scat analysis. I calculated the relative abundance of prey species for comparison with kill-site data based only on camera sites that fell within the 95% kernel home range areas of the three leopards.

CHAPTER 5: LEOPARD DIET

Prey preference was calculated using Jacobs index, which provides a measure of prey preference by comparing the extent to which species are preyed upon compared to their relative availability (Jacobs 1974). Jacobs' index uses the following equation:

$$D = r_i - p_i / (r_i + p_i - 2r_i p_i)$$

Where r_i is the proportion of all scats or kills containing species i , and p_i is the relative abundance of species i , as determined by the camera trap-based relative abundance index. I excluded photographs of the collared leopards from prey preference calculations based on kill sites. Jacobs' index has been used extensively in carnivore research to measure prey preferences in lions (*Panthera leo*) (Hayward & Kerley 2005; Valeix et al. 2012), tigers (*Panthera tigris*) (Hayward et al. 2012), wolves (*Canis lupus*) (Wagner et al. 2012; Hosseini-Zavarei et al. 2013), black-backed jackals (*Canis mesomelas*) (Klare et al. 2010) and leopards (Rautenbach 2010; Brackowski et al. 2012).

When determining the relative abundance of prey species for the kill site data, camera trap photos of animals weighing less than 10 kg were excluded, as these were unlikely to be located at kill sites. Although Martins et al. (2011) frequently found rock hyrax remains at kill sites, I did not locate any during the course of this study, despite scat analysis suggesting that leopards frequently prey upon rock hyrax in the Little Karoo (see results below). This suggests that leopards killed and ate rock hyraxes in too short a period for these events to be identified using my protocol for identifying kill sites. I compared prey preferences amongst the individual leopards by calculating Jacobs' indices for each individual, based on kills located and the relative abundance of prey species at camera trap sites that fell within a 95% kernel home range area.

CHAPTER 5: LEOPARD DIET

5.4 Results

5.4.1 Scat analysis

A total of 94 scat samples were collected, but hair could only be obtained from 76 of these. Hairs within the remaining 18 scats had disintegrated and no other identifiable remains were found in these scats. A total of 21 species were identified from the hairs found in the scats using cross-sections. Cuticle-scale imprints from eight scats were also examined to aid identification. Rock hyrax (17.3%), kudu (11.5%) and Karoo or bush rats (*Otomys* spp. – 9.6%) were the most frequently found prey items (see Table 5-2). Small mammals weighing less than one kilogramme (*Otomys* spp., four-striped field mouse, *Rhabdomys pumilio* and the small grey mongoose, *Galarella pulverulenta*) together accounted for 17.3% of all prey items.

The total biomass of all prey items found in the leopard scats was 4696.5 kg. Kudu and eland were the dominant food sources, accounting for over 62% of the total biomass of prey items. Rock hyrax, although the most frequently consumed prey item, accounted for a little over one percent of prey biomass (see Table 5-2). Small mammals (less than one kg mass) accounted for less than one percent of prey biomass. Livestock, however, were a relatively important food source, accounting for 10% of the total biomass of prey killed by leopards. Donkeys comprised ~9% of biomass consumed, but were not categorized as livestock as there is a substantial feral donkey population in the area and it is likely that the vast majority of donkeys killed by leopards were from feral, rather than domestic, populations.

When converted from naive biomass using the formula developed by Ackerman (1984), the total biomass represented by the scat samples was reduced to 390.9 kg. Kudu (24%) and eland (21%) remained the two most important food sources, but rock hyrax accounted for a far larger percentage of the biomass consumed (10%). The relative importance of smaller species, such as *Otomys* spp. also increased (see Table 5-2).

CHAPTER 5: LEOPARD DIET

Table 5-2. Prey items recorded in leopard scats (n=76) collected in the Little Karoo region of the Western Cape, South Africa. Number of occurrences shows the number of scats in which each prey item was found. Frequency of occurrence is the percentage of each prey species relative to the total number of prey items identified. Corrected frequency of occurrence shows the percentage of each prey species after occurrence totals had been corrected to account for the presence of multiple prey items in some scats. The percent of prey biomass shows the percentage of each prey item of the estimated total biomass of all prey items found in scat samples using the corrected frequency of occurrence. The corrected prey biomass is the biomass of prey consumed converted using the formula developed by Ackerman (1984).

Prey species	Prey mass (kg)	Number of occurrences (total=104)	Frequency of occurrence (%)	Corrected frequency of occurrence (%)	Total biomass of all prey items (%)	Corrected prey biomass (%)
Rock hyrax (<i>Procavia capensis</i>)	3.6	18	17.3	19.1	1.1	10.3
Kudu (<i>Tragelaphus strepsiceros</i>)	110.9	12	11.5	12.9	28.3	24.2
Karoo/ Bush rats (<i>Otomys sp.</i>)	0.2	10	9.6	8.1	0.9	0.3
Baboon (<i>Papio hamadryas</i>)	22.9	8	7.7	8.6	3.2	6.1
Goat (<i>Capra hircus</i>)	40.0	8	7.7	8.3	5.4	7.2
Common duiker (<i>Sylvicapria grimmia</i>)	16.1	7	6.7	6.4	1.66	4.1
Eland (<i>Tragelaphus oryx</i>)	267.0	7	6.7	7.2	31.2	21.0
Striped field mouse (<i>Rhabdomys pumilio</i>)	0.04	6	5.8	3.5	0.04	0.04
Klipspringer (<i>Oreotragus oreotragus</i>)	11.9	6	5.8	6.5	1.4	3.6
Donkey (<i>Equus asinus</i>)	175.0	3	2.9	3.0	8.7	6.4

CHAPTER 5: LEOPARD DIET

Prey species	Prey mass (kg)	Number of occurrences (total=104)	Frequency of occurrence (%)	Corrected frequency of occurrence (%)	Total biomass of all prey items (%)	Corrected prey biomass (%)
Hare (<i>Lepus</i> spp.)	2.0	3	2.9	3.3	0.1	1.7
Porcupine (<i>Hystrix africaeaustralis</i>)	12.2	3	2.9	3.1	0.6	1.9
Cattle (<i>Bos taurus</i>)	108.0	2	1.9	2.6	4.6	3.9
Gemsbok (<i>Oryx gazelle</i>)	225.0	2	1.9	2.0	7.2	5.0
Grey rhebok (<i>Pelea capreolus</i>)	20.0	2	1.9	1.3	0.4	0.9
Small grey mongoose (<i>Galarella pulverulenta</i>)	0.8	2	1.923	1.3	0.01	0.3
Aardwolf (<i>Proteles cristatus</i>)	9.2	1	1.0	0.4	0.06	1.1
Black wildebeest (<i>Connochaetes gnou</i>)	130.0	1	1.0	0.7	1.4	1.1
Bushpig (<i>Potamochoerus larvatus</i>)	70.1	1	0.962	0.7	0.7	0.7
Nyala (<i>Tragelaphus angasii</i>)	61.8	1	0.962	0.4	0.4	0.5
Hewitt's red rock rabbit (<i>Pronolagus saundersiae</i>)	1.6	1	0.962	0.4	0.01	0.2

CHAPTER 5: LEOPARD DIET

The species accumulation curve for the scat samples did not reach an asymptote (see Figure 5-3). The Incidence-based Cover Estimator (ICE) and Abundance-based Cover Estimator (ACE) of species richness (Chazdon et al. 1998) had means of 24.3 and 24.9, respectively, suggesting that between three and four potential prey species may not have been detected by the scat analysis.

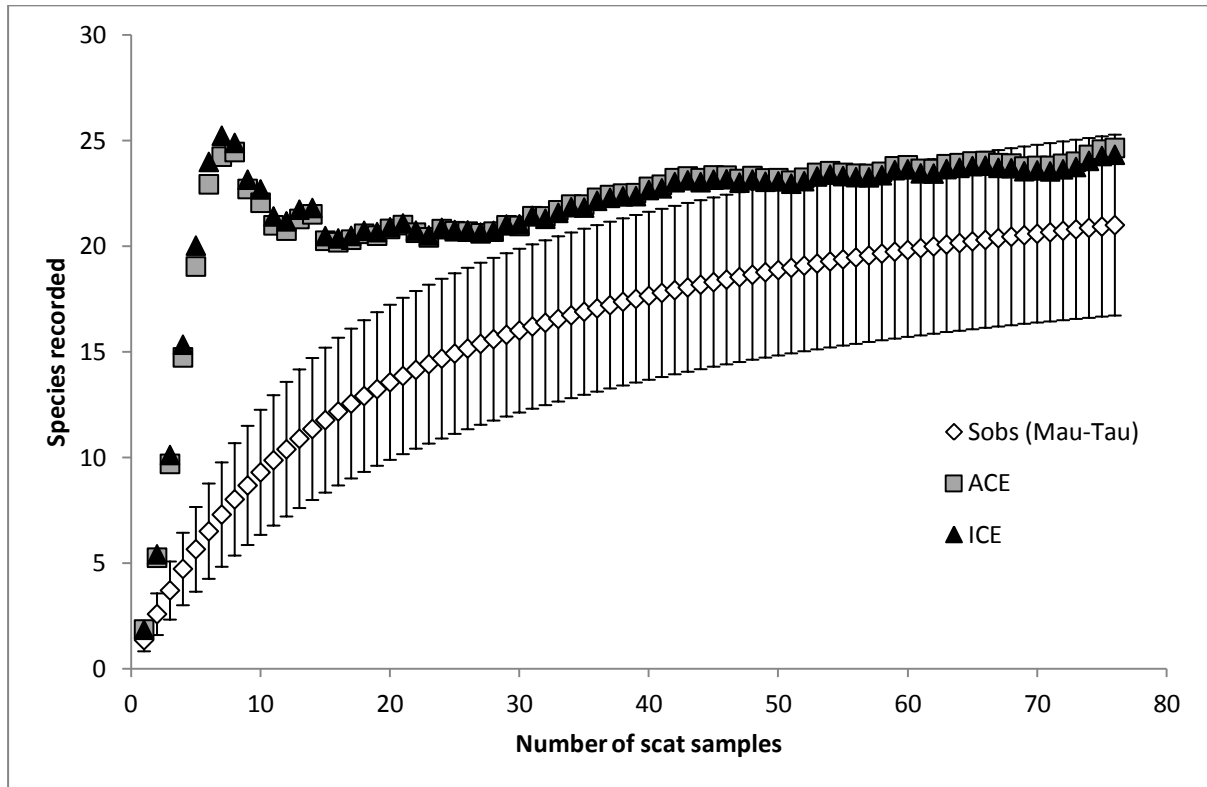


Figure 5-3. Mau-Tau species accumulation curve with 95% confidence intervals (50 randomised iterations; ACE mean 24.88, ICE mean 24.33) for 21 prey types recorded in 76 scat samples collected in the Little Karoo. ACE and ICE provide estimates of the number of species at which the curve is likely to reach an asymptote, and thus represent an estimate of the total number of species likely to be present in leopard scats in the area.

In 1986, all leopard prey items were found to fall into the small (1-10 kg weight) and medium (10-40 kg weight) categories (Norton et al. 1986; Rautenbach 2010). In 2008, substantial changes were observed, with small mammals weighing less than one kilogram accounting for 28.5% of all prey items (see Figure 5-4). My study found that large species weighing over 40 kg accounted for a far larger proportion of prey items (35.6%), while reliance on smaller prey species appeared to have been reduced.

CHAPTER 5: LEOPARD DIET

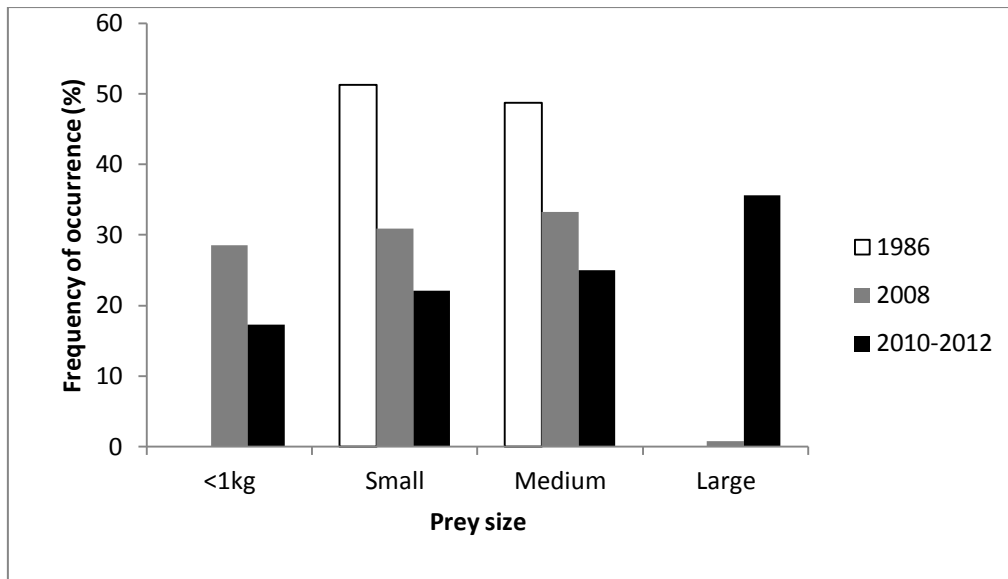


Figure 5-4. Comparison of uncorrected frequency of occurrence of four categories of leopard prey in 1986 (Norton et al. 1986), 2008 (Rautenbach 2010) and 2010-2012 (this study), all of which collected scats from similar areas (see Figure 5-1). Prey were categorised according to biomass; species weighing less than one kilogramme (<1 kg'), small species weighing between one and 10 kg ('Small'), medium sized species weighing between 10 and 40 kg ('Medium') and large species weighing over 40 kg ('Large').

While Norton et al. (1986) and Rautenbach (2010) did not explicitly calculate the biomass of prey consumed, the two studies had near identical results, with over 70% of all prey biomass coming from species weighing between 10 and 40 kg (see Figure 5-5). In contrast, my study found a far greater reliance on large prey species (50.2% of all biomass consumed), while domestic species also accounted for a larger proportion of prey biomass than has previously been observed (see Figure 5-5).

CHAPTER 5: LEOPARD DIET

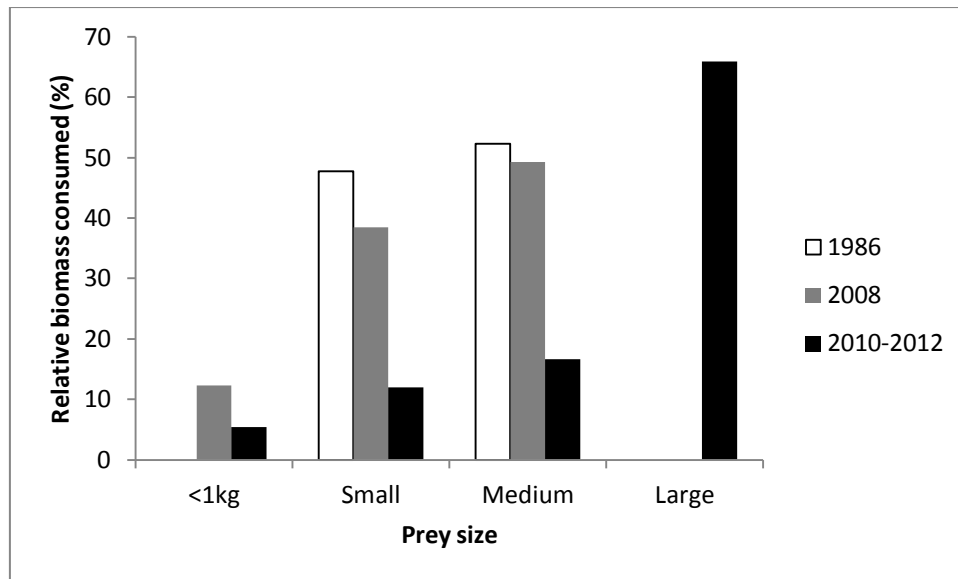


Figure 5-5. Relative biomass obtained from different prey size categories in 1986 (Norton et al. 1986), 2008 (Rautenbach 2010) and 2010-2012 (this study). Prey were categorised according to biomass; species weighing less than one kilogramme ('<1 kg'), small species weighing between one and 10 kg ('Small'), medium sized species weighing between 10 and 40 kg ('Medium'), large species weighing over 40 kg ('Large'). Relative biomass was calculated using the correction formula developed by Ackerman (1984).

5.4.2 Kill-site prey composition

The three male leopards were tracked for periods ranging from 140 to 609 days, providing a total of 946 days of observation. During this time, the three collars attempted to take 5678 GPS fixes, of which 4845 (85.3%) were successful (see Table 5-3). A total of 117 potential kill sites were identified and visited. Prey remains were found at 96 of the 117 sites. I was not able to identify three of the prey items as I could not find sufficient remains to make an accurate identification. The mean search time for prey remains was 27.5 minutes (± 17.3 minutes, range: 1-60). The probability of finding prey remains increased with the number of consecutive GPS points at the cluster (i.e. the amount of time that a leopard spent at a kill). Leopards spent significantly more time on average (Mann-Whitney U-test, $Z=3.181$, $p<0.01$) at sites at which prey remains were subsequently discovered (mean= 56.8 ± 32.3 hours) than at sites where no remains were found (mean= 32.5 ± 11.3 hours). The majority of kill remains (85.3%) were found in closed habitat (i.e., under or amongst trees and bushes) with only 14.7% found in open areas. Of the kills found in open areas, 90.9% were large prey species (weighing over 40 kg). Large species comprised 48.4% of all kills located, and were

CHAPTER 5: LEOPARD DIET

significantly more likely to be found in open areas than smaller prey (Fishers exact test $p=0.009$). No kills were found cached in trees.

Table 5-3. Summary of GPS collar data from three leopards collared in the Little Karoo. 'GPS fixes' represents the total number of attempts the collar made to obtain a GPS fix while still active. Successful fixes shows how many of these fixes were actually obtained. The 'Days' column shows how long each collar was active. 'Potential kills' refers to the number of possible kill sites that were identified based on GPS clusters exceeding 24 hours and visited, while 'Kills found' is the number of these sites at which prey remains were found. The 'Kill rate' is the average number of days in between confirmed kill events (i.e. successfully located kills). 'Maximum kill rate' is the average number of days in between all potential kills.

Leopard	GPS fixes	Successful fixes	Days	Potential kills	Kills found	Kill rate	Maximum kill rate
GM1	1178	1017 (86.3%)	196	26	22	8.9	7.6
GM2	3082	3082 (84.2%)	609	66	53	27.7	9.2
GM9	841	746 (88.7%)	140	26	21	6.4	5.4

A total of 18 species were identified from prey remains at kill sites. Baboons were the most commonly killed prey item, followed by donkeys and common duikers (see Table 5-4).

The estimated total biomass of all kills was 5478.9 kg. The smallest prey item found at a kill site was a hare (~2 kg), although a leopard cub that was killed and eaten may have been of a similar weight. A species accumulation curve based on the remains found at kill sites reached an asymptote (see Figure 5-6). The mean ACE was 18.0, while the mean ICE was 18.5. This suggests that almost all large prey species were found at the kill sites.

CHAPTER 5: LEOPARD DIET

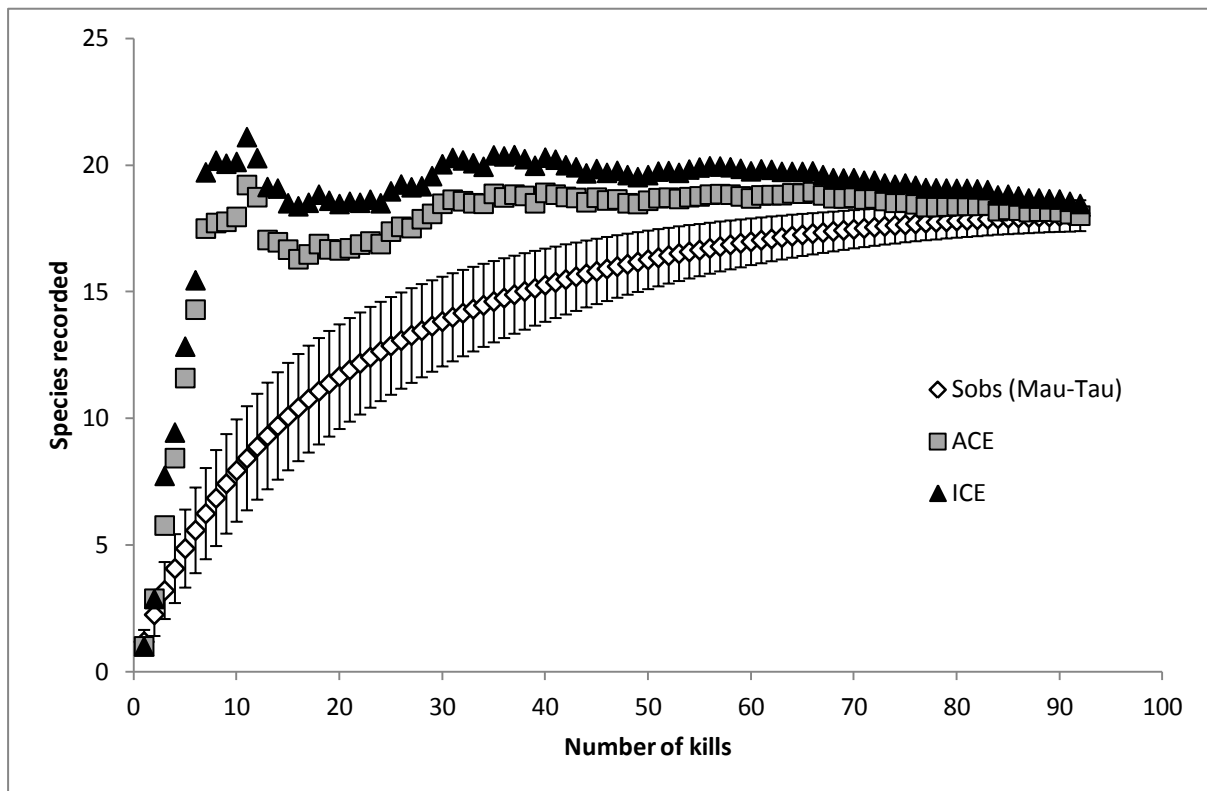


Figure 5-6. Mau-Tau species accumulation curve with 95% confidence intervals (50 randomised iterations, ACE = 18.00, ICE=18.46) for species found at leopard kill sites (n=93). ACE and ICE provide estimates of the number of species at which the curve is likely to reach an asymptote, and thus represent an estimate of the total number of species likely to be present at leopard kill sites in the area.

The mean biomass of prey species located at kill sites was 62.2 kg (± 70.6 kg). Eland constituted the largest percentage of the total biomass consumed by leopards (34.0%), followed by donkeys, cattle and baboons (see Table 5-4). Livestock species (cattle, goats and ostriches (*Struthio camelus*) accounted for 18.3% of all biomass consumed.

CHAPTER 5: LEOPARD DIET

Table 5-4. Summary of prey items identified from leopard kill sites identified by GPS clusters (n=93). Remains at three kill sites could not be identified and were not included in this analysis. Number of occurrences shows the number of kills at which each prey item was found. Frequency of occurrence is the percentage (of all prey items) made up by each prey item. The percent of prey biomass shows the percentage of each prey item of the estimated total biomass of all prey items found at kill sites.

Prey species	Prey mass (kg)	Number of occurrences (total = 93)	Frequency of occurrences (%)	Percent of total prey biomass
Baboon (<i>Papio hamadryas</i>)	22.9	22	23.7	7.1
Donkey (<i>Equus asinus</i>)	175.0	11	11.8	27.2
Common duiker (<i>Sylvicapria grimmia</i>)	16.1	10	10.8	2.3
Eland (<i>Tragelaphus oryx</i>)	267.0	9	9.7	34.0
Goat (<i>Capra hircus</i>)	40.0	8	8.6	4.5
Cattle (<i>Bos taurus</i>)	108.0	7	7.5	10.7
Klipspringer (<i>Oreotragus oreotragus</i>)	11.9	6	6.5	1.1
Grysbok (<i>Raphicerus melanotis</i>)	10.3	3	3.226	0.4
Kudu (<i>Tragelaphus strepsiceros</i>)	110.9	3	3.2	4.5
Ostrich (<i>Struthio camelus</i>)	88.3	3	3.2	3.0
Porcupine (<i>Hystrix africaeaustralis</i>)	12.2	3	3.2	0.5
Aardvark (<i>Orycteropus afer</i>)	43.3	2	2.2	1.2

CHAPTER 5: LEOPARD DIET

Prey species	Prey mass (kg)	Number of occurrences (total = 93)	Frequency of occurrences (%)	Percent of total prey biomass
Bontebok (<i>Damaliscus pyrgargus pyrgargus</i>)	61.0	1	1.1	0.9
Grey rhebok (<i>Pelea capreolus</i>)	20.0	1	1.1	0.3
Hare (<i>Lepus</i> sp.)	2.0	1	1.1	0.0
Leopard (<i>Panthera pardus</i>)	1.0	1	1.1	0.0
Red hartebeest (<i>Alcelaphus buselaphus</i>)	120	1	1.1	1.7
Springbok (<i>Antidorcas marsupialis</i>)	31.5	1	1.1	0.4

CHAPTER 5: LEOPARD DIET

Leopards usually killed juvenile and sub-adult individuals of the larger prey species (eland, kudu, and cattle). However, two of the eland killed were adult females, suggesting that leopards in the area are capable of killing large prey weighing over 300 kg. This trend was less obvious for the donkeys which were killed, as many of the remains found appeared to come from adult (or close to adult-sized) individuals. One incident of cannibalism was recorded, where a leopard cub had seemingly been killed and eaten by one of the collared leopards.

The majority (81.8%) of baboon kills were of female or sub-adult individuals, but adult male carcasses were found at four (18.2%) of the sites. At one site, a leopard (GM1) had killed two baboons; a juvenile and an adult male. The majority (61.9%) of baboon kills appear to have been made during the day. However, this figure may be as high as 85.7%, as kills made between 04:00 and 08:00, and between 16:00 and 20:00 may also have occurred during daylight hours. The percentage of baboons killed during the day was unusually high in comparison to other prey (see Figure 5-7), but there was no significant difference in the time of day at which baboon kills took place relative to other prey ($D=0.33$, $p>0.10$).

CHAPTER 5: LEOPARD DIET

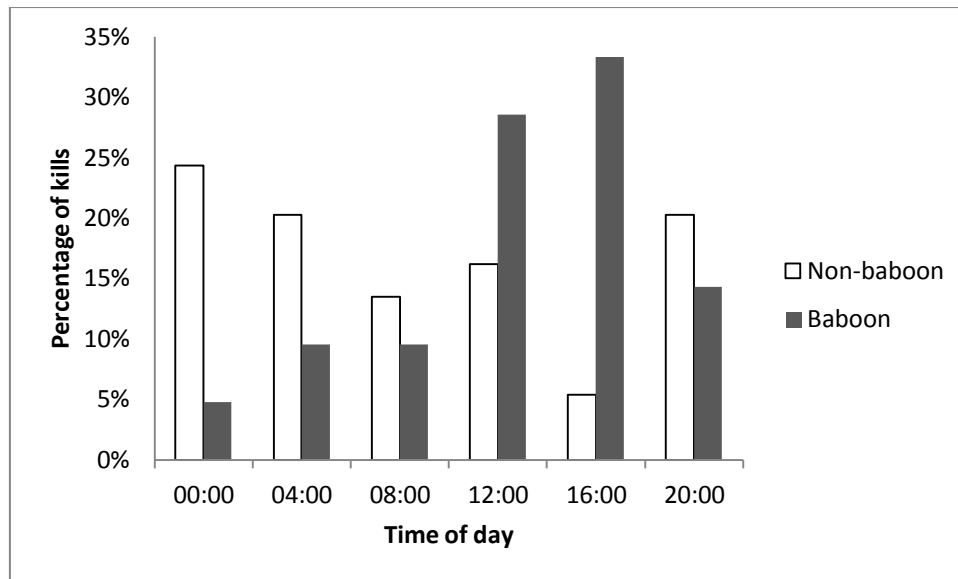


Figure 5-7. Comparison of the timing of kills of baboons (n=21) to kills of other species (n=74) by three collared leopards.

The average biomass of prey killed by leopard GM1 was 67.6 kg. GM2's prey had an average biomass of 90.7 kg, while GM9's prey had an average biomass of 48.8 kg. These differences in average prey size were not significant (One-way ANOVA, $F_{(2,30)}=0.65$ $p=0.528$). Leopard GM2 had the longest average period in between kills of the three leopards, (see Table 5-3), but also killed the greatest average biomass of prey per day (8.3 kg/day). The other two leopards, GM1 and GM9 averaged 6.4 and 6.8 kg of prey killed per day, respectively. This suggests that although GM2 tended to make kills less frequently than the other two leopards he generally killed larger prey items.

5.4.3 Prey abundances and preference

Relative abundances of prey species were calculated based on 103 camera traps set within areas classified as leopard habitat within the study area. Jacobs' index values for prey remains found in scats were negative for all species except rock hyrax, suggesting that all other large prey species were taken at lower rates than would be expected based on their relative abundance (see Figure 5-8). Nevertheless, the negative scores for goats, kudu, klipspringer, eland and donkeys are sufficiently close to zero to assume that these species are not being avoided. Hayward et al. (2006) defined Jacobs' index scores of -0.5 and lower as representing definite avoidance of a particular prey species. Many of the species with Jacobs' index scores below this threshold, such as gemsbok,

CHAPTER 5: LEOPARD DIET

bushpigs, baboons, porcupines, black-backed jackals, caracals, honey badgers and Cape mountain zebras have been identified as posing a potential threat to leopards (Hayward et al. 2006). Of the prey species that were not avoided, only kudu and eland are thought to be potentially dangerous to leopards. However, the assessment of Hayward et al. (2006) did not include donkeys, which are also likely to pose a substantial risk of injury to a leopard.

Many of the species that were not preyed upon appeared to only occur at low densities within the study area (see Table 5-5). Of the 28 large species for which no leopard depredation was documented in this study, 19 had a relative abundance of less than one percent, suggesting that they are rarely found in leopard habitat. The cumulative relative abundance of these 19 species was 4.78%.

The relative abundances of prey species were calculated using data obtained from 44 camera traps set within 95% home range kernels of the territories of the three collared leopards (see Table 5-6). Jacobs' index values based on kill site analysis showed slight preferences for cattle, ostriches, springbok, grey rhebok and bontebok (see Figure 5-9). However, of these species, only cattle were actually recorded by camera traps in the area, and even these had a very low relative abundance (0.3%). Donkeys had a slightly negative Jacobs' index score, suggesting that they are preyed upon in almost direct proportion to their abundance, although their overall relative abundance was low (1.6%). Given these low relative abundances, it is to be expected that Jacobs' index scores for these species are too low to show any definite preference.

CHAPTER 5: LEOPARD DIET

Table 5-5. Summary of the relative abundance indices (RAI) of prey species throughout leopard habitat areas in the Little Karoo. Jacobs' indices were calculated for each species based on the corrected frequency of occurrence (CFO) of species in 76 scats collected in the area.

Species	Photos	RA	Scat CFO	Jacobs Index
baboon	715	19.0	9.7	-0.66
Cape porcupine	460	12.2	3.5	-0.79
common duiker	267	7.1	7.2	-0.46
black-backed jackal	184	4.9	0.0	-1.00
rock hyrax	174	4.6	21.6	0.03
cattle	168	4.5	3.0	-0.59
small grey mongoose	146	3.9	1.5	-0.72
leopard	145	3.8	0.0	-1.00
kudu	141	3.7	14.6	-0.07
caracal	113	3.0	0.0	-1.00
grysbok	113	3.0	0.0	-1.00
African wild cat	107	2.8	0.0	-1.00
eland	94	2.5	8.2	-0.16
gemsbok	89	2.4	2.2	-0.50
large-spotted genet	85	2.3	0.0	-1.00
Cape/scrub hare	81	2.1	3.7	-0.34
klipspringer	73	1.9	7.4	-0.14
aardvark	69	1.8	0.0	-1.00
bushpig	58	1.5	0.7	-0.67
honey badger	54	1.4	0.0	-1.00
Cape mountain zebra	51	1.4	0.0	-1.00
goat	49	1.3	9.4	-0.03
aardwolf	47	1.2	0.5	-0.72
donkey	37	1.0	3.5	-0.19
steenbok	34	0.9	0.0	-1.00
small-spotted genet	25	0.7	0.0	-1.00
waterbuck	24	0.6	0.0	-1.00
black wildebeest	21	0.6	0.7	-0.42
grey rhebok	20	0.5	1.5	-0.25
nyala	19	0.5	0.5	-0.50
giraffe	13	0.3	0.0	-1.00
cat (domestic)	10	0.3	0.0	-1.00
mountain reedbuck	10	0.3	0.0	-1.00
plains zebra	9	0.2	0.0	-1.00
water mongoose	9	0.2	0.0	-1.00
Hewitt's red rock rabbit	9	0.2	0.5	-0.32
red hartebeest	8	0.2	0.0	-1.00
striped polecat	8	0.2	0.0	-1.00
ostrich	6	0.2	0.0	-1.00
vervet monkey	6	0.2	0.0	-1.00
red lechwe	5	0.1	0.0	-1.00
yellow mongoose	5	0.1	0.0	-1.00

CHAPTER 5: LEOPARD DIET

Species	Photos	RA	Scat CFO	Jacobs Index
African clawless otter	2	0.1	0.0	-1.00
impala	2	0.1	0.0	-1.00
springbok	2	0.1	0.0	-1.00
African striped weasel	1	0.0	0.0	-1.00
bat-eared fox	1	0.0	0.0	-1.00

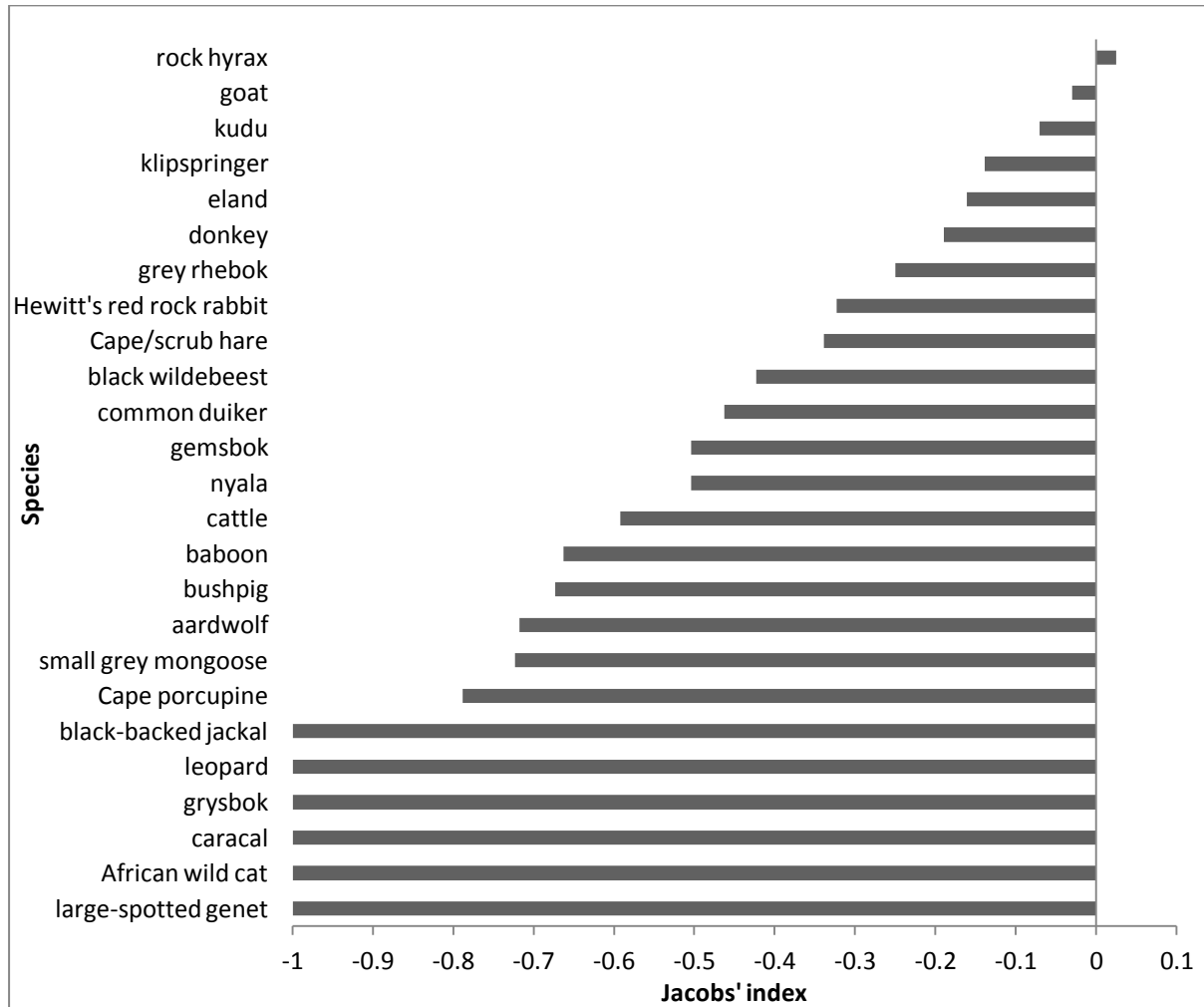


Figure 5-8. Jacobs' index scores for potential leopard prey species in the Little Karoo, based on corrected frequency of occurrence of prey items in leopard scats and the relative abundance of these prey species within areas of leopard habitat. Scores of less than -0.5 indicate that leopards avoid preying on those species. Species with very low relative abundances (<1%) are not shown; these accounted for 249 of the 3769 photos recorded (6.6%) and contained four prey species identified from scats, all of which had low corrected frequencies of occurrence; Hewitt's red rock rabbit (0.04%), nyala (0.04%), grey rhebok (1.3%) and black wildebeest (0.07%).

CHAPTER 5: LEOPARD DIET

Table 5-6. Summary of relative abundance indices (RAI) of prey species recorded within the 95% kernel home ranges of three collared male leopards. The total number of photographs is shown in brackets below the RAI. Photographs were recorded at 17 sites in GM1's territory, 15 sites in GM2's territory, and 13 sites in GM9's territory. Kills shows the percentage of successfully located kills of each prey species, and the total number of kills is shown in brackets below. Jacobs' index scores for each prey species are also shown.

