Characteristics, determinants and management of farmer-predator conflict in a multi-use dryland system, South Africa

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Happiness is not at the top of the mountain, but in how to climb.

Confucius

Sunset after a great day of work, Central Karoo, South Africa © Nathalie Houdin & Denis Palanque – The Karoo Predator Project.

ABSTRACT

Extensive livestock farming provides an important source of food and fibre for humans and is often the only commercially viable land use in the more arid regions of the globe. Pastoralism can however lead to natural habitat degradation, fragmentation of landscape by fencing and conflict between livestock farmers and predators. Collectively these impacts have been identified as major threats to biodiversity in general and predators in particular. In the semi-arid Central Karoo region of South Africa, extensive small-livestock farming is the primary use of land and provides local predators with a plentiful supply of unguarded, easy-to-catch sheep in addition to permanent artificial water sources. The result is a widespread and pervasive conflict between farmers and predators and amongst diverse stakeholders on how to best manage both livestock and predators to reduce such conflict. A major impediment to understanding human-predator conflict on farmland and its impacts on biodiversity is the paucity of relevant applied research. Most research on mesopredators in South Africa has been conducted in protected areas (PA) or at the level of a single farm, precluding the generalisation of results to broader regions, and therefore limiting our understanding of the conflict on farmlands more generally. In this thesis I sought to better understand farmer-predator conflict in the Karoo region of South Africa with an emphasis on measuring the impacts of livestock farming on wildlife in general and how predators in particular impact livestock. I hypothesized that ecological, environmental and socio-economic factors would all contribute to the negative interactions between predators and small-livestock farmers, and to the persistence of the two most prevalent predators in the region, the black-backed jackal (*Canis mesomelas*) and the caracal (*Caracal caracal*), despite sustained lethal control. I addressed this hypothesis by first using camera trapping surveys to compare wildlife species richness on farmland with a nearby and similar-sized PA to assess the impacts of small-livestock farming on wildlife diversity and occupancy, notably predators. I then used scat analysis to compare the diet of jackal and caracal with those of conspecifics living in the PA to understand whether predators on farmland are targeting livestock or simply including them opportunistically in their diet. I also used Global Positioning System (GPS) clusters from collars affixed to mesopredators to determine whether jackal and caracal actively kill versus scavenge on livestock. Finally, I performed spatially-explicit interviews using semi-structured questionnaires with farmers to assess the distribution and severity of the conflict with jackal, caracal and chacma baboon (*Papio ursinus*), to explore the potential environmental and socio-economic drivers of reported livestock losses, the attitudes to predators and the use of lethal methods to control predators. Contrary to predictions, species richness was similar on farmland and the PA while community structure, diversity and composition all differed with land use. Species richness and probability of use both varied with environmental factors but not with human disturbance. Diet differed markedly for jackal and caracal between the two land uses, with micromammals and plants dominating mesopredator diet in the PA and livestock on farmland. By combining the results of the biodiversity surveys with the diet analysis, I was able to assess prey preference by predators on medium and large vertebrates. The results revealed that while both jackal and caracal consumed more livestock on farmland than wild prey, only jackal showed a preference for livestock. The results of scat and GPS cluster analyses were consistent reinforcing the findings that mesopredators actively killed livestock on farmland but not from within the PA, even when individuals crossed onto neighbouring farms. Survey results showed that farmers perceive the severity of the conflict with jackal, caracal and baboon to be increasing, especially since the 2000s. There was a positive relationship between perceived livestock losses and both environmental (e.g. terrain ruggedness) and socio-economic (e.g. decrease in farm worker numbers) factors. Surprisingly, negative attitudes towards jackal and caracal were not significantly linked to the percentage of lamb losses but rather to their belief that predators should be confined to PAs. Tolerance was best explained by the perceived aesthetic appeal of both jackal and caracal. Finally, I showed that farmers preferred to use lethal versus non-lethal control methods to manage predation, including poison, because non-lethal methods were considered to be expensive, unpractical, labour intensive and less effective. The use of poison was driven by ecological (e.g. having jackal, caracal and baboon as the top three predators on the farm) and socio-economic (e.g. decrease in farm worker numbers) factors. Together, my results suggest that jackal and caracal, like many other mesocarnivores worldwide, display a remarkable ability to adapt to human-modified landscape, using both rangeland and the PA to feed on a diverse range of prey species. Even if small-livestock farms in the Central Karoo still host important components of indigenous biodiversity, the lack of government support and incentives to protect wildlife, the changes in farming practices, the associated increase in natural habitat from which predators can recolonise commercial farmland, and the reduced labour force may together result in farmers increasing their reliance on non-selective lethal control methods to protect their livestock. Of particular concern is the widespread use of illegal poisoning. If we are to find an appropriate balance between farming and conserving biodiversity on farmland, then a new approach will be required to this very old problem. Resource-constrained conservation authorities will need to be backed by multi-stakeholders' engagements. Farmers will need to be supported through funds to increase farm worker numbers on farms and through improved livestock husbandry measures based on scientific research conducted at the appropriate temporal and spatial scales. The conflict between predators and farmers in the Karoo is complex and multifactorial, involving environmental, ecological, and socioeconomic factors. Finding solutions to limit its impacts is a societal decision at the crux of the debate between conservation and development and requires better use of available funding and multidisciplinary teams to tackle the issue.