Species	GM1			GM2			GM9			Total		
	RAI (n=291)	Kills (%) (n=22)	Jacobs' index	RAI (n=369)	Kills (%) (n=49)	Jacobs' index	RAI (n=379)	Kills (%) (n=21)	Jacobs' index	RAI (n=1039)	Kills (%) (n=92)	Jacobs' index
baboon	25.2	13.6	-0.66	23.0	22.4	-0.43	20.8	33.3	-0.18	23.1	23.9	-0.40
Cape porcupine	12.3	0.0	-1.00	12.5	6.1	-0.67	11.3	0.0	-1.00	12.0	3.3	-0.80
eland	0.0	4.5	0.05	6.0	16.3	-0.13	20.8	0.0	-1.00	11.4	9.8	-0.50
common duiker	11.3	4.5	-0.72	9.2	12.2	-0.36	6.9	19.0	-0.10	9.9	10.9	-0.42
caracal	12.3	0.0	-1.00	5.4	0.0	-1.00	4.7	0.0	-1.00	6.7	0.0	-1.00
gemsbok	1.7	0.0	-1.00	12.7	0.0	-1.00	0.0	0.0	-1.00	5.9	0.0	-1.00
grysbok	4.3	4.5	-0.47	6.0	2.0	-0.75	5.5	4.8	-0.52	4.2	3.3	-0.55
aardvark	2.7	0.0	-1.00	7.3	2.0	-0.79	0.5	4.8	-0.05	4.1	2.2	-0.65
Cape mountain zebra	7.0	0.0	-1.00	2.7	0.0	-1.00	0.0	0.0	-1.00	3.5	0.0	-1.00
kudu	3.3	0.0	-1.00	3.8	4.1	-0.46	2.1	4.8	-0.27	3.3	3.3	-0.49
goat	0.0	22.7	0.23	0.0	6.1	0.06	6.9	0.0	-1.00	2.9	8.7	-0.18
klipspringer	5.3	18.2	-0.07	2.2	2.0	-0.51	1.1	4.8	-0.14	2.7	6.5	-0.24
steenbok	6.0	0.0	-1.00	0.5	0.0	-1.00	3.4	0.0	-1.00	2.3	0.0	-1.00
waterbuck	0.0	0.0	-1.00	0.0	0.0	-1.00	5.3	0.0	-1.00	2.3	0.0	-1.00
leopard	6.0	4.5	-0.34	0.8	0.0	-1.00	4.5	0.0	-1.00	1.7	1.1	-0.61
donkey	2.3	9.1	-0.13	0.0	18.4	0.18	2.1	0.0	-1.00	1.6	12.0	0.00
bushpig	0.3	0.0	-1.00	1.6	0.0	-1.00	0.3	0.0	-1.00	0.8	0.0	-1.00
plains zebra	0.0	0.0	-1.00	0.0	0.0	-1.00	1.8	0.0	-1.00	0.8	0.0	-1.00
red hartebeest	0.0	0.0	-1.00	0.5	2.0	-0.19	1.1	0.0	-1.00	0.7	1.1	-0.38
cattle	0.0	9.1	0.09	0.0	2.0	0.02	0.8	19.0	0.15	0.3	7.6	0.03
ostrich	0.0	9.1	0.09	0.0	0.0	-1.00	0.0	4.8	0.05	0.0	3.3	0.03
bontebok	0.0	0.0	-1.00	0.0	2.0	0.02	0.0	0.0	-1.00	0.0	1.1	0.01
grey rhebok	0.0	0.0	-1.00	0.0	2.0	0.02	0.0	0.0	-1.00	0.0	1.1	0.01
springbok	0.0	0.0	-1.00	0.0	0.0	-1.00	0.0	4.8	0.05	0.0	1.1	0.01

CHAPTER 5: LEOPARD DIET

Most of the prey species seemingly avoided by leopards were potentially dangerous; these included porcupines, other leopards, caracal, Cape mountain zebra, waterbuck, plains zebra, gemsbok and bushpig. Low relative abundances were also common amongst the avoided species; only gemsbok (5.9%) caracals (6.4%) and porcupines (15.2%) had relative abundance scores of over five percent.

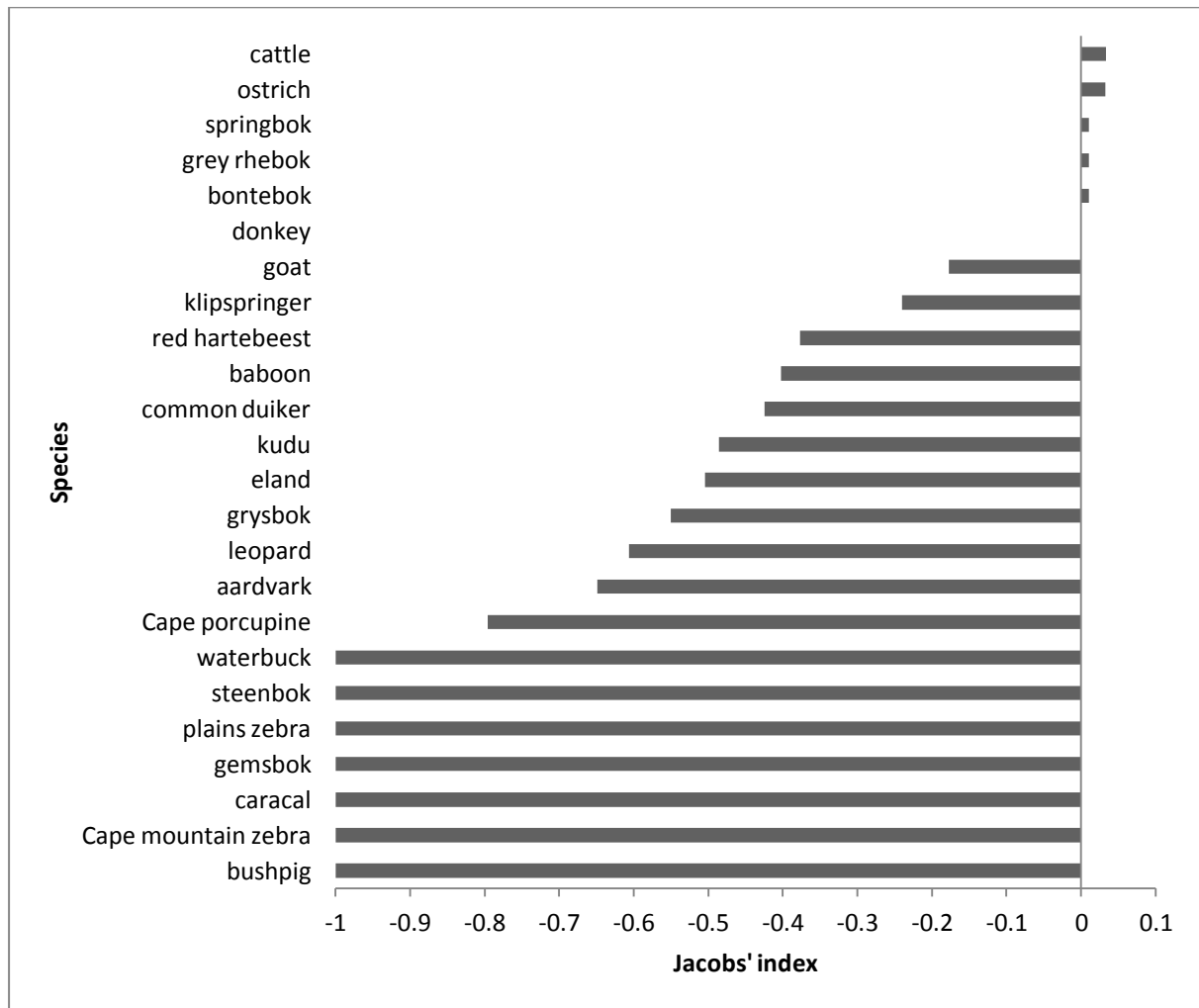


Figure 5-9. Jacobs' index scores for leopard prey based on remains found at kills made by three male leopards. Relative abundances were calculated using camera traps set within the territories of the three male leopards. Species weighing less than 9 kg were excluded from this analysis due to the difficulties of locating kills of relatively small prey species.

5.4.4 Similarity of kill site and scat data

Bray-Curtis compositional similarity analysis calculated a 49.75% similarity between the prey abundances found using scat analysis and kill sites to determine diet composition. When small species weighing less than 10 kg were excluded from the scat samples, compositional similarity between scat and kill site samples rose to 62.39%.

CHAPTER 5: LEOPARD DIET

SIMPER analysis showed high levels of dissimilarity (93.98%) between kill site and scat sample data. The highest contributors to this dissimilarity were baboons (13.68%) and rock hyrax (10.93%), while kudu, common duikers, goats and eland and donkeys all contributed to approximately eight percent of total dissimilarity. Excluding smaller species did not substantially increase similarity according to SIMPER analysis, as average dissimilarity between scat and kill samples remained high at 93.47%. Baboons (18.30%), common duiker (11.28%), eland (10.20%) and goat (10.07%) were the major contributors to this dissimilarity.

The results obtained by Rautenbach (2010), which were based on scat analysis, showed strong dissimilarities to scat (88.65% dissimilarity) data collected during my study. Rock hyrax and klipspringers accounted for a large portion (33.12%) of the overall dissimilarity due to their greater abundance in samples obtained by Rautenbach (2010). The data used by Norton et al. (1986) were not available for a similar comparison.

There were high levels of dissimilarity between the diets of the three collared leopards, ranging from 89.31% (between GM2 and GM9) and 94.29% (GM1 and GM2). GM1 preyed upon goats and klipspringers more frequently than the other two leopards (see Table 5-7). This contributed substantially to the high dissimilarity observed between the species killed by GM1 and the other two leopards. Baboons were an important prey species for all three individuals. The average probability of finding a baboon kill was 0.22 at GM1 and GM2's kill sites and 0.33 for GM9. GM9 also killed cattle and common duiker more frequently than the other two leopards. Although baboons were the prey species most frequently killed by GM2, this leopard also often preyed upon donkeys and eland, which were seldom killed by the other two individuals (see Table 5-7).

CHAPTER 5: LEOPARD DIET

Table 5-7. Main prey species (average abundance >0.1) of the three collared leopards. Average abundance shows the number of each prey species found per kill site for each individual, while the contribution to dissimilarity shows the proportion of all dissimilarity found by SIMPER analysis that was due to differences in the abundance of that particular prey species.

Leopard	Prey species	Average abundance/kill	Contribution to dissimilarity		
			GM1	GM2	GM9
GM1	Goat	0.28	-	16.11	15.07
	Klipspringer	0.22	-	12.36	13.44
	Baboon	0.22	-	17.98	22.44
GM2	Baboon	0.22	17.98	-	22.85
	Donkey	0.18	9.56	-	10.28
	Eland	0.16	8.50	-	9.14
	common duiker	0.12	6.37	-	14.91
GM9	Baboon	0.33	22.44	22.85	-
	Cattle	0.19	12.01	11.37	-
	common duiker	0.19	10.14	14.91	-

Further differences between individuals were apparent when comparing the Jacobs' indices between individuals (see Figure 5-10). While all three individuals showed a preference for domestic prey species such as goats and cattle, there were substantial differences in preference for some wild prey species. For example, two of the most abundant prey species, baboons and common duikers, were killed in almost direct proportion to their relative abundance by GM9, but were avoided by GM1 and GM2. However, GM9 avoided preying on eland, which were regularly killed by GM1 and GM2.

CHAPTER 5: LEOPARD DIET

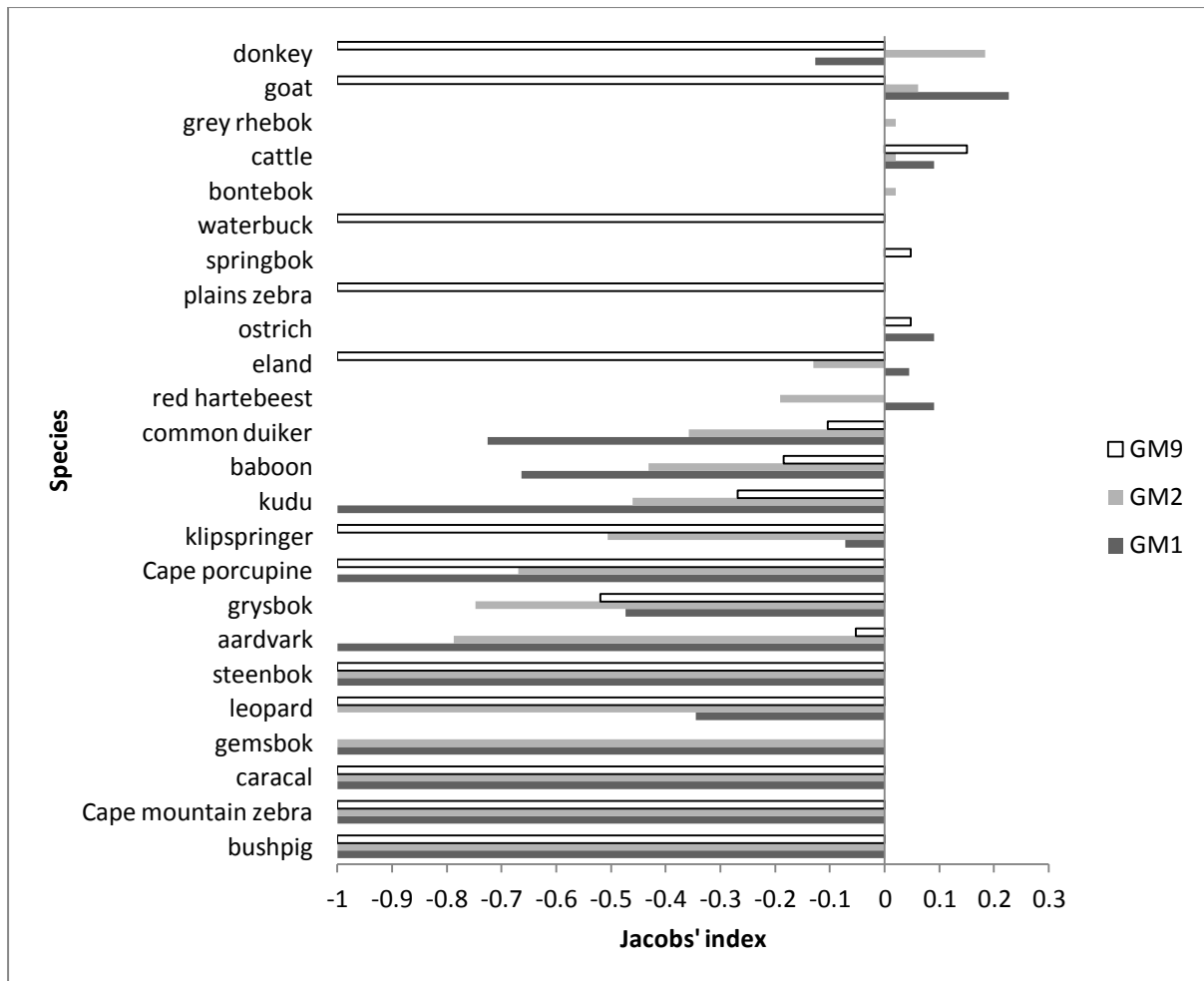


Figure 5-10. Comparison of Jacobs' index values for prey species based on kills made by each of the three collared male leopards and the relative abundance of prey within a 95% kernel home range of each leopard. The absence of a bar for a species indicates that it was not recorded within the home range of that leopard.

CHAPTER 5: LEOPARD DIET

5.5 Discussion

Leopards are generalist predators in the Little Karoo, which is an area with relatively low prey abundance. While leopards have long been considered to be opportunistic predators with a catholic diet (Bailey 1993; Estes 2012), more recent research has suggested that leopards do exhibit some selectivity, actively targeting medium-sized ungulates (Hayward et al. 2006). In an area where prey of this type is relatively scarce, it is likely that leopards will exhibit greater opportunism and hunt a broader range of prey. Previous studies have shown that leopard diet can shift towards smaller prey in the absence of a sufficient prey base within the preferred size range (Henschel et al. 2005; Ott et al. 2007; Aryal & Kreigenhofer 2009). However, the absence of preferred sized prey species may also result in increased predation on livestock and domestic animals (Mizutani 1999; Edgaonkar & Chellam 2002; Anwar et al. 2011). The results of my study show evidence of both of these trends, as leopards preyed heavily upon smaller species, such as rock hyrax, but were highly opportunistic hunters of livestock. Furthermore, leopards regularly preyed upon relatively large prey that exceeded the threshold of 40 kg which Hayward et al. (2006) considered to be the upper limit of the preferred prey of leopards.

Rock hyraxes were the species most frequently found in scat samples, a similar trend to that observed in previous studies in the Little Karoo (Norton et al. 1986; Rautenbach 2010). The abundance of rock hyrax in scat samples in my study was substantially lower than that observed by Rautenbach (2010), which was in turn lower than that found by Norton (1986). Rautenbach (2010) suggested that leopards in the Gamkaberg may have undergone a dietary shift towards small mammals, which reduced their reliance on rock hyrax, the predominant prey species found by Norton (1986). As the only species to have a positive Jacobs' Index score based on my scat analysis data, would seem that rock hyraxes remain a favoured prey species for leopards in the Little Karoo. Reduced reliance on rock hyraxes may therefore reflect reduced availability of this prey species rather than a change in the dietary preferences of leopards in the area. One possible explanation for this may be a decline in the rock hyrax population due to pulmonary infection, which has been

CHAPTER 5: LEOPARD DIET

reported elsewhere in the Western Cape (Parsons et al. 2008). However, no assessment has been done of potential infection rates in the Little Karoo, and in the absence of sustained monitoring of the rock hyrax population, one can only speculate as to whether there has been any genuine decline in the Little Karoo rock hyrax population.

In contrast to the findings of Rautenbach (2010), the results of my study suggest a shift in the opposite direction; that leopards in the Little Karoo may be increasingly reliant upon larger prey species, a finding common to both methods of dietary analysis employed in this study. These larger prey species exceed the preferred prey range of leopards, which is thought to be between 10 and 40 kg (Hayward et al. 2006). One potential explanation for this trend is that large prey has become more available in the area due to the establishment of several game farms within my study area, with subsequent introductions of large game such as eland, kudu and red hartebeest (*Alcelaphus buselaphus camaa*).

The introduction of carnivores into a system in which ungulates are established has been shown to have major impacts on ungulate populations, both in terms of demographics and behaviour (Ripple & Beschta 2004; White & Garrott 2005; Gorini et al. 2012). African ungulates have been shown to increase vigilance behaviour over time when subjected to predation pressure, but ungulates in areas without predators show low levels of vigilance (Hunter & Skinner 1998). It is thus likely that game species introduced into the Little Karoo may be predator-naïve, particularly if they originate from an area from which predators have been extirpated. This would increase their vulnerability to leopard predation, which may enable leopards to hunt larger prey species than would otherwise be possible (Gorini et al. 2012). As leopards are cryptic, and predation rates are relatively low compared to savannah systems with a full suite of large predators, vigilance levels amongst large ungulates may have remained low, facilitating continued leopard predation.

Although increased abundance of large game species may explain the shift to larger prey in the period between the study done by Norton et al. (1986) and this study, most of the game farms in the

CHAPTER 5: LEOPARD DIET

area were well-established in 2008, when samples were collected by Rautenbach (2010). Although there was extensive spatial overlap between the samples analysed by Rautenbach (2010) and my study, I collected more scats from the western side of the study area in an area dominated by game farms (see Figure 5-1). Notwithstanding the large home ranges typical of leopards in the Little Karoo, this almost certainly increased the likelihood of finding scats containing remains of large game species killed in the area.

The trend of greater reliance on large prey becomes particularly apparent when biomass, rather than number of prey items consumed, is considered. Previous studies in the Little Karoo did not record predation on any species weighing in excess of 40 kg (Norton et al. 1986; Rautenbach 2010), but these larger prey species accounted for almost one quarter of all prey items identified from the scats analysed during my study. Furthermore, the average biomass of prey killed by each of the three collared leopards exceeded 40 kg. While this may be due to a genuine shift in leopard diet, it is also likely that the differences between the areas in which scats were collected on a local scale may have contributed to this finding.

The total number of prey species found in scat samples in my study (21) is comparable to that found by Rautenbach (2010), who identified 22 prey species, but much higher than Norton et al. (1986) who only identified seven prey species. The low number of prey species identified by Norton et al. (1986) falls well below the species accumulation curves based on subsequent studies in the area (Rautenbach 2010, present study). The ICE means obtained by my study (24.33) and Rautenbach (2010) (24.8) are consistent. My study found a total of six species at kill sites that were not present in any scats, which increased the total number of prey species found to 27, higher than the ICE estimate. Of these, only aardvark ($n=2$), grysbok ($n=3$) and ostrich ($n=3$) were present at more than one kill site, suggesting that the other species (bontebok, red hartebeest and springbok) are probably seldom killed by leopards in the Little Karoo. The ICE mean of between 24 and 25 species would thus appear to be a reasonable estimate of the number of leopard prey species in my study

CHAPTER 5: LEOPARD DIET

area. It is unlikely that any of the species that were not sampled accounted for more than five percent of the leopard's overall diet (following Trites & Joy 2005). This finding lends further weight to the argument that the differences in results between this study and that of Rautenbach (2010) may be due to sampling locations, although observer bias in identifying hair samples from scats may also have influenced results (Verma et al. 2002). It is also possible that the scat samples collected during my study were biased towards male leopards, which tend to make greater use of the pathways and trails where the vast majority of my samples were opportunistically collected. When applied to jaguars (*Panthera onca*) similar scat collection methods resulted in a sample comprising over 80% male scats (Palomares et al. 2012). However, similarly opportunistic sampling was employed in the previous studies in the Little Karoo (Norton et al. 1986; Rautenbach 2010), and it is thus likely that the bias towards males has remained relatively constant across the different studies.

Analysis of kill sites provides strong corroborative evidence of the importance of larger prey species in the diet of leopards in the Little Karoo. Although this method is inherently biased towards larger prey (Ackerman et al. 1984; Martins et al. 2011; Pitman et al. 2012), the sheer number of large prey items found at kill sites demonstrates the importance of these larger species to the collared leopards. Leopards are thought to require between 1.6 and 4.9 kg of meat per day to maintain their body mass (Bothma & Le Riche 1984; Bailey 1993; Stander et al. 1997; Hayward et al. 2006). The three collared leopards in this study killed an average of 7.18 kg (± 1.01 kg) of prey per day, well above this threshold. The biomass of prey killed does not necessarily equate to the biomass of prey eaten, particularly as larger prey items contain a higher percentage of indigestible material (large bones, etc.). Nevertheless, even if the collared leopards only consumed half of the total biomass of their prey, they would still be meeting their nutritional requirements from these large prey species alone. Leopards in the Little Karoo can maximise the amount of biomass consumed from prey without interference as there are no competing predators or scavengers capable of chasing leopards off their kills, which has been shown to reduce leopard feeding efficiency elsewhere (Bailey 1993). Leopards have also been recorded shifting their diet towards smaller prey in response to an increase

CHAPTER 5: LEOPARD DIET

in the local tiger (*Panthera tigris*) population (Harihar et al. 2011). Lack of intra-guild competition may thus contribute to the extensive depredation of large prey observed in this study (Linnell & Strand 2000).

There were high levels of dissimilarity between the diets of the individual leopards. Such high dissimilarity is somewhat unexpected, given they were all adult males with adjoining territories. This implies that extrapolations of these results to make broad generalizations about leopard diet throughout my study area should be treated with caution. Furthermore, it is likely that the diet of female and sub-adult leopards is based upon smaller prey species than those typically utilised by males (Bailey 1993). The observed dissimilarity between male leopard diet in this study is most likely to be due to the relative availability of prey within the territory of each leopard (Shehzad et al. 2012). For example, donkeys were an important part of leopard GM2's diet. GM2's territory included communal lands south of the settlement of Zoar, where there is a large feral donkey population (pers. obs.). While feral donkeys were occasionally present in other areas, they appeared to be at far lower densities, hence there was less chance of the other individuals encountering them. GM2 also preyed heavily on eland. While all three collared leopards moved through game farms on which eland were present, approximately 30 eland escaped from a local game farm and appeared to remain within GM2's territory. These eland were not recaptured, and several of them were killed by GM2. Both GM2 and GM1 killed eland in approximate proportion to their relative abundance, while GM9 appeared to avoid them. This trend appeared unrelated to the size of prey; GM9 appeared to prefer kudu to a far greater extent than GM1 and GM2, while the three individuals showed marked differences in preference for common duiker, which were fairly common throughout the study area. Despite being by far the largest of the three individuals, GM1 frequently preyed upon klipspringer, one of the smaller ungulates present in the study area. However, the relative abundance of klipspringer was far higher within GM1's territory than that of the other two individuals (see Table 5-6). These results suggest that spatial variations in prey abundance have a strong effect on the diet of individual leopards, particularly when overall prey abundances are low.

CHAPTER 5: LEOPARD DIET

Hayward et al. (2006) hypothesised that leopards may avoid prey species that have the ability to inflict significant injury, as these can be potentially fatal to solitary predators. This hypothesis may explain the observed avoidance of species such as porcupines, which had one of the highest relative abundances within the study area, but also have a well-developed defence mechanism. Other dangerous prey species that were avoided included the two zebra species, neither of which had a very high relative abundance within the study area and may reflect their preference for more open terrain. Zebras are also known to harass potential predators through kicking and biting (Berger 1979), and are therefore likely to represent formidable prey for a solitary predator such as a leopard. Most of the less threatening prey species that were avoided (aardvark, steenbok, bushpig, grysbok and caracal) had relatively low abundances within the territories of the collared leopards. As these species are usually killed in proportion to their abundance (Hayward et al. 2006), the avoidance recorded in my study is more likely to be due to the low abundance of these species within the study area than any genuine avoidance behaviour by leopards. Grysbok and caracal are an exception to this, as Hayward et al. (2006) found that they were strongly avoided by leopards. This may be due to crypsis or an effective predator evasion technique that is currently undocumented (Hayward et al. 2006).

Baboons were the only prey species that comprised over 10% of the kills of all three individual leopards. Baboons are highly adaptable generalists, and had the highest relative abundance of the large prey species in the study area, both overall and within the territories of each collared leopard. Leopards were found to be the most frequent predators of baboons in the Kruger National Park (Pienaar 1969), but subsequent research has suggested that leopards only prey upon primates when other prey is scarce (Seidensticker 1983; Hayward et al. 2006). In the Western Cape, where leopards occur at low densities and prey is thought to be relatively scarce, previous studies have shown that leopards tend to avoid preying on baboons, despite baboons being one of the more abundant potential prey species (Rautenbach 2010; Brackowski et al. 2012). Other studies in the Western Cape have noted relatively low predation on baboons, which have been assumed to be amongst the

CHAPTER 5: LEOPARD DIET

most abundant of potential prey species (Norton et al. 1986; Ott et al. 2007; Martins et al. 2011). Baboons are group-living, and male baboons have large canines that can severely injure, or even kill leopards (Cowlshaw 1994). Cowlshaw (1994) found that male baboons retaliating to leopard attacks killed the leopard involved in four of 11 occasions. The risks involved in hunting baboons are thus significant.

Leopards can mitigate these risks by hunting baboons at night, or in dense cover where visibility is reduced (Cowlshaw 1994). Leopards in the Little Karoo appear to have adopted the latter strategy, as the majority of baboon kills seem to have occurred during daytime, as inferred from the time that the first points of GPS clusters at baboon kills were recorded (following Jooste et al. 2012). While it was seldom possible to determine exactly where a kill had occurred due to the lengthy delay in investigating many kill sites, 77% of baboon carcasses were found in thicket or dense riverine vegetation, which would have offered cover and potential refuge to the leopard. The remaining kills were found in drainage lines in fynbos vegetation, which would also have provided more opportunity for both ambushing baboons and escaping potential retaliation. However, these inferences remain speculative, as the baboon carcasses could easily have been dragged to these locations. Leopards also seemed to mitigate injury risk by targeting female and juvenile baboons. One of the four male carcasses was found at the same site as a juvenile baboon carcass, suggesting either an unsuccessful attempt at retaliation against the leopard or that the male was ambushed while he was carrying the juvenile, and thus in a more vulnerable state.

These findings are in stark contrast to those of Cowlshaw (1994), who found that leopards showed a clear preference for male baboons. However, the study by Cowlshaw (1994) was largely based upon data from a baboon population that slept predominantly in trees and they may thus have been more vulnerable to nocturnal depredation than baboons in this study which slept almost exclusively on cliffs (pers. obs.). Baboons in my study area are thus likely to be most vulnerable during the day when they are foraging in areas without access to cliff refuges. Jooste et al. (2012) recorded similarly

CHAPTER 5: LEOPARD DIET

high levels of daytime baboon predation by leopards in the Waterberg Mountains in northern South Africa, but did not find any evidence of preference for either sex. It has been suggested that leopards can learn hunting strategies to successfully prey upon certain species (Bothma & Walker 1999; Jooste et al. 2012), and while the frequent predation on baboons by all three collared leopards would suggest that this behaviour may be widespread, a larger sample size would be required to confirm this.

The use of camera-trap based relative abundance indices is acknowledged as a weakness of this study. Accurate calculation of relative abundance assumes that all species are equally detectable, or that any differences in detectability between species has been taken into account (Buckland et al. 2001). Other studies have used line transects or aerial game counts to estimate prey densities (Karanth & Sunquist 1995; Karanth et al. 2004; Balme et al. 2007; Klare et al. 2010), and it has been suggested that one of these methods be used to provide an index against which relative abundance indices derived from camera traps can be suitably adjusted (Carbone et al. 2001, 2002). The low densities of prey species in the Little Karoo, as well as difficult terrain and differences in detection probability between different habitat types made formulating independent estimates of prey species densities difficult.

A number of studies have found substantial variation in camera trap detection probability between species (Weckel et al. 2006; Larrucea et al. 2007; Harmsen et al. 2010b; Sollmann et al. 2013). A framework has been developed to allow the estimation of densities for species in which the identification of individuals is not possible, but this requires totally random camera placement (Rowcliffe et al. 2008). This could not be accommodated in the camera survey design used in my study, and would probably have resulted in extremely low numbers of photographs being recorded as I expected animal movement to be biased towards paths. The relative abundance and prey preferences calculated should thus be treated with some caution.

CHAPTER 5: LEOPARD DIET

However, detection probability does show a general increase with abundance (McCarthy et al. 2012). Furthermore, the camera trap survey design specifically sought to avoid bias towards roads by placing the majority of cameras on game trails or along drainage lines or other natural ‘funnels’ (*sensu* Harmsen et al. 2010). Roads are often associated with skewed detection probabilities, and placing cameras away from roads is likely to have reduced differences in detectability for some species (Weckel et al. 2006; Harmsen et al. 2010b; Sollmann et al. 2013). All kill sites investigated in this study were from male leopards, and it is likely that the majority of the scats collected were also of male leopard origin. As male leopards in the Little Karoo tend to use roads and trails far more than females (see Chapter 4), it is likely that their relative foraging effort was also greater around these more obvious pathways through the landscape. Prey species that were frequently detected by camera traps set up along these pathways were thus more likely to encounter male leopards, which would in turn increase predation risk (Gorini et al. 2012), and consequently, the probability of remains being detected at a kill site or in a scat sample.

My results suggest that small prey species make a minor contribution to the total biomass consumed by leopards in the Little Karoo. Similar results have been reported in the Cederberg Mountains, where small prey contributed less than one percent of biomass consumed, despite being present in over 20% of analysed scats (Martins et al. 2011). Inclusion of smaller prey species obtained from lion (*Panthera leo*) scats also did not significantly alter lion diet composition estimates derived from kill sites (Tambling et al. 2012). Kill site analysis may thus represent a more reliable means of estimating leopard diet composition than scat analysis, as it appears to yield results that are more representative of overall biomass intake by collared individuals. Furthermore, prey remains at kill sites are usually fairly easy to identify, and are thus likely to be less prone to observer bias and consequent misidentification than hair samples in scats. However, implementation of this method requires the capture and collaring of sufficient individuals to yield a reasonable sample size, an extremely challenging and expensive proposition in areas with low leopard population density, such as the Little Karoo. Kill site analysis was somewhat hampered by my inability to regularly obtain data

CHAPTER 5: LEOPARD DIET

from collared leopards, resulting in lengthy delays (of up to almost two years) before some kill sites could be investigated. However, the absence of large scavengers such as brown hyaenas (*Parahyaena brunnea*) from my study area meant that carcasses remained largely intact, which aided kill location and identification. Kill site analysis may prove less effective in areas where large scavengers are present, particularly if kills cannot be investigated promptly.

In contrast, scat analysis is non-invasive, and offers a far more economical means of estimating diet composition. All scat analyses of leopards in the Little Karoo have been based upon relatively small numbers of scat samples, ranging from 59 (Norton et al. 1986) to 77 (Rautenbach 2010). A larger sample of scats may have provided a diet estimate more similar to that generated from kill site analysis. Scat-based dietary studies are often biased towards smaller prey species, particularly if no correction factor is applied to account for differences in body mass (Weaver 1993; Karanth & Sunquist 1995; Klare et al. 2011; Tambling et al. 2012). In contrast, using kill sites as the sole means of determining diet composition is likely to result in a bias towards larger prey species as the brief time taken to consume small precludes their detection using GPS clusters (Anderson & Lindzey 2003; Sand et al. 2005; Tambling et al. 2012; Pitman et al. 2012). The contrasting results obtained using these two methods in my study suggests that they should be viewed as complementary as together they provide a more robust estimate of leopard diet.

CHAPTER 5: LEOPARD DIET

5.6 Conclusion

The results of my study suggest that leopard diet largely reflects prey abundance, with most prey species killed in proportion to their local abundance. Estimates of leopard diet based on both scat and kill site data from the same region differed markedly. These results are largely expected given that scat analyses typically under represent large prey species while kill site data is generally incapable of detecting smaller species consumed. As such, dietary studies on elusive carnivores will benefit from a combination of both approaches. Intraspecific comparisons using kill site data revealed marked differences in diet suggesting that individual leopard diet may be influenced by prey availability at local scales or varying prey preferences of individuals. This has ramifications for future dietary studies based on scat analysis, as spatial heterogeneity in prey availability may result in misleading conclusions if the results are applied to a broader study area. Scat sampling thus needs to be done systematically over a broad area, covering the territories of several leopards, to ensure that results are not biased by the dietary preferences of one or two leopards. This is less of a problem for kill site data, as the number and sex of sampled individuals is known, and associated biases can be taken into account. However, scat analysis tends to focus more on the number of scats collected rather than the spatial distribution of those scats, and any potential bias caused by uneven sampling. Similarly, analyses based on kill-site location should aim to track a large number of individuals to ensure a more representative sample of prey species.

CHAPTER 5: LEOPARD DIET

5.8 Appendix 5A - Trapping and collaring of leopards

All trapping and collaring activities were done with the authorisation of the Rhodes University Ethical Standards Committee (ethical clearance number: ZOOL-02-2010) and CapeNature (Permit number: AAA004005920035). Leopards were caught in walk-through cage traps (2 m x 0.75 m x 0.8 m in size), with a central pressure plate that triggered the release of the cage doors. These were placed on paths which had been identified as being frequently used by leopards (either by camera trapping or spoor). Traps were fitted with a VHF transmitter (Telonics TBT500, Mesa, Arizona, USA) that was triggered when the trap doors closed. Only one leopard (GM9) was captured using this method. A sub-adult male leopard (GM10) was captured in a cage trap, but released without being collared. As sub-adult leopards can disperse large distances (Fattebert et al. 2013), tracking and recapturing the leopard to remove the collar may have been difficult, and automatically triggered collar drop-off devices were deemed unsuitable due to the difficulties of locating and retrieving the collar in the rugged terrain of the Little Karoo mountains. Leopard neck girth tends to increase substantially on adulthood (Balme et al. 2012), and therefore I considered putting a collar on a sub-adult leopard to be unethical, given the high probability that I would not be able to remove the collar before it became excessively tight.

The cage traps proved relatively unsuccessful, recording only two successful captures in 384 trap nights. I used three cage traps in 2010, and two in 2011. All available traps were active each night, and traps were only closed when weather conditions were unsuitable (heavy rain or snow) or when logistical constraints prevented them being checked. On two other occasions, a leopard was captured in the cage trap but managed to escape before a veterinarian could arrive to immobilize the leopard. On the first occasion the veterinarian arrived approximately three hours after the leopard was observed in the trap. The second escape occurred after a substantially lengthier delay (approximately seven hours). Neither escape was observed, as Cape Leopard Trust protocol at the time was to minimize disturbance around the trap until the veterinarian arrived to immobilize the leopard. This protocol was subsequently changed, and trapped leopards were kept under continuous

CHAPTER 5: LEOPARD DIET

observation, albeit from a distance of approximately 100 m to reduce stress. No evidence of injury to the leopard (blood in or around the trap, tooth or claw fragments) was found after either of the escape incidents. Although the identity of the escapee leopard could not be established, it is most likely to have been GM1, particularly as this individual appeared to avoid cage traps after the second incident (based on camera trap photographs recorded close to cage traps that remained undisturbed).

In August and September 2010 I was trained to use foot-loop traps (Frank et al. 2003). These traps make use of a stainless steel cable snare to capture leopards by the foot, and are considered to be more effective and potentially safer than cage traps (Frank et al. 2003; Balme et al. 2007; Jooste et al. 2012; Pitman et al. 2013). Traps were visually monitored at least twice daily, in addition to checks using VHF transmitters (Telonics TBT-500, Mesa, Arizona, USA) attached to the trap. Foot-loop traps were more successful than cage traps, recording five leopard captures in 664 trapping nights. I typically deployed a larger number of foot-loop traps simultaneously in relatively close proximity to one another; in 2010 I had 11 foot-loop traps running simultaneously, although in 2012 I only used a maximum of four traps at once. This inflated the number of trapping nights for foot-loop traps; in terms of the actual number of nights spent trapping, foot-loop traps were far more effective than cage traps.

Triggered traps were investigated immediately and non-target species captured in cage traps were released immediately. Non-target species captured in cage traps included African wild cat (*Felis sylvestris*, n=5), Cape porcupine (n=5), baboon (n=3), aardwolf (*Proteles cristatus*, n=1), caracal (n=1) and grysbok (n=1) No injuries were recorded on either non-target species or leopards caught in the cage traps. No non-target species were captured in the foot-loop snare traps.

Once it was ascertained that a leopard had been caught in the trap, all possible steps were taken to ensure that the area around the trap was kept clear to minimize disturbance to the animal. The trap was visually monitored until a veterinarian arrived with the necessary equipment to sedate the

CHAPTER 5: LEOPARD DIET

leopard. The veterinarian made the decision on whether to proceed with immobilization and collaring of the leopard. All reasonable steps were taken to minimize the amount of time that any animal spends in the trap prior to immobilization and/or release.

All immobilizations were done by a fully qualified veterinarian with experience of working with wildlife. Two veterinarians assisted with the study; in 2010 all immobilizations (n=4) were done by Dr. Glen Carlisle (Oudtshoorn Veterinary Clinic, practice number FCC 02/5572), while Dr. Willem Burger (Dr. Willem Burger Consulting, Wildlife Veterinarian, SA Veterinary Council registration number D90/2995) assisted with captures in 2011 and 2012 (n=3). In this study, leopards were immobilized using a mixture of medetomidine (ORION PHARMA, Espoo, Finland) and ketamine (Anaket-V Bayer Pty Ltd., Isando, South Africa). Zoletil® (Virbac South Africa (Pty) Ltd., Isando, Centurion, South Africa) was used to sedate a leopard on one occasion, the dosage used was 5 mg/kg. The size of the leopard was visually assessed by the veterinarian and a dosage of 70 µg/kg of medetomidine and 3 mg/kg of ketamine was used (Jalanka 1989; Hoogesteijn et al. 1996). Top-ups of the sedating drugs were administered when required (see Table 5-8). The drugs were administered with a CO₂-pressurized dart gun (DAN-INJECT, Aps, Denmark) from a distance of approximately eight metres, and top-up doses were administered with a hand-syringe. All darting and injections were done by the supervising veterinarian.

CHAPTER 5: LEOPARD DIET

Table 5-8. Summary of leopard captures made during this project. Trap type refers to the sort of trap used (cage or footloop trap). Capture time is the time at which the leopard was first observed in the trap, although leopards could realistically have been caught any time in the preceding four hours. Dosage shows the amount of immobilising drugs used to immobilise the leopard, as well as the time and amount of any top-up drugs administered. Time darted and time to recumbancy show the time at which the leopard was darted, and how long it took for the leopard to actually be immobilised. The time of reversal is the time at which Antisedan was administered to counter the effects of the medetomidine to accelerate the leopards' recovery from immobilisation. The exact time until the first walk was only recorded for the first capture of GM9; for subsequent captures it shows the time at which the leopard was found to have left the area in which it had been placed to recover. First walk times should thus be regarded as being accurate to within 10 minutes of actual first walk time.

Leopard	Trap type	Capture time	Dosage	Time darted	Time of recumbancy	Time reversal	First walk
GM9	Cage	07:25	20 mg Meditomidine. 90 mg ketamine	10:32	10:52	11:46	12:30
GM1	Foot-loop	06:30	20 mg Meditomidine. 90 mg ketamine + 80 mg ketamine (at 10:04) + 100 mg ketamine (at 10:30)	09:40	09:55	11:10	11:25
GM9	Foot-loop	06:19	20 mg Meditomidine. 90 mg ketamine	10:28	10:42	11:24	11:40
GM2	Foot-loop	07:15	20 mg Meditomidine. 90 mg ketamine	12:30	12:50	13:20	13:40
GM10	Cage	07:10	100 mg Zoletil	11:15	11:25	NA	14:00
GM10	Foot-loop	07:15	20 mg Meditomidine. 90 mg ketamine	09:20	09:33	10:02	10:20
GM2	Foot-loop	07:05	35 mg Meditomidine. 70 mg ketamine + 15 mg med, 30 mg ketamine (at 09:50)	09:34	09:58	10:14 25 mg antisedan	10:25

CHAPTER 5: LEOPARD DIET

Spray-on antibiotics (such as Cetrigen wound spray (Virbac South Africa (Pty) Ltd, Centurion, South Africa)) were administered to any minor injuries sustained prior to or during the trapping process. One leopard (GM1) had large wounds on his shoulder and back, although a camera trap photograph from two days prior to his capture proved that the shoulder wound pre-dated his capture. I was unaware of this at the time of the capture, and assumed that GM1 had been injured in the trap. The wounds were thus treated and stitched closed by Dr. Glen Carlisle, the veterinarian who supervised the leopard immobilisation.

When the leopard had spent a long period in the trap and become dehydrated, a fluid drip was used to aid rehydration. This was done at the veterinarian's discretion, and was only required on hot days when slow response time on the part of the veterinarian resulted in the leopard only being darted in the late morning or mid-day. Veterinarian response time was a major problem in this study, despite my effort to trap in relatively accessible locations. The nearest veterinarians were based in the town of Outdshoorn, approximately 75 km from the most frequently used trap sites on Groenefontein Nature Reserve. The poor quality of the roads on Groenefontein Nature Reserve itself negatively affected response times (the last seven kilometres to the trap site took approximately 25 minutes to drive), but the major delay usually stemmed from the veterinarians themselves. Veterinarians were seldom able to respond to leopard captures immediately, despite being informed of captures early in the morning before their usual clinic/ consulting hours. Leopard captures were infrequent and unpredictable, and therefore employing a full-time vet to work on the project was not feasible. The delay caused by waiting for veterinarians substantially increased the time that leopards spent in the traps, and is thus likely to have increased both the stress and the risk of injury to captured leopards. Latex gloves were worn by all personnel who handled the leopard during the capture process. Once all the procedures to be carried out during immobilisation had been completed, the veterinarian injected the leopard with a 1.5 ml dose of Antisedan (ORION PHARMA, Espoo, Finland) to accelerate the recovery process by reversing the medetomidine component of the immobilizing drugs. This typically results in the animal being fully recovered within 10 minutes of the Antisedan being

CHAPTER 5: LEOPARD DIET

administered (Jalanka 1989). Exact recovery time was seldom recorded; once the leopard began to show signs of recovery, such as moving limbs and raising its' head, we retreated to vehicles parked between 100 and 200 metres away, out of the leopards view, but within earshot of the capture site. We visually checked the capture site after approximately 15 minutes to see whether the leopard was ambulatory. If the leopard was no longer visible, we assumed that it was ambulatory and left the area.

While the animal was immobilized, the following procedures were carried out:

- The animal was examined for general body condition, injuries, tooth damage and exoparasites (see Figure 5-11).
- Morphometric measurements: weight, head-to-tail length (straight and curved), tail length, chest girth, neck girth, head length, head circumference, shoulder height, paw length and width.
- Age was estimated from tooth wear (after (Stander 1997)
- Samples of tissue (< 8 mm²) were taken from the ear and stored in 70% alcohol. Hair and whisker samples (two from each side of the head) were also collected.
- Physiological data such as body temperature was measured and recorded.
- Photographs were taken of both sides of the face, teeth, body and tail to aid future identification.
- A GPS collar was fitted.

CHAPTER 5: LEOPARD DIET



Figure 5-11. Photographic record of injuries suffered by leopard GM1 prior to capture. The top photograph was taken three days prior to GM1's capture and shows the large wound on his back, which is also shown in the middle picture. The lowest picture shows a smaller gash across the shoulders. Dr. Glen Carlisle is treating the larger back wound, which he stitched up. This accounted for the unusually long handling time of leopard GM1.

Leopards were fitted with VECTRONICS GPS Plus 1 collars (VECTRONICS Aerospace GmbH, Berlin, Germany), with a nominal neck circumference of 45cm. These collars weigh ~350 g and provide an

CHAPTER 5: LEOPARD DIET

average of approximately 1700 GPS fixes (Q. Martins, unpublished data). Leopards were tracked using a vehicle-mounted omni-directional whip antenna and VHF receiver. When the tracking signal from a collar is detected, its position will be identified using a directional four element yagi antenna, linked to a VECTRONICS hand-held receiver. Data were downloaded from the collar using the yagi antenna and VECTRONICS hand-held receiver. The collars were not fitted with drop-off devices, as the extreme conditions and rugged terrain of the study site were likely to result in drop-off devices being damaged and malfunctioning (Q. Martins unpublished data). I thus attempted to recapture all collared leopards to remove the collars.



Figure 5-12. Comparison of tooth wear for three leopards; GM1 (left), estimated age ~8 years, GM2 (top right) estimated age ~12 years and GM10 (bottom right), estimated age ~3 years. Ages were estimated using the criteria suggested by Stander (1997).

Two of the collared individuals, GM1 and GM9 could not be located. The last sighting of GM9 was in October 2010, while the last download from GM1 was in November 2011. Neither of these two leopards were recorded on any camera traps after this time, despite extensive search effort (13 camera traps within GM9's 95% home range kernel and 17 camera stations within GM1's 95% home

CHAPTER 5: LEOPARD DIET

range kernel, all stations active for ~90 days) and extensive searches (both on the ground and with tracking flights), they could not be located using their tracking collars. These two leopards were thus assumed to either be dead or to have left the area, and thus could not be recaptured.

CHAPTER 6: SPOTTING TROUBLE: ATTITUDES TOWARDS WILDLIFE AND CONSERVATION IN THE LITTLE KAROO

6.1 Abstract

Human persecution as a result of conflict poses a major threat to the persistence of large carnivores in the existing matrix of natural and human transformed habitats. Species such as leopards (*Panthera pardus*), black-backed jackals (*Canis mesomelas*), caracals (*Caracal caracal*) and baboons (*Papio hamadryas*) have historically caused significant economic damage to agriculture in South Africa. This damage results in conflict, both between humans and wildlife, and secondary conflicts between farmers and conservation organisations. Despite farmers frequently citing wildlife damage as a major source of economic loss, there has been little analysis of the problem to assess patterns of conflict, identify which species are responsible for damage, and determine the efficacy of various management options. To gather data on these issues, I interviewed 53 landowners in the Little Karoo between March 2011 and November 2012 using structured questionnaires. Respondents were asked to provide information on economic losses incurred due to wildlife and how (if at all) they had attempted to mitigate such losses. A range of questions were used to derive indices that reflect tolerance for damage causing wildlife, livestock husbandry methods, effort and effectiveness of the formal conservation sector in mitigating conflict and the respondent's general knowledge of wildlife. Farmers estimates of economic losses to wildlife were high (US\$3.69 per hectare per year), with stock farmers losing, on average, 6.6% of their total stock value to predators each year. Baboons, black-backed jackals and caracals were the species most frequently cited as causing damage to agricultural produce, with black-backed jackals considered to be the species responsible for the most economic damage across the study area (US\$103 294 per year). Stock farmers suffered significantly greater losses than other land users, and together with crop farmers had significantly lower tolerance of wildlife than game farmers or non-agricultural landowners. Despite stock farmers generally making more effort to protect small stock, such as sheep (*Ovis aries*) and goats (*Capra hircus*) (e.g. through kraaling, herders and livestock-guarding dogs), they still suffered higher

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

depredation rates than those who farmed with large stock (e.g. cattle (*Bos taurus*) and ostriches (*Struthio camelus*)). Despite this, both herding and livestock-guarding dogs were considered to be effective means of reducing stock depredation. Perceptions of conservation authorities were heavily influenced by the amount of damage that a respondent had suffered, although equal numbers of respondents approved/disapproved of current wildlife management policies and practices in the area. My results suggest that wildlife damage is a significant cause of economic loss to pastoralists in the Little Karoo. Implementation of more intensive livestock husbandry measures, such as improved protection of young stock and the use of livestock-guarding dogs or herders, coupled with advice and expertise from conservation authorities and NGOs, may mitigate these losses. Conservation authorities can assist in reducing conflict through greater engagement with the agricultural community, both on a provincial and local scale. An improvement in the relationship between the local conservation agency (CapeNature) and the agricultural community is also likely to aid the implementation of landscape-level biodiversity conservation plans for the Little Karoo.

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

6.2 Introduction

Human-wildlife conflict has been defined as 'the situation that arises when a non-pest, wild animal species poses a direct and recurring threat to the livelihood or safety of a person or a community and, in response, persecution of the species ensues' (Inskip & Zimmerman 2009). Human-wildlife conflict is an ancient phenomenon (Treves & Naughton-Treves 1999; Woodroffe et al. 2005), but one that is becoming increasingly prevalent as anthropogenic activities reduce and fragment areas of natural habitat (Siex & Struhsaker 1999; Elmore et al. 2007; Dickman 2010). Species that are reliant on specific types of habitat are often rapidly extirpated if they are in direct competition with humans (Beinart 1998; Naughton-Treves et al. 2003), or become confined to small habitat patches, coming into conflict with humans when they disperse (Vijayan & Pati 2002). Species with broader habitat tolerance and/or greater behavioural flexibility may be able to survive in a human-modified landscape, and can thus come into competition with humans, resulting in their persecution as pest species (Beinart 1998; Siex & Struhsaker 1999; Naughton-Treves et al. 2003; Elmore et al. 2007; Linkie et al. 2007; Herr et al. 2009; Hoffman & O'Riain 2010). Successful conservation interventions can also increase conflict, as wildlife populations recover and re-colonise areas from which they were previously extirpated (Treves et al. 2004; Boitani et al. 2010).

Conflict is not restricted to predators, as other wildlife species may also become embroiled in conflict with humans (McIvor & Conover 1994; Conover 1998; Elmore et al. 2007). Crop raiding behaviour by large ungulates, primates and rodents can be a significant cause of conflict (Naughton-Treves 1997; Siex & Struhsaker 1999; Pimentel et al. 2005; Linkie et al. 2007). Furthermore, these conflicts can have a large range of indirect impacts upon human communities, including the need to delegate workers to guard fields, removing children from school to guard fields, increased risk of injury from wildlife, and increased exposure to disease (Naughton-Treves 1997; Hill 2004). People tend to be less tolerant of wildlife when their own safety and livelihoods are put at risk as a result of these interactions (Reiter et al. 1999; Daley et al. 2004). Human-wildlife conflict can occur in situations where wildlife species have successfully adapted to urban or near-urban environments

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

(Webber 1997; Herr et al. 2009; Hoffman & O’Riain 2010; Yirga et al. 2012). However, human-wildlife conflict is often more prevalent in rural areas, where damage inflicted by wildlife can directly impact on the economic activities of farmers and hunters (McIvor & Conover 1994). Communities living close to the boundaries of protected areas are often particularly vulnerable to wildlife conflict (Naughton-Treves 1997; Vijayan & Pati 2002). Moreover, state protection of wildlife by designated conservation authorities can ban lethal control methods for predators, which can cause resentment amongst communities who suffer the direct costs of losses to predators (Naughton-Treves 1997; Hill 2004).

Human-wildlife conflicts are of particular concern when they involve a threatened or endangered species (Inskip & Zimmerman 2009). Many large African carnivore populations are particularly vulnerable as they require large ranges (Ray et al. 2005) and are thus most susceptible to habitat loss and fragmentation (Terborgh 1992; Estes et al. 2011). Carnivores are also more likely to come into conflict with humans due to their dietary requirements, and the threat that they pose to human safety (Linnell et al. 2001; Thirgood et al. 2005; Sillero-Zubiri et al. 2007). At a more local scale, predators are often persecuted due to their impact, both real and perceived, on human economic activities, particularly predation on livestock, which is probably the most common cause of human-wildlife conflict (Terborgh 1992; Beinart 1998; Thirgood et al. 2005; Gusset et al. 2007; Estes et al. 2011).. Although most large carnivores in Africa are officially protected, there are few incentives for private landowners to conserve them (Holmern et al. 2007). Tourism and trophy hunting are often touted as economic benefits that stem from the presence of large carnivores, however income from these sources is seldom shared with farming communities, which causes reduces tolerance of large carnivores and causes resentment towards conservation authorities (Holmern et al. 2007).

Human-wildlife conflict in South Africa dates back to pre-historic times, but intensified with the arrival of European settlers in the 17th century (Beinart 1998; Skead 2011). Large and visible predators, such as lions (*Panthera leo*), cheetahs (*Acinonyx jubatus*), spotted hyaenas (*Crocuta*

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

crocota) and African wild dogs (*Lycaon pictus*) were extirpated from most areas soon after the arrival of European settlers (Beinart 1998; Skead 2011). The predators that survived were either cryptic, such as leopards (*Panthera pardus*) or were able to adapt their behaviour to survive despite persecution, such as black-backed jackals (*Canis mesomelas*, hereafter referred to simply as 'jackals') and caracals (*Caracal caracal*). European settlers originally kept livestock in kraals, relatively small, enclosed areas designed to exclude predators, to protect their stock (Beinart 1998). Farmers were encouraged to abandon kraaling of stock at night in favour of large, fenced camps due to the greater vegetation impacts and risk of disease transmission caused by bringing stock back to a kraal each night (Beinart 1998). Jackals proved adept at catching and killing predator-naïve Merino sheep (*Ovis aries*) introduced from Europe, and rapidly became a major problem to small-stock farmers, with stock losses to jackals reaching 12% annually in some areas by the 1910's (Beinart 1998; Nattrass & Conradie 2013).

Leopards have also been implicated in conflict due to livestock depredation. The first published study of leopard diet in the Cape examined stomachs of leopards killed due to stock raiding (Stuart 1981). Of the 36 stomachs examined, 19 were found to contain livestock remains, but the results of this study were not necessarily representative of the leopard population as a whole as it was biased towards individuals that had depredated livestock (Stuart 1981). Although incidents of leopard damage appear to be relatively infrequent, retaliatory and 'preventative' killing of leopards was historically widespread, with large bounties being offered for leopard pelts (Beinart 1998). Incomplete records from the Cederberg Mountains, Western Cape, South Africa suggest that leopards were being killed at an average rate of 4.9 leopards per year between 1940 and 2006, and it is likely that many incidents in which leopards were killed went unreported (Martins & Martins 2006). From 2004 to 2010, CapeNature (the Western Cape Nature Conservation Board; the statutory body responsible for nature conservation in the province) issued 89 leopard trapping permits in the Western Cape, excluding trapping done for research purposes (Theresa van der Westhuizen, CapeNature, pers. comm.). Only four of these were for the Little Karoo, of which two permits were

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

issued for the Uniondale area about 100 km to the east of my study area. No permits have been issued for the use of leg-hold or 'gin' traps to capture leopards in the Western Cape since July 2004, and other than cage traps, the only means of legally capturing or killing leopards has been through the use of poisonous collars on livestock (two permits) and hunting at night (one permit).

Conflict mitigation strategies in South Africa have historically been heavily reliant on lethal control, with implementation being encouraged through incentives such as bounties on jackal, leopard, baboon and caracal pelts and subsidies for poison and hunting dog clubs (Beinart 1998). These measures resulted in the death of large numbers of predators, and over 317 000 jackal bounties were paid between 1914 and 1923 (Beinart 1998; Nattrass & Conradie 2013). The South African government continued to pay bounties until the mid-1950's, after which alternative support was provided to farmers in the form of subsidies and technical aid to hunting clubs (Nattrass & Conradie 2013). The latter were phased out by 1993, leaving farmers to control problem wildlife on their own (Nattrass & Conradie 2013).

By this time, small-stock farming had become significantly less profitable (Nattrass & Conradie 2013) and many farms were sold and the new owners engaged in alternative land use activities. National changes to labour laws, including increased minimum wages, in addition to fears concerning land claims by labourers resulted in many farmers no longer employing a dedicated predator trapper. These, and other factors, caused a reduction in predator control efforts that are generally perceived to have allowed jackals and other predator populations to recover, recolonising areas from which they had previously been extirpated and escalating levels of conflict (Nattrass & Conradie 2013).

Jackals and caracals are estimated to cause over US\$12 235 000 in direct damage (i.e. livestock killed) per year in the Western Cape, and thus have a major economic impact on the agricultural sector (van Niekerk 2010). In 2008, CapeNature banned the use of leg-hold, or 'gin', traps, one of the more popular forms of lethal control used by farmers, due to their impact on non-target species, welfare concerns and a lack of evidence that this method targeted damage causing individuals and

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

hence reduces stock losses (Stahl et al. 2002; Treves & Naughton-Treves 2005; Conradie & Piesse 2013). This decision exacerbated tensions between farmers and conservation authorities, which had adverse knock-on effects on other large-scale conservation initiatives (see Lombard et al. 2010). The continued use of leg-hold traps by many farmers has also raised the ire of conservation NGO's and sectors of the general public who regard such methods as barbaric (Nattrass & Conradie 2013).

Currently, a lack of data on the effectiveness of conflict mitigation methods, both lethal and non-lethal, has fuelled what Nattrass & Conradie (2013) refer to as 'rival narratives' amongst farmers and the scientific and conservation community. While new initiatives, such as the establishment of the Western Cape Predator Management Forum in 2012, have fostered dialogue between these two groups, data on the management of wildlife conflict remains of vital importance in identifying effective management strategies to reduce human-wildlife conflict in the Western Cape. The lack of government support for lethal control methods may have contributed to farmers experimenting with non-lethal alternatives, including livestock-guarding dogs, herders and electronic shepherd devices. However, these are often regarded with suspicion by farmers, who tend to view these methods as expensive and ineffective, despite being widely used elsewhere in the world (Ogada et al. 2003; Rigg 2004; Breitenmoser et al. 2005; Stein et al. 2010; van Niekerk 2010; Nattrass & Conradie 2013). Non-lethal predator management practices are therefore perceived as being a supplement to essential lethal control methods (van Niekerk 2010; Nattrass & Conradie 2013).

In this chapter, I investigate human-wildlife conflict in the Little Karoo. As leopard activity tends to be restricted to mountainous areas where there is little farming activity, I broadened the scope of this investigation to include all potentially damage-causing species found in the area. I attempted to identify successful management strategies that may mitigate this conflict, and assess the attitudes of farmers towards wildlife, conservation authorities and conservation in general.

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

6.3 Methods

6.3.1 Data collection

I personally conducted structured questionnaire interviews with landowners in the period from March 2011 to November 2012. Landowners were informed that their answers would remain confidential, and were part of a study to assess wildlife conflict in the area. To ensure even geographical coverage of the study area, I attempted, wherever possible, to interview landowners who had allowed me to set up camera traps on their land as part of my camera trap survey (see Chapter 4). Although the interviews were structured, I encouraged landowners to provide additional comments and inputs beyond the scope of individual questions where relevant. The questionnaire used is attached as Appendix 6A.

Interviews opened with a series of socio-economic questions, including the size of the property, number and type of stock owned, the economic importance of existing livestock (if it was not the principal source of income for the landowner), and how long the landowner had owned the property and lived in the area. Many stock farmers had more than one type of livestock with goats (*Capra hircus*), sheep (*Ovis aries*), ostriches (*Struthio camelus*) and cattle (*Bos taurus*) all commonly farmed in the area. These species are hereafter referred to as 'stock types'. Stock farmers were asked to rate the significance of a range of potential problems, including disease, drought, unreliable markets and predation on a five-point Likert scale (Pollock et al. 1994; Lafon et al. 2003; Zimmermann et al. 2005; Knight et al. 2010).

Landowners were asked to identify any species which they considered to be pests and to supply details on the type of damage caused by each species, the approximate annual cost of this damage, and what steps they had taken to mitigate this damage. I also asked whether they perceived that there had been changes in the abundance of any wildlife species during the previous 10 years, and whether any new species had been observed on the property during this period.

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

I investigated attitudes towards CapeNature, the statutory conservation body, by asking a series of questions regarding the landowner's relationship with CapeNature. Landowners were asked if they had suffered any losses due to predators, whether they had reported these (or any other losses, such as crop damage) to CapeNature or any other governmental (such as the Department of Agriculture, Forestry and Fisheries) or conservation body, and what action had been taken as a result. Landowners were asked if they felt that CapeNature did a good job of managing damage-causing wildlife, and if there were any other organisations that should rather assume responsibility for this perceived threat to food security and livelihoods. A series of short questions were used to assess the attitude of landowners towards predators. I asked whether landowners had ever removed predators from their property, how they had removed predators, how target-specific these methods had been, and how many predators were removed in a year. When interviewing landowners who did not own livestock, I broadened these questions to include other potential pest species and other potential forms of economic loss.

The next sequence of questions focused specifically on the attitude of stock farmers towards leopards. I asked farmers whether they would accept stock losses due to leopard predation, and whether a compensation scheme for leopard-related losses would increase their acceptance of leopard depredation of their stock. Farmers were asked to describe any livestock losses over the previous two years that could be attributed to leopards, including the type and number of animals killed, when and where the incident took place, and why they thought that a leopard had been responsible for the damage.

I asked all stock farmers about livestock husbandry practices, with a focus on how they protected stock from predators. I requested details on what protection measures were implemented during the day, at night and during the breeding season for each livestock type. Stock farmers rated the effectiveness of herders and livestock-guarding dogs on a five-point Likert scale, and provided details of any livestock husbandry changes that they had made in response to predator losses. I asked stock

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

farmers whether they felt that conflict with predators was increasing, declining or stable, and why they felt that this might be occurring. I concluded the interview with a series of questions that I used to assess respondent knowledge of leopards and attitudes towards predators in general. Finally, landowners were asked to mark the location of their property on an A2-sized map of the area, and provided some basic demographic information such as age and highest education level. Asking demographic questions at the end of a survey has been shown to improve response rates (Roberson & Sundstrom 1990).

Farm locations were mapped using ArcGIS 9.3 software (ESRI, Redlands, California, USA). Farm areas and perimeters were calculated, as well as the distances (m) to the nearest protected area and conservancy. Protected areas refer to formally proclaimed nature reserves owned or managed by CapeNature, the statutory conservation body, while conservancies are defined as 'a voluntary association of environmentally-conscious landowners who co-operatively manage environmental resources in a sustainable manner' (National Association of Conservancies and Stewardship South Africa, www.nacsa.org.za, accessed on 27/12/2013). I calculated the length (m) of any boundaries shared with protected areas and/or conservancies, and used this to determine the percentage of the total farm perimeter shared with protected areas and conservancies. I calculated the mean Normalised Differential Vegetation Index (NDVI), terrain ruggedness, elevation, habitat condition, distance to the nearest town and distance to the nearest river for each property using Zonal tools in ArcGIS 9.3 (see Chapter 3 for further details on how these environmental variables were calculated).

Respondent answers may have been influenced by self-imposed pressure to deliver answers that I would deem to be socially acceptable (Lindsey et al. 2006). My affiliation to the Cape Leopard Trust (CLT) was well-known, and the vehicle that I used to travel to interviews was also clearly marked with the CLT logo. There was little that I could do to influence this, other than to stress that I was a PhD student registered at an academic institution and that the interview was part of my overall research into wildlife conflict, while acting in a generally agreeable manner in order to foster an

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

open and honest dialogue with the respondent (Groves et al. 1992; Holbrook et al. 2003). I further stressed that I was not a representative of CapeNature or any other Government-mandated body and that the purpose of my research was ultimately to provide useful feedback to farmers to improve management practices. As I was clearly strongly associated with a leopard conservation NGO, some respondents may have exaggerated their tolerance of leopards for my benefit. However, negative sentiment towards other damage-causing species was strong, and I suspect that the majority of questions relating to species other than leopards were answered honestly.

6.3.2 Wildlife damage

The estimated total South African rands (ZAR) value of damage caused by each wildlife species was summed to produce an overall value of total damage attributed to wildlife. Respondents gave figures of damage cost in ZAR, which I converted to US dollars (\$US) at a rate of 8.50 rands to one dollar, an approximation of the median exchange rate in 2012. To assess damage intensity, I divided the amount of damage (in \$US) by the total size of the farms (hectares) to calculate the mean damage per hectare caused by each species. Respondents who were not able to provide an estimate of the damage caused by a particular species were not included in these calculations. The total amount of wildlife-related damage was also calculated for each farm, and divided by farm size to provide an estimate of mean damage per hectare both for total damage caused by wildlife and total damage caused by predators.

Incidents involving leopards were examined in greater detail. As leopard depredation of livestock is relatively rare in the area (Theresa van der Westhuizen, CapeNature, pers. comm.), farmers provided details over a two year period, as opposed to an annual tally for all other species. The types of livestock depredated were compared to the number of separate incidents to assess the number of livestock killed in each leopard depredation event.

Stock farmers were asked to score the severity of a range of other challenges to farming including, disease, drought, infertility, poor grazing, unreliable market, predators, theft, livestock road kill and

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

lack of herders on a five-point Likert scale, where a score of one indicated that it was not a problem, and five indicated it was a major problem. Farmers could also suggest and score any additional problems on the same scale. Farmers were asked to identify their biggest problem if the highest score was shared by two or more categories. I calculated a mean Likert scale score for each problem (McIvor & Conover 1994; Lafon et al. 2003) across all farmers. If farmers had removed pest species from their property (irrespective of the method used) I asked them to provide details on how the animal was killed or captured.

6.3.3 Predictive models

I assessed which variables (see Table 6-1) were most important in influencing total damage caused by wildlife, livestock losses to predation, tolerance of wildlife, and conservation index score using Generalised Linear Models (GLZ) run in Statistica version 11 (Statsoft Inc., Tulsa, Oklahoma, USA). All variables were tested for normality and co-linearity prior to analysis (Freckleton 2011). Variables that were not normally distributed were root or log-transformed to obtain a normal distribution. When predictive variables were co-linear, I excluded the variables that were likely to explain less of the response term variance (Freckleton 2011). Landscape characteristic variables (elevation, terrain ruggedness index, NDVI and habitat condition) were strongly co-linear ($r^2 > 0.9$, $p < 0.05$ for all combinations), and I opted to use habitat condition as the proxy for these variables. The habitat condition layer is a measure of land degradation, and was thus likely to provide insight into farm management and stocking rates, which could in turn influence predation risk (Kirkwood 2010).

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

Table 6-1. Variables used in generalized linear models to predict total damage, predator damage, tolerance of wildlife and attitudes towards conservation authorities. Unless otherwise stated all information was obtained directly from respondents during the interviews.

Respondent characteristics			
Variable	Type	Transformation	Notes
Age (years)	Continuous	None	The age of the respondent
Gender	Categorical	None	The gender of the respondent
Years owned	Continuous	None	The number of years that the respondent had owned or managed his/her property
Tourism (yes/no)	Categorical	None	Whether the respondent generated any income from tourism
Gouritz Initiative participation	Categorical	None	Had the respondent participated in the Gouritz Initiative, or its successor, the Gouritz Corridor Biosphere Reserve?
Landowner type	Categorical	None	Landowners were divided into four categories: Stock farmers, crop farmers, game farmers or recreational.
Stock role	Categorical	None	The economic importance of livestock to the farmer – classified as either being the main source of income, a supplementary source of income, or none (if the respondent did not own livestock or derived no income from livestock)
Education level	Categorical	None	The highest level of education obtained by the landowner; classified as either ‘matric’ (finished high school), ‘diploma’ (a one or two-year tertiary qualification) or ‘degree’ (a university degree and above, including post-graduate qualifications). All respondents had at least a ‘matric’ level of education.
Lethal control	Categorical	None	Use of lethal methods to remove damage-causing wildlife

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

Non-lethal	Categorical	None	Use of at least one non-lethal husbandry method (herders, guardian dogs or kraals to protect livestock, electric fencing or crop-guarding to protect crops).
Property characteristics			
Variable	Type	Transformation	Notes
Natural vegetation (%)	Continuous	log and square root	The percentage of the property made up of natural vegetation (i.e. non-irrigated land). Neither transformation achieved a normal distribution, as most properties had high proportions of natural vegetation (median = 95% of farm area). This variable was not included in any analyses.
Property area	Continuous	log	Total area (hectares) of the respondent's property
PA perimeter (%)	Continuous	log	The percentage of the respondent's property's perimeter that was shared with a formally conserved area (CapeNature reserve), a private nature reserve or a property that formed part of a local conservancy. This was measured after plotting property and protected area locations in ArcGIS 9.3.
PA distance (m)	Continuous	log and square root	The Euclidean distance to the nearest protected area (including conservancy land, private nature reserves and CapeNature reserves). Most respondent properties (79.2%) bordered a protected area or conservancy, and these values were zero-inflated and could not be transformed to a normal distribution. I used the percentage of boundary shared with a protected area (PA perimeter %) as a substitute for distance, as this was normally distributed once log-transformed.

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

Habitat condition	Categorical	none	Mean habitat condition of the respondent's property, according to the Western Cape Biodiversity Framework habitat layer, produced for CapeNature in 2010. Each 100 mx100 m cell was assigned the following score based on habitat condition: natural = 1, near-natural = 2, degraded = 3, no natural habitat = 4. A mean score was calculated for each property using Zonal tools in ArcGIS 9.3.
Terrain ruggedness index	Continuous	none	The mean terrain ruggedness index (Riley et al. 1999) for the property was calculated from the terrain ruggedness index score of each 100 m x 100 m cell within the property using Zonal tools in ArcGIS 9.3.
Elevation (m)	Continuous	none	Mean elevation was calculated for each property based on the elevation of each 100 m x 100 m cell within the property, using Zonal tools in ArcGIS 9.3. Elevation data were obtained from Shuttle Radar Topography Mission (http://www2.jpl.nasa.gov/srtm/africa_radar_images.htm) accessed on 04/04/2013
Normalised differential vegetation index (NDVI)	Continuous	none	NDVI scores were generated for each 100 m by 100 m cell within each property based on Moderate Resolution Imaging Spectroradiometer (MODIS) satellite data, (http://reverb.echo.nasa.gov/reverb/), accessed on 01/04/2013
Distance to town (m)	Continuous	none	The Euclidean distance to the nearest town, averaged for all 100 m x 100 m cells within the property, calculated using Zonal tools in ArcGIS 9.3.
Distance to river (m)	Continuous	none	The Euclidean distance to the nearest river, averaged for all 100 m x 100 m cells within the property, calculated using Zonal tools in ArcGIS 9.3. Many of these rivers were non-perennial, but drainage lines could potentially provide cover for predators.

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

Economic characteristics			
Variable	Type	Transformation	Notes
Stock value	Continuous	square root	The total value of the respondent's livestock holdings, calculated at \$US 117.65 per goat and sheep, \$US 176.47 per ostrich and \$US 588.24 per cow, based on mean values supplied by respondents.
Total damage	Continuous	square root	The sum of all damage (in \$US) caused by wildlife species on the respondent's property per year.
Predator damage	Continuous	square root	The sum of all damage (in \$US) caused by predators on the respondent's property per year.
Predator damage (%)	Continuous	square root	The percentage of total stock value lost to predators per year.

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

Variable subsets were ranked according to Akaike's Information Criterion (AIC), which was adjusted for small sample size (AIC_c) (Akaike 1974; Burnham & Anderson 2002; Symonds & Moussalli 2011). I determined the number of variables to use in each model based on a guideline of 15 samples per variable (Ellison & Gotelli 2004). Therefore, models that incorporated all respondents ($n=53$) were based on three variables, while those based solely on stock farmers ($n=34$) used two predictor variables. I calculated AIC_c weights for all suitable models, and used model averaging to identify important variables if none of the candidate variable subsets had an AIC_c weight of less than 0.9 (Burnham & Anderson 2002). Models were averaged by summing the AIC_c scores for subsets in which each variable appeared (Burnham & Anderson 2002). After identifying suitable variables, I fitted a General Linear Model (GLM) to the data and calculated F-ratios using Type II-adjusted sums of squares (Hill & Lewicki 2007).

Unless specifically stated, I included all respondents when modelling variables influencing my response terms viz. total damage, tolerance of wildlife and conservation index in separate GLZs and subsequent GLMs, as these were issues likely to be relevant to all landowners. I grouped respondents into one of four broad categories largely defined by their relative extent of stock or their relative economic reliance on stock farming:

- Stock farmers were landowners who derived income from farming livestock. Respondents who owned small numbers of livestock, but did not farm them for commercial purposes were not considered as stock farmers. When I was interested in variables unique to stock farming, I divided stock farmers into two subgroups to reflect whether livestock was the main or supplementary source of income for that landowner. Most stock farmers also grew some crops (typically lucerne (*Medicago sativa*) for feed).
- Crop farmers were classified as farmers who derive their income solely from agricultural produce and did not own any stock.

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

- Game farmers were landowners who did not derive any income from stock farming and had introduced large ungulates such as eland (*Tragelaphus oryx*), kudu (*Tragelaphus strepsiceros*), zebra (*Equus quagga*) and gemsbok (*Oryx gazella*) to their properties. Although most of the game farms in the area were managed for recreational, rather than commercial, purposes, game farmers frequently expressed concern about the impact of predators on the game species that they had introduced.
- Recreational landowners had not introduced game, and either derived income from tourism or from other sources not related to agricultural production on the property. This group included owners of private nature reserves, managers of provincial nature reserves, retirees and people involved in various tourism-related activities, as well as people who simply used their property for relaxation or lifestyle purposes.

Stock farming was the most prevalent land-use in the study area, and I therefore developed separate models based solely on stock farmer responses. When modeling predator damage, landowners who did not have livestock were excluded. Game farmers in the area were also excluded, despite some of them reporting predator damage. Game farmers do not have the same suite of husbandry tools available to them as livestock farmers (e.g. livestock-guarding dogs, herders, kraals, etc.), and losses are thus likely to be influenced by different factors that fell beyond the scope of my assessment.

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

6.3.4 Wildlife tolerance

I used data from the interviews to generate an index that described tolerance of wildlife for each landowner (Mehta & Kellert 1998; Walpole & Goodwin 2001; Zimmermann et al. 2005). The wildlife tolerance index was based on the answers given to questions asked of all interview respondents (see Table 6-2). The wildlife tolerance index is the sum of points obtained for all questions – a high score (maximum of 26) shows high tolerance of predators/wildlife. Respondents were grouped by land-use type (stock farming, crop farming, game farming or recreational) and wildlife tolerance index scores were compared among groups using a one-way ANOVA.

Table 6-2. Questions and scores used to calculate the wildlife tolerance index for respondents. Points in the 'Yes', 'No' and 'Maybe' columns indicate the points awarded for those respective answers. A higher score indicates greater tolerance.

Question	Yes	No	Maybe
28. Do you expect compensation for wildlife damage?	0	2	1
30. Would you be happier if all predators were removed from the Little Karoo?	0	2	1
32. Should game farms kill predators that prey on introduced game?	0	2	1
33. Would you kill/remove predators if you suffered stock losses?	0	2	1
34. Would you shoot a predator if you encountered one on your farm?	0	2	1
35. Have you removed wildlife from your property in the past?	0	2	1
38. Have you used snares/gin traps?	0	2	1
40. Would you accept livestock losses to leopard predation?	2	0	1
41. Would you accept these (leopard) losses if you were compensated?	2	0	1
73. Can you tolerate leopards being present on your neighbour's property?	2	0	1
74. Would the Little Karoo be a better place without leopards?	0	2	1
76. Does the presence of leopards add value to a property?	2	0	1
79. Are there too many leopards in the Little Karoo?	0	2	1

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

To assess whether respondents were more tolerant of leopards than of other predators, I compared the answers given to the questions, 'Should efforts to protect leopards in the Little Karoo continue?'(Q68), and 'Do predators currently have too much legal protection?' (Q29). While not directly analogous, these questions are similar enough to allow for a broad comparison of attitudes. Answers were grouped according to the respondents desire for further protection of leopards and predators respectively, i.e. 'Yes' for Q68 and 'No' for Q29 were treated as being in favour of conservation. Frequencies of answers in favour, against and with neutral attitudes towards future conservation were compared using a Chi-square (χ^2) goodness-of-fit test.

A second test of comparative tolerance was conducted by comparing answers to question 33 ('Would you try to kill/remove a predator in future if you lost livestock to predation?') and question 40 ('Will you accept it if leopards kill any of your livestock?'). A positive answer to Q40 and a negative answer to Q33 were treated as equivalent, and vice versa. Results were also compared using a Chi-square (χ^2) goodness-of-fit test.

GLMs were fitted to the wildlife tolerance index data to investigate factors that might influence wildlife tolerance, firstly for all respondents and then for stock farmers using the procedure described above.

6.3.5 Livestock husbandry

All livestock husbandry analyses were restricted to stock farmers. Points were awarded based on three criteria (see Table 6-3); husbandry measures implemented during the day, at night, and during the breeding/birthing season. Points were summed for each criterion, and a total derived for each livestock type/ farmer. A high score implied greater protection effort.

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

Table 6-3. Summary of the scoring of wildlife husbandry measures used to determine the wildlife husbandry index for each species. 'Free roam' refers to animals kept in large camps, usually with jackal-proof fencing of varying quality. 'Feedlots' are small camps with little or no vegetation that would serve as cover for predators, but without predator-proof fencing. Small fenced camps are usually in irrigated land, with well-maintained, often electrified fencing. 'Kraals' are relatively small, predator-proof enclosures designed to keep livestock contained and protected at night.

Day		Night		Birthing season	
Action	Points	Action	Points	Action	Points
Free roam	0	Free roam	0	No change	0
In feedlot	1	In feedlot	1	In feedlot, close to house	1
Protected by dog, or in small fenced camp	2	In predator-proof kraal, or protected by dog/herder	2	Kept in kraal/protected by dog or herder	2
Protected by herder	3				

As most stock farmers had a range of stock types, I calculated a score for each stock type by scoring the husbandry methods employed by stock farmers during the day, night and in the birthing season for each stock type. These were summed to provide a husbandry score for each stock type for each farmer. I then calculated a mean husbandry score for each stock type, and used the difference between this stock mean and the farmer's individual score to calculate the relative husbandry effort for a particular stock type. I then calculated the total value of the livestock owned by each farmer, and determined the proportion of this total contributed by each stock type in the area. This was used to weight the husbandry scores for each stock type, and these weighted scores were summed to provide an overall husbandry score for that farmer. This can be summarised in the following equation;

$$Husbandry_{wt} = [(x_1 - \bar{x}_1) \times V_{x1}] + [(x_2 - \bar{x}_2) \times V_{x2}] + \dots [(x_n - \bar{x}_n) \times V_{xn}]$$

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

Where x_n is a farmer's husbandry score for a particular stock type, $\bar{x}_n$ is the average husbandry score for that stock type, and V_{xn} is the proportion contributed by that stock type to the total value of all livestock owned by the farmer.

Livestock prey preferences (and consequently, stock vulnerability), for all predators and for leopards in particular, were calculated using Jacobs' index (Jacobs 1974). Jacobs' index measures prey preference using a comparison of depredation rates and relative prey abundance, based on the following equation:

$$D = r_i - p_i / (r_i + p_i - 2r_i p_i)$$

Where r_i is the proportion of all depredation events where species i , was depredated, and p_i is the relative abundance of species i , as determined by the stock numbers provided by interviewed stock farmers. This assumes that predators had equal access to all livestock types, which is unlikely to have been the case. Ideally I would have mapped the areas used by each livestock type, but given the length of the questionnaire and the difficulties inherent in accurately mapping seasonal variation in habitat use by the various livestock species I decided against this, and present the above analysis as a broad-level comparison of the vulnerability of different stock types to depredation.

I compared the herd size of farmers who used either livestock-guarding dogs or herders to protect stock to those who used neither method using a one-way ANOVA. The use of kraals to protect livestock was also compared between the two groups. Differences in the sizes of herds guarded by herders and dogs were assessed using a student's t-test. I assessed the perceived effectiveness of herders and dogs using a five-point Likert scale, and compared effectiveness scores allocated by respondents who currently use one of these two methods to scores volunteered by respondents who did not. This allowed me to investigate whether there was a disparity in opinion between respondents who made use of active livestock guards (herders or dogs) and those who did not.

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

I calculated a second index, 'husbandry_{crops}' to account for damage caused by species such as baboons, porcupines (*Hystrix africaeaustralis*), bushpigs (*Potamochoerus larvatus*) and birds to crops, in addition to stock losses. The measures used to deter each species were scored on a scale from zero to two (Rigg 2004; Marker et al. 2005). A farmer who made no effort to mitigate losses from a species scored a zero for that species, while sporadic, reactive deterrence measures (chasing away, shooting, etc.) were allocated a score of one. Farmers who instituted crop defense measures such as netting (for birds) or electric fences got a score of two. I calculated the average crop protection score, and used the difference between the farmer's score and the mean to calculate each farmer's relative crop protection effort for each species. As farmers often suffered crop damage from multiple species, I weighted protection effort by multiplying the farmer's relative crop protection effort (for each species) by the proportion of crop damage caused by that species. These weighted scores were summed to provide a crop protection score for each farmer. When farmers had both crops and livestock, I summed the two scores. I did not weight the relative contribution of crops and stock as I did not know the relative contribution of stock and crops to the net turnover of most respondents.

6.3.6 Perceptions regarding CapeNature

I divided respondents into two groups based on their response to question 24; respondents who had reported wildlife-related problems to CapeNature (the 'reporting' group), and those who had not ('non-reporting'). The percentage of the non-reporting group who had suffered wildlife-related damage, or who considered at least one wildlife species to be a pest, was calculated. The percentage of respondents from each group who thought that CapeNature provided an appropriate and professional service for managing damage-causing animals (Q25) was calculated, and the results compared using a Chi-square goodness-of-fit test. The two groups response to question 26 ('Who do you think should be responsible for managing damage-causing animals?') were compared using a Fisher's exact test.

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

6.3.7 Conservation index

This index quantified attitudes and perceptions of conservation management, both in terms of actions carried out by CapeNature and other formal conservation mechanisms, such as legislation (see Table 6-4).

Table 6-4. Questions used to calculate the conservation index. Points in the 'Yes', 'No' and 'Maybe' columns indicate the points awarded for those respective answers. The conservation index was calculated as the sum of points obtained for all questions – a high score (maximum of 16) shows a favourable attitude towards conservation. * - 2 points are awarded if the respondent felt that CapeNature should continue to manage damage-causing wildlife, 1 point if the respondent felt that it should be managed by CapeNature together with farmers or another agency, and 0 points if the respondent felt that CapeNature should be excluded from the managing damage-causing wildlife.

Question	Yes	No	Maybe
26. Do CapeNature do a good job of managing damage-causing wildlife?	2	0	1
27. Who should be responsible for managing damage-causing wildlife?	*	*	*
23. Are you concerned about the future of wildlife in the Karoo?	2	0	1
30. Does wildlife receive too much legal protection?	0	2	1
68. Should leopard conservation efforts continue?	2	0	1
75. Can leopards bring tourism benefits to you/the community?	2	0	1
80. Can you assist leopard conservation efforts in some way?	2	0	1
81. Are you willing to work with conservation groups to reduce wildlife conflict?	2	0	1

6.3.8 Knowledge index

The knowledge index attempted to quantify the respondent's knowledge of wildlife. As leopards were the most high-profile species in the area, knowledge of leopards was used as a proxy for knowledge of wildlife in general (see Table 6-5).

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

Table 6-5. Questions used to calculate the respondent knowledge index. Points in the 'Yes', 'No' and 'Maybe' columns indicate the points awarded for those respective answers. The knowledge index is the sum of points obtained for all questions; a high score (maximum of 14) shows greater awareness/ knowledge of leopard issues. As the answers to some questions were uncertain, scoring was adjusted to reflect this uncertainty.

Question	Yes	No	Maybe
64. Are leopards likely to attack people?	0	2	1
65. Can leopards move unseen across your property?	2	0	1
69. Do leopards play an important role in the ecosystem?	2	0	1
70. Do leopards control the populations of smaller predators?	1	2	1
71. Do leopards help to control the baboon population?	2	0	1
77. Will low game densities increase the risk of livestock predation by leopards?	1	1	2
82. What is the conservation status of leopards?	Protected (2 points), 1 point for 'vulnerable', 'rare' or 'endangered', 0 points for 'don't know' or 'common'		

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

6.4 Results

6.4.1 Demographic characteristics

I interviewed 53 landowners who collectively owned or managed approximately 154 000 hectares of land in the Little Karoo (see Figure 6-1). Mean farm size was 2918 (± 4414) hectares. Respondents ranged in age from 27 to 75 years old (mean: 54.56 $\pm$ 10.58 years old). Only one female respondent was interviewed, and all but one respondent was of Caucasian descent. All respondents had at least a grade 12 qualification (i.e. completed secondary school), 12 had completed a tertiary diploma (one or two-year course), while 23 respondents had a university degree. Thirty four landowners farmed stock, and livestock was the main source of income for 21 of these landowners. Livestock was a supplementary source of income for other landowners, with the majority of their income derived from crop farming (five respondents) or non-agricultural activities (eight respondents). Of the landowners who did not have livestock, four were crop farmers, five had game farms and 10 used their properties exclusively for tourism or recreation-related activities. Most respondents (79.24%) had properties that bordered either a formally conserved nature reserve or some form of conservancy land.

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

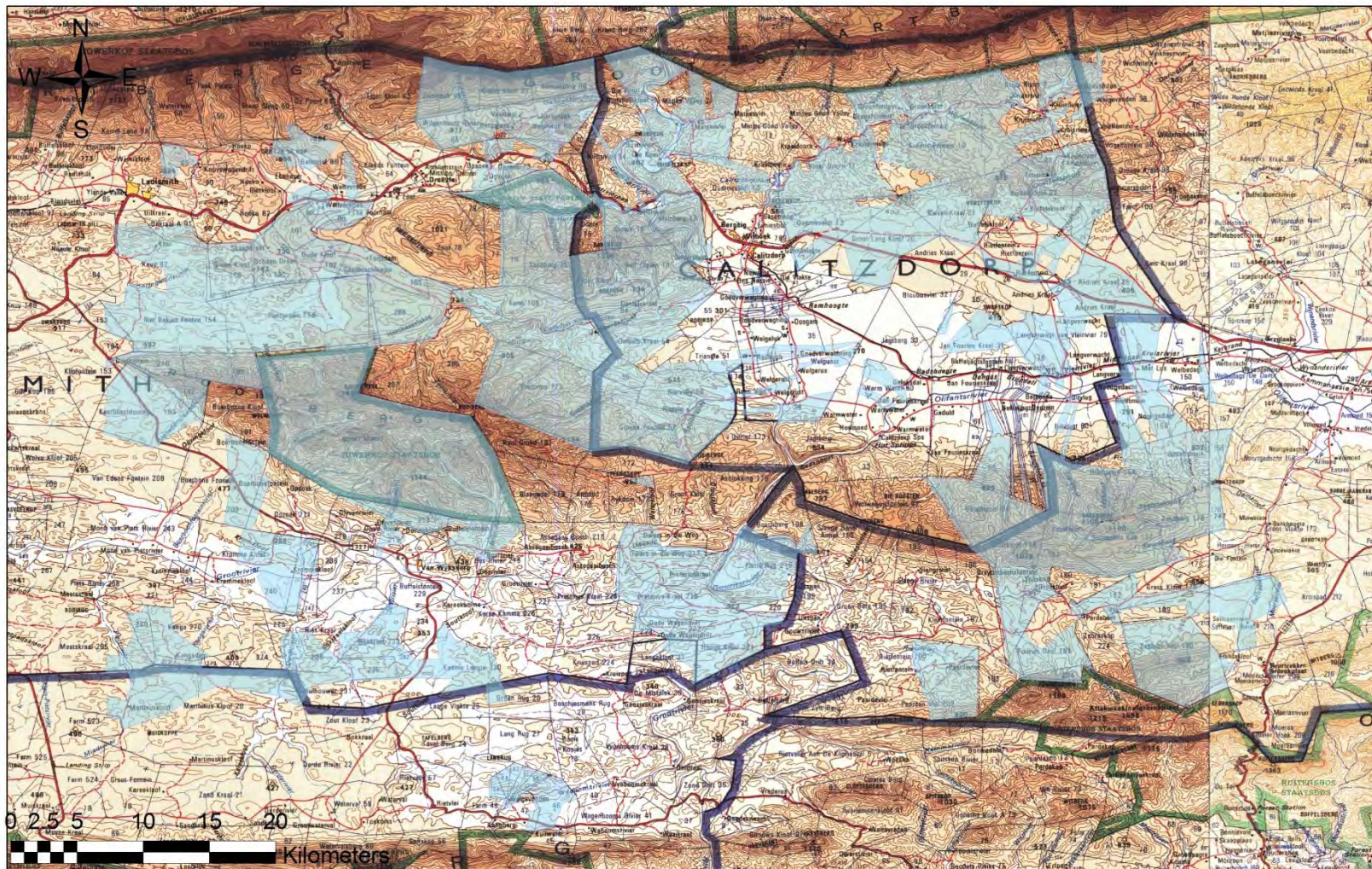


Figure 6-1. Map showing the extent (blue-shaded areas) and distribution of properties belonging to, or managed by, interview respondents

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

6.4.2 Damage causing animals

A total of 19 damage-causing species were identified by respondents (see Table 6-6). Baboons were most frequently identified as problematic (56% of respondents), followed by black-backed jackals (51%), caracals (21%), porcupines (19%) and leopards (17%). Jackals were responsible for the most damage in total (\$US 103 000), followed by baboons (\$US 64 941), feral dogs (\$US 18 235), leopards (\$US 15 882) and passerine birds (\$US 14 236). Total damage figures for all species are shown in Table 6-6.

Table 6-6. Summary of perceived damage caused by wildlife in the Little Karoo, arranged by total damage caused. Landowners affected, shows the number of landowners who identified each species as a pest. Cost shows the sum of all damage caused by each species per year in US dollars, while area shows the total area of all properties affected. Cost per hectare shows the mean amount of damage caused by each species per hectare each year. Properties belonging to landowners who were unable to provide an estimate of the damage caused by a particular species were excluded when calculating the damage per hectare for that species.

Species	Landowners affected	Cost (\$US)	Area (ha)	Cost/ha
black-backed jackal (<i>Canis mesomelas</i>)	27	103 000	67600	1.52
baboon (<i>Papio hamadryas</i>)	30	64 941	72449	0.90
feral dogs (<i>Canis lupus familiaris</i>)	7	18 235	12529	1.45
leopard (<i>Panthera pardus</i>)	9	15 882	24090	0.66
birds (passerine)	5	14 236	7742	1.84
caracal (<i>Caracal caracal</i>)	11	9 706	22163	0.44
aardvark (<i>Orycteropus afer</i>)	2	5 882	2199	2.67
Verreaux's Eagle (<i>Aquila vereauxii</i>)	2	5 294	3440	1.54
Cape porcupine (<i>Hystrix africaeaustralis</i>)	10	4 000	4729	0.85
meerkat (<i>Suricata suricatta</i>)	3	2 353	6578	0.36
bushpig (<i>Potamochoerus larvatus</i>)	6	2 235	7771	0.29
small grey mongoose (<i>Galarella pulverulenta</i>)	2	1 119	2610	0.43
pied crow (<i>Corvus albus</i>)	4	471	8510	0.06
yellow mongoose (<i>Cynictis penicillata</i>)	3	353	6777	0.05

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

Species	Landowners affected	Cost (\$US)	Area (ha)	Cost/ha
feral cats (<i>Felis catus</i>)	1	118	4448	0.03
mongoose (unspecified)	2	unknown	2775	unknown
African Fish Eagle (<i>Haliaeetus vocifer</i>)	2	unknown	3210	unknown
donkeys (<i>Equus asinus</i>)	1	unknown	1080	unknown
Egyptian Goose (<i>Alopochen aegyptiacus</i>)	1	unknown	2013	unknown
Cape clawless otter (<i>Aonyx capensis</i>)	1	unknown	2330	unknown

Aardvark (*Orycteropus afer*) inflicted the most damage per hectare on farms on which they were identified as being problematic (\$US 2.67), but were only identified as a problem species by two farmers. Passerine birds inflicted the next highest damage per hectare (\$US 1.84), largely due to damage to vineyards and other crops (e.g. apricots (*Prunus armeniaca*)) that are farmed intensively on relatively small pieces of land. Verreaux's Eagle (*Aquila verreauxii*), more commonly known as the Black Eagle in the Little Karoo, was only identified as being problematic on two farms, but caused the most damage per hectare of the carnivore species (\$US 1.54), closely followed by jackals (\$US 1.52) and feral dogs (\$US 1.46). Despite being the most frequently-cited damage-causing species, baboons caused far less damage per hectare (\$US 0.90), a similar amount to that caused by porcupines (\$US 0.85), while leopard damage amounted to \$US 0.66 per hectare.

Stock farmers suffered mean predator damage of 6.59% ($\pm 17.52\%$, range: 0% - 100%) of their stock value. Five stock farmers suffered losses exceeding 10% of their total stock value. One farmer claimed to have lost all of his livestock (30 sheep) to predators in the preceding year; however these represented a supplementary source of income for this landowner. With this outlier excluded, mean percentage of stock value lost per year was 3.76% ($\pm 5.98\%$). Of stock farmers for whom livestock provided the main source of income, mean stock loss was 5.17% ($\pm 7.42\%$), and the highest percentage of losses suffered by an individual was 30.58%. Farmers who used stock farming as a

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

supplementary source of income tended to suffer lower losses ($2.28\% \pm 3.59\%$). However, this rose to $8.02\% (\pm 23.96\%)$ with the inclusion of the landowner who lost all of his stock. Apart from this individual, the highest loss suffered by an individual farmer was 12.91% of the total stock value.

In total, leopards were thought to have been responsible for the loss of 103 head of livestock over a two year period. Of these, goats (44.7%), cattle (29.1%) and sheep (22.3%) made up the vast majority of the stock lost. Goat losses were heavily influenced by two leopard attacks in which 22 and 17 goats were killed respectively, although leopard culpability for the second attack was not confirmed. Other than this, leopard attacks seldom resulted in the loss of more than one head of livestock. Approximately half (53.3%) of the cattle allegedly lost to leopards could not be definitively confirmed to be leopard damage either, as no carcasses were found. When carcasses were located, leopards were most frequently (35.5%) deemed to be responsible because of tracks found in the vicinity of the carcass. Leopard kills were also often inferred from the size of the prey (32.3% of kills) or, less frequently, from examination of the carcass itself (22.6%). On rare occasions (6.5% of kills), leopards were sighted near the carcass, and on one occasion a leopard was captured when it returned to feed on a carcass. However, a substantial portion of kills supposedly made by leopards (12.9%) were attributed to leopards without any direct evidence of their involvement.

The mean damage caused by wildlife was \$US 3.69 ($\pm$ \$US 6.84) per hectare per year. The highest rate of damage was \$US 33.55 per hectare. Stock farmers suffered above-average damage rates (\$US 4.27 $\pm$ \$US 6.33/hectare each year). Stock damage from predators amounted to an average of \$US 2.98 ($\pm$ \$US 5.92) per hectare, ranging from no losses to \$US 28.76 per hectare each year.

On average, stock farmers identified predators as their biggest problem. On a five-point Likert scale, predator damage had the highest mean score (2.89 ± 1.52 , see Figure 6-2), followed by drought (2.37 ± 1.42), poor grazing (1.92 ± 1.10) and theft (1.82 ± 1.25). Fifteen stock farmers (44%) identified predator damage as their biggest problem. Drought was identified as the biggest concern by six farmers (18%), while five farmers (15%) identified poor grazing (and in particular poisonous plants)

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

as their biggest concern. Two farmers (6%) cited the rising cost of electricity, while another two farmers felt that theft was their biggest problem. Only one farmer (3%) said that disease was the biggest problem. Five farmers said that they had no major problems; however, all of them used livestock as a supplementary source of income.

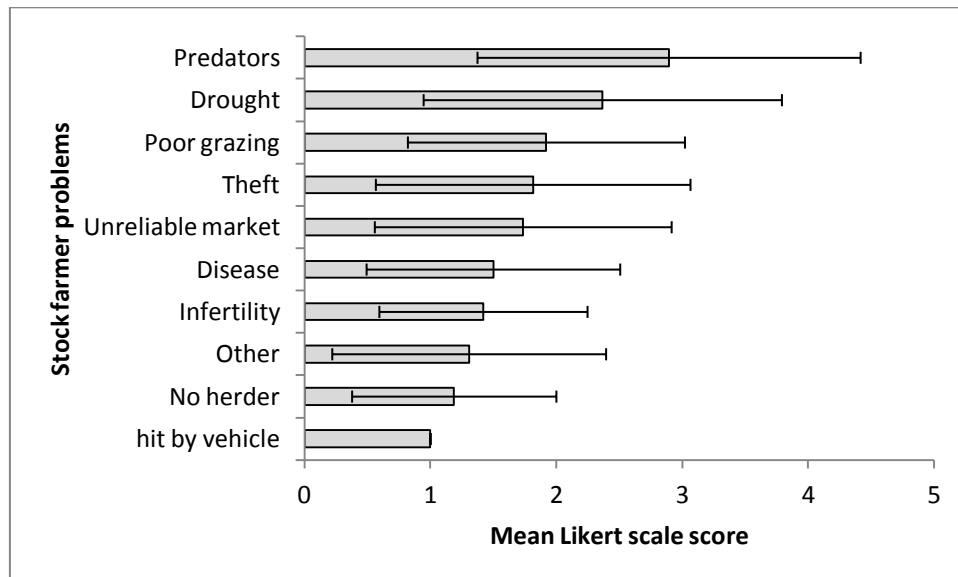


Figure 6-2. Mean Likert scale scores for the magnitude of problems facing 31 stock farmers. Farmers ranked problems on a scale from one to five, where one indicated that there was no problem, and five indicated a major problem. The error bars show the standard deviation.

In total, 67.9% of respondents had removed wild animals from their property, mostly using lethal control methods. Of these 40 landowners, 27 (67.5%) had removed animals by shooting them, 20 (50%) had trapped and shot animals (while in the trap), and only 5 respondents (12.5%) had used poison. Other removal methods included the unintentional killing of wildlife by the landowner's dogs, and one landowner had caught porcupines in a cage trap and released them on a neighbouring conservation property. More respondents (39.62%) thought that wildlife conflict levels were increasing than those who thought it was decreasing (9.44%) or remaining stable (22.64%), while 7.55% of landowners were unsure. Most of the landowners (57.14%) who thought that conflict was increasing attributed this to a decline in stock farming in the area, with fewer landowners practicing lethal control, while a further 33.33% of respondents cited an increase in predator numbers without explicitly linking this to land-use change. Ironically, 60% of respondents who felt that conflict has

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

decreased also attributed this to land-use change, stating that the reduction in the number of active farms had reduced the potential for conflict. The vast majority (85.71%) of respondents who felt that conflict was increasing were stock farmers, and this accounted for 52.94% of the stock farmers interviewed. Only four stock farmers (11.75% of stock farmers) felt that conflict was decreasing, with the remainder either unsure or believing that conflict levels remained stable.

6.4.3 Predictors of total stock value (%) lost to predators

A set of nine candidate predictor variables of the percentage of stock value lost to predators (square root transformed) was assessed; age, PA perimeter, knowledge, stock value, husbandry_{wt}, education level, stock role, introduced game and lethal control. The GLZ model-building routine identified 200 variable subsets. As 34 stock farmers were interviewed, only subsets containing a maximum of two variables were used for further analysis, and subsets containing three or more variables were excluded (Ellison & Gotelli 2004). This reduced the number of candidate variable subsets to 45. Of these, the subset comprising the 'knowledge' index and 'percentage protected area perimeter' received by far the highest AIC_c weighting of 0.965. The subsets were ranked according to AIC_c score (Burnham & Anderson 2002; Symonds & Moussalli 2011). The five highest-ranking subsets are shown in Table 6-7.

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

Table 6-7. The top five variable subsets used to predict the percentage of livestock lost to predators annually. Subsets are arranged in descending order according to AIC_c weight. ‘Knowledge’ refers to the knowledge index score, ‘PA perimeter’ to the percentage of the property boundary shared with a protected area or conservancy, ‘Husbandry_{wt}’ is the weighted husbandry index score, ‘Introduced game’ refers to whether the landowner had introduced large game species to the property, and ‘Stock value’ represents the total value of a farmer’s livestock holdings.

Variable	Variable	Degrees of freedom	AIC _c	ΔAIC _c	AIC _c weight
Knowledge	PA perimeter (%)	2	124.080	0	0.965
Knowledge	Husbandry _{wt}	2	131.521	7.441	0.023
Knowledge	Introduced game	2	135.256	11.175	0.004
Knowledge	-	1	136.650	12.570	0.002
Knowledge	Stock value	2	137.147	13.067	0.001

A GLM was fitted to the data using knowledge index score and PA perimeter (%) as predictor variables of damage cause by predators. Predator damage had a positive relationship with the proportion of the property boundary shared with a protected area, but this effect was not significant ($F_{1,31}=1.32$, $p=0.25$). The farmer’s knowledge index score was significantly and positively related to the percentage of stock lost to predators ($F_{1,31}=5.506$, $p=0.03$). The overall model fit was weak ($r^2=0.17$).

6.4.4 Total damage

The value of the total amount of damage sustained by landowners was assessed using eleven candidate variables; age, years owned, PA perimeter, area, knowledge, husbandry_{crop}, landowner type, stock role, introduced game, education level and tourism income. Unlike the predator damage model, total damage includes all landowners, as all individuals are presumed to have the potential to suffer some form of wildlife damage. This increased the sample size to 53 individuals, and I could thus include sets of up to three predictor variables. The subset consisting of the landowner type, area and husbandry_{crop} variables had the highest AIC_c weight (see Table 6-8).

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

Table 6-8. The top five subsets of variables used to predict the total damage caused by wildlife on individual properties. The subsets are arranged in descending order according to AIC_c weight. 'Landowner type' refers to whether the landowner is a farmer (stock, fruit, game) or a recreational landowner, 'Area' is the total size of the property, 'Husbandry_{crop}' is the husbandry index, adjusted to take crop protection measures into account. The age of the landowner is represented by the 'Age' variable, while 'Education level' is the highest education level attained by the landowners

Variable	Variable	Variable	Degrees of freedom	AIC_c	ΔAIC_c	AIC_c weight
Landowner type	Area	Husbandry _{crop}	5	648.671	0	0.110
Landowner type	Area		4	649.035	0.364	0.092
Landowner type	Area	Age	5	649.710	1.038	0.065
Landowner type	Area	Education level	5	650.703	2.031	0.040
Landowner type			3	650.716	2.044	0.038

The variables selected in the first subset had the three highest averaged scores. Landowner type had the highest score (0.928), followed by area (0.561). Husbandry_{crops} (0.201) and age (0.205) were the next highest variables. As the weightings of the age and husbandry_{crops} variables were relatively low, these were not included in the GLM fitted to total wildlife damage. The total damage suffered by farmers was significantly influenced by landowner type ($F_{3,48}=7.22$, $p<0.01$), while the log of total area of the property had a near-significant effect ($F_{1,48}=3.60$, $p=0.06$), with larger properties suffering more damage. Stock farmers suffered significantly more damage than other landowner types, and the model explained about 35% of the variation in the total damage suffered by respondents ($r^2 = 0.351$).

6.4.5 Wildlife tolerance

There were significant differences in wildlife tolerance index scores among the different groups of landowners ($F_{3,49}=4.78$, $p<0.01$). Recreational (21.4 ± 1.96 , $n=10$) and game farmers (20.4 ± 2.88 , $n=5$)

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

had higher tolerance index scores than crop farmers (17.75 ± 4.5 , $n=4$) and stock farmers (17.00 ± 3.79 , $n=34$). Landowners tended to be more tolerant of leopards than of predators in general. Almost all landowners (94.3%) felt that leopards should continue to be protected, with the remaining three landowners answering 'Maybe', rather than saying that leopards should not be conserved in future. In contrast, 43.4% of landowners agreed with the statement that predators receive too much legal protection, with 47.1% disagreeing and 9.4% undecided. This showed a significant difference between attitudes to formal protection of leopards in comparison to predators in general ($\chi^2=48.8$, $df=2$, $p<0.01$).

A similar trend was observed for tolerance of losses to leopards compared to other predators. The majority (58.5%) of landowners said that they would kill predators in response to losses, but a larger proportion (66.0%) were prepared to accept losses caused by leopards without compensation, a significant difference in attitude ($\chi^2=199.0$, $df=2$, $p<0.01$). Stock farmers were significantly more likely to accept leopard losses if compensation was paid ($\chi^2=6.04$, $df=2$, $p<0.05$). However, respondents (both stock and game farmers) who had experienced leopard damage within the previous two years ($n=12$) had significantly lower wildlife tolerance index scores (15.16 ± 4.18) than stock farmers who had not suffered any damage from leopards during this period (18.48 ± 3.48 ; $F_{1,33}=6.75$, $p<0.05$).

A set of 10 candidate predictor variables was assessed for the wildlife tolerance model; total damage (square root transformed), stock role, knowledge, education level, introduced game, PA perimeter (% - log transformed), area (log-transformed), age, years owned and landowner type. All landowners were included in this analysis ($n=53$), and sets of up to three predictor variables were assessed using AIC_c . The subset comprising of the total damage and stock role variables was found to be best, but had a low AIC_c weight (see Table 6-9).

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

Table 6-9. Model selection of the top five subsets of predictor variables for wildlife tolerance for all landowners. Variable subsets are arranged in descending order according to AIC_c weight. 'Total damage' represents the total cost of damage caused by wildlife, 'Stock role' denotes whether the landowner's livestock are a main, supplementary or not a source of income to the landowner. 'Knowledge' is the landowner's knowledge index score, 'PA perimeter' is the percentage of the property boundary shared with a nature reserve or conservancy, while 'Education level' is the highest level of education attained by the landowner. 'Years owned' is the number of years that the landowner has owned (or been living on) the property.

Variable	Variable	Variable	Degrees of freedom	AIC_c	ΔAIC_c	AIC_c weight
Total damage	Stock role		3	273.965	0	0.161
Knowledge	Total damage	Stock role	4	275.277	1.312	0.084
PA perimeter (%)	Total damage	Stock role	4	275.324	1.359	0.082
Total damage	Education level	Stock role	4	275.535	1.570	0.074
Years owned	Total damage	Stock role	4	275.715	1.75	0.065

Due to the low AIC_c weighting of the best subset, I averaged the models to identify the most important variables. Total damage (1.00) and stock role (0.673) had the highest scores, with the third most important variable, knowledge, scoring substantially lower (0.195). I fitted a GLM to the data using total damage and stock role as predictor variables.

Tolerance of wildlife was significantly influenced by two factors; the total damage caused by wildlife ($F_{1,49}=10.66$, $p<0.01$) and the role of livestock ($F_{2,49}=4.25$, $p<0.05$). Landowners for whom livestock were the main source of income were significantly less tolerant of wildlife than those who did not own livestock or were not reliant on livestock for income. However, this model only explained 38.8% of variation in wildlife tolerance.

To further examine factors that influence tolerance of wildlife, I restricted the analysis to stock farmers, who tended to have a lower tolerance of wildlife. Eight candidate variables were assessed; stock role, total damage, PA perimeter, knowledge, education level, stock value, years owned and

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

age. The model containing the total damage and stock role variables was selected as most powerful based on AIC_c weighting (see Table 6-10).

Table 6-10. The top five subsets of variables used to predict wildlife tolerance amongst stock farmers. Subsets are arranged in descending order according to AIC_c weight. 'Total damage' represents the total cost of damage caused by wildlife, 'Stock role' denotes whether the landowner's livestock are a main, supplementary or not a source of income to the landowner. 'Stock value' is the total value of the landowner's livestock holdings. 'Education level' is the highest level of education attained by the landowner, while the landowner's age is represented by the 'Age' variable.

Variable	Variable	Degrees of freedom	AIC_c	ΔAIC_c	AIC_c weight
Total damage	Stock role	2	184.219	0	0.237
Stock role		1	185.835	1.616	0.106
Stock role	Education level	2	187.142	2.923	0.055
Stock role	Stock value	2	187.262	3.043	0.052
Stock role	Age	2	187.436	3.217	0.047

The stock role (0.618) and total damage (0.416) variables had the highest weightings. I fitted a GLM to the wildlife tolerance index scores for stock farmers using these two variables. Amongst stock farmers, tolerance of wildlife was significantly negatively influenced by both the total amount of damage sustained due to wildlife ($F_{1,31}=5.91$, $p<0.05$) and the role of livestock, with farmers whose main income came from livestock being less tolerant ($F_{1,31}=4.92$, $p<0.05$). The r^2 value of the model was 0.27.

6.4.6 Livestock husbandry

Cattle (n=26 respondents), ostriches (20), sheep (18) and goats (11) were the most frequently farmed stock types. Goats had the highest mean husbandry index score (6.09 ± 1.04 , n=11), followed by sheep (4.27 ± 1.93 , n=18), ostriches (2.4 ± 1.60 , n=20) and cattle (0.89 ± 0.97 , n=27). The differences in husbandry scores for these stock types were significant ($F_{3,72}=42.19$, $p<0.01$). Other livestock types (donkeys, horses, ponies and chickens) were all farmed at low levels (only on single

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

properties, except for horses, which were present on three farms), and were not included in the analyses presented below.

Losses of stock, as a proportion of the total population owned by respondents, showed that sheep suffered higher predation rates than other livestock types (14.5%). Goats (4.1%), ostrich (2.5%) and cattle (0.5%) all had substantially lower predation rates. Jacobs' indices suggested that sheep were the livestock type most likely to be preferred by predators (see Table 6-11), although this preference was relatively weak. All other livestock suffered depredation at lower proportions than expected by their abundance alone, and ostriches and cattle appeared to be strongly avoided. Leopards did not show strong preferences for any livestock, as cattle, goats and sheep were all depredated in proportion to their abundance, although ostriches appeared to be avoided.

Table 6-11. Jacobs' indices for stock depredation by all predators (including leopards), and leopards only. Calculations for all predators are based on estimates of annual losses provided by stock farmers, while leopard losses are based on incidents over a two-year period. Total numbers refers to the total number of a stock type summed for all interviewed landowners, while the number killed is the total number of each stock type depredated by all predators and leopards respectively. Jacobs' index values were calculated separately for leopards.

Stock type	Total numbers	Leopard		All predators	
		Number killed	Jacobs' index	Number killed	Jacobs' index
Cattle	2515	30	-0.05	13	-0.89
Goats	4289	46	0.02	175	-0.40
Sheep	2375	23	-0.17	344	0.16
Ostriches	12159	4	-0.97	298	-0.74

Of the 34 stock farmers interviewed, 24 had herds of sheep or goats (hereafter referred to as small stock). Twelve farmers either used or had recently employed a herder, while seven used livestock-guarding dogs (all of these were Anatolian shepherd dogs). Farmers that used either a herder or a dog tended to have larger small stock herds (mean = 409.5 ± 405.5). The majority (73.7%) of these

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

farmers kept their stock in a kraal at night, and all but two kept lambs confined to a predator-proof kraal.

Nine small-stock farmers used neither herders nor dogs to protect their stock, but kept their small stock in a kraal at all times ($n=2$) or at night ($n=7$). These farmers had an average herd size of 91.3 (± 83.6) small stock, significantly less than farmers that used herders or dogs ($F_{1,22}=5.31$, $p=0.03$). Stock farming was the main source of income for six of these farmers, although small stock accounted for less than 50% of the value of their total stock holdings, the remainder being made up of less vulnerable species such as cattle and ostriches.

Herders usually guarded larger herds (mean = 235 ± 165.3) than dogs (mean = 193.5 ± 189.8), although the difference between herd sizes was not significant ($t=0.49$, $df=17$, $p=0.62$). There was significant difference in opinion on the efficacy of herders ($t=3.14$, $df=19$, $p<0.01$); respondents who employed herders gave them a mean ranking of 4.25 (± 1.14 , $n=12$) on a five-point Likert scale, while other respondents perceived herders as being far less effective, assigning a mean ranking of 2.56 (± 1.26 , $n=10$). There was far greater consensus about the effectiveness of guardian dogs; farmers who used them ranked them highly on the five point Likert scale (4.29 ± 0.49 , $n=7$), and other farmers also viewed them favourably (mean ranking 4.00 ± 0.00 , $n=9$).

6.4.7 Perceptions of CapeNature

Thirty-one of the 53 respondents (58.9%) said that they had suffered damage due to wildlife. Of these, 18 (34.0%) had reported damage-causing wildlife incidents to CapeNature, of which 12 (66.7%) had a CapeNature representative physically investigate the incident. Of the 35 respondents who had not reported wildlife problems, 13 respondents had suffered damage from wildlife, while another 13 considered at least one wildlife species to be a pest, although they had not suffered any actual damage. These two groups accounted for 74.8% of the respondents who had not reported wildlife damage to CapeNature. Respondents who genuinely had no wildlife-related problems comprised a small minority (nine respondents, 17.0%).

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

Respondents who had reported losses to CapeNature were evenly split on the question of whether CapeNature did a good job of managing damage-causing animals. Equal numbers of respondents answered 'Yes' and 'No' (n=8, 44.4%), with a further two undecided. The majority of the group had not reported damage to CapeNature were undecided (n=18, 51.4%), but slightly more respondents (n=9, 25.7%) viewed CapeNature's management of damage-causing animals negatively than positively (n=8, 22.9%). Differences in perception of CapeNature's management efficacy were significantly different ($\chi^2=62.7$, df=2, $p<0.01$). When respondents who were unsure or had neutral attitudes about CapeNature's management were removed from the sample, the differences in perception between groups who had reported damage and those who had not were not significant ($\chi^2=0.4$, df=1, $p>0.54$). Despite the generally ambivalent perceptions of CapeNature's current management, the majority of respondents in both groups (66.7% of the reported group, 60% of the not reported group), felt that CapeNature should continue to be responsible for managing damage-causing animals. Previous reporting of damage-causing incidents did not result in any significant difference between the number of respondents who felt that CapeNature should continue to manage damage-causing animals and those who felt that damage-causing animals should be managed by another group or organisation (Fishers exact test, $p=1.0$).

In response to the question on the type of assistance that they would like from CapeNature, 15 respondents wanted CapeNature to remove problematic wildlife, 23 wanted advice on how to reduce damage and implement their own management actions and three respondents wanted CapeNature to provide compensation for damage caused by wildlife. Five respondents requested subsidies to improve management and livestock husbandry practices. Other forms of assistance requested were for CapeNature to assist with the control of invasive alien vegetation (one respondent) and for more assistance to aid the introduction of game species to private property (two respondents).

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

6.4.8 Conservation index

For all landowners, a set of ten candidate variables were assessed; total damage, knowledge, landowner type, age, years owned, introduced game, PA perimeter, area(log-transformed), education level and stock role. The total damage and knowledge index variables had the highest AIC_c weight, although this was very low (see Table 6-12).

Table 6-12. The top five subsets of variables used to predict conservation index score for all landowners. Subsets are arranged in descending order according to AIC_c weight. 'Total damage' represents the total cost of damage caused by wildlife, 'Knowledge' represents the landowner's knowledge index score. The 'Tourism' variable denotes whether the landowner generates income from tourism (yes/no), 'PA perimeter' is the percentage of the property boundary shared with a nature reserve of conservancy. 'Years owned' is the number of years that the landowner has owned (or been living on) the property.

Variable	Variable	Variable	Degrees of freedom	AIC _c	ΔAIC _c	AIC _c weight
Total damage	Knowledge		2	229.903	0	0.072
Total damage	Knowledge	Tourism	3	230.067	0.164	0.067
Total damage			1	230.737	0.834	0.048
Total damage	Knowledge	PA perimeter	3	230.845	0.942	0.046
Total damage	Knowledge	Years owned	3	230.856	0.952	0.035

The models were averaged to estimate the relative importance of variables. Total damage (square root) scored highest (1.000), followed by knowledge (0.402) and tourism income (0.202). A GLM was fitted using total damage, knowledge and tourism as predictor variables. Attitude towards conservation was significantly negatively affected by total damage sustained ($F_{1,49}=14.46$, $p<0.01$) and positively influenced by knowledge ($F_{1,49}=4.22$, $p<0.05$). The tourism variable did not have a significant effect ($F_{1,49}=1.47$, $p=0.23$). The model had low explanatory power ($r^2=0.31$) for attitudes towards conservation by respondents.

For stock farmers, a set of nine candidate variables were assessed; total damage, knowledge, age, years owned, introduced game, PA perimeter, education level, stock role and stock value. The subset

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

of age and years owned was selected as the best combination of variables (see Table 6-13), but the AIC_c weighting was low (0.08), indicating low explanatory power.

Table 6-13. The top five subsets of variables used to predict conservation index score amongst stock farmers. Subsets are arranged in descending order according to AIC_c weight. The age of the landowner is represented by the 'Age' variable, while 'Years owned' is the number of years that the landowner has owned (or lived on) the property. 'Stock value' gives the total value of the landowner's livestock holdings, while total damage is the cost of all damage caused by wildlife.

Variable	Variable	Degrees of freedom	AIC_c	ΔAIC_c	AIC_c weight
Age	Years owned	2	151.153	0	0.083
Age		1	151.823	0.671	0.059
Years owned		1	152.333	1.181	0.046
Stock value		1	152.685	1.532	0.039
Total damage		1	152.708	1.556	0.038

The weightings of individual variables were also low, with age ranked the highest (0.320), followed by years owned (0.273) and total damage (0.193). Nevertheless, I fitted a GLM using age and years owned as predictor variables for conservation index. Neither the age of the farmer ($F_{1,31}=2.71$, $P=0.11$), nor the number of years that the farmer had owned the property ($F_{1,31}=2.29$, $p=0.14$) had a significant effect on the conservation index score. The model explained very little variation in conservation index scores amongst stock farmers ($r^2=0.11$).

6.4.9 Knowledge index

Knowledge index scores were similar for all groups, and generally quite high, with a mean score of 10.11 (± 1.30) out of a maximum score of 14. Stock farmers had the lowest mean knowledge index score (9.84 ± 1.31), while game farmers had the highest (10.8 ± 1.14). Crop farmers and recreational landowners had mean scores of 10.6 (± 1.10) and 10.4 (± 1.35) respectively. There was no significant difference between the knowledge index scores of difference landowner groups ($F_{3,51}=1.33$, $p=0.27$).

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

6.5 Discussion

6.5.1 Damage-causing wildlife

The results of my study show generally high levels of conflict with predators and other potentially damage-causing wildlife in the Little Karoo. Stock-loss rates were high, regardless of whether livestock were the main or a supplementary source of income. The mean stock loss rate of 6.59% is substantially higher than losses of 2.77% reported in a similar study in the north-west of South Africa (Thorn et al. 2012), the 1.4% reported in Namibia (Marker et al. 2003a), 2.2% in Botswana (Schiess-Meier et al. 2007; Hemson et al. 2009) and 4.5% in Tanzania (Holmern et al. 2007). However, the percentage of stock farmers who reported suffering extremely high losses (10% or more) was similar, 14.75% for this study compared to 17% reported by Thorn et al. (2012). While studies elsewhere in Africa have typically focused on livestock losses due to large predators such as lions (*Panthera leo*), leopards and spotted hyaenas (*Crocuta crocuta*) (Ogada et al. 2003; Kolowski & Holekamp 2006; Holmern et al. 2007; Schiess-Meier et al. 2007), the bulk of livestock depredation in my study area was by jackals, a similar result to that found by Thorn et al. (2012). Jackals are highly adaptable generalist species that readily persist in heavily disturbed areas, despite continuous persecution (Beinart 1998; Nattrass & Conradie 2013).

Jackals may also have benefitted from meso-predator release following the extirpation of many large carnivores from the Little Karoo by the mid-19th century (Beinart 1998; Skead 2011). Meso-predator release has been defined as, 'the expansion in density or distribution, or the change in behaviour of a middle-rank predator, resulting from a decline in the density or distribution of an apex predator' (Prugh et al. 2009). The introduction of exotic, predator-naïve small stock to the Little Karoo may have facilitated the success of jackals by providing an abundant, predator naïve and easily accessible food source (Beinart 1998; Prugh et al. 2009). Jackals are thus likely to have benefitted from the simultaneous removal of top-down (i.e. superior predators) and bottom-up (i.e. food availability) constraints. Attempts have been made to restore top-down control of the jackal population through lethal control. However, effective control of meso-predators often requires intensive, sustained

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

action, which is expensive (Goodrich & Buskirk 1995). Jackals are known to be able to recover quickly after 'spot' culling events, suggesting that a sustained culling effort would be required to effectively control their population (Bingham & Purchase 2002). Jackals, caracals and baboons have endured centuries of human persecution in South Africa, suggesting that their behavioural plasticity makes them difficult to eradicate (Cardillo et al. 2004). Nevertheless, my results suggest that farmers who suffered greater losses were generally more knowledgeable about wildlife. Much like the surviving wildlife, farmers in the Little Karoo have also gained considerable experience in conflict situations, and their (albeit largely anecdotal) knowledge should not be discounted without strong evidence to the contrary (Sillero-Zubiri et al. 2007).

The implementation of successful lethal control measures is confounded by the high prevalence of protected areas or conservancies within the study area. Most farms share a boundary with such an area, and these are likely to provide a constant source population of wildlife that can disperse onto productive farms (Bothma 2002; Ray et al. 2005). Farmers are aware of this, and frequently made the association between a change in land-use from stock farming to other uses with an increase in predators and associated losses. Although extensive efforts have been made to control or even eliminate jackals within the Western Cape (Beinart 1998; Nattrass & Conradie 2013), these appear to have lacked the intensity required to reduce stock depredation by jackals, particularly in the absence of government subsidies or other incentives (Beinart 1998; Nattrass & Conradie 2013). This support is unlikely to be forthcoming, particularly given the controversy caused by the mere issuing of permits for lethal control of predators (<http://mg.co.za/article/2012-03-16-zille-attacked-over-predator-cull>, accessed 1 December 2013). Lethal control methods, used in isolation, are therefore unlikely to reduce losses to a level acceptable to farmers.

Baboons were the species most likely to be identified as a pest by respondents in my study. Much like jackals, baboons may also benefit from meso-predator release extending their home ranges into low-lying flat areas where they can exploit young stock and crops (Prugh et al. 2009). Baboons

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

caused damage in a wide variety of ways, including crop-raiding, damaging plants (e.g. vines, fruit trees) and infrastructure, killing young sheep and goats, breaking ostrich eggs and raiding ostrich feed. All respondents who identified baboons as a pest suffered some form of economic damage from baboons, suggesting that negative perceptions of baboons may have been caused by negative experiences rather than prejudice.

Despite widespread negative sentiment towards baboons, and the broad variety of landowners who suffered baboon damage, few landowners had instituted any consistent means of controlling or mitigating baboon damage on their land. The reasons for this are unclear, but are likely to be linked to the sheer difficulty and high effort required to effectively exclude baboons from an area (Prugh et al. 2009; Brashares et al. 2010; Kaplan 2013). The majority (86.7%) of landowners sporadically instituted measures such as shooting, chasing baboons away or catching and shooting baboons in cage traps, but of these, only one landowner actually monitored the baboon population on his property and instituted lethal control measures when he felt that the population was growing too large. All other control measures were instituted on a purely reactive basis, either in response to the landowner encountering baboons on his property, or to damage to property. Two landowners who complained of baboon damage instituted no control measures at all. Only two landowners had instituted preventative measures against baboon damage in the form of electric fencing around vineyards (one landowner) or employing workers specifically to guard orchards against baboons (one landowner). Both landowners found that their respective measures were effective in reducing damage caused by baboons and the latter respondent also intends to build electric fences around his orchards. Electric fencing has been found to be a particularly effective means of excluding baboons from dense residential areas with high food rewards (Kaplan 2013), but the relatively large capital investment required to construct baboon-proof fencing is likely to deter the majority of farmers from implementing this option. One respondent claimed to have abandoned apricot farming due to baboon raiding, with a resultant opportunity cost of \$US 17 647 per annum. In situations such as

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

this, where high-value crops are grown in a relatively small area, the cost-benefit ratio of electric fencing would favour this method.

Damage caused by passerine birds represents a particularly interesting case of potential conflict between different types of agriculture. While not formally monitored, a number of respondents linked growth in passerine bird populations to the availability of ostrich feed. This phenomenon has been recorded in the Eastern Cape province of South Africa (Whittington-Jones 1997) and was associated with increased damage to seasonal fruit such as grapes (*Vitis vinifera*). In 2011, an outbreak of H5N2 avian influenza amongst farmed ostriches in the Little Karoo caused a halt in ostrich meat exports and the culling of 40 000 birds in an attempt to contain the disease (Howerth et al. 2012; Van Helden et al. 2012; Mather 2014). The ban on meat exports caused many farmers to abandon, or reduce the scale of their ostrich farming activities (pers. obs.). This reduced the amount of feed available to birds, and there was a noticeable decline in the passerine bird population around Calitzdorp (pers. obs.). Most of the respondents who complained of passerine bird damage were located in the vicinity of ostrich farms, and two respondents felt that they had suffered reduced losses since 2011, when the avian influenza outbreak occurred.

Ostriches were widely farmed in my study area (20 respondents), and it is likely that most ostrich farmers suffered losses as a result of the ban of meat exports, which is estimated to have cost the ostrich industry in excess of \$US 117.5 million

(<http://www.farmersweekly.co.za/news.aspx?id=33627&h=Ostrich-industry-on-the-rebound>,

accessed 22/11/2013). The outbreak was discovered in March 2011, and meat exports were halted immediately (Van Helden et al. 2012). All interviews with stock farmers occurred while the export ban was in place, but few stock farmers identified disease as their biggest problem. Rather, predators were most frequently cited as the biggest problem, and also received the highest mean score on a Likert scale of problem severity. These results may have been influenced by stock farmers who did not farm ostriches, but these were a minority amongst the stock farmers interviewed (14

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

respondents, 41.2%). The remaining 58.8% of stock farmers were thus affected by the avian influenza outbreak, which makes the overall trend of predators being perceived as a greater threat than disease rather puzzling. Viewed in isolation, ostrich farmers gave disease a mean score of 1.81 (± 1.25) on a five-point Likert scale of threat severity, while predators scored a mean of 3.57 (± 1.29).

It is difficult to assess whether economic losses due to predation genuinely exceeded those caused by the avian influenza outbreak. Ostrich farmers were still able to generate some income from ostriches through the sale of feathers from live birds, although this tended to reduce reproduction rates amongst plucked birds (Richard Barry, ostrich farmer, pers. comm.), and a relatively low proportion (2.5%) of the ostrich population were lost to predators compared to other stock types. Furthermore, only one farmer that I interviewed actually had his ostriches slaughtered due to the influenza outbreak, and received compensation (albeit at less than market value), while most other farmers scaled back ostrich farming activities and accepted significantly reduced profits until the influenza outbreak had been controlled. Predator damage on other stock types may have exacerbated the financial pressure on ostrich farmers already struggling due to the influenza outbreak. Nevertheless, the example of ostrich farmers suggests that stock farmers may have exaggerated perceptions of the degree to which predators threaten their livelihoods relative to other threats. A similar trend was observed in the North-West province of South Africa, where farmers tended to perceive predation pressure as disproportionately high, given actual stock-loss rates (Thorn et al. 2012). A possible explanation for this trend is that predator damage is a highly visible manifestation of economic loss in comparison to more subtle, yet potentially more damaging factors such as drought or disease (Rasmussen 1999; Schumann et al. 2012). Nevertheless, the perception of high predator damage is important, as behaviour is driven by perceived losses, regardless of the actual magnitude of losses (Mishra 1997; Schumann et al. 2012). This means that reduction in livestock depredation levels does not always result in a corresponding increase in tolerance of the species responsible (Marker et al. 2003a). Exposing gaps between perceived and actual threat levels may be helpful in reducing conflict (Dickman 2010), but landowners who are

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

directly reliant on their property for income are less likely to consider the aesthetic and intrinsic value of wildlife (Daley et al. 2004). Tolerance of wildlife damage is likely to remain low given the increasingly marginal profits derived from stock farming in an arid area such as the Karoo (Nattrass & Conradie 2013).

Landowner tolerance of leopards appears greater than that of other potential pest species. This may provide some indication of the amount of damage farmers are prepared to accept from a predator before resorting to lethal control methods. There are, however, several problems with using leopards as a proxy for broader tolerance of damage-causing wildlife. The first is that leopard distribution is geographically restricted within the Little Karoo (see Chapter 3), and there is thus a strong possibility that many farmers suffered no leopard damage because there was simply no overlap between leopards and the economically active portion of the farmers property. My position as a representative of the Cape Leopard Trust may also have influenced landowners to exaggerate their tolerance of leopards for my benefit, which could have influenced these results. However, my study found that respondents who were exposed to leopard damage had significantly lower tolerance of wildlife than stock farmers, the group least tolerant of predators. In general, farmers owning livestock and living close to felids are most likely to be affected by them and this may affect their tolerance (Holmern et al. 2007; Hemson et al. 2009).

Even within their preferred habitat, leopards tend to be less visible than other potentially damage-causing wildlife (pers. obs.). This is a consequence of the generally cryptic nature of leopards and their low population density within the Little Karoo (see Chapter 4). Highly visible species are more likely to be perceived as threats and persecuted (Naughton-Treves 1997; Naughton-Treves & Treves 2005; Dickman 2010). Baboons and jackals are frequently detected by farmers in the Little Karoo; either by sight or by their loud, distinctive calls. In contrast, leopards are rarely seen, and even leopard sign is infrequently detected due to the hard, rocky ground that characterises much of the Little Karoo. Consequently, leopards are (correctly) perceived as being rare, and appeals from

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

CapeNature and NGOs such as the Cape Leopard Trust of the need to protect leopards are likely to be deemed more credible than similar calls to reduce jackal or baboon persecution. Baboon depredation by leopards also contributes to greater tolerance, as leopards are commonly viewed as the only natural enemy of baboons in the area (Pienaar 1969; Cowlshaw 1994). These factors may explain why there was near-universal acceptance of continued conservation of leopards, even amongst landowners who had previously experienced leopard damage.

6.5.2 Livestock husbandry practices

Sheep were the most depredated livestock type relative to the total number owned by respondents, and also had the highest Jacobs' index score of all stock types. This vulnerability was not reflected in husbandry measures; sheep were typically less protected than goats, which suffered lower depredation rates. These results suggest that protecting sheep to the same degree as goats could substantially reduce losses, however protecting sheep may be more difficult to accomplish due to behavioural differences between sheep and goats. Dorper sheep are the most popular breed in the Little Karoo due to their tolerance of relatively unpalatable grazing resources and high meat yield (Brand 2000). However, Dorper sheep do not have a strong flocking instinct, and thus tend to spread out over a large area making their management with either herders or guard dogs less efficient and hence effective (G. Laubscher, C. Fourie, D. van der Vyver, pers. comm.). Livestock depredation risk has been shown to be higher in areas with dense bush, presumably because this limits the ability of the dog or herder to monitor all individuals and to detect predators (Woodroffe et al. 2006), and it is likely that having to monitor a flock of sheep dispersed over a broad area would have a similarly negative effect on the efficacy of these husbandry measures.

Farmers who did not use herders tended to view them with suspicion, raising concerns about stock theft, the poaching of game by herders, and simply a lack of workers who would be willing to undertake such a physically arduous task. Other farmers felt that employing herders was not financially viable due to current labour laws, a factor that has probably contributed to a decline in the use of herders throughout the Western Cape (Nattrass & Conradie 2013). Farmers who use

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

herders viewed them in a more favourable light, but tended to farm in more accessible areas where the herder could return the stock to a kraal each evening. Two farmers who used herders said that the herder's main purpose was to prevent stock from wandering off, although both conceded that herders probably helped to prevent stock theft and depredation. Other farmers noted that the expense of employing a herder could only be justified if there was a suitably large herd of stock to protect. While herders undoubtedly offer a potentially effective means of preventing livestock depredation (Ogada et al. 2003; Woodroffe et al. 2006), 50% of small stock farmers viewed them as an unfeasible option. While more stringent labour laws (e.g. The Basic Conditions of Employment Act, No. 75 of 1997) in South Africa have certainly contributed to this, changes to land-tenure legislation (the Extension of Security of Land Tenure Act (no. 62 of 1997)) in South Africa have also made many farmers reluctant to allow workers to live on their farms due to the increased difficulty in evicting workers and their families should they no longer be needed (Crane 2006; Cousins & Hall 2011). Livestock herding thus runs counter to prevailing socio-political trends in South African rural areas, and it is unlikely that herders will be used on a broad scale without legislative changes or some other external intervention, such as subsidies for herders from conservation agencies or meat retailers.

Livestock-guarding dogs were viewed positively by both farmers who used them, and those who did not. Dogs have previously been shown to be an effective means of protecting stock from wildlife depredation (Marker et al. 2005; Gehring et al. 2010; Potgieter et al. 2013) and have generally been perceived to be a satisfactory stock protection measure by farmers (Marker et al. 2005; Potgieter et al. 2013). Most farmers reported a dramatic reduction in stock losses following the introduction of livestock-guarding dogs. Some respondents raised concerns about the impact of the dogs on game species, although perceptions of the degree of impact varied amongst respondents. Some respondents felt that the dogs would occasionally chase, but seldom catch, small game, while others suspected that the dogs regularly killed game. Although farmers took a negative view of their dogs chasing ungulates and lagomorphs, the killing of jackals was greeted with universal approval. It is

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

possible that the tendency to chase game varied between individual dogs as exemplified from research in Namibia where only 15% of livestock-guarding dogs chased wildlife (Potgieter et al. 2013).

Of greater concern to farmers was the possibility of the dogs chasing and killing livestock, particularly ostriches. Two of the farmers who used livestock-guarding dogs to protect small stock also farmed with ostriches, but the remainder either had no ostriches or just a small breeding group confined to a small area. Ostriches are easily startled, and can sustain serious injuries from running into fences, after which they are often euthenased by the farmers. While some farmers claimed to have habituated their dogs to ostriches by training them while young, others had euthenased dogs after they had been seen chasing ostriches on neighbouring farms. A further behavioural problem associated with livestock-guarding dogs is the dog staying at home rather than accompanying stock in the field (Marker et al. 2005; Potgieter et al. 2013). Only one respondent had a single dog that remained at home, but this respondent was, however, generally satisfied with the performance of his other dogs, and was breeding dogs to sell to other farmers in the area.

In comparison to herders, livestock-guarding dogs appear to represent a relatively uncomplicated and effective means of protecting stock. Although promoted by the Cape Leopard Trust, livestock-guarding dogs appear to have gained popularity due to their perceived efficacy at protecting stock, rather than due to farmers wishing to act in a conservation-friendly manner (pers. obs.). Farmers who used livestock-guarding dogs also tended to have either abandoned or greatly reduced their use of leg-hold traps, poison and other lethal control measures that could impact on a wide range of wildlife. Training methods seemed to vary between farmers, and may have explained some of the perceived behavioural variation experienced by different respondents. Undesirable behaviour in livestock-guarding dogs can often be corrected with appropriate training (Marker et al. 2005), and farmers in the Little Karoo may benefit from formal instruction in livestock-guarding dog training,

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

either through a workshop or training seminar, or through the provision of dogs from a centralised and professional breeding centre.

Despite long-standing concerns over their contribution to veld degradation and the spread of disease (Beinart 2008), the use of kraals remains widespread in the Little Karoo. In contrast to other parts of Africa, where carnivores are able to break into kraals or cause cattle to stampede out (Ogada et al. 2003; Schiess-Meier et al. 2007; Hemson et al. 2009), depredation of kraaled stock in the Little Karoo appears to be rare. Kraals were usually used in conjunction with either a herder or a livestock-guarding dog, and less than 30% of small stock farmers used kraals without employing some other form of protection. This suggests that for the majority of farmers in the Little Karoo, the use of kraals alone is not sufficient to keep small stock depredation at acceptable levels. Daytime depredation of stock was often reported, and one respondent claimed to have lost an entire herd (30 sheep) to daytime depredation, despite keeping the sheep kraaled each night.

Ostriches and cattle were depredated at much lower rates than small stock, and husbandry effort was typically much lower. Ostrich egg depredation by jackals and baboons was a major problem that farmers sought to mitigate by collecting eggs at regular intervals. Egg collection was hampered by difficulty in locating nests, and concern that collecting eggs too frequently could lead to ostriches abandoning the nest. Some farmers had experimented with placing deterrents, such as pipes around nests, or using bright lights to deter jackals, but found that these methods became less effective over time, presumably as jackals became habituated to the various deterrent measures. One respondent claimed to have had great success using a '*jakkalsjaer*' (literally translated as 'jackal-chaser'), an electronic shepherd device that intermittently plays radio or a siren, combined with flashing light to disorientate and deter predators. This method is relatively cheap to implement, and may work on a broader scale. More expensive measures, such as electrifying fencing around the often-extensive breeding camps are likely to be effective (Breitenmoser et al. 2005; Kaplan 2013), but may be too expensive to represent an attractive option to most farmers (Woodroffe et al. 2006).

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

Ostrich chicks, which are vulnerable to a range of smaller predators, such as yellow mongoose (*Cynictis penicillata*), meerkat (*Suricata suricatta*) and pied crows (*Corvus albus*) as well as jackals and caracals, were typically well-protected in small, predator-proof enclosures located close to human habitation.

Cattle appear to be immune to depredation by all predators other than leopards, and husbandry effort was correspondingly low. Cattle are typically allowed to wander in large camps, hundreds of hectares in size with no supervision other than occasional counts that were typically done every two weeks. These camps often encompass mountainous areas where there is overlap with existing leopard habitat (see Chapter 3). Although leopards undoubtedly do predate on cattle (see Chapter 5), quantifying the true depredation rates by leopards is difficult, as farmers are seldom able to locate the carcasses of missing cattle. There are a number of other factors that could cause cattle to go missing, such as falling and injuring themselves in difficult mountainous terrain, mortality from snake bites or exposure, roaming off the property through poorly maintained fences and stock theft. Most farmers are willing to accept these as potential causes of cattle disappearance, but consider leopard depredation to be the most likely cause of these losses (pers. obs.). Azevedo & Murray (2007) found that predation accounted for only 19% of mortality of cattle in Brazil, and a similar trend may occur in my study area, although this is difficult to quantify without intensive monitoring of cattle. Less than half of the cattle presumed to have been depredated in this study could be attributed to leopards without reasonable doubt, but even if leopards were responsible for all losses, the overall depredation rate of 0.5% of standing stock is relatively low, and similar to that observed in Brazil (Azevedo & Murray 2007).

When predators prey upon species that are difficult to catch and subdue, they are more likely to target sub-standard individuals (Temple 1987). As solitary felids, leopard prey selection is likely to be selected by size, and they are thus more likely to predate upon smaller individuals of larger species, such as cattle (Temple 1987; Hayward et al. 2006). Although I did not gather data on the relative

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

proportions of calves compared to adult cattle in herds, calves accounted for at least one third of the cattle killed (two farmers who had lost 17 head of cattle between them did not specify how many were calves), and are likely to be more vulnerable to leopard depredation than adult cattle. Disproportionate calf depredation by jaguars (*Panthera onca*) has been recorded in South America (Hoogesteijn 2001; Polisar et al. 2003; Michalski et al. 2006; Azevedo & Murray 2007).

It is likely that conflict between cattle farmers and leopards will persist in this area given that free ranging cattle provide local farmers with the only means of exploiting the large tracts of mountainous land on their farms. Herders are likely to provide the best means of protecting cattle from large predators (Ogada et al. 2003; Kolowski & Holekamp 2006), but are unlikely to be a practical solution given the issues discussed above, and the remote and difficult mountainous terrain. Restricting young calves (up to a minimum of three months old) to a better-protected pasture away from preferred leopard habitat (mountainous areas) or close to human habitation is arguably the most sensible way of reducing current depredation rates (Ackerman et al. 1984; Hoogesteijn 2001; Polisar et al. 2003; Michalski et al. 2006). These precautions, combined with a more synchronised breeding season will allow for more efficient management of calves (Hoogesteijn 2001; Polisar et al. 2003). Polisar et al. (2003) recommend only allowing cattle over one or two years of age into areas where predation risk is high, and to use these areas for only bulls or horned cows that are better able to defend themselves. Protection of wildlife populations has also been proposed as a means of reducing stock depredation by ensuring that there are adequate alternative natural prey resources (Hoogesteijn 2001; Polisar et al. 2003).

6.5.3 Formal conservation perceptions

Conservation conflicts have been defined as, 'situations that occur when two or more parties with strongly held opinions clash over conservation objectives, and one party is perceived to assert its interests at the expense of another' (Redpath et al. 2013). While wildlife conflicts may be viewed as a natural consequence of competition between humans and wildlife for access to resources, conservation conflicts occur between groups of people (Redpath et al. 2013). As the government-

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

mandated conservation authority, CapeNature is responsible for the conservation and management of wildlife in the Little Karoo. This potentially puts them in conflict with landowners who suffer damage from wildlife. Conflict between CapeNature's conservation mandate and agricultural land-uses has previously hampered implementation of large-scale conservation plans in the Gouritz Corridor, an area of 33 000 km² extending from the Swartberg Mountains to the Indian Ocean, of which the Little Karoo forms an integral part (Lombard et al. 2010). Landowner perceptions of CapeNature are thus an important indicator of the degree of conservation conflict in the area, and understanding and improving relationships between private landowners and government conservation agencies is a critical aspect of implementing effective conservation plans in the area.

The vast majority of respondents had suffered annual wildlife-related damage and considered select species to be pests. Landowners typically did not report damage to CapeNature for two reasons; either the landowner felt that the problem was not severe enough to be worth reporting, or the landowner felt that nothing would be gained from involving CapeNature, and that it would be better to attempt to resolve the problem without official assistance. Opinions of the efficacy of CapeNature's management were generally ambivalent when viewed as a whole, although some landowners had strongly negative opinions of the current management strategy.

The conservation perception index, which measured attitudes towards conservation organisations, showed a negative relationship with the total amount of wildlife damage sustained. This suggests that farmers who suffered greater amounts of damage were typically less confident in the ability of conservation authorities to effectively manage damage-causing wildlife. No clear pattern emerged amongst stock farmers, suggesting considerable unexplained variation in attitudes towards conservation authorities.

A common sentiment amongst respondents was that legal protection of predators, in particular, is excessive, with the implication that this is either causing them to act illegally or preventing them from reacting to wildlife damage. Farmers suffering severe levels of damage are more likely to resort

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

to lethal control measures (McIvor & Conover 1994), and the current lack of financial and/or infrastructural support for lethal control methods is likely to be a major contributor to landowner frustration (Nattrass & Conradie 2013).

The ban on the use of certain forms of lethal control, such as poison and leg-hold traps without a permit is likely to be perceived by some farmers as an imposition of a conservation agenda that they consider unfair due to the failure of CapeNature to effectively prevent wildlife damage to their crops and livestock. Conservation practitioners may use legislation to impose their interests on other groups, which may lead to conservation success, but also often results in conflict (Redpath et al. 2013) and resentment when they are perceived to prevent the implementation of reasonable measures to protect stock or crops, and can lead to illegal retaliation (Naughton-Treves 1997; Zimmermann 2004; Kolowski & Holekamp 2006; Linkie et al. 2007; Mateo-Tomas et al. 2012). Customary law dictates that farmers provide compensation for any damage done by stock on a neighbouring property (Naughton-Treves 1997), and that they institute appropriate measures to contain their own animals. Stock farmers were more likely than other groups to believe that conflict levels were increasing, and most attributed this to an increase in predator numbers, often brought about by a shift from agricultural land use to protected areas or game farms. While game farms and other non-productive land owned by private individuals are perceived to be part of the problem, these individuals do not impose legal restrictions on farmer's actions in the same manner as government agencies. Damage caused by animals perceived to be 'belonging' to the Government (or in this case, CapeNature) is thus particularly resented (Naughton-Treves 1997) as it is perceived as a failure on CapeNature's part to adequately contain or control 'their' animals.

While leopards appear to be regarded with more tolerance than other predators, some farmers who experienced leopard damage expressed frustration at CapeNature's management of damage-causing leopards. CapeNature's formal protocol (Theresa van der Westhuizen, CapeNature Conservation Services, pers. comm.) for dealing with damage-causing leopards involves visiting the

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

farm concerned and inspecting the damage within 24 hours of the loss being reported. Prior to any attempts to capture the leopard concerned, mitigating measures such as the deployment of a *jakkalsjaer* or bell collars must be implemented. If available, camera traps may be deployed to attempt to identify the 'problem' leopard. If the problem continues despite mitigation measures, a trapping permit may be issued, and a cage trap deployed for a limited period of up to five days. Upon capture, the leopard is immobilised and examined by a veterinarian. If the leopard is considered to be incapable of hunting natural prey, either due to age or injury, the official in charge of trapping the leopard will inform the Wildlife Advisory Committee through the Wildlife Program Manager and Area Manager. The Wildlife Advisory Committee may then submit a recommendation for euthanasia to the Executive Director of CapeNature. Otherwise the leopard is released in the same area in which it was captured, with the expectation that the negative experience of being captured will cause it to avoid the area in future. Although this policy was formalised in July 2013, it differs little from the policy followed from 2010 to 2012, during which I accompanied CapeNature representatives to several of these incidents.

This policy appears to have a firm scientific basis. Indiscriminate removal of individuals may exacerbate conflict by allowing more leopards to move into the area (Bailey 1993), and translocating leopards has been shown to be problematic (Athreya 2006; Athreya et al. 2011). The risks involved in removing leopards has been poorly communicated to farmers, some of whom view conservation authorities as 'leopard apologists', who are unwilling to sanction the killing of leopards regardless of the situation. This perception may have some basis in fact; in January 2011 I was informed of an incident in which two Welsh ponies had been attacked by a leopard, one of which was killed. The attack occurred close to the farmer's house, and he expressed concern about the safety of his young children. The leopard was subsequently captured by CapeNature personnel and immobilised by a veterinarian. Upon inspection it was apparent that the leopard's canines had been almost entirely worn down, suggesting extreme age (Stander 1997). However, despite the attending veterinarian recommending that the leopard be euthenased, CapeNature officials opted to release the leopard,

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

allegedly in a wilderness area approximately 10 km from the farm. The farmer identified leopard tracks on his property less than 48 hours later, and assumed that the same leopard had returned. I subsequently visited the farmer on several occasions, and he reported no further damage. However, he was extremely hostile towards CapeNature, as he viewed their management actions as having potentially threatened his family's safety. While this was a single, isolated incident, many farmers were subsequently made aware of what had happened and are likely to have developed negative perceptions of CapeNature as a result.

The controversy surrounding leopard management has been exacerbated by strong criticism of CapeNature by conservation NGOs on occasions when leopard kill permits have been issued (<http://www.iol.co.za/news/south-africa/western-cape/fur-flies-over-illegal-leopard-killing-1.1191728#.UpR2rcSjySo>, accessed 26 November 2013). The public pressure resulting from this incident could potentially cause CapeNature to issue fewer permits to kill leopards in future, and the somewhat unwieldy process in authorising the euthanasia of trapped leopards appears indicative of a desire to avoid the controversy that accompanies leopard euthanasia. However, selective removal of 'problem' leopards may increase approval of protecting the species as a whole (Treves & Karanth 2003). This particular aspect of the conflict highlights differences in perceptions of wildlife between farmers and the non-farming, urban community, who are less likely to endorse lethal control methods (McIvor & Conover 1994). While there would be fewer legal killings of leopards in the Western Cape, there may be a compensatory increase in illegal retaliatory leopard killings unless there is a substantial reduction in actual conflict (e.g. Bangs et al. 2005). Legal permission, in the form of a permit, is not thought to significantly influence the willingness of South African farmers to kill predators (St John et al. 2011).

Nevertheless, several stock farmers expressed a desire for greater co-operation with CapeNature and felt that greater dialogue between the CapeNature and farmers would improve relationships and wildlife management. Stakeholder participation has been shown to be effective in building

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

stronger relationships, improving levels of trust between parties and ultimately in reducing conflict (Ansell & Gash 2007; Jones-Walters & Çil 2011; Redpath et al. 2013). While livestock predation may represent a local conservation conflict, effective management of this conflict may be hampered by provincial and national legislation and policies (Young et al. 2010). The recent (2012) formation of the Predator Management Forum

(<http://www.capenature.co.za/news.htm?sm%5Bp1%5D%5Baction%5D=content&sm%5Bp1%5D%5Bcntid%5D=2080&sm%5Bp1%5D%5Bpersistent%5D=1>, accessed 26 November 2013), a collaborative initiative between CapeNature, agricultural organizations, researchers and various other NGOs has provided a platform for engagement between farmers and the authorities. In August 2013, the Predator Management Forum produced draft guidelines for the management of damage-causing jackals, caracals and bushpigs (*Potamochoerus larvatus*) in the Western Cape, which have been endorsed by CapeNature. While conservation conflicts are seldom resolved (Redpath et al. 2013), this is an important step in improving trust and relations between the conservation and agricultural fraternity. This important step should be matched by greater engagement between CapeNature and farmers at a local scale.

6.6 Conclusion

This chapter examined three elements of human-wildlife conflict; the losses experienced by landowners and their willingness to tolerate such losses, the effectiveness of the husbandry measures implemented to reduce losses, and the relationship between landowners and the regional conservation authority. Stock losses in the Little Karoo appear relatively high compared to other areas, but may be a consequence of inadequate or ineffective livestock husbandry practices. The continued reliance on lethal control as the default response to livestock losses may also be a contributing factor, as the increasingly patchy application of lethal control methods is likely to have drastically reduced their efficacy. The implementation of lethal control measures is likely to remain a contentious issue between farmers, conservation groups, and the broader public. The general satisfaction amongst farmers who have implemented husbandry measures such as livestock-

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

guarding dogs and herders suggest that these methods are more effective than lethal control. This would imply that more farmers will gradually adopt these methods. However, an outright ban on lethal control is likely to alienate farmers, potentially increasing the use of illegal poisons and leg-hold traps, and could compromise long-term conservation plans. Although wildlife damage represents a significant cost to most farmers, other economic factors, such as disease or weak markets may have an even greater effect on farmers livelihoods, resulting in ever-decreasing profit margins for Karoo stock farmers (Nattrass & Conradie 2013). Therefore, farmers may remain intolerant of even low levels of wildlife damage for which they hold conservation authorities at least partially responsible. Improving the relationship between farmers and conservation bodies is thus critical to ensuring that biodiversity goals for the area are met. This can be achieved through visits to individual farms and by CapeNature officials' regular attendance of quarterly farmer's union meetings. Such measures will not eradicate conflict between farmers and conservation authorities but may well reduce levels of conflict to levels that allow for improved general co-operation between farmers and conservation organisations mandated to achieving long-term biodiversity goals. Farmer outreach should thus be regarded as a priority for conservation organisations, and should be coupled with improved service when farmers request assistance.

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

APPENDIX 6A – QUESTIONNAIRE

LITTLE KAROO LANDOWNER SURVEY

GENERAL

1) Date: _____ 2) Investigator: _____

3) Name: _____ 4) Phone Number: _____

5) Age: _____ 6) Gender: _____ 7) Job: _____ 8) Education Level: _____

9) Property details (indicate residential farm with *)

Farm name			
Farm size (ha)			
Years occupied			
Proportion natural veld			
Distance to CN area			

10) How long have you lived in the area? _____ 11) Main source of family income? _

Yes	No
-----	----

12) Do you generate any income from tourism?

13) Have you ever been involved in the Gouritz Initiative or an environmental club/ society?

Yes	No
-----	----

14) How many stock/domestic animals do you keep?

	Cattle	Sheep	Goats	Donkeys	Horses	Pigs	Ostriches	Chickens	Other
quantity									

15) What is the role of livestock if they are not the main source of income? _____

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

16) What are the main problems facing you as a livestock owner?

Score Significance: 1 to 5 where 1 = no problem 3 = occasional problem 5 = Major problem

Disease	Drought	Infertility	Poor Grazing	Unreliable Market	Predators	Theft	Hit by vehicle	No herder	Other

17) If several are equally scored, which is the biggest problem? _____

18) Have you introduced any game species to your property?

Species	Eland	Kudu	Gemsbok	Red hartebeest	Giraffe	Other	Other
Quantity							

19) In general, do you think that there has been a decline in the natural population of game species (antelope, hares, etc.) in the area over the past ten years?

Yes	No
-----	----

If yes, why? _____

20) Are there any wild animals on your property that you consider to be pests? Which animals do the most damage?

Species	Damage type	Cost of damage/year	Present daily/weekly monthly/seasonal?	How do you control or manage this problem?

21) Are there any wild animals that you feel have declined significantly or become more scarce in the area over the past 5 – 10 years?

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

22) Are there any wild animals that have significantly increased in number over the past 5 – 10 years?

23) Are you concerned about the future of wildlife in the Little Karoo?

Yes	No	Maybe
-----	----	-------

24) Do you lose livestock to predators?

Yes	No
-----	----

25) Who were the attacks reported to?

	Name	Attack investigated		Response
CapeNature		Yes	No	
Cape Leopard Trust		Yes	No	
Other		Yes	No	
Not reported				

26) Do you think that CapeNature do a good job of managing damage causing animals?

Yes	No
-----	----

27) Who do you think should be responsible for managing damage causing animals?

CapeNature	Provincial government	Municipality	Department of Agriculture	Agricultural associations	Individual farmers	Other
------------	-----------------------	--------------	---------------------------	---------------------------	--------------------	-------

28) What sort of assistance would you like to receive?

Compensation	Advice	Subsidise improved livestock husbandry	Predator removal	Other
--------------	--------	--	------------------	-------

29) Do you expect financial compensation for livestock losses to any predators?	Yes	No	Maybe
30) Do you believe predators receive too much legal protection	Yes	No	Maybe
31) Do you believe you would be a happier if all predators were removed?	Yes	No	Maybe
32) Do you believe that the predator population has increased in the last 5 years?	Yes	No	Maybe
33) Should game farmers be allowed to kill predators that kill introduced antelope, etc?	Yes	No	Maybe
34) Do you believe you would try to kill/remove a predator in future if you lost livestock to predation?	Yes	No	Maybe
35) If you were carrying a weapon on your property and you saw a predator do you believe you would try to kill it?	Yes	No	Maybe

36) Have you ever successfully removed a predator or pest animal?

Yes	No
-----	----

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

37) If yes, explain how?

Shot	Poisoned	Live Trap	Other
------	----------	-----------	-------

38) How many predators do you remove per year? _____

39) Do you use snares or gin traps to catch problem animals? _____

40) Have you even seen domestic animals or livestock caught in a snare/trap?

Yes	No
-----	----

41) Will you accept it if leopards kill any of your livestock?	Yes	No	Maybe
42) If compensation was to be paid for leopard-related losses would you then accept such losses?	Yes	No	Maybe

43) Explain any leopard-related livestock loss over the past 2 years:

< 6 months ago 6 month – 1 year ago 1 year – 2 years ago	Type and number of livestock killed	Season	How predator identified (spoor, faeces, call, carcass)	Incident took place in daylight or dark	Distance to nearest dwelling of incident site

LIVESTOCK HUSBANDRY

44) What husbandry protection practices are employed for your livestock?

	In a camp	Kraal	Guarded by Human or Dog	Other
Day				
Night				

45) Which stock do you kraal at night?

All	Some	Small stock only	Young animals
-----	------	------------------	---------------

46) During birthing seasons do you make any husbandry changes to further protect offspring or mothers?

Yes	No
-----	----

47) Explain: _____

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

48) Are your enclosures designed to keep predators out?

Yes	No
-----	----

49) If you use a herder, is the herder a

Paid Worker	Child	Other
-------------	-------	-------

1=Strongly Disagree	2=Disagree	3=Neither Agree nor Disagree	4=Agree	5=Strongly Agree
---------------------	------------	------------------------------	---------	------------------

Please score your opinion of the following statements based on the rating given above:

50) The herder is effective at protecting livestock?

1	2	3	4	5
---	---	---	---	---

51) How much is a herder paid/month? _____

52) How many animals does one herder guard? _____

53) How many animals does one dog guard? _____

54) The dog(s) is effective at protecting livestock?

1	2	3	4	5
---	---	---	---	---

Explain: _____

55) Give details of any husbandry changes following all attacks: _____

56) Have your changes been successful?

Yes	No
-----	----

57) Are there methods you think will be more effective at protecting livestock?

Yes	No
-----	----

58) Are you considering these alternative methods in response to threats experienced or as a result of public information campaigns which have explained new options?

59) Explain: _____

60) Why do you not use these now? _____

61) Do you believe improved husbandry practices will prevent predator related losses?

Yes	No
-----	----

62) Do you believe the conflict with predators is increasing, decreasing or stable? _____

63) Can you give reasons why you believe this is occurring? _____

CHAPTER 6: ATTITUDES TOWARDS WILDLIFE

EDUCATION

Do you believe?

64) Leopards are likely to attack humans?	Yes	No	Maybe
65) Leopards can pass through your land or community unseen/ unnoticed?	Yes	No	Maybe
66) Leopards can live in or pass through your property without killing livestock?	Yes	No	Maybe
67) Leopards in the Karoo are increasing in number?	Yes	No	Maybe
68) Efforts should continue to protect leopards in the Karoo?	Yes	No	Maybe
69) Leopards have a role to play in the ecosystem?	Yes	No	Maybe
70) Leopards control smaller predators, such as caracal and jackals?	Yes	No	Maybe
71) Leopards control the baboon population?	Yes	No	Maybe
72) Leopards are an important part of the Little Karoo's natural heritage?	Yes	No	Maybe
73) You could tolerate leopards being present on neighbouring land?	Yes	No	Maybe
74) The Karoo would be a better place without leopards?	Yes	No	Maybe
75) Leopards could create tourism related benefits for you or your community?	Yes	No	Maybe
76) Leopards add value to your property	Yes	No	Maybe
77) Low game densities in an area may result in leopards killing livestock?	Yes	No	Maybe
78) It is important to educate communities on how to react when they see leopards or leopard sign?	Yes	No	Maybe
79) There are too many leopards?	Yes	No	Maybe
80) You could actively assist leopard protection efforts in some way?	Yes	No	Maybe
81) You would cooperate with conservation groups to reduce conflict with predators?	Yes	No	Maybe

82) Do you know if leopards have a particular conservation status?

Common	Endangered	Protected	Threatened	Vulnerable	Other	Don't know
--------	------------	-----------	------------	------------	-------	------------

83) Would you be interested in learning more about leopards?

Yes	No
-----	----

CHAPTER 7: SYNTHESIS

7.1 Introduction

The Cape Leopard Trust has been conducting leopard research in the Little Karoo since September 2007, but pre-2010 activities were limited to using a small number ($n = \sim 10$) of camera traps to broadly identify leopard presence in the area and the opportunistic collection of scats. In addition, the Cape Leopard Trust organised meetings with farmers and other members of the local community to raise awareness of the threats to leopards, the important ecological role they fulfill and to encourage farmers to implement improved livestock husbandry methods. When my study commenced in 2010, knowledge of the Little Karoo leopard population was thus limited to two dietary studies (Norton et al. 1986; Rautenbach 2010), and photographs ($n = 126$) from the ad-hoc camera trapping survey, which suggested the presence of approximately 25 leopards from 36 camera stations arranged stochastically (both spatially and temporally) over an area of approximately 1300 km².

The goal of my study was to add substantially to this knowledge base for leopards in the Little Karoo and for leopards generally in the Western Cape of South Africa. Using standard techniques including camera traps, tracking collars and scat analysis I have quantified leopard density and diet in different habitat types, in addition to identifying important potential movement corridors that link large tracts of natural land in mountainous areas within the mosaic of land that has been transformed for crops or is currently being used for livestock farming. Formally protected areas (nature reserves and national parks) cover approximately 8% of South Africa, but 20% of the country is thought to comprise suitable leopard habitat, of which only 32% occurs within protected areas (Swanepoel et al. 2013). In the Western Cape, 70% of suitable leopard habitat occurs outside protected areas, and therefore privately-owned land is critical to the future conservation of leopards (Balme et al. 2013; Swanepoel et al. 2013). In addition, I have explored landowner attitudes towards leopards and other potentially damage-causing wildlife in the area with a view to understanding the long-term threats

CHAPTER 7: SYNTHESIS

to leopards posed by the agricultural sector in the Little Karoo. In this final chapter, I discuss the implications of my research for ongoing leopard conservation in the Little Karoo, Western Cape and South Africa and suggest possible improvements to methods for future long-term monitoring of leopard populations living outside of protected areas and carnivores in general.

7.2 Conservation status of leopards in the Little Karoo

The results of my study suggest that the Little Karoo has one of the lowest densities of leopards ever recorded in South Africa (see Chapter 4). While historical persecution may have contributed to this, conflict between stock farmers and leopards appears to be at their lowest since the arrival of European settlers in the area approximately 250 years ago (Beinart 2008; Skead 2011). Furthermore, tolerance of leopards by the farmers I interviewed is high, particularly in comparison to other wildlife, including other predators (see Chapter 6). The low leopard population densities are thus more likely to be due to low prey densities, which may in part be attributed to the loss of access to more productive low-lying land much of which has been transformed for agricultural purposes. Even when wildlife do access transformed low-lying areas, both overstocking and poor stock management have resulted in significant habitat degradation (Cupido 2005), ultimately reducing the carrying capacity of such land for wild prey. Together these factors may all contribute to the extremely low leopard population density in the Little Karoo relative to studies done elsewhere in South Africa (see Chapter 4). Furthermore, most other leopard research in South Africa has been done within protected areas (Balme et al. 2013), thus this is the first study to estimate leopard population density in a highly-transformed region. In KwaZulu-Natal, South Africa leopard densities have been shown to decline from 11.11 leopards/100km² in protected areas to 2.49 leopards/100km² in unprotected areas (Balme et al. 2010a), but In India, leopards have been shown to be able to persist at high densities (4.8 adults/100km²) despite high human population densities of over 300 people/100km² (Athreya et al. 2013). Jaguar (*Panthera onca*) and puma (*Puma concolor*) densities have also been shown to decrease in fragmented habitat outside protected areas in Belize, central America (Foster et al. 2010). Studies in similarly transformed mixed-use landscapes

CHAPTER 7: SYNTHESIS

elsewhere in South Africa are thus necessary, not only to provide a broader context to the results of my study, but also to assess the impact of habitat transformation on leopard populations outside protected areas.

Despite the current low levels of conflict between leopards and farmers in my study area and the potential bias in the survey that may be ascribed to my close association with a leopard conservation NGO, my data suggest that conflict between leopards and stock farmers is nevertheless a concern. Diet analyses revealed that livestock were depredated frequently, accounting for between 10 and 15% of the diet of leopards in the area (see Chapter 5). Although farmers often blamed leopards for the disappearance of cattle (*Bos taurus*), there were also several occasions when farmers were unaware of leopard depredation incidents. One farmer confidently informed me that leopards had avoided his farm since he had started using livestock-guarding dogs; but I subsequently found that a GPS-collared leopard had killed three goats (*Capra hircus*) on his farm in the preceding six months. This highlights the need for an independent scientific assessment of both losses and the efficiency of current stock management and conflict mitigation methods.

Game farms (properties on which large ungulates have been introduced for ranching, hunting or viewing) are a further source of potential conflict with predators including leopards, as has been found elsewhere in South Africa (Lindsey et al. 2005; Thorn et al. 2012). None of the game farms in my study area were commercial operations; in general large antelope had simply been introduced for the viewing pleasure of the owner their family and friends. Nevertheless, leopard depredation of game on these properties caused considerable resentment (Chapter 6) and at least one leopard was trapped and killed on one of these game farms prior to my study taking place (Theresa van der Westhuizen, CapeNature, pers. comm.). Furthermore, the only landowner who prohibited me from working on his property did so after a (non-collared) leopard killed two recently introduced eland (*Tragelaphus oryx*) on his property in late 2011. This landowner subsequently set a cage trap on his

CHAPTER 7: SYNTHESIS

property, although he denied that this was done in attempt to capture leopards (T. van der Westhuizen, CapeNature, pers. comm.).

Careful management of these conflict situations involving leopards is required to prevent an escalation of leopard persecution in the Little Karoo. CapeNature, the local conservation authority responsible for the management of damage-causing wildlife, will have to continue to walk the fine line between protecting a locally-endangered species and appeasing farmers suffering livestock losses. Striking this balance is always difficult (Naughton-Treves & Treves 2005; Redpath et al. 2013), but developing and maintaining good relationships between government level authorities and farmers outside of conflict situations is likely to make a difficult task somewhat easier.

Educating and interacting with stakeholders is frequently cited as a means of alleviating human-wildlife conflict situations (Reiter et al. 1999; Lafon et al. 2003; Ogada et al. 2003; Treves & Karanth 2003; Lindsey et al. 2005; Zimmermann et al. 2005; Wang & Macdonald 2006; Liu et al. 2011). However, any educational campaign needs to be evidence-based, with the aim of reducing landowner vulnerability to wildlife conflict rather than simply telling farmers that their current practices are 'wrong' or passively recording stock-loss incidents (Sillero-Zubiri et al. 2007).

Other than conflict with humans over livestock losses, the major threat to leopards in the Little Karoo is likely to be further habitat transformation. Leopard habitat in the Little Karoo is relatively unfragmented, and is likely to remain so due to the rugged, mountainous nature of the terrain (see Chapter 3). Nevertheless, some key low-lying areas, such as the Huisrivier Pass and the area south of Gamkaberg, appear to function as important links between the mountainous areas that provide the core habitat for leopards in this area. Based on camera trap data, at least one male leopard has a territory that straddles the Huisrivier Pass, and potential movement corridors have been identified to the south of Gamkaberg (see Chapter 3). Leopard conservation management and planning should prioritise these areas to ensure that future development does not impact on these potentially important dispersal corridors that link existing core areas. It is my hope that the leopard habitat map

CHAPTER 7: SYNTHESIS

developed in Chapter 3 may serve as a template that could be applied across a much broader area, and may ultimately lead to the development of a simulated leopard habitat map for the entire Western Cape.

7.3 Camera trapping: time for a sex-specific approach?

Camera traps have rapidly become the favoured tool for estimating population densities of individually identifiable felids such as leopards (Balme et al. 2009). Despite the emergence of improved analytical tools, such as spatially-explicit capture-recapture (SECR) methods (Efford 2004; Borchers & Efford 2008; Royle et al. 2009a), the overall design of camera trap surveys has changed little in 18 years, with the majority of researchers adhering closely to the methods described by Karanth & Nichols (1998). In recent years, a variety of recommendations have been made regarding the size of the overall camera survey area, spacing of cameras, reporting of results, and incorporation of sex covariates into SECR models – all in an effort to improve the accuracy of the estimates (Sollmann et al. 2011; Foster & Harmsen 2012; Tobler & Powell 2013).

My study found a substantial bias (2.17:1) towards male leopards, both in terms of the photographic capture rate and the number of individuals ‘captured’ by camera traps (see Chapter 4). Female leopards have been found to occupy smaller territories than males, and assuming that they are territorial and occupy all available habitat are thus predicted to occur at densities two to three times higher than males (Bailey 1993; Mizutani & Jewell 1998; Simcharoen et al. 2008; Stein et al. 2011; Martins & Harris 2013). Up to six females have been reported within the territory of a single male (Bailey 1993). Assuming a higher female density, I thus concluded that a large number of resident female leopards had gone undetected in my survey, and therefore my density estimates were underestimates.

Biases towards males in camera trap surveys are common; a ratio of 2.16 males: females was found in a review of 39 jaguar population studies (Maffei et al. 2011) while a sex ratio of 2.5 males per female has been recorded in a cougar camera trapping study (Negrões et al. 2010), and a ratio of

CHAPTER 7: SYNTHESIS

1.3:1 in favour of males has been recorded for snow leopards (*Panthera uncia*) (Jackson et al. 2006). Few studies have reported the sex ratio of tigers (*Panthera tigris*); and of those that did the ratio ranges from 0.4:1 (Simcharoen et al. 2007) to 1.3:1 (Karanth 1995), although many other tiger studies have not reported these data (Karanth & Nichols 1998; O'Brien et al. 2003; Karanth et al. 2004; Kawanishi & Sunquist 2004; Johnson et al. 2006; Lynam et al. 2009; Wang & Macdonald 2009a). Only ocelot (*Felis pardalis*) studies have shown a consistently less-pronounced bias (0.95 males: females overall), ranging from 0.5 to 1.2 males: females (Trolle & Kery 2003; Maffei et al. 2005; Di Bitetti et al. 2006; Dillon & Kelly 2007, 2008).

In this context, previous studies of leopards (for which sex ratios have been reported) appear more representative of expected population trends, with females generally outnumbering males (see Table 7-1). Home range size estimates suggest that male: female sex ratios should fall between 0.3 and 0.5 (i.e. 2-3 females for every male), and by this criterion, only the sex ratio obtained in the Cederberg of South Africa (Martins 2010) seems representative (see Table 7-1). Females tend to be under-represented, both in terms of the numbers of captures and the numbers of individuals recorded. This is based on the assumption that female felids are evenly distributed within areas in which males occur, which may not always be the case, particularly in fragmented habitat. Furthermore, the number of photographs recorded has usually been heavily biased towards male leopards, with the sole exception being a study conducted in the Soutpansberg Mountains, South Africa (see Table 7-1).

CHAPTER 7: SYNTHESIS

Table 7-1. Summary of sex ratios obtained from leopard population studies using camera trap data. The authors and area in which the study was done are shown, as well as the number of males and females recorded by the camera traps. When available, the number of independent photographs ('captures') of each sex is shown in brackets next to the number of individuals recorded. The number of cameras per minimum home range recorded in the area was calculated by dividing the approximate grid cell size reported by each study by the minimum leopard home range size reported for the area. This assumes that cameras were arranged in an evenly-spaced grid, which is unlikely to be the case, and these figures should therefore only be viewed as a rough approximation of camera-trap intensity. Only studies that used camera traps and published the number of recorded individuals of each sex are included.

Study	Area	Male individuals (no. captures)	Female individuals (no. captures)	Sex ratio (males: females)	Cameras/min home range
Chapman & Balme (2010)	Zululand Rhino Reserve, South Africa	3 (14)	3 (4)	1:1	±3.5
Martins (2010)	Cederberg Mountains, South Africa	2 (118)	5 (46)	0.4:1	8.2
Chase-Grey (2011)	Soutpansberg Mountains, South Africa	10 (44)	14 (57)	0.7:1	±6.5
Grant (2012)	Matobo Hills, Zimbabwe	5	8	0.6:1	±3.0
Gray & Prum (2012)	Mondulkiri Protected Forest, Cambodia	5 (51)	7 (9)	0.7:1	Home range size not reported
My study	Little Karoo, South Africa	13 (111)	6 (22)	2.17:1	±3.0

These data suggest that most camera trap studies do not reflect the probable composition of leopard populations. As most of the studies referenced above were predominantly done within protected areas, I consider the assumption of an even female distribution to be reasonable. Males are likely to be more detectable due to their larger home ranges (presumably because these large areas include a greater number of cameras), greater daily distances moved and greater use of trails and roads than females (Martins & Harris 2013). These differences in detection probability can be

CHAPTER 7: SYNTHESIS

accounted for using the M_h jackknife estimator, which is usually selected as the most appropriate model for non-spatial capture-recapture analysis (Otis et al. 1978; White et al. 1982; Karanth & Nichols 1998). However, this estimator has been shown to be unreliable when there is high heterogeneity in capture probability between individuals and when overall capture probabilities are low (Harmsen et al. 2010a).

Minimum recorded female home ranges are typically used as the basis for determining the spacing of camera traps to ensure that all individuals within the study area can be recorded (following Karanth & Nichols 1998). However, my study found that the distance between cameras could be drastically increased with minimal loss of accuracy or precision of SECR-derived population density estimates (see Chapter 4). A consequence of the greater distance between cameras is that some female territories within the study area may not overlap with a camera station, violating one of the assumptions of capture-recapture analysis (White et al. 1982). However, as females were likely to have been under-sampled in the 'full' survey, this did not significantly influence density estimates.

Monitoring of female leopard population densities may be more effective when cameras are arranged at high densities. Martins (2010) had a distance of approximately 3km between camera stations, based on a presumed minimum female home range of 25km². However, subsequent tracking data obtained from female leopards fitted with GPS collars revealed home range sizes of between 74 and 203km², suggesting that the camera trap survey was done at an excessively fine resolution, based on the standard procedure suggested by Karanth & Nichols (1998). However, this relatively intense camera trapping may have contributed to Martins (2010) obtaining what is likely to be a more representative sample of the population, with 2.5 female individuals recorded for each male although those males were still photographed more frequently than females. This appears to be a more intensive trapping effort than the other leopard studies that reported sex-specific data (see Table 7-1). Camera trap studies of jaguar populations have also recorded more females when

CHAPTER 7: SYNTHESIS

camera trapping has been done at a fine spatial resolution relative to home ranges in the respective areas (Paviolo et al. 2008; Núñez-Pérez 2011).

This finding leads to an intriguing question: would future surveys be better off by ignoring females altogether? There are compelling arguments to be made in favour of this approach. Firstly, males are more detectable, and thus easier to survey, therefore it is likely that estimates of the density of male leopards would be more accurate. Secondly, males tend to have larger home ranges, allowing for detection by cameras spaced further apart, and consequently allowing for a larger area to be surveyed than would be possible by determining trap grid resolution by female home range size. Thirdly, male leopards are more likely to be recorded on paths and roads; these are typically more accessible to researchers and reduce the logistical difficulty and costs of performing a camera trap survey. Finally, male leopards tend to suffer greater anthropogenic mortality than females (Balme & Hunter 2004; Balme et al. 2010b), which would suggest that effective monitoring of the male population may provide a better estimate of threats and conflict levels, in addition to providing important data for the management of male numbers in areas where trophy hunting occurs (Balme et al. 2012). Separate calculation of male and female population densities has been suggested before (Foster 2008; Harmsen et al. 2010a; Foster & Harmsen 2012), but here I am suggesting that the design of camera trap surveys should take advantage of the intersexual variation in detectability to improve our understanding of leopard movement and habitat use outside of protected areas.

7.4 Conclusion

My study was conducted in challenging conditions. Leopards in the Little Karoo are highly elusive. At no time during my three years of fieldwork was I able to directly observe free-ranging leopards. The low densities of the leopard population made data collection a slow, painstaking process, which necessarily had to be carried out over a large area. Working on private land brought its own challenges including the time taken to establish the identity of the landowner, make contact, and arrange access to the property. Trapping leopards was also extremely difficult and time-consuming, and the heavy reliance on data from only three leopards, all adult males, is a major weakness of my

CHAPTER 7: SYNTHESIS

study. While I have tried to compensate for this whenever possible, it is an inescapable fact that a larger, more diverse sample of collared leopards would have made the results obtained in this study far more robust.

Nevertheless, I believe that my research has answered fundamental questions about the ecology of leopards in the Little Karoo, and has provided a valuable baseline for future research and monitoring in the area. Leopard research in South Africa has been criticised for failing to address conservation needs (Balme et al. 2013). However, my study has produced results that will be useful to conservation managers in an area where data on the leopard population was poor. In doing so, my study meets many of the recommendations made by Balme et al. (2013), particularly as this research will contribute to the management of leopards outside of protected areas where their survival is more tenuous but which is likely to comprise a large proportion of the total South African population (Balme et al. 2013; Swanepoel et al. 2013).

Future research in the Little Karoo should empirically test the monitoring programme suggested by my study, while detailed testing of the efficacy of various livestock husbandry methods should also be a high priority. The leopard habitat model developed in this study could be further refined with additional data, and potential leopard habitat corridors linking the Gamkaberg/Rooiberg Mountains with the Langeberg and Outeniqua Mountains to the south should be investigated to determine whether these are genuine dispersal corridors. Finally, leopard researchers should continue to work closely with both conservation authorities and local landowners to ensure that future leopard management is implemented in a holistic manner, with buy-in from private landowners.

CHAPTER 8: REFERENCES

CHAPTER 8: REFERENCES

- ACKERMAN, B. B., LINDZEY, F. G. & HEMKER, T. P. 1984. Cougar food habits in southern Utah. *The Journal of Wildlife Management* **48**: 147–155.
- AKAIKE, H. 1974. A new look at statistical model identification. *IEEE Transactions on Automatic Control* **19**: 716–723.
- ALLEN, B. L., FLEMING, P. J. S., HAYWARD, M., ALLEN, L. R., ENGEMAN, R. M., BALLARD, G. & LEUNG, L. K. 2012. Top-predators as biodiversity regulators: contemporary issues affecting knowledge and management of dingoes in Australia. In: *Biodiversity Enrichment in a Diverse World*, (ed) G. A. Lameed, p. 86-132. InTech, Rijeka, Croatia.
- ANDELMAN, S. J. & FAGAN, W. F. 2000. Umbrellas and flagships: efficient conservation surrogates or expensive mistakes? *Proceedings of the National Academy of Sciences of the United States of America* **97**: 5954–5959.
- ANDERSON, C. R. & LINDZEY, F. G. 2003. Estimating cougar predation rates from GPS location clusters. *The Journal of Wildlife Management* **67**: 307–316.
- ANILE, S., AMICO, C. & RAGNI, B. 2012. Population density estimation of the European wildcat (*Felis silvestris silvestris*) in Sicily using camera trapping. *Wildlife Biology in Practice* **8**: 1–12.
- ANONYMOUS. 1999. Klein Karoo Streeksinligtingsdokument. Oudtshoorn Proefplaas, Oudtshoorn.
- ANSELL, C. & GASH, A. 2007. Collaborative governance in theory and practice. *Journal of Public Administration Research and Theory* **18**: 543–571.
- ANWAR, M. B., JACKSON, R., NADEEM, M. S., JANEČKA, J. E., HUSSAIN, S., BEG, M. A., MUHAMMAD, G. & QAYYUM, M. 2011. Food habits of the snow leopard *Panthera uncia* (Schreber, 1775) in Baltistan, Northern Pakistan. *European Journal of Wildlife Research* **57**: 1077–1083.
- ARYAL, A. & KREIGENHOFER, B. 2009. Summer diet composition of the common leopard *Panthera pardus* (Carnivora: Felidae) in Nepal. *Journal of Threatened Taxa* **1**: 562–566.
- ATHREYA, V. 2006. Is relocation a viable management option for unwanted animals? – The case of the leopard in India. *Conservation and Society* **4**: 419–423.
- ATHREYA, V., ODDEN, M., LINNELL, J. D. C. & KARANTH, K. U. 2011. Translocation as a tool for mitigating conflict with leopards in human-dominated landscapes of India. *Conservation biology : the journal of the Society for Conservation Biology* **25**: 133–41.
- ATHREYA, V., ODDEN, M., LINNELL, J. D. C., KRISHNASWAMY, J. & KARANTH, U. 2013. Big cats in our backyards: persistence of large carnivores in a human dominated landscape in India. *PLoS ONE* **8**: e57872.
- AZEVEDO, F. C. C. DE & MURRAY, D. L. 2007. Evaluation of potential factors predisposing livestock to predation by jaguars. *Journal of Wildlife Management* **71**: 2379–2386.

CHAPTER 8: REFERENCES

- BACON, M. M., BECIC, G. M., EPP, M. T. & BOYCE, M. S. 2011. Do GPS clusters really work? Carnivore diet from scat analysis and GPS telemetry methods. *Wildlife Society Bulletin* **35**: 409–415.
- BAILEY, T. N. 1993. *The African leopard: ecology and behaviour of a solitary felid*. The Blackburn Press, Caldwell, New Jersey.
- BALME, G. A., HUNTER, L. & BRACZKOWSKI, A. R. 2012. Applicability of age-based hunting regulations for African leopards. *PloS one* **7**: e35209.
- BALME, G. A., HUNTER, L. T. B., GOODMAN, P., FERGUSON, H., CRAIGIE, J. & SLOTOW, R. 2010a. An adaptive management approach to trophy hunting of leopards (*Panthera pardus*): a case study from KwaZulu-Natal, South Africa. In: *Biology and Conservation of Wild Felids*, (eds) D. W. Macdonald & A. Loveridge, pp. 341–352. Oxford University Press, Oxford.
- BALME, G. A., HUNTER, L. T. B. & SLOTOW, R. 2009. Evaluating methods for counting cryptic carnivores. *Journal of Wildlife Management* **73**: 433–441.
- BALME, G. A., LINDSEY, P. A., SWANEPOEL, L. H. & HUNTER, L. T. B. 2013. Failure of research to address the rangewide conservation needs of large carnivores: leopards in South Africa as a case study. *Conservation Letters* **7**: 3-11.
- BALME, G. A., SLOTOW, R. & HUNTER, L. T. B. 2010b. Edge effects and the impact of non-protected areas in carnivore conservation: leopards in the Phinda-Mkhuze Complex, South Africa. *Animal Conservation* **13**: 315–323.
- BALME, G., HUNTER, L. & SLOTOW, R. 2007. Feeding habitat selection by hunting leopards *Panthera pardus* in a woodland savanna: prey catchability versus abundance. *Animal Behaviour* **74**: 589–598.
- BALME, G. & HUNTER, L. T. B. 2004. Mortality in a protected leopard population, Phinda Private Game Reserve, South Africa: a population in decline? *Ecological Journal* **6**: 1–6.
- BANGS, E. E., FONTAINE, J. A., JIMENEZ, M. D., MEIER, T. J., BRADLEY, E. H., NIEMEYER, C. C., SMITH, D. W., MACK, C. M., ASHER, V. & OAKLEAF, J. K. 2005. Managing wolf-human conflict in the northwestern United States. In: *People and wildlife: conflict or coexistence?*, (eds) R. Woodroffe, S. Thirgood & A. R. Rabinowitz, pp. 340–356. Cambridge University Press, Cambridge.
- BEAN, W. T., STAFFORD, R. & BRASHARES, J. S. 2012. The effects of small sample size and sample bias on threshold selection and accuracy assessment of species distribution models. *Ecography* **35**: 250–258.
- BEINART, W. 1998. The night of the jackal: sheep, pastures and predators in the Cape. *Past and Present* **158**: 172–206.
- BEINART, W. 2008. *The rise of conservation in South Africa: settlers, livestock and the environment 1770-1950*. Oxford University Press, Oxford.
- BERGER, J. 1979. “Predator harassment” as a defensive strategy in ungulates. *American Midland Naturalist* **102**: 197–199.

CHAPTER 8: REFERENCES

- BEYER, H. L. 2004. Hawth's Analysis Tools for ArcGIS. <http://www.spatialecology.com/htools>
- BICKFORD-SMITH, V. 1995. *Ethnic pride and racial prejudice in Victorian Cape Town*. Cambridge University Press, Cambridge.
- BINGHAM, J. & PURCHASE, G. K. 2002. Reproduction in the jackals *Canis adustus* Sundevall, 1846 , and *Canis mesomelas* Schreber, 1778 (Carnivora: Canidae), in Zimbabwe. *African Zoology* **37**: 21–26.
- BISSETT, C. 2004. The feeding ecology, habitat selection and hunting behaviour of re-introduced cheetah on Kwandwe Private Game Reserve, Eastern Cape Province. MSc thesis, Rhodes University, Grahamstown, South Africa.
- BLAKE, S. & HEDGES, S. 2004. Sinking the flagship: the case of forest elephants in Asia and Africa. *Conservation Biology* **18**: 1191–1202.
- BOITANI, L., CIUCCI, P. & RAGANELLA-PELLICCIONI, E. 2010. Ex-post compensation payments for wolf predation on livestock in Italy: a tool for conservation? *Wildlife Research* **37**: 722–730.
- BORCHERS, D. 2010. A non-technical overview of spatially explicit capture–recapture models. *Journal of Ornithology* **152**: 435–444.
- BORCHERS, D. L. & EFFORD, M. G. 2008. Spatially explicit maximum likelihood methods for capture-recapture studies. *Biometrics* **64**: 377–385.
- BOSHOFF, A. F., KERLEY, G. I. H. & COWLING, R. M. 2001. A pragmatic approach to estimating the distributions and spatial requirements of the medium- to large-sized mammals in the Cape Floristic Region, South Africa. *Diversity and Distributions* **7**: 29–43.
- BOTHMA, J. DU P. 2002. *Game ranch management*. Van Schaik, Pretoria.
- BOTHMA, J. DU P., KNIGHT, M. H., LE RICHE, E. A. N. & VAN HENSBERGEN, H. J. 1997a. Range size of southern Kalahari leopards. *South African Journal of Wildlife Research* **27**: 94–100.
- BOTHMA, J. DU P. & LE RICHE, E. A. N. 1984. Aspects of the ecology and the behaviour of the leopard *Panthera pardus* in the Kalahari desert. *Koedoe* **84**: 259–279.
- BOTHMA, J. DU P., VAN ROOYEN, N. & LE RICHE, E. A. N. 1997b. Multivariate analysis of the hunting tactics of Kalahari leopards. *Koedoe* **40**: 41–56.
- BOTHMA, J. DU P. & WALKER, C. 1999. *Larger carnivores of the African savannahs*. J.L. Van Schaik, Pretoria.
- BOWKETT, A. E., ROVERO, F. & MARSHALL, A. R. 2007. The use of camera-trap data to model habitat use by antelope species in the Udzungwa Mountain forests, Tanzania. *African Journal of Ecology* **46**: 479–487.
- BOX, E. O., HOLBEN, B. N. & KALB, V. 1989. Accuracy of the AVHRR vegetation index as a predictor of biomass, primary productivity and net CO₂ flux. *Vegetatio* **80**: 71–89.

CHAPTER 8: REFERENCES

- BRACZKOWSKI, A., WATSON, L., COULSON, D. & RANDALL, R. 2012. Diet of leopards in the southern Cape, South Africa. *African Journal of Ecology* **50**: 377–380.
- BRAND, T. S. 2000. Grazing behaviour and diet selection by Dorper sheep. *Small ruminant research : the journal of the International Goat Association* **36**: 147–158.
- BRASHARES, J. S., PRUGH, L. R., STONER, C. J. & EPPS, C. W. 2010. Ecological and conservation implications of mesopredator release. In: *Trophic cascades: predators, prey, and the changing dynamics of nature*, (eds) J. Terborgh & J. A. Estes, pp. 221–240. Island Press, Washington D.C.
- BREITENMOSER, U., ANGST, C., LANDRY, J.-M., BREITENMOSER-WÜRSTEN, C., LINNELL, J. D. C. & WEBER, J.-M. 2005. Non-lethal techniques for reducing predation. In: *People and wildlife: conflict or coexistence?*, (eds) R. Woodroffe, S. Thirgood & A. R. Rabinowitz, pp. 49–71. Cambridge University Press, Cambridge.
- BUCKLAND, S. T., ANDERSON, D. R., BURNHAM, K. P., LAAKE, J. L., BORCHERS, D. L. & THOMAS, L. 2001. *Introduction to distance sampling: estimating abundance of biological populations*. Oxford University Press, Oxford.
- BURKE, A. 2004. Range management systems in arid Namibia — what can livestock numbers tell us? *Journal of Arid Environments* **59**: 387–408.
- BURNHAM, K. P. & ANDERSON, D. R. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. Springer-Verlag, New York.
- BURNHAM, K. P. & OVERTON, W. S. 1978. Estimation of the size of a closed population when capture probabilities vary among animals. *Biometrika* **65**: 625–633.
- BUSBY, J. R. 1991. BIOCLIM - a bioclimate analysis and prediction system. *Plant Protection Quarterly* **6**: 8–9.
- CANTOR, S. B., SUN, C. C., TORTOLERO-LUNA, G., RICHARDS-KORTUM, R. & FOLLEN, M. 1999. A comparison of C/B ratios from studies using receiver operating characteristic curve analysis. *Journal of clinical epidemiology* **52**: 885–92.
- CARBONE, C., CHRISTIE, S., CONFORTI, K., COULSON, T., FRANKLIN, N., GINSBERG, J. R., GRIFFITHS, M., HOLDEN, J., KAWANISHI, K., KINNAIRD, M., LAIDLAW, R., LYNAM, A., MACDONALD, D. W., MARTYR, D., MCDUGAL, C., NATH, L., O'BRIEN, T. G., SEIDENSTICKER, J., D.J.L., S., SUNQUIST, M., TILSON, R. & WAN SHAHRUDDIN, W. N. 2001. The use of photographic rates to estimate densities of tigers and other cryptic mammals. *Animal Conservation* **4**: 75–79.
- CARBONE, C., CHRISTIE, S., CONFORTI, K., COULSON, T., FRANKLIN, N., GINSBERG, J. R., GRIFFITHS, M., HOLDEN, J., KINNAIRD, M., LAIDLAW, R., LYNAM, A., MACDONALD, D. W., MARTYR, D., MCDUGAL, C., NATH, L., O'BRIEN, T., SEIDENSTICKER, J., SMITH, J. L. D., TILSON, R. & WAN SHAHRUDDIN, W. N. 2002. The use of photographic rates to estimate densities of cryptic mammals: response to Jennelle et al. *Animal Conservation* **5**: 121–123.
- CARBONE, C. & GITTLEMAN, J. 2002. A common rule for the scaling of carnivore density. *Science* **295**: 2273–2276.

CHAPTER 8: REFERENCES

- CARBONE, C., MACE, G. M., ROBERTS, S. C. & MACDONALD, D. W. 1999. Energetic constraints on the diet of terrestrial carnivores. *Nature* **402**: 286–288.
- CARBONE, C., TEACHER, A. & ROWCLIFFE, J. M. 2007. The costs of carnivory. *PLoS biology* **5**: e22.
- CARDILLO, M., PURVIS, A., SECHREST, W., GITTLEMAN, J. L., BIELBY, J. & MACE, G. M. 2004. Human population density and extinction risk in the world's carnivores. *PLoS biology* **2**: 909–914.
- CHAME, M. 2003. Terrestrial mammal feces: a morphometric summary and description. *Memorias do Instituto Oswaldo Cruz* **98**: 71–94.
- CHAPMAN, S. & BALME, G. 2010. An estimate of leopard population density in a private reserve in KwaZulu-Natal, South Africa, using camera-traps and capture–recapture models. *South African Journal of Wildlife Research* **40**: 114–120.
- CHASE-GREY, J. N. 2011. Leopard population dynamics, trophy hunting and conservation in the Soutpansberg Mountains, South Africa. PhD thesis, Durham University, Durham, UK.
- CHAZDON, R. L., COLWELL, R. K., DENSLOW, J. S. & GUARIGA, M. R. 1998. Statistical methods for estimating species richness of woody regeneration in primary and secondary forests of NE Costa Rica. In: *Forest biodiversity research, monitoring and modelling: conceptual background and Old World case studies*, (eds) F. Dallmeier & J. A. Comiskey, pp. 285–309. Pathenon Publishing, Paris.
- CLARKE, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of ecology* **118**: 117–143.
- CLARKE, K. R. & GORLEY, R. N. 2006. PRIMER v6: User manual/tutorial. PRIMER-E, Plymouth.
- COLWELL, R. K. 2006. EstimateS: Statistical estimation of species richness and shared species from samples. www.purl.oclc.org/estimates
- COLWELL, R. K. & CODDINGTON, J. A. 1994. Estimating terrestrial biodiversity through extrapolation. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **345**: 101–18.
- CONOVER, M. R. 1998. Perceptions of American agricultural producers about wildlife on their farms and ranches. *Wildlife Society Bulletin* **26**: 597–604.
- CONRADIE, B. & PIESSE, J. 2013. The effect of predator culling on livestock losses: Ceres, South Africa, 1979-1987. Working paper 319, Centre for Social Science Research, University of Cape Town, Cape Town, South Africa.
- COUSINS, B. & HALL, R. 2011. Rights without illusions: the potential and limits of rights-based approaches to securing land tenure in rural South Africa. Working paper 18, Institute for Poverty, Land and Agrarian Studies, Bellville, South Africa.
- COWLISHAW, G. 1994. Vulnerability to predation in baboon populations. *Behaviour* **131**: 293–304.

CHAPTER 8: REFERENCES

- CRABTREE, I. D. 1973. Sabi Sand Wildtuin: Wardens report for the year ended 30th April 1973. Circular no. 452. In: BAILEY, T. N. 1993. *The African leopard: ecology and behaviour of a solitary felid*. The Blackburn Press, Caldwell, New Jersey.
- CRABTREE, I. D. 1974. Sabi Sand Wildtuin: Wardens report for the year ended 30th April 1974. Circular no. 483. In: BAILEY, T. N. 1993. *The African leopard: ecology and behaviour of a solitary felid*. The Blackburn Press, Caldwell, New Jersey.
- CRANE, W. 2006. Biodiversity conservation and land rights in South Africa: Whither the farm dwellers? *Geoforum* **37**: 1035–1045.
- CREEL, S. & CHRISTIANSON, D. 2009. Wolf presence and increased willow consumption by Yellowstone elk: implications for trophic cascades. *Ecology* **90**: 2454–66.
- CROOKS, K. R., BURDETT, C. L., THEOBALD, D. M., RONDININI, C. & BOITANI, L. 2011. Global patterns of fragmentation and connectivity of mammalian carnivore habitat. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **366**: 2642–51.
- CUELLAR, E., MAFFEI, L., ARISPE, R. & NOSS, A. 2006. Geoffroy's cats at the northern limit of their range: activity patterns and density estimates from camera trapping in Bolivian dry forests. *Studies on Neotropical Fauna and Environment* **41**: 169–177.
- CUPIDO, C. F. 2005. Assessment of veld utilisation practices and veld condition in the Little Karoo. MSc. thesis, University of Stellenbosch, Stellenbosch, South Africa.
- DALEY, S. S., COBB, D. T., BROMLEY, P. T. & SORENSON, C. E. 2004. Landowner attitudes regarding wildlife management on private land in North Carolina. *Wildlife Society Bulletin* **32**: 209–219.
- DANELL, A. C. & ANDRÉN, H. 2010. Precision beats interval: appropriate monitoring efforts for management of a harvested Eurasian lynx *Lynx lynx* population. *Wildlife Biology* **16**: 409–418.
- DAWSON, D. K. & EFFORD, M. G. 2009. Bird population density estimated from acoustic signals. *Journal of Applied Ecology* **46**: 1201–1209.
- DENNIS, T. E. & SHAH, S. F. 2012. Assessing acute effects of trapping , handling , and tagging on the behavior of wildlife Using GPS telemetry: a case study of the common brushtail possum. *Journal of Applied Animal Welfare Science* **15**: 189–207.
- DESMET, P. G. & COWLING, R. M. 1999. The climate of the Little Karoo - a functional approach. In: *The Karoo: ecological patterns and processes*, (eds) W. R. J. Dean & S. J. Milton, pp. 3–16. Cambridge University Press, Cambridge.
- DI BITETTI, M. S., PAVIOLO, A. & DE ANGELO, C. 2006. Density, habitat use and activity patterns of ocelots (*Leopardus pardalis*) in the Atlantic Forest of Misiones , Argentina. *Journal of Zoology* **270**: 153–163.
- DICKMAN, A. J. 2010. Complexities of conflict: the importance of considering social factors for effectively resolving human–wildlife conflict. *Animal Conservation* **13**: 458–466.
- DILLON, A. & KELLY, M. J. 2007. Ocelot *Leopardus pardalis* in Belize: the impact of trap spacing and distance moved on density estimates. *Oryx* **41**: 469–477.

CHAPTER 8: REFERENCES

- DILLON, A. & KELLY, M. J. 2008. Ocelot home range, overlap and density: comparing radio telemetry with camera trapping. *Journal of Zoology* **275**: 391–398.
- DO LINH SAN, E., MALONGWE, N. B., FIKE, B., SOMERS, M. J. & WALTERS, M. 2009. A diverse autumn diet without dominant prey for opportunistic black-backed jackals *Canis mesomelas*. *Wildlife Biology in Practice* **5**: 96–103.
- DOUGLAS, R. M. 1989. A new method of cross-sectioning hair of larger mammals. *South African Journal of Science* **19**: 73–76.
- EDGAONKAR, A. & CHELLAM, R. 2002. Food habit of the leopard, *Panthera pardus*, in the Sanjay Gandhi National Park, Maharashtra, India. *Mammalia* **66**: 353–360.
- EFFORD, M. 2004. Density estimation in live-trapping studies. *Oikos* **3**: 598–610.
- EFFORD, M. G., DAWSON, D. K. & BORCHERS, D. L. 2009. Population density estimated from locations of individuals on a passive detector array. *Ecology* **90**: 2676–2682.
- EFFORD, M. G., DAWSON, D. K. & ROBBINS, C. S. 2004. DENSITY: software for analysing capture – recapture data from passive detector arrays. *Animal Biodiversity and Conservation* **27**: 217–228.
- ELITH, J., GRAHAM, C. H., ANDERSON, R. P., DUDIK, M., FERRIER, S., GUISAN, A., HIJMANS, R. J., HUETTMANN, F., LEATHWICK, J. R., LEHMANN, A., LI, J., LOHMANN, L. G., LOISELLE, B. A., MANION, G., MORITZ, C., NAKAMURA, M., NAKAZAWA, Y., OVERTON, J. M., PETERSON, A. T., PHILLIPS, S. J., RICHARDSON, K., SCACHETTI-PEREIRA, R., SCHAPIRE, R. E., SOBERON, J., WILLIAMS, S., WISZ, M. S. & ZIMMERMANN, N. E. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* **29**: 129 – 151.
- ELITH, J., KEARNEY, M. & PHILLIPS, S. 2010. The art of modelling range-shifting species. *Methods in Ecology and Evolution* **1**: 330–342.
- ELITH, J., PHILLIPS, S. J., HASTIE, T., DUDÍK, M., CHEE, Y. E. & YATES, C. J. 2011. A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* **17**: 43–57.
- ELLIS, F. & LAMBRECHTS, J. J. N. 1986. Soils. In: *The karoo biome: a preliminary synthesis. Part 1 - physical environment*, (eds) R. M. Cowling, P. W. Roux & A. J. H. Pieterse, pp. 18–38. Council for Scientific and Industrial Research, Pretoria.
- ELLISON, A. M. & GOTELLI, N. J. 2004. *A primer of ecological statistics*. Sinauer Associates Inc., Sunderland, Massachusetts.
- ELMHAGEN, B. & RUSHTON, S. P. 2007. Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? *Ecology Letters* **10**: 197–206.
- ELMORE, R. D., MESSMER, T. A. & BRUNSON, M. W. 2007. Perceptions of wildlife damage and species conservation : lessons learned from the Utah prairie dog. *Human-Wildlife Conflicts* **1**: 78–88.
- ESTES, J. A, TERBORGH, J., BRASHARES, J. S., POWER, M. E., BERGER, J., BOND, W. J., CARPENTER, S. R., ESSINGTON, T. E., HOLT, R. D., JACKSON, J. B. C., MARQUIS, R. J., OKSANEN, L., OKSANEN, T.,

CHAPTER 8: REFERENCES

- PAINE, R. T., PIKITCH, E. K., RIPPLE, W. J., SANDIN, S. A., SCHEFFER, M., SCHOENER, T. W., SHURIN, J. B., SINCLAIR, A. R. E., SOULÉ, M. E., VIRTANEN, R. & WARDLE, D. A. 2011. Trophic downgrading of planet Earth. *Science* **333**: 301–6.
- ESTES, R. D. 2012. *The behaviour guide to African mammals*. The University of California Press, Berkely.
- FATTEBERT, J., DICKERSON, T., BALME, G., SLOTOW, R. & HUNTER, L. 2013. Long-distance natal dispersal in leopard reveals potential for a three-country metapopulation. *South African Journal of Wildlife Research* **43**: 61–67.
- FERRAZ, K. M. P. M. B., BEISIEGEL, B. M., PAULA, R. C. DE, SANA, D. A., CAMPOS, C. B. DE, OLIVEIRA, T. G. DE & DESBIEZ, A. L. J. 2012. How species distribution models can improve cat conservation - jaguars in Brazil. *CATnews* **7**: 38–42.
- FIELDING, A. H. & BELL, J. F. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* **24**: 38–49.
- FORBES, R. W. 2011. The diet of black-backed jackal (*Canis Mesomelas*) on two contrasting land-use types in the Eastern Cape province, South Africa and the validation of a new analytical method of mammalian hair identification. MSc. thesis, Rhodes University, Grahamstown, South Africa.
- FORMAN, D. W. 2005. An assessment of the local impact of native predators on an established population of British water voles (*Arvicola terrestris*). *Journal of Zoology, London* **266**: 221–226.
- FOSTER, R. J. 2008. The ecology of jaguars (*Panthera onca*) in a human-influenced landscape. PhD thesis, University of Southampton, Southampton, UK.
- FOSTER, R. J. & HARMSSEN, B. J. 2012. A critique of density estimation from camera-trap data. *The Journal of Wildlife Management* **76**: 224–236.
- FOSTER, R. J., HARMSSEN, B. J. & DONCASTER, C. P. 2010. Habitat use by sympatric jaguars and pumas across a gradient of human disturbance in Belize. *Biotropica* **42**: 724–731.
- FRANK, L., SIMPSON, D. & WOODROFFE, R. 2003. Foot snares: an effective method for capturing African lions. *Wildlife Society Bulletin* **31**: 309–314.
- FRECKLETON, R. P. 2011. Dealing with collinearity in behavioural and ecological data: model averaging and the problems of measurement error. *Behavioural Ecology and Sociobiology* **65**: 91–101.
- FRIEDMAN, B. J., HASTIE, T. & TIBSHIRANI, R. 2000. Additive logistic regression: a statistical view of boosting. *The Annals of Statistics* **28**: 337–407.
- FRIEDMANN, Y. & DALY, B. 2004. *Red data book of the mammals of South Africa: a conservation assessment*. Conservation Breeding Specialist Group & Endangered Wildlife Trust, Johannesburg.
- FUNSTON, P. J., FRANK, L., STEPHENS, T., DAVIDSON, Z., LOVERIDGE, A., MACDONALD, D. M., DURANT, S., PACKER, C., MOSSER, A. & FERREIRA, S. M. 2010. Substrate and species constraints

CHAPTER 8: REFERENCES

- on the use of track incidences to estimate African large carnivore abundance. *Journal of Zoology* **281**: 56–65.
- GARDNER, B., REPUCCI, J., LUCHERINI, M. & ROYLE, J. A. 2010. Spatially explicit inference for open populations: estimating demographic parameters from camera trap studies. *Ecology* **91**: 3376–3383.
- GAVASHELISHVILI, A. & LUKAREVSKIY, V. 2008. Modelling the habitat requirements of leopard *Panthera pardus* in west and central Asia. *Journal of Applied Ecology* **45**: 579–588.
- GEHRING, T. M., VERCAUTEREN, K. C., PROVOST, M. L. & CELLAR, A. C. 2010. Utility of livestock-protection dogs for deterring wildlife from cattle farms. *Wildlife Research* **37**: 715.
- GIBBS, J. P. & ENE, E. 2010. Program Monitor: estimating the statistical power of ecological monitoring programs. Version 11.0.0. www.esf.edu/ef/gibbs/monitor
- GILKS, W. R., THOMAS, A. & SPIEGELHALTER, D. J. 1994. A language and program for complex Bayesian modelling. *The Statistician* **43**: 169–178.
- GOLDSMITH, B. 1991. *Monitoring for conservation and ecology*. Chapman and Hall, London.
- GOLICHER, D., FORD, A., CAYUELA, L. & NEWTON, A. 2012. Pseudo-absences, pseudo-models and pseudo-niches: pitfalls of model selection based on the area under the curve. *International Journal of Geographical Information Science* **26**: 2049–2063.
- GOODRICH, J. M. & BUSKIRK, S. W. 1995. Control of abundant native vertebrates for conservation of endangered species. *Conservation Biology* **9**: 1357–1364.
- GORINI, L., LINNELL, J. D. C., MAY, R., PANZACCHI, M., BOITANI, L., ODDEN, M. & NILSEN, E. B. 2012. Habitat heterogeneity and mammalian predator-prey interactions. *Mammal Review* **42**: 55–77.
- GRAHAM, K., BECKERMAN, A. P. & THIRGOOD, S. 2005. Human–predator–prey conflicts: ecological correlates, prey losses and patterns of management. *Biological Conservation* **122**: 159–171.
- GRANT, T. 2012. Leopard population density, home range size and movement patterns in a mixed landuse area of the Mangwe district of Zimbabwe. MSc. thesis, Rhodes University, Grahamstown, South Africa.
- GRAUPNER, E. D. & GRAUPNER, O. F. 1971. Predator-prey interrelationships in a natural big game population. Final report TN.6.4.1/4F. Pretoria. In: BAILEY, T. N. 1993. *The African leopard: ecology and behaviour of a solitary felid*. The Blackburn Press, Caldwell, New Jersey.
- GRAY, T. N. E. & PRUM, S. 2012. Leopard density in post-conflict landscape, Cambodia: Evidence from spatially explicit capture-recapture. *The Journal of Wildlife Management* **76**: 163–169.
- GRIMBEEK, A. M. 1992. The ecology of the leopard (*Panthera pardus*) in the Waterberg. MSc. thesis, University of Pretoria, Pretoria, South Africa.
- GROVES, R. M., CIALDINI, R. B. & COUPER, M. P. 1992. Understanding the decision to participate in a survey. *Public Opinion Quarterly* **56**: 475–495.

CHAPTER 8: REFERENCES

- GUISAN, A. & THUILLER, W. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters* **8**: 993–1009.
- GUSSET, M. & BURGNER, N. 2005. Estimating larger carnivore numbers from track counts and measurements. *African Journal of Ecology* **43**: 320–324.
- GUSSET, M., MADDOCK, A. H., GUNTHER, G. J., SZYKMAN, M., SLOTOW, R., WALTERS, M. & SOMERS, M. J. 2007. Conflicting human interests over the re-introduction of endangered wild dogs in South Africa. *Biodiversity and Conservation* **17**: 83–101.
- GUTIERREZ-GONZALEZ, C. E., GOMEZ-RAMIREZ, M. A. & LOPEZ-GONZALEZ, C. A. 2012. Estimation of the density of the near threatened jaguar *Panthera onca* in Sonora, Mexico, using camera trapping and an open population model. *Oryx* **46**: 431–437.
- HARIHAR, A., PANDAV, B. & GOYAL, S. P. 2011. Responses of leopard *Panthera pardus* to the recovery of a tiger *Panthera tigris* population. *Journal of Applied Ecology* **48**: 806–814.
- HARMSSEN, B. J., FOSTER, R. J. & DONCASTER, C. P. 2010a. Heterogeneous capture rates in low density populations and consequences for capture-recapture analysis of camera-trap data. *Population Ecology* **53**: 253–259.
- HARMSSEN, B. J., FOSTER, R. J., SILVER, S., OSTRO, L. & DONCASTER, C. P. 2010b. Differential use of trails by forest mammals and the implications for camera-trap studies: a case study from Belize. *Biotropica* **42**: 126–133.
- HAYWARD, G. D., MIQUELLE, D. G., SMIRNOV, E. N. & NATIONS, C. 2002. Monitoring Amur tiger populations : characteristics of track surveys in snow. *Wildlife Society Bulletin* **30**: 1150–1159.
- HAYWARD, M. W., HENSCHER, P., O'BRIEN, J., HOFMEYER, M., BALME, G. & KERLEY, G. I. H. 2006. Prey preferences of the leopard (*Panthera pardus*). *Journal of Zoology, London* **270**: 298–313.
- HAYWARD, M. W., JEDRZEJEWSKI, W. & JEDRZEWSKA, B. 2012. Prey preferences of the tiger *Panthera tigris*. *Journal of Zoology* **286**: 221–231.
- HAYWARD, M. W. & KERLEY, G. I. H. 2005. Prey preferences of the lion (*Panthera leo*). *Journal of Zoology, London* **267**: 309–322.
- HEBBLEWHITE, M. & HAYDON, D. T. 2010. Distinguishing technology from biology : a critical review of the use of GPS telemetry data in ecology. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **365**: 2303–2312.
- HEMSON, G., MACLENNAN, S., MILLS, G., JOHNSON, P. & MACDONALD, D. 2009. Community, lions, livestock and money: A spatial and social analysis of attitudes to wildlife and the conservation value of tourism in a human–carnivore conflict in Botswana. *Biological Conservation* **142**: 2718–2725.
- HENSCHER, P. 2008. The conservation biology of the leopard *Panthera pardus* in Gabon: Status , threats and strategies for conservation. PhD. thesis, Georg-August-Universität zu Göttingen, Göttingen, Germany.

CHAPTER 8: REFERENCES

- HENSCHER, P., ABERNETHY, K. A. & WHITE, L. J. T. 2005. Leopard food habits in the Lope National Park, Gabon, Central Africa. *African Journal of Ecology* **43**: 21–28.
- HENSCHER, P., HUNTER, L. T. B., BREITENMOSER, U., PACKER, C., KHOROZYAN, I. G., BAUER, H., MARKER, L. L., SOGBOHOSSOU, E. & BREITENMOSER-WÜRSTEN, C. 2009. *Panthera pardus*. In: IUCN 2013. IUCN Red List of Threatened Species. www.iucnredlist.org.
- HERNANDEZ, P. A., GRAHAM, C. H., MASTER, L. L. & ALBERT, D. L. 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* **29**: 773–785.
- HERR, J., SCHLEY, L. & ROPER, T. J. 2009. Stone martens (*Martes foina*) and cars: investigation of a common human–wildlife conflict. *European Journal of Wildlife Research* **55**: 471–477.
- HILL, C. M. 2004. Farmers' perspectives of conflict at the wildlife–agriculture boundary: some lessons Learned from African subsistence farmers. *Human Dimensions of Wildlife* **9**: 279–286.
- HILL, T. & LEWICKI, P. 2007. *Statistics: methods and applications*. STATSOFT, Tulsa, Oklahoma.
- HINES, J. E., NICHOLS, J. D., ROYLE, J. A., MACKENZIE, D. I., GOPALASWAMY, A. M., SAMBA KUMAR, N. & KARANTH, K. U. 2010. Tigers on trails: occupancy modelling for cluster sampling. *Ecological Applications* **20**: 1456–1466.
- HIRST, S. M. 1969. Predation as a regulating factor of wild ungulate populations in a Transvaal lowveld nature reserve. *Zoologica Africana* **4**: 199–230.
- HIRZEL, A. H., HAUSSER, J., CHESSEL, D. & PERRIN, N. 2002. Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? *Ecology* **83**: 2027–2036.
- HOFFMAN, T. S. & O'RIAIN, M. J. 2010. The spatial ecology of chacma baboons (*Papio ursinus*) in a human-modified environment. *International Journal of Primatology* **32**: 308–328.
- HOLBROOK, A. L., GREEN, M. C. & KROSNIK, J. A. 2003. Telephone versus face-to-face interviewing of national probability samples with long questionnaires: comparisons of respondent satisficing and social desirability response bias. *Public Opinion Quarterly* **67**: 79–125.
- HOLMERN, T., NYAHONGO, J. & RØSKAFT, E. 2007. Livestock loss caused by predators outside the Serengeti National Park, Tanzania. *Biological Conservation* **135**: 518–526.
- HOOGESTEIJN, R. 2001. Manual on the problem of predation caused by jaguars and pumas on cattle ranches. Wildlife Conservation Society and Cat Specialist Group, IUCN. Prohesa, Venezuela.
- HOOGESTEIJN, R., MCBRIDE, R., SUNQUIST, M., HOOGESTEIJN, A. & FARRELL, L. 1996. Medetomidine and rubber-padded leg-hold traps in Venezuelan cat studies. *Cat News* **25**: 22–23.
- HOSSEINI-ZAVAREI, F., FARHADINIA, M. S., BEHESHTI-ZAVAREH, M. & ABDOLI, A. 2013. Predation by grey wolf on wild ungulates and livestock in central Iran. *Journal of Zoology* **290**: 127–134.
- HOWERTH, E. W., OLIVIER, A., FRANCA, M., STALLKNECHT, D. E. & GERS, S. 2012. Pathobiology of highly pathogenic avian influenza virus H5N2 infection in juvenile ostriches from South Africa. *Avian Diseases* **56**: 966–968.

CHAPTER 8: REFERENCES

- HUNTER, L. T. B. & SKINNER, J. D. 1998. Vigilance behaviour in African ungulates: the role of predation pressure. *Behaviour* **135**: 195–211.
- INSKIP, C. & ZIMMERMAN, A. 2009. Human-felid conflict: a review of patterns and priorities worldwide. *Oryx* **43**: 18–34.
- JACKSON, R. M., ROE, J. D., WANGCHUK, R. & HUNTER, D. O. 2006. Estimating snow leopard population abundance using photography and capture-recapture techniques. *Wildlife Society Bulletin* **34**: 772–781.
- JACOBS, J. 1974. Quantitative measurement of food selection: a modification of the forage ratio and Ivlev's Electivity Index. *Oecologia* **14**: 413–417.
- JALANKA, H. H. 1989. Medetomidine- and Ketamine-induced immobilization of snow leopards (*Panthera uncia*): doses, evaluation, and reversal by Atipamezole. *Journal of Zoo and Wildlife Medicine* **20**: 154–162.
- JAYNES, E. T. 1957. Information Theory and Statistical Mechanics. *Physical Review* **106**: 620 – 630.
- JIMÉNEZ-VALVERDE, A. 2012. Insights into the area under the receiver operating characteristic curve (AUC) as a discrimination measure in species distribution modelling. *Global Ecology and Biogeography* **21**: 498–507.
- JOHNSON, A., VONGKHAMHENG, C., HEDEMARK, M. & SAITHONGDAM, T. 2006. Effects of human – carnivore conflict on tiger (*Panthera tigris*) and prey populations in Lao PDR. *Animal Conservation* **9**: 421–430.
- JONES-WALTERS, L. & ÇİL, A. 2011. Biodiversity and stakeholder participation. *Journal for Nature Conservation* **19**: 327–329.
- JOOSTE, E., PITMAN, R. T., VAN HOVEN, W. & SWANEPOEL, L. H. 2012. Unusually high predation on chacma baboons (*Papio ursinus*) by female leopards (*Panthera pardus*) in the Waterberg Mountains, South Africa. *Folia primatologica; International Journal of Primatology* **83**: 353–60.
- JOST, L., CHAO, A. & CHAZDON, R. L. 2011. Compositional similarity and beta diversity. In: *Biological diversity: frontiers in measurement and assessment*, (eds) A. E. Magurran & B. J. McGill, pp. 66–84. Oxford University Press, Oxford.
- KALLE, R., RAMESH, T., QURESHI, Q. & SANKAR, K. 2011. Density of tiger and leopard in a tropical deciduous forest of Mudumalai Tiger Reserve, southern India, as estimated using photographic capture–recapture sampling. *Acta Theriologica* **56**: 335–342.
- KAPLAN, B. 2013. In pursuit of a panacea: mitigating human-baboon conflict in the Cape Peninsula, South Africa. PhD. thesis, University of Cape Town, Cape Town, South Africa.
- KARANTH, K. U. 1995. Estimating tiger *Panthera tigris* populations from camera-trap data using capture-recapture models. *Biological Conservation* **71**: 333–338.
- KARANTH, K. U., GOPALASWAMY, A. M., KUMAR, N. S., VAIDYANATHAN, S., NICHOLS, J. D. & MACKENZIE, D. I. 2011. Monitoring carnivore populations at the landscape scale: occupancy modelling of tigers from sign surveys. *Journal of Applied Ecology* **48**: 1048–1056.

CHAPTER 8: REFERENCES

- KARANTH, K. U. & NICHOLS, J. D. 1998. Estimation of tiger densities in India using photographic captures and recaptures. *Ecology* **79**: 2852–2862.
- KARANTH, K. U., NICHOLS, J. D., KUMAR, N. S. & HINES, J. E. 2006. Assessing tiger population dynamics using photographic capture-recapture sampling. *Ecology* **87**: 2925–2937.
- KARANTH, K. U., NICHOLS, J. D., KUMAR, N. S., LINK, W. A & HINES, J. E. 2004. Tigers and their prey: predicting carnivore densities from prey abundance. *Proceedings of the National Academy of Sciences of the United States of America* **101**: 4854–8.
- KARANTH, K. U., NICHOLS, J. D., SEIDENSTRICKER, J., DINERSTEIN, E., SMITH, J. L. D., MCDUGAL, C., JOHNSINGH, A. J. T., CHUNDAWAT, R. S. & THAPAR, V. 2003. Science deficiency in conservation practice: the monitoring of tiger populations in India. *Animal Conservation* **6**: 141–146.
- KARANTH, K. U. & SUNQUIST, M. E. 1995. Prey selection by tiger, leopard and dhole in tropical forests. *Journal of Animal Ecology* **64**: 439–450.
- KARANTH, K. U. & SUNQUIST, M. E. 2000. Behavioural correlates of predation by tiger (*Panthera tigris*), leopard (*Panthera pardus*) and dhole (*Cuon alpinus*) in Nagarhole, India. *Journal of Zoology, London* **250**: 255–265.
- KAUNDA, S. K. K. & SKINNER, J. D. 2003. Black-backed jackal diet at Mokolodi Nature Reserve, Botswana. *African Journal of Ecology* **41**: 39–46.
- KAWANISHI, K. & SUNQUIST, M. E. 2004. Conservation status of tigers in a primary rainforest of Peninsular Malaysia. *Biological Conservation* **120**: 329–344.
- KEOGH, H. J. 1983. A photographic reference system of the microstructure of the hair of African bovids. *South African Journal of Wildlife Research* **13**: 89–132.
- KHOROZYAN, I. G. & MALKHASYAN, A. G. 2002. Ecology of the leopard (*Panthera pardus*) in Khosrov Reserve, Armenia: implications for conservation - Scientific Reports n. 6. Societa Zoologica "la Torbiera", Italy.
- KIRKWOOD, D. 2010. Western Cape Biodiversity Framework - Garden Route and Little Karoo - Habitat conditions. Western Cape Nature Conservation Board, Stellenbosch.
- KLARE, U., KAMLER, J. F. & MACDONALD, D. W. 2011. A comparison and critique of different scat-analysis methods for determining carnivore diet. *Mammal Review* **41**: 294–312.
- KLARE, U., KAMLER, J. F., STENKEWITZ, U. & MACDONALD, D. W. 2010. Diet, prey selection, and predation impact of black-backed jackals in South Africa. *Journal of Wildlife Management* **74**: 1030–1042.
- KNIGHT, A. T., COWLING, R. M., DIFFORD, M. & CAMPBELL, B. M. 2010. Mapping human and social dimensions of conservation opportunity for the scheduling of conservation action on private land. *Conservation Biology* **24**: 1348–1358.
- KNIGHT, A. T., COWLING, R. M., ROUGET, M., BALMFORD, A., LOMBARD, A. T. & CAMPBELL, B. M. 2008. Knowing but not doing: selecting priority conservation areas and the research-implementation gap. *Conservation Biology* **22**: 610–7.

CHAPTER 8: REFERENCES

- KOŁOWSKI, J. M. & HOLEKAMP, K. E. 2006. Spatial, temporal, and physical characteristics of livestock depredations by large carnivores along a Kenyan reserve border. *Biological Conservation* **128**: 529–541.
- LAFON, N. W., MCMULLIN, S. L. & STEFFEN, D. E. 2003. Knowledge and opinions of stakeholders of black bear management in Virginia. *Ursus* **14**: 55–64.
- LAHOZ-MONFORT, J. J., GUILLERA-ARROITA, G., MILNER-GULLAND, E. J., YOUNG, R. P. & NICHOLSON, E. 2010. Satellite imagery as a single source of predictor variables for habitat suitability modelling: how Landsat can inform the conservation of a critically endangered lemur. *Journal of Applied Ecology* **47**: 1094–1102.
- LARRUCEA, E. S., BRUSSARD, P. F., JAEGER, M. M. & BARRETT, R. H. 2007. Cameras, coyotes, and the assumption of equal detectability. *Journal of Wildlife Management* **71**: 1682–1689.
- LAURANCE, W. F., KOSTER, H., GROOTEN, M., ANDERSON, A. B., ZUIDEMA, P. A., ZWICK, S., ZAGT, R. J., LYNAM, A. J., LINKIE, M. & ANTEN, N. P. R. 2012. Making conservation research more relevant for conservation practitioners. *Biological Conservation* **153**: 164–168. Elsevier Ltd.
- LI, W., GUO, Q. & ELKAN, C. 2011. Can we model the probability of presence of species without absence data? *Ecography* **34**: 1096–1105.
- LINDENMAYER, D. B., LIKENS, G. E., ANDERSEN, A., BOWMAN, D., BULL, C. M., BURNS, E., DICKMAN, C. R., HOFFMANN, A. A., KEITH, D. A., LIDDELL, M. J., LOWE, A. J., METCALFE, D. J., PHINN, S. R., RUSSELL-SMITH, J., THURGATE, N. & WARDLE, G. M. 2012. Value of long-term ecological studies. *Austral Ecology* **37**: 745–757.
- LINDSEY, P. A., ALEXANDER, R., FRANK, L. G., MATHIESON, A. & ROMANACH, S. S. 2006. Potential of trophy hunting to create incentives for wildlife conservation in Africa where alternative wildlife-based land uses may not be viable. *Animal Conservation* **9**: 283–291.
- LINDSEY, P. A., DU TOIT, J. T. & MILLS, M. G. L. 2005. Attitudes of ranchers towards African wild dogs *Lycaon pictus*: Conservation implications on private land. *Biological Conservation* **125**: 113–121.
- LINKIE, M., CHAPRON, G., MARTYR, D. J., HOLDEN, J. & LEADER-WILLIAMS, N. 2006. Assessing the viability of tiger subpopulations in a fragmented landscape. *Journal of Applied Ecology* **43**: 576–586.
- LINKIE, M., DINATA, Y., NOFRIANTO, A. & LEADER-WILLIAMS, N. 2007. Patterns and perceptions of wildlife crop raiding in and around Kerinci Seblat National Park, Sumatra. *Animal Conservation* **10**: 127–135.
- LINNELL, J. D. C. & STRAND, O. 2000. Interference interactions, co-existence and conservation of mammalian carnivores. *Diversity and Distributions* **6**: 169–176.
- LINNELL, J. D. C., SWENSON, J. E. & ANDERSEN, R. 2001. Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. *Animal Conservation* **4**: 345–349.
- LIU, C., BERRY, P. M., DAWSON, T. P. & PEARSON, R. G. 2005. Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* **28**: 385–393.

CHAPTER 8: REFERENCES

- LIU, C., WHITE, M. & NEWELL, G. 2013. Selecting thresholds for the prediction of species occurrence with presence-only data. *Journal of Biogeography* **40**: 778–789.
- LIU, F., MCSHEA, W. J., GARSHELIS, D. L., ZHU, X., WANG, D. & SHAO, L. 2011. Human-wildlife conflicts influence attitudes but not necessarily behaviors: factors driving the poaching of bears in China. *Biological Conservation* **144**: 538–547. Elsevier Ltd.
- LOBO, J. M., JIMÉNEZ-VALVERDE, A. & REAL, R. 2008. AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography* **17**: 145–151.
- LOCKIE, J. D. 1959. The estimation of the food of foxes. *The Journal of Wildlife Management* **23**: 224–227.
- LOMBARD, A. T., COWLING, R. M., VLOK, J. H. J. & FABRICIUS, C. 2010. Designing conservation corridors in production landscapes: assessment methods, implementation issues, and lessons learned. *Ecology and Society* **15**: 7.
- LOVERIDGE, A. J. & MACDONALD, D. W. 2003. Niche separation in sympatric jackals (*Canis mesomelas* and *Canis adustus*). *Journal of Zoology, London* **259**: 143–153.
- LYNAM, A. J., RABINOWITZ, A., MYINT, T., MAUNG, M., LATT, K. T. & PO, S. H. T. 2009. Estimating abundance with sparse data: tigers in northern Myanmar. *Population Ecology* **51**: 115–121.
- MACKENZIE, D. I., NICHOLS, J. D., LACHMAN, G. B., DROEGE, S., ROYLE, J. A. & LANGTIMM, C. A. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* **83**: 2248–2255.
- MACKENZIE, D. I., NICHOLS, J. D., SUTTON, N., KAWANISHI, K. & BAILEY, L. L. 2005. Improving inferences in population studies of rare species that are detected imperfectly. *Ecology* **86**: 1101–1113.
- MACKENZIE, D. I. & ROYLE, J. A. 2005. Designing occupancy studies: general advice and allocating survey effort. *Journal of Applied Ecology* **42**: 1105–1114.
- MAFFEI, L., CUELLAR, E. & NOSS, A. 2004. One thousand jaguars (*Panthera onca*) in Bolivia's Chaco. Camera trapping in the Kaa-Iya National Park. *Journal of Zoology, London* **262**: 295–304.
- MAFFEI, L. & NOSS, A. J. 2008. How small is too small? Camera trap survey areas and density estimates for ocelots in the Bolivian Chaco. *Biotropica* **40**: 71–75.
- MAFFEI, L., NOSS, A. J., CUÉLLAR, E. & RUMIZ, D. I. 2005. Ocelot (*Felis pardalis*) population densities, activity, and ranging behaviour in the dry forests of eastern Bolivia: data from camera trapping. *Journal of Tropical Ecology* **21**: 349–353.
- MAFFEI, L., NOSS, A. J., SILVER, S. C. & KELLY, M. J. 2011. Abundance/density case study: jaguars in the Americas. In: *Camera Traps in Animal Ecology: Methods and Analyses*, (eds) A. F. O'Connell, J. D. Nichols & K. U. Karanth, pp. 119–144. Springer, New York.
- MAGURRAN, A. E. 2004. *Measuring biological diversity*. Blackwell Science Ltd., Malden, Massachusetts.

CHAPTER 8: REFERENCES

- MARKER, L. L., DICKMAN, A. J. & MACDONALD, D. W. 2005. Perceived effectiveness of livestock-guarding dogs placed on Namibian farms. *Rangeland Ecology & Management* **58**: 329–336.
- MARKER, L. L., MILLS, M. G. L. & MACDONALD, D. W. 2003a. Factors influencing perceptions of conflict and tolerance toward cheetahs on Namibian farmlands. *Conservation Biology* **17**: 1290–1298.
- MARKER, L. L., MUNTIFERING, J. R., DICKMAN, A. J., MILLS, M. G. L. & MACDONALD, D. W. 2003b. Quantifying prey preferences of free-ranging Namibian cheetahs. *South African Journal of Wildlife Research* **33**: 43–53.
- MARNEWICK, K., FUNSTON, P. J. & KARANTH, K. U. 2008. Evaluating camera trapping as a method for estimating cheetah abundance in ranching areas. *South African Journal of Wildlife Research* **38**: 59–65.
- MARQUES, T. A., THOMAS, L., MARTIN, S. W., MELLINGER, D. K., JARVIS, S., MORRISSEY, R. P., CIMINELLO, C.-A. & DIMARZIO, N. 2010. Spatially explicit capture–recapture methods to estimate minke whale density from data collected at bottom-mounted hydrophones. *Journal of Ornithology* **152**: 445–455.
- MARTIN, R. B. & DE MEULENAAR, T. 1988. *Survey of the status of the leopard (Panthera pardus) in sub-Saharan Africa*. CITES Secretariat, Lausanne, Switzerland.
- MARTINS, Q. E. 2010. The ecology of the leopard *Panthera pardus* in the Cederberg Mountains. PhD. thesis, University of Bristol, Bristol, UK.
- MARTINS, Q. & HARRIS, S. 2013. Movement, activity and hunting behaviour of leopards in the Cederberg mountains, South Africa. *African Journal of Ecology* **51**: 571–579.
- MARTINS, Q., HORSNELL, W. G. C., TITUS, W., RAUTENBACH, T. & HARRIS, S. 2011. Diet determination of the Cape Mountain leopards using global positioning system location clusters and scat analysis. *Journal of Zoology* **283**: 81–87.
- MARTINS, Q. & MARTINS, N. 2006. Leopards of the Cape : conservation and conservation concerns. *International Journal of Environmental Studies* **63**: 579–585.
- MARTINS, S. DE S., SANDERSON, J. G. & SILVA-JUNIOR, J. DE S. E. 2007. Monitoring mammals in the Caxiuna National Forest , Brazil – First results from the Tropical Ecology, Assessment and Monitoring (TEAM) program. *Biodiversity & Conservation* **16**: 857–870.
- MATEO-TOMÁS, P. & OLEA, P. P. 2010. Anticipating knowledge to inform species management: predicting spatially explicit habitat suitability of a colonial vulture spreading its range. *PloS one* **5**: e12374.
- MATEO-TOMAS, P., OLEA, P. P., SANCHEZ-BARBUDO, I. S. & MATEO, R. 2012. Alleviating human-wildlife conflicts: identifying the causes and mapping the risk of illegal poisoning of wild fauna. *Journal of Animal Ecology* **49**: 376–385.
- MATHER, C. 2014. Avian influenza multiple: Enacting realities and dealing with policies in South Africa’s farmed ostrich sector. *Journal of Rural Studies* **33**: 99–106.

CHAPTER 8: REFERENCES

- MAZZOLLI, M. 2010. Mosaics of exotic forest plantations and native forests as habitat of pumas. *Environmental Management* **46**: 237–53.
- MCCARTHY, K. P., FULLER, T. K., MING, M., MCCARTHY, T. M., WAITS, L. & JUMABAEV, K. 2008. Assessing estimators of snow leopard abundance. *Journal of Wildlife Management* **72**: 1826–1833.
- MCCARTHY, M. A., MOORE, J. L., MORRIS, W. K., PARRIS, K. M., GARRARD, G. E., VESK, P. A., RUMPFF, L., GILJOHANN, K. M., CAMAC, J. S., BAU, S. S., FRIEND, T., HARRISON, B. & YUE, B. 2012. The influence of abundance on detectability. *Oikos* **122**: 717–726.
- MCCARTHY, T. M., FULLER, T. K. & MUNKHTSOG, B. 2005. Movements and activities of snow leopards in Southwestern Mongolia. *Biological Conservation* **124**: 527–537.
- MCDONALD, J. E. & FULLER, T. K. 2005. Effects of spring acorn availability on black bear diet, milk composition and cub survival. *Journal of Mammalogy* **86**: 1022–1028.
- MCIVOR, D. E. & CONOVER, M. R. 1994. Perceptions of farmers and non-farmers toward management of problem wildlife. *Wildlife Society Bulletin* **22**: 212–219.
- MEHTA, J. N. & KELLERT, S. R. 1998. Local attitudes toward community-based conservation policy and programmes in Nepal: a case study in the Makalu-Barun Conservation Area. *Environmental Conservation* **25**: 320–333.
- MICHALSKI, F., BOULHOSA, R. L. P., FARIA, A. & PERES, C. A. 2006. Human-wildlife conflicts in a fragmented Amazonian forest landscape: determinants of large felid depredation on livestock. *Animal Conservation* **9**: 179–188.
- MILLER, B., DUGELBY, B., FOREMAN, D., MARTINEZ DEL RIO, C., NOSS, R., PHILLIPS, M., READING, R., SOULÉ, M. E., TERBORGH, J. & WILLCOX, L. 2001. The importance of large carnivores to healthy ecosystems. *Endangered Species Update* **18**: 202–210.
- MILLS, L. S., CITTA, J. J., LAIR, K. P., SCHWARTZ, M. K. & TALLMON, D. A. 2000. Estimating animal abundance using noninvasive DNA sampling: promise and pitfalls. *Ecological Applications* **10**: 283–294.
- MILLS, M. G. L. 1990. *Kalahari hyenas: comparative behavioral ecology of two species*. The Blackburn Press, Caldwell, New Jersey.
- MILLS, M. G. L. & HARVEY, M. 2002. *African predators*. Struik Publishers, Cape Town.
- MINNIE, L. 2009. Socio-economic and ecological correlates of leopard-stock farmer conflict in the Baviaanskloof Mega-Reserve, Eastern Cape. MSc. thesis, Nelson Mandela Metropolitan University, Port Elizabeth, South Africa.
- MISHRA, C. 1997. Livestock depredation by large carnivores in the Indian trans-Himalaya: conflict perceptions and conservation prospects. *Ecological Conservation* **24**: 338–343.
- MITTERMEIER, R. A., GIL, P. R., HOFFMAN, M., PILGRIM, J., BROOKS, T., MITTERMEIER, C. G., LAMOREUX, J. & DA FONSECA, G. A. B. 2005. *Hotspots revisited. Earth's biologically richest and most endangered terrestrial ecoregions*. Conservation International, Sierra Madre.

CHAPTER 8: REFERENCES

- MIZUTANI, F. 1999. Impact of leopards on a working ranch in Laikipia , Kenya. *African Journal of Ecology* **37**: 211–225.
- MIZUTANI, F. & JEWELL, P. A. 1998. Home-range and movements of leopards (*Panthera pardus*) on a livestock ranch in Kenya. *Journal of Zoology, London* **244**: 269–286.
- MOHD. AZLAN, J. & SHARMA, D. S. K. 2003. Camera trapping the IndoChinese tiger, *Panthera tigris corbetti*, in a secondary forest in Peninsular Malaysia. *Raffles Bulletin of Zoology* **51**: 421–427.
- MONDAL, K., GUPTA, S., BHATTACHARJEE, S., QURESHI, Q. & SANKAR, K. 2012a. Response of leopards to re-introduced tigers in Sariska Tiger Reserve, Western India. *International Journal of Biodiversity and Conservation* **4**: 228–236.
- MONDAL, K., SANKAR, K. & QURESHI, Q. 2013. Factors influencing the distribution of leopard in a semiarid landscape of Western India. *Acta Theriologica* **58**: 179–187.
- MONDAL, K., SANKAR, K., QURESHI, Q., GUPTA, S. & CHOURASIA, P. 2012b. Estimation of population and survivorship of leopard *Panthera pardus* (Carnivora: Felidae) through photographic capture-recapture sampling in western India. *World Journal of Zoology* **7**: 30–39.
- MOREHOUSE, A. T. & BOYCE, M. S. 2011. From venison to beef: seasonal changes in wolf diet composition in a livestock grazing landscape. *Frontiers in Ecology and the Environment* **9**: 440–445.
- MUCINA, L. & RUTHERFORD, M. C. (eds). 2006. *The vegetation of South Africa, Lesotho and Swaziland*. South African National Biodiversity Institute, Pretoria.
- MYERS, N. 1990. The biodiversity challenge: expanded hot-spots analysis. *The Environmentalist* **10**: 243–56.
- MYERS, N., MITTERMEIER, R. A., MITTERMEIER, C. G., DA FONSECA, G. A. & KENT, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* **403**: 853–8.
- NATTRASS, N. & CONRADIE, B. 2013. Jackal narratives and predator control in the Karoo, South Africa. Working paper 324, Centre for Social Science Research, University of Cape Town, Cape Town, South Africa.
- NAUGHTON-TREVES, L. 1997. Farming the forest edge: vulnerable places and people around the Kibale National Park, Uganda. *Geographical Review* **87**: 27–46.
- NAUGHTON-TREVES, L., MENA, J. L., TREVES, A., ALVAREZ, N. & RADELOFF, V. C. 2003. Wildlife survival beyond park boundaries: the impact of slash-and-burn agriculture and hunting on mammals in Tambopata, Peru. *Conservation Biology* **17**: 1106–1117.
- NAUGHTON-TREVES, L. & TREVES, A. 2005. Socio-ecological factors shaping local support for wildlife: crop-raiding by elephants and other wildlife in Africa. In: *People and wildlife: conflict or coexistence?*, (eds) R. Woodroffe, S. Thirgood & A. Rabinowitz, pp. 252–277. Cambridge University Press, Cambridge.
- NEGRÕES, N., SARMENTO, P., CRUZ, J., EIRA, C., REVILLA, E., FONSECA, C., SOLLMANN, R., TÔRRES, N. M., FURTADO, M. M., JÁCOMO, A. T. A. & SILVEIRA, L. 2010. Use of camera-trapping to

CHAPTER 8: REFERENCES

- estimate puma density and influencing factors in central Brazil. *Journal of Wildlife Management* **74**: 1195–1203.
- NEGROES, N., SOLLMANN, R., FONSECA, C., JACOMO, A. T. A., REVILLA, E. & SILVEIRA, L. 2012. One or two cameras per station? Monitoring jaguars and other mammals in the Amazon. *Ecological Research* **27**: 639–648.
- NEWTON, A. R., SHONE, R. W. & BOOTH, P. W. K. 2006. The Cape Fold Belt. In: *The geology of South Africa*, (eds) M. R. Johnson, C. R. Annhaeusser & R. J. Thomas, pp. 521–530. Geological Society of South Africa, Johannesburg/ Council for Geoscience, Pretoria, Cape Town.
- NICHOLS, J. D. & WILLIAMS, B. K. 2006. Monitoring for conservation. *Trends in ecology & evolution* **21**: 668–73.
- NORTON, P. M. 1986. Historical changes in the distribution of leopards in the Cape Province, South Africa. *Bontebok* **5**: 1–9.
- NORTON, P. M. 1990. How many leopards? A criticism of Martin and de Meulenaer's population estimates for Africa. *South African Journal of Science* **86**: 218–219.
- NORTON, P. M. & HENLEY, S. R. 1987. Home range and movements of male leopards in the Cedarberg Wilderness Area, Cape Province. *South African Journal of Wildlife Research* **17**: 41–48.
- NORTON, P. M. & LAWSON, A. B. 1985. Radio tracking of leopards and caracals in the Stellenbosch area, Cape Province. *South African Journal of Wildlife Research* **16**: 47–52.
- NORTON, P. M., LAWSON, A. B., HENLEY, S. R. & AVERY, G. 1986. Prey of leopards in four mountainous areas of the south-western Cape Province. *South African Journal of Wildlife Research* **16**: 47–52.
- NOSS, A. J., GARDNER, B., MAFFEI, L., CUÉLLAR, E., MONTAÑO, R., ROMERO-MUNOZ, A., SOLLMAN, R. & O'CONNELL, A. F. 2012. Comparison of density estimation methods for mammal populations with camera traps in the Kaa-Iya del Gran Chaco landscape. *Animal Conservation* **15**: 527–535.
- NOSS, A., POLISAR, J., MAFFEI, L., GARCIA, R. & SILVER, S. 2013. Evaluating jaguar densities with camera traps. Wildlife Conservation Society, New York.
- NÚÑEZ-PÉREZ, R. 2011. Estimating jaguar population density using camera-traps: a comparison with radio-telemetry estimates. *Journal of Zoology* **285**: 39–45.
- O'BRIEN, T. G., KINNAIRD, M. F. & WIBISONO, H. T. 2003. Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. *Animal Conservation* **6**: 131–139.
- O'CONNELL, A. F., NICHOLS, J. D. & KARANTH, K. U. (eds). 2011. *Camera traps in Animal Ecology Methods and Analyses*. Springer, Tokyo.
- OBBARD, M. E., HOWE, E. J. & KYLE, C. J. 2010. Empirical comparison of density estimators for large carnivores. *Journal of Applied Ecology* **47**: 76–84.

CHAPTER 8: REFERENCES

- ODDEN, J., LINNELL, J. D. C., MOA, P. F., HERFINDAL, I., KVAM, T. & ANDERSEN, R. 2002. Lynx depredation on domestic sheep in Norway. *Journal of Wildlife Management* **66**: 98–105.
- ODDEN, M. & WEGGE, P. 2005. Spacing and activity patterns of leopards *Panthera pardus* in the Royal Bardia National Park, Nepal. *Wildlife Biology* **11**: 145–152.
- OGADA, M. O., WOODROFFE, R., OGUGE, N. O. & FRANK, L. G. 2003. Limiting depredation by African carnivores: the role of livestock husbandry. *Conservation Biology* **17**: 1521–1530.
- OLIVEIRA-SANTOS, L. G. R., ZUCCO, C. A., ANTUNES, P. C. & CRAWSHAW, P. G. 2010. Is it possible to individually identify mammals with no natural markings using camera-traps? A controlled case-study with lowland tapirs. *Mammalian Biology* **75**: 375–378.
- OTIS, D. L., BURNHAM, K. P., WHITE, G. C. & ANDERSON, D. R. 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monographs* **62**: 3–135.
- OTT, T., KERLEY, G. I. H. & BOSHOFF, A. F. 2007. Preliminary observations on the diet of leopards (*Panthera pardus*) from a conservation area and adjacent rangelands in the Baviaanskloof region, South Africa. *African Zoology* **42**: 31–37.
- PALOMARES, F., ROQUES, S., CHÁVEZ, C., SILVEIRA, L., KELLER, C., SOLLMANN, R., DO PRADO, D. M., TORRES, P. C., ADRADOS, B., GODOY, J. A., DE ALMEIDA JÁCOMO, A. T., TÔRRES, N. M., FURTADO, M. M. & LÓPEZ-BAO, J. V. 2012. High proportion of male faeces in jaguar populations. *PLoS one* **7**: e52923.
- PARSONS, S., SMITH, S. G. D., MARTINS, Q., HORSNELL, W. G. C., GOUS, T. A., STREICHER, E. M., WARREN, R. M., VAN HELDEN, P. D. & GEY VAN PITTIUS, N. C. 2008. Pulmonary infection due to the dassie bacillus (*Mycobacterium tuberculosis* complex sp.) in a free-living dassie (rock hyrax — *Procavia capensis*) from South Africa. *Tuberculosis* **88**: 80–83.
- PAVIOLO, A., DE ANGELO, C. D., DI BLANCO, Y. E. & DI BITETTI, M. S. 2008. Jaguar *Panthera onca* population decline in the Upper Paraná Atlantic Forest of Argentina and Brazil. *Oryx* **42**: 554–561.
- PEARSON, R. G., RAXWORTHY, C. J., NAKAMURA, M. & TOWNSEND PETERSON, A. 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography* **34**: 102–117.
- PEREIRA, J. A., BITETTI, M. S. DI, FRACASSI, N. G., PAVIOLO, A., ANGELO, C. D. DE, BLANCO, Y. E. DI & NOVARO, A. J. 2011. Population density of Geoffroy's cat in scrublands of central Argentina. *Journal of Zoology* **283**: 37–44.
- PETTORELLI, N., RYAN, S., MUELLER, T., BUNNEFELD, N., JEDRZEJEWSKA, B., LIMA, M. & KAUSRUD, K. 2011. The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. *Climate Research* **46**: 15–27.
- PHILLIPS, S. 2012. Inferring prevalence from presence-only data: a response to “Can we model the probability of presence of species without absence data?” *Ecography* **35**: 385–387.
- PHILLIPS, S. J., ANDERSON, R. P. & SCHAPIRE, R. E. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* **190**: 231–259.

CHAPTER 8: REFERENCES

- PHILLIPS, S. J. & DUDIK, M. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* **31**: 161–175.
- PIENAAR, U. DE V. 1969. Predator-prey relationships amongst the larger mammals of the Kruger National Park. *Koedoe* **12**: 108–176.
- PIMENTEL, D., ZUNIGA, R. & MORRISON, D. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* **52**: 273–288.
- PITMAN, R. T., MULVANEY, J., RAMSAY, P. M., JOOSTE, E. & SWANEPOEL, L. H. 2013. Global Positioning System-located kills and faecal samples: a comparison of leopard dietary estimates. *Journal of Zoology*: DOI: 10.1111/jzo.12078.
- PITMAN, R. T., SWANEPOEL, L. H. & RAMSAY, P. M. 2012. Predictive modelling of leopard predation using contextual Global Positioning System cluster analysis. *Journal of Zoology* **288**: 222–230.
- POLISAR, J., MAXIT, I., SCOGNAMILLO, D., FARRELL, L., SUNQUIST, M. E. & EISENBERG, J. F. 2003. Jaguars, pumas, their prey base, and cattle ranching: ecological interpretations of a management problem. *Biological Conservation* **109**: 297–310.
- POLLOCK, K. H., JONES, C. M. & BROWN, T. L. 1994. *Angler survey methods and their applications in fisheries management*. American Fisheries Society, Bethesda, Maryland.
- POTGIETER, G. C., MARKER, L. L., AVENANT, N. L. & KERLEY, G. I. H. 2013. Why Namibian farmers are satisfied with the performance of their livestock guarding dogs. *Human Dimensions of Wildlife* **18**: 403–415.
- PRUGH, L. R., STONER, C. J., EPPS, C. W., BEAN, W. T., RIPPLE, W. J., LALIBERTE, A. S. & BRASHARES, J. S. 2009. The rise of the mesopredator. *BioScience* **59**: 779–791.
- RADLOFF, F. G. T. 2008. The ecology of large herbivores native to the coastal lowlands of the Fynbos Biome in the Western Cape, South Africa. PhD thesis, Stellenbosch University, Stellenbosch, South Africa.
- RADLOFF, F. G. T. & DU TOIT, J. T. 2004. Large predators and their prey in a southern African savanna: a predator's size determines its prey size range. *Journal of Animal Ecology* **73**: 410–423.
- RAES, N., ROOS, M. C., SLIK, J. W. F., VAN LOON, E. E. & STEEGE, H. TER. 2009. Botanical richness and endemism patterns of Borneo derived from species distribution models. *Ecography* **32**: 180–192.
- RAMAKRISHNAN, U., COSS, R. G. & PELKEY, N. W. 1999. Tiger decline caused by the reduction of large ungulate prey: evidence from a study of leopard diets in southern India. *Biological Conservation* **89**: 113–120.
- RASMUSSEN, G. S. . 1999. Livestock predation by the painted hunting dog *Lycaon pictus* in a cattle ranching region of Zimbabwe: a case study. *Biological Conservation* **88**: 133–139.

CHAPTER 8: REFERENCES

- RAUTENBACH, T. 2010. Assessing the diet of the Cape Leopard (*Panthera pardus*) in the Cederberg and Gamka Mountains, South Africa. MSc. thesis, Nelson Mandela Metropolitan University, Port Elizabeth, South Africa.
- RAY, J. C., HUNTER, L. & ZIGOURIS, J. 2005. Setting conservation and research priorities for larger African carnivores. Wildlife Conservation Society, New York.
- REDPATH, S. M., YOUNG, J., EVELY, A., ADAMS, W. M., SUTHERLAND, W. J., WHITEHOUSE, A., AMAR, A., LAMBERT, R. A., LINNELL, J. D. C., WATT, A. & GUTIÉRREZ, R. J. 2013. Understanding and managing conservation conflicts. *Trends in Ecology & Evolution* **28**: 100–9.
- REITER, D. K., BRUNSON, M. W. & SCHMIDT, R. H. 1999. Public attitudes toward wildlife damage management and policy. *Wildlife Society Bulletin* **27**: 746–758.
- RENNER, I. W. & WARTON, D. I. 2013. Equivalence of MAXENT and Poisson point process models for species distribution modeling in ecology. *Biometrics* **69**: 274–281.
- REYNOLDS, J. C. & AEBISCHER, N. J. 1991. Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the Fox *Vulpes vulpes*. *Mammal Review* **21**: 97–122.
- RIGG, R. 2004. The extent of predation on livestock by large carnivores in Slovakia and mitigating carnivore-human conflict using livestock guarding dogs. MSc. thesis, University of Aberdeen, UK.
- RILEY, S. J., DEGLORIA, S. D. & ELLIOT, R. 1999. A terrain ruggedness index that quantified topographic heterogeneity. *Intermountain Journal of Sciences* **5**: 23–27.
- RÍOS-UZEDA, B., GÓMEZ, H. & WALLACE, R. B. 2007. A preliminary density estimate for Andean bears using camera-trapping methods. *Ursus* **18**: 124–128.
- RIPPLE, W. J. & BESCHTA, R. L. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? *BioScience* **54**: 755–766.
- RIPPLE, W. J. & BESCHTA, R. L. 2008. Trophic cascades involving cougar, mule deer, and black oaks in Yosemite National Park. *Biological Conservation* **141**: 1249–1256.
- RIPPLE, W. J., ESTES, J. A., BESCHTA, R. L., WILMERS, C. C., RITCHIE, E. G., HEBBLEWHITE, M., BERGER, J., ELMHAGEN, B., LETNIC, M., NELSON, M. P., SCHMITZ, O. J., SMITH, D. W., WALLACH, A. D. & WIRSING, A. J. 2014. Status and ecological effects of the world's largest carnivores. *Science* **343**: 1241484–1–1241484–11.
- ROBERGE, J.-M. & ANGELSTAM, P. 2004. Usefulness of the Umbrella Species Concept as a conservation tool. *Conservation Biology* **18**: 76–85.
- ROBERSON, M. T. & SUNDSTROM, E. 1990. Questionnaire design, return rates and response to favorableness in an employee attitude questionnaire. *Journal of Applied Psychology* **75**: 354–357.
- ROUGET, M., COWLING, R. M., LOMBARD, A. T., KNIGHT, A. T. & KERLEY, G. I. H. 2006. Designing large-scale conservation corridors for pattern and process. *Conservation Biology* **20**: 549–561.

CHAPTER 8: REFERENCES

- LE ROUX, P. G. & SKINNER, J. D. 1989. A note on the ecology of the leopard (*Panthera pardus* Linnaeus) in the Londolozi Game Reserve. *African Journal of Ecology* **27**: 167–171.
- ROUX, P. W. & THERON, G. K. 1986. Vegetation change in the Karoo biome. In: *The karoo biome: a preliminary synthesis. Part 2 - vegetation and history*, (eds) R. M. Cowling, P. W. Roux & A. J. H. Pieterse, pp. 50–69. Council for Scientific and Industrial Research, Pretoria.
- ROWCLIFFE, J. M., FIELD, J., TURVEY, S. T. & CARBONE, C. 2008. Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology* **45**: 1228–1236.
- ROWE-ROWE, D. T. 1983. Black-backed jackal diet in relation to food availability in the Natal Drakensberg. *South African Journal of Wildlife Research* **13**: 17–23.
- ROYLE, J. A., KARANTH, K. U., GOPALASWAMY, A. M. & KUMAR, N. S. 2009a. Bayesian inference in camera trapping studies for a class of spatial capture-recapture models. *Ecology* **90**: 3233–44.
- ROYLE, J. A., NICHOLS, J. D., KARANTH, K. U. & GOPALASWAMY, A. M. 2009b. A hierarchical model for estimating density in camera-trap studies. *Journal of Applied Ecology* **46**: 118–127.
- SAMPSON, C. G. 1986. Veld damage in the Karoo caused by its pre-trekboer inhabitants: preliminary observations in the Seacow River valley. *Naturalist* **30**: 37–42.
- SAND, H., ZIMMERMANN, B., WABAKKEN, P., ANDRÈN, H. & PEDERSEN, H. C. 2005. Using GPS technology and GIS cluster analyses to estimate kill rates in wolf – ungulate ecosystems. *Wildlife Society Bulletin* **33**: 914–925.
- SARMENTO, P. B., CRUZ, J. P., EIRA, C. I. & FONSECA, C. 2010. Habitat selection and abundance of common genets *Genetta genetta* using camera capture-mark-recapture data. *European Journal of Wildlife Research* **56**: 59–66.
- SCHEEPERS, R. & SCHOCH, A. E. 2006. The Cape Granite Suite. In: *The geology of South Africa*, (eds) M. R. Johnson, C. R. Annhaeusser & R. J. Thomas, pp. 421–432. Geological Society of South Africa, Johannesburg/ Council for Geoscience, Pretoria, Cape Town.
- SCHIESS-MEIER, M., RAMSAUER, S., GABANAPELO, T. & KÖNIG, B. 2007. Livestock predation — insights from problem animal control registers in Botswana. *Journal of Wildlife Management* **71**: 1267–1274.
- SCHUMANN, B., WALLS, J. L. & HARLEY, V. 2012. Attitudes towards carnivores: the views of emerging commercial farmers in Namibia. *Oryx* **46**: 604–613.
- SEIDENSTICKER, J. 1983. Predation by Panthera cats and measures of human influence on habitats of South Asian monkeys. *International Journal of Primatology* **4**: 323–326.
- SERGIO, F., CARO, T., BROWN, D., CLUCAS, B., HUNTER, J., KETCHUM, J., MCHUGH, K. & HIRALDO, F. 2008. Top predators as conservation tools: ecological rationale, assumptions, and efficacy. *Annual Review of Ecology, Evolution, and Systematics* **39**: 1–19.

CHAPTER 8: REFERENCES

- SERGIO, F., NEWTON, I., MARCHESI, L. & PEDRINI, P. 2006. Ecologically justified charisma: preservation of top predators delivers biodiversity conservation. *Journal of Applied Ecology* **43**: 1049–1055.
- SHARMA, R. K., JHALA, Y., QURESHI, Q., VATTAKAVEN, J., GOPAL, R. & NAYAK, K. 2010. Evaluating capture – recapture population and density estimation of tigers in a population with known parameters. *Animal Conservation* **13**: 94–103.
- SHEHZAD, W., MCCARTHY, T. M., POMPANON, F., PUREVJAV, L., COISSAC, E., RIAZ, T. & TABERLET, P. 2012. Prey preference of snow leopard (*Panthera uncia*) in South Gobi, Mongolia. *PloS one* **7**: 1–8.
- SHONE, R. W. 2006. Onshore post-Karoo Mesozoic deposits. In: *The geology of South Africa*, (eds) M. R. Johnson, C. R. Annhaeusser & R. J. Thomas, pp. 541–552. Geological Society of South Africa, Johannesburg/ Council for Geoscience, Pretoria, Cape Town.
- SIEX, K. S. & STRUHSAKER, T. T. 1999. Colobus monkeys and coconuts: a study of perceived conflicts. *Journal of Applied Ecology* **36**: 1009–1020.
- SILLERO-ZUBIRI, C., SUKUMAR, R. & TREVES, A. 2007. Living with wildlife: the roots of conflict and the solutions. In: *Key topics in conservation biology*, (eds) D. W. Macdonald & K. Service, pp. 255–272. Blackwell Science Ltd., Malden, Massachusetts.
- SILVEIRA, L., JACOMO, A. T. A. & DINIZ-FILHO, J. A. F. 2003. Camera trap , line transect census and track surveys : a comparative evaluation. *Biological Conservation* **114**: 351–355.
- SILVER, S. 2004. Assessing jaguar abundance using remotely triggered cameras. Wildlife Conservation Society, New York.
- SILVER, S. C., OSTRO, L. E. T., MARSH, L. K., MAFFEI, L., NOSS, A. J., KELLY, M. J., WALLACE, R. B., GÓMEZ, H. & AYALA, G. 2004. The use of camera traps for estimating jaguar *Panthera onca* abundance and density using capture/recapture analysis. *Oryx* **38**: 148–154.
- SIMBERLOFF, D. 1998. Flagships, umbrellas, and keystones: is single-species management passe in the landscape era. *Biological Conservation* **83**: 247–257.
- SIMCHAROEN, S., BARLOW, A. C. D., SIMCHAROEN, A. & SMITH, J. L. D. 2008. Home range size and daytime habitat selection of leopards in Huai Kha Khaeng Wildlife Sanctuary, Thailand. *Biological Conservation* **141**: 2242–2250.
- SIMCHAROEN, S., PATTANAVIBOOL, A., KARANTH, K. U., NICHOLS, J. D. & KUMAR, N. S. 2007. How many tigers *Panthera tigris* are there in Huai Kha Khaeng Wildlife Sanctuary, Thailand? An estimate using photographic capture-recapture sampling. *Oryx* **41**: 447–453.
- SKEAD, C. J. 2011. *Historical incidence of the larger land mammals in the broader Western and Northern Cape*, (A. F. Boshoff, G. I. H. Kerley, and P. H. Lloyd (eds)). Centre for African Conservation Ecology, Nelson Mandela Metropolitan University, Port Elizabeth.
- SKINNER, J. D. & CHIMIMBA, C. T. 2005. *The mammals of the Southern African subregion*. Cambridge University Press, Cambridge.

CHAPTER 8: REFERENCES

- SMITH, A. B. 1999. Hunters and herders in the karoo landscape. In: *The Karoo: ecological patterns and processes*, (eds) S. J. Milton & W. R. J. Dean, pp. 243–256. Cambridge University Press, Cambridge.
- SOISALO, M. K. & CAVALCANTI, S. M. C. 2006. Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture – recapture sampling in combination with GPS radio-telemetry. *Biological Conservation* **9**: 487–496.
- SOLLMANN, R., FURTADO, M. M., GARDNER, B., HOFER, H., JÁCOMO, A. T. A. A., TÔRRES, N. M., SILVEIRA, L., MALZONI, M. & MUNDIM, N. 2011. Improving density estimates for elusive carnivores: accounting for sex-specific detection and movements using spatial capture–recapture models for jaguars in central Brazil. *Biological Conservation* **144**: 1017–1024. Elsevier Ltd.
- SOLLMANN, R., MOHAMED, A., SAMEJIMA, H. & WILTING, A. 2013. Risky business or simple solution – Relative abundance indices from camera-trapping. *Biological Conservation* **159**: 405–412.
- SPALTON, J. A., AL HIKMANI, H. M., WILLIS, D. & SAID, A. S. B. 2006. Critically Endangered Arabian leopards *Panthera pardus nimr* persist in the Jabal Samhan Nature Reserve, Oman. *Oryx* **40**: 287.
- ST JOHN, F. A. V., KEANE, A. M., EDWARDS-JONES, G., JONES, L., YARNELL, R. W. & JONES, J. P. G. 2011. Identifying indicators of illegal behaviour: carnivore killing in human-managed landscapes. *Proceedings of the Royal Society B: Biological Sciences* **279**: 804–812.
- STAHL, P., VANDEL, J. M., RUETTE, S., COAT, L., COAT, Y. & BALESTRA, L. 2002. Factors affecting lynx predation on sheep in the French Jura. *Journal of Applied Ecology* **39**: 204 – 216.
- STANDER, P. E. 1997. Field age determination of leopards by tooth wear. *African Journal of Ecology* **35**: 156–161.
- STANDER, P. E. 1998. Spoor counts as indices of large carnivore populations: the relationship between spoor frequency, sampling effort and true density. *Journal of Applied Ecology* **35**: 378–385.
- STANDER, P. E., HADEN, P. J., KAQECE, // & GHOU, //. 1997. The ecology of asociality in Namibian leopards. *Journal of Zoology, London* **242**: 343–364.
- STEIDL, R. J., CONWAY, C. J. & LITT, A. R. 2013. Power to detect trends in abundance of secretive marsh birds: Effects of species traits and sampling effort. *The Journal of Wildlife Management* **77**: 445–453.
- STEIN, A. B., FULLER, T. . K., DAMERY, D. T., SIEVERT, L. & MARKER, L. L. 2010. Farm management and economic analyses of leopard conservation in north-central Namibia. *Animal Conservation* **13**: 419–427.
- STEIN, A. B., FULLER, T. K., DESTEFANO, S. & MARKER, L. L. 2011. Leopard population and home range estimates in north-central Namibia. *African Journal of Ecology* **49**: 383–387.

CHAPTER 8: REFERENCES

- STEIN, A. B., FULLER, T. K. & MARKER, L. L. 2008. Opportunistic use of camera traps to assess habitat-specific mammal and bird diversity in northcentral Namibia. *Biodiversity & Conservation* **17**: 3579–3587.
- STEYN, P. D. V. 2007. The socio-spatial organisation of leopards (*Panthera pardus*) in the northern Tuli Game Reserve, Botswana. MTech. thesis, Tshwane University of Technology, Pretoria, South Africa.
- STOCKWELL, D. 1999. The GARP modelling system: problems and solutions to automated spatial prediction. *International Journal of Geographical Information Science* **13**: 143–158.
- STUART, C. T. 1981. Notes on the mammalian carnivores of the Cape Province, South Africa. *Bontebok* **1**: 1–58.
- STUART, C. T., MACDONALD, I. A. W. & MILLS, M. G. L. 1985. History, current status and conservation of large mammalian predators in Cape Province, Republic of South Africa. *Biological Conservation* **31**: 7–19.
- STUART, C. T. & STUART, M. D. 1991. Cederberg leopard monitoring project - unpublished report. African carnivore survey, Niewoudtville.
- SWANEPOEL, L. H. 2009. Ecology and conservation of leopards, *Panthera pardus*, on selected game ranches in the Waterberg region, Limpopo, South Africa. MSc. thesis, University of Pretoria, Pretoria, South Africa.
- SWANEPOEL, L. H. 2012. Viability of leopards *Panthera pardus* (Linnaeus, 1758) in South Africa. PhD thesis, University of Pretoria, Pretoria, South Africa.
- SWANEPOEL, L. H., LINDSEY, P., SOMERS, M. J., VAN HOVEN, W. & DALERUM, F. 2013. Extent and fragmentation of suitable leopard habitat in South Africa. *Animal Conservation* **16**: 41–50.
- SYFERT, M. M., SMITH, M. J. & COOMES, D. A. 2013. The effects of sampling bias and model complexity on the predictive performance of MaxEnt species distribution models. *PLoS ONE* **8**: e55158.
- SYMONDS, M. R. E. & MOUSSALLI, A. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioural Ecology and Sociobiology* **65**: 13–21.
- TAMBLING, C. J., LAURENCE, S. D., BELLAN, S. E., CAMERON, E. Z., DU TOIT, J. T. & GETZ, W. M. 2012. Estimating carnivore diets using a combination of carcass observations and scats from GPS clusters. *Journal of Zoology* **286**: 102–109.
- TEMPLE, S. A. 1987. Do predators always capture substandard individuals disproportionately from prey populations? *Ecology* **68**: 669–674.
- TERBORGH, J. 1988. The big things that run the world - a sequel to E. O Wilson. *Conservation Biology* **2**: 402–403.
- TERBORGH, J. 1992. Maintenance of Diversity in Tropical Forests. *Biotropica* **24**: 283–292.

CHAPTER 8: REFERENCES

- THAMM, A. G. & JOHNSON, M. R. 2006. The Cape Supergroup. In: *The geology of South Africa*, (eds) M. R. Johnson, C. R. Annhaeusser & R. J. Thomas, pp. 443–461. Geological Society of South Africa, Johannesburg/ Council for Geoscience, Pretoria, Cape Town.
- THIRGOOD, S., WOODROFFE, R. & RABINOWITZ, A. R. 2005. The impact of human-wildlife conflict on human lives and livelihoods. In: *People and wildlife: conflict or coexistence?*, (eds) R. Woodroffe, S. Thirgood & A. R. Rabinowitz, pp. 13–26. Cambridge University Press, Cambridge.
- THORN, M., GREEN, M., DALERUM, F., BATEMAN, P. W. & SCOTT, D. M. 2012. What drives human–carnivore conflict in the North West Province of South Africa? *Biological Conservation* **150**: 23–32.
- TOBLER, M. W. 2007. CameraBase version 1.4. Botanical Research Institute of Texas. <http://www.atrium-biodiversity.org/tools/camerabase/>
- TOBLER, M. W., CARRILLO-PERCASTEGUI, S. E., ZÚÑIGA HARTLEY, A. & POWELL, G. V. N. 2013. High jaguar densities and large population sizes in the core habitat of the southwestern Amazon. *Biological Conservation* **159**: 375–381. Elsevier Ltd.
- TOBLER, M. W. & POWELL, G. V. N. 2013. Estimating jaguar densities with camera traps: problems with current designs and recommendations for future studies. *Biological Conservation* **159**: 109–118. Elsevier Ltd.
- TREVES, A. & KARANTH, K. U. 2003. Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology* **17**: 1491–1499.
- TREVES, A. & NAUGHTON-TREVES, L. 1999. Risk and opportunity for humans coexisting with large carnivores. *Journal of Human Evolution* **36**: 275–282.
- TREVES, A. & NAUGHTON-TREVES, L. 2005. Evaluating lethal control in the management of human-wildlife conflict. In: *People and wildlife: conflict or coexistence?*, (eds) R. Woodroffe, S. Thirgood & A. R. Rabinowitz, pp. 87–106. Cambridge University Press, Cambridge.
- TREVES, A., NAUGHTON-TREVES, L., HARPER, E. K., MLADENOFF, D. J., ROSE, R. A., SICKLEY, T. A. & WYDEVEN, A. P. 2004. Predicting human-carnivore conflict: a spatial model derived from 25 years of data on wolf predation on livestock. *Conservation Biology* **18**: 114–125.
- TRITES, A. W. & JOY, R. 2005. Dietary analysis from fecal samples: how many scats are enough? *Journal of Mammalogy* **86**: 704–712.
- TROLLE, M. & KERY, M. 2003. Estimation of ocelot density in the Pantanal using capture-recapture analysis of camera-trapping data. *Journal of Mammalogy* **84**: 607–614.
- TROLLE, M., NOSS, A. J., LIMA, E. D. S. & DALPONTE, J. C. 2006. Camera-trap studies of maned wolf density in the Cerrado and the Pantanal of Brazil. *Biodiversity and Conservation* **16**: 1197–1204.
- TUYTTENS, F. A. M., MACDONALD, D. W. & RODDAM, A. W. 2002. Effects of radio-collars on European badgers (*Meles meles*). *Journal of Zoology, London* **257**: 37–42.

CHAPTER 8: REFERENCES

- VALEIX, M., HEMSON, G., LOVERIDGE, A. J., MILLS, G. & MACDONALD, D. W. 2012. Behavioural adjustments of a large carnivore to access secondary prey in a human-dominated landscape. *Journal of Applied Ecology* **49**: 73–81.
- VAN HELDEN, L. S., GREWAR, J. D., VISSER, D., DYASON, E. & KOEN, P. 2012. An outbreak of highly pathogenic avian influenza in domestic ostriches: the current situation in South Africa. In: *Proceedings of the annual congress of the Southern African Society for Veterinary Epidemiology and Preventive Medicine* 1-3 August 2012, pp. 11–12.
- VAN NIEKERK, H. N. 2010. The cost of predation on small livestock in South Africa by medium-sized predators. MSc. thesis, University of the Free State, Potchefstroom, South Africa.
- VAN TONDER, J. & VAN HORSTEN, L. 1998. *The Little Karoo*. Human & Rousseau (Pty) Ltd, Cape Town.
- VELOZ, S. D. 2009. Spatially autocorrelated sampling falsely inflates measures of accuracy for presence-only niche models. *Journal of Biogeography* **36**: 2290–2299.
- VENTER, J. M., MOCKE, C. & DE JAGER, J. M. 1986. Climate. In: *The karoo biome: a preliminary synthesis. Part 1 - physical environment*, (eds) R. M. Cowling, P. W. Roux & A. J. H. Pieterse, pp. 39–52. Council for Scientific and Industrial Research, Pretoria.
- VERMA, M. S., PRATT, L., GANESH, C. & MEDINA, C. 2002. Hair-MAP: a prototype automated system for forensic hair comparison and analysis. *Forensic Science International* **129**: 168–186.
- VIJAYAN, S. & PATI, B. P. 2002. Impact of changing cropping patterns on man-animal conflicts around Gir Protected Area with specific reference to Talala Sub-District, Gujarat, India. *Population and Environment* **23**: 541–559.
- VISSER, J. N. J. 1986. Geology. In: *The karoo biome: a preliminary synthesis. Part 1 - physical environment*, (eds) R. M. Cowling, P. W. Roux & A. J. H. Pieterse, pp. 1–17. Council for Scientific and Industrial Research, Pretoria.
- VLOK, J. H. J., COWLING, R. M. & WOLF, T. 2005. A vegetation map for the Little Karoo. Unpublished maps and report for a SKEP project funded by CEPF grant no. 1064410304.
- VLOK, J. H. J. & SCHUTTE-VLOK, A. L. 2010. *Plants of the Klein Karoo*. Umdaus Press, Hatfield.
- WAGNER, C., HOLZAPFEL, M., KLUTH, G., REINHARDT, I. & ANSORGE, H. 2012. Wolf (*Canis lupus*) feeding habits during the first eight years of its occurrence in Germany. *Mammalian Biology* **77**: 196–203. Elsevier GmbH.
- WALLACE, R. B., GOMEZ, H., AYALA, G. & ESPINOZA, F. 2003. Camera trapping for Jaguar (*Panthera onca*) in the Tuichi Valley, Bolivia. *Journal of Neotropical Mammalogy* **10**: 133–139.
- WALPOLE, M. J. & GOODWIN, H. J. 2001. Local attitudes towards conservation and tourism around Komodo National Park, Indonesia. *Environmental Conservation* **28**: 160–166.
- WANG, S. W. & MACDONALD, D. W. 2006. Livestock predation by carnivores in Jigme Singye Wangchuck National Park, Bhutan. *Biological Conservation* **129**: 558–565.

CHAPTER 8: REFERENCES

- WANG, S. W. & MACDONALD, D. W. 2009a. The use of camera traps for estimating tiger and leopard populations in the high altitude mountains of Bhutan. *Biological Conservation* **142**: 606–613.
- WANG, S. W. & MACDONALD, D. W. 2009b. Feeding habits and niche partitioning in a predator guild composed of tigers, leopards and dholes in a temperate ecosystem in central Bhutan. *Journal of Zoology* **277**: 275–283.
- WARREN, D. L., GLOR, R. E. & TURELLI, M. 2010. ENMTools: a toolbox for comparative studies of environmental niche models. *Ecography* **33**: 607–611.
- WARREN, D. L. & SEIFERT, S. N. 2011. Ecological niche modeling in Maxent : the importance of model complexity and the performance of model selection criteria. *Ecological Applications* **21**: 335–342.
- WARTON, D & AARTS, G. 2013. Advancing our thinking in presence-only and used-available analysis. *Journal of Animal Ecology* **82**: 1125–1134.
- WATKEYS, M. K. 1999. Soils of the arid south-western zone of Africa. In: *The Karoo: ecological patterns and processes*, (eds) S. J. Milton & W. R. J. Dean, pp. 17–26. Cambridge University Press, Cambridge.
- WEAVER, J. L. 1993. Refining the equation for interpreting prey occurrence in gray wolf scats. *The Journal of Wildlife Management* **57**: 534–538.
- WEBBER, K. 1997. Urban coyotes (*Canis latrans* Say, 1823) in the Lower Mainland, British Columbia: public perceptions and education. MSc. thesis, University of British Columbia, Vancouver, Canada.
- WECKEL, M., GIULIANO, W. & SILVER, S. 2006. Jaguar (*Panthera onca*) feeding ecology: distribution of predator and prey through time and space. *Journal of Zoology* **270**: 25–30.
- WHITE, G. C., ANDERSON, D. R., BURNHAM, K. P. & OTIS, D. L. 1982. *Capture-Recapture and Removal Methods for Sampling Closed Populations*. Los Alamos National Laboratory, Los Alamos, New Mexico, USA.
- WHITE, P. J. & GARROTT, R. A. 2005. Yellowstone's ungulates after wolves – expectations, realizations, and predictions. *Biological Conservation* **125**: 141–152.
- WHITTINGTON-JONES, C. A. 1997. Apparent range expansion of the Redbilled Quelea Quelea quelea in the Eastern Cape Province of South Africa. *Ostrich* **68**: 97–103.
- WILLIAMS, R. L., GOODENOUGH, A. E. & STAFFORD, R. 2012. Statistical precision of diet diversity from scat and pellet analysis. *Ecological Informatics* **7**: 30–34.
- WOODROFFE, R., FRANK, L. G., LINDSEY, P. A., OLE RANAH, S. M. K. & ROMANACH, S. 2006. Livestock husbandry as a tool for carnivore conservation in Africa's community rangelands: a case-control study. *Biodiversity and Conservation* **16**: 1245–1260.
- WOODROFFE, R. & GINSBERG, J. R. 1998. Edge effects and the extinction of populations inside protected areas. *Science* **280**: 2126–2128.

CHAPTER 8: REFERENCES

- WOODROFFE, R., THIRGOOD, S. & RABINOWITZ, A. R. 2005. The impact of human-wildlife conflict on natural systems. In: *People and wildlife: conflict or coexistence?*, (eds) R. Woodroffe, S. Thirgood & A. R. Rabinowitz, pp. 13–26. Cambridge University Press, Cambridge.
- YASUDA, M. 2004. Monitoring diversity and abundance of mammals with camera traps: a case study on Mount Tsukuba, central Japan. *Mammal Study* **29**: 37–46.
- YIRGA, G., DE IONGH, H. H., LEIRS, H., GEBRIHIWOT, K., DECKERS, J. & BAUER, H. 2012. Adaptability of large carnivores to changing anthropogenic food sources: diet change of spotted hyena (*Crocuta crocuta*) during Christian fasting period in northern Ethiopia. *Journal of Animal Ecology* **81**: 1052–1055.
- YOUNG, J. C., MARZANO, M., WHITE, R. M., MCCracken, D. I., REDPATH, S. M., CARSS, D. N., QUINE, C. P. & WATT, A. D. 2010. The emergence of biodiversity conflicts from biodiversity impacts: characteristics and management strategies. *Biodiversity and Conservation* **19**: 3973–3990.
- ZELLER, K. A., NIJHAWAN, S., SALOM-PÉREZ, R., POTOSME, S. H. & HINES, J. E. 2011. Integrating occupancy modeling and interview data for corridor identification: A case study for jaguars in Nicaragua. *Biological Conservation* **144**: 892–901.
- ZIMMERMANN, A., WALPOLE, M. J. & LEADER-WILLIAMS, N. 2005. Cattle ranchers' attitudes to conflicts with jaguar *Panthera onca* in the Pantanal of Brazil. *Oryx* **39**: 406.
- ZIMMERMANN, F. 2004. Conservation of the Eurasian lynx (*Lynx lynx*) in a fragmented landscape – habitat models, dispersal and potential distribution. PhD thesis, Universite de Lausanne, Lausanne, Switzerland.