PLAGIARISM DECLARATION

This thesis/dissertation has been submitted to the Turnitin module and I confirm that my main supervisor has seen my report and any concerns revealed by such have been resolved with my main supervisor.

This thesis is my own unaided work, both in concept and execution, and apart from the normal guidance from my supervisors, I have received no assistance.

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Date: 02/02/2019

This research complied with protocols approved by the Science Faculty Animal Ethics Committee (SFAEC) of the University of Cape Town and adhered to South African legal requirements. All research methods were approved and conducted with permission and relevant permits from CapeNature (permit AAA007-00074-0056).

DEDICATION

This work is dedicated to Piet and Marijke Gouws without whom this thesis would not have been possible.

Small-livestock farm in the Central Karoo, South Africa © Marine Drouilly – The Karoo Predator Project.

FOREWORD

This PhD was conducted under the Karoo Predator Project, which is the name I gave to the inter-disciplinary collaboration between a team of ecologists, social scientists and economists at the University of Cape Town in South Africa. In 2012, A. Prof. Beatrice Conradie gave a talk in Beaufort West in the Central Karoo on the economics of farming in the region. There, she was approached by two sheep farmers, Lukas Botes and Piet Gouws, who invited her to conduct research on farm economics and predator ecology in their area (the Koup). This meeting was the first one of many that followed and saw the creation of the Karoo Predator Project when I joined the project in September 2012 and started this PhD in 2013.

Red hartebeests at a waterhole in Anysberg Nature Reserve, South Africa © Nathalie Houdin & Denis Palanque – The Karoo Predator Project.

ACKNOWLEDGEMENTS

I keep this memory of myself being really excited, a bit apprehensive, with a huge smile on my face while approaching the trap where my first caracal was caught… This moment took me back to my childhood when I was about 10, drawing in my room with the book "Les félins – toutes les espèces du monde" by Peter Jackson and Adrienne Farrell Jackson in front of me. The book was open on the caracal page and I was trying to reproduce the drawings of Robert Dallet and Johan De Crem, while learning how to say caracal in 6 different languages (the book provided the name of each cat species in the major languages spoken across their distributional range). If this little girl had known that many years later, she would have been studying caracal for her PhD and even have the opportunity to adopt an orphan caracal, she would probably have died of happiness!

Although this project and my PhD thesis presented many difficulties that included (but were not limited to) getting stuck for 24 hours far from anyone after my Toyota completely sank in a mud slide after a huge storm, with no satellite phone; coming back, limping, from a solo night trail run in the veld with a sprain ankle and calf after falling in an aardvark hole and having to run a charity half marathon 2 weeks later; saving a jackal from drowning with bare hands and hoping that it would not bite me; house-sitting for one of my supervisors and ending up having to save their house and dog pack from the flames of the wildfire coming down from Table Mountain in Cape Town; finishing up my analysis while the east of France (where I had decided to stay for a while to be with my family) was getting flooded; finally deciding to finish this thesis in South Africa, with no running water while Cape Town was going through its most severe drought in history, and in fact finishing it while working on the Eurasian lynx in the Alps… This thesis is, before anything, the realization of a personal project that evolved with the encounters I had along the way and the opportunities that arose. It became an interesting puzzle made of different disciplines, languages, cultures, species and horizons. I have been extremely privileged to spend three full years in the veld tracking predators off the beaten tracks in this beautiful and remote part of the world named the Karoo. I have also been very fortunate to have incredible support from a wide variety of people and organizations along the way. I would like to thank them for making this project possible:

To my supervisors and other academic support

First and foremost, I would like to thank my (numerous!) supervisors for allowing me to start this long journey of a PhD, for their academic guidance and advice, for the logistic and interdisciplinary help they provided throughout. Beatrice, for introducing me to the farmer community and giving me a chance to tackle this project even if you thought that a non-Afrikaans student was not the best idea. Allan, for your patience while explaining Bayesian statistics to me and for our exchange of emails when we were both feeling like "an octopus that is being pulled by all tentacles at the same time". Nicoli, for your edits and ideas on the human dimensions of this thesis and for introducing me to this new field I didn't know at all, for your help each time I needed funding or equipment to continue my research, for the nice dinners at Hunters Way with Jeremy and for lending me your wolf pack to go and run in the mountains. And most of all, thank you for providing a great field assistant. Justin, thank you for your incredible support and advice all along this PhD, even when I was working in France and finishing the last chapters. Most of all, thank you for believing in my abilities to complete this big book, especially when my self-confidence was at the lowest. Thanks for your help when dealing with the various logistical problems that arose along the way over the past six years and for helping with the funding of my PhD. Thank you for creating this fun and relax atmosphere at the Institute, for your jokes and your positive energy (I liked the "*Jour-bon*!" every morning). Finally, thank you for giving me time to mature my project and my ideas and for giving me freedom to lead my research as I wanted (and all the side projects that took time off the PhD) while building up my self-reliance. I grew and learnt a lot and completely enjoyed the experience.

To my sponsors / funders

I am extremely grateful to the Nedbank WWF Green Trust for providing substantial funding to the Karoo Predator Project, for covering three years of my PhD, and for generally broadening the scope of the project.

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To the organizations

The Institute for Communities and Wildlife in Africa provided funding to finish my PhD and for me to register at national (AZEF, SAWMA) and international (ICCB in France, IMC in Australia) conferences where I was able to mingle with local and international experts and find collaborators.

CapeNature provided me with extensive support throughout my project, from issuing my permit to work on wild carnivores to inviting me to give talks and present the Karoo Predator Project at several of their meetings. Thank you to all of you and particularly to Coral Briss, Corne Claassen and Annelise Vlok.

Thank you to the Pôle Grands Prédateurs in France for sharing my research through blog posts and for inviting me to talk to their annual international conference in the Jura Mountains that led to my actual job on Eurasian lynx in France.

Thank you to the South African Weather Service for providing the weather data for my study area.

I am grateful to the Flood Museum in Laingsburg for providing me with regular opportunities to present my findings to the farmer community.

Thank you to UCT for hosting my research.

To the farmer community

Most 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 to set camera traps (despite being afraid of being caught in the act of doing a number two in front of one of them without knowing it), to collect carnivores scats and search for carnivores kills. I am particularly grateful to those farmers who sat through lengthy interviews and showed great patience while replying to each one of my question in English. A particular thank you goes to the farmers who let me collar mesopredators on their farms, despite the risk it represented for their livestock and the sleepless nights the results of some of the GPS data have surely provoked! Without you, this project would never have existed. Thank you for your support, your trust, your daily help, your advice, stories about the veld and animals. I never thought that I would find such a strong and helpful community. A particular thank you goes to the farmers of the Koup and to the Lund family in Beaufort West. My gratitude goes far beyond those lines and I hope you know it. I hope this thesis brings some more understanding about the biodiversity present on your farm and the ecology of mesocarnivores in the Karoo.

To other key individuals

A huge thank you to Marius Brand, his wife Adri and the great ranger team at Anysberg Nature Reserve to have supported my research in many ways: from offering a nice spot in their campsite and allowing me to have a desk at their headquarters, to dealing with the large amount of battery chargers plugged everywhere to charge the camera traps, as well as for adopting Jynx and giving him another chance in the wild. Thank you to the rangers who helped collecting scats and to Ismail Wambi and Hanlo Fouche for coming with me to the field to remove cameras, especially when it involved "driving" on the crazy jeep track on top of the mountain. Thanks to my friend Quinn Harrison for joining for some captures and GPS cluster investigations. Your experience with wolves and cougars was greatly appreciated.

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40

LIST OF PUBLICATIONS COMING FROM THIS PHD AND ASSOCIATED FIELDWORK

Peer-reviewed

- Nattrass, N., **Drouilly, M.** and O'Riain, M.J. (2019) Learning from science and history about black-backed jackal Canis mesomelas and their conflict with sheep farmers in South Africa. Mammal Review.
- Nattrass, N., Conradie, B., Stephens, J. and **Drouilly, M.** (2019). Culling recolonizing mesopredators increases livestock losses: Evidence from the South African Karoo. Ambio.
- **Drouilly, M.** and O'Riain, M.J. (2019) Wildlife winners and losers of extensive small-livestock farming: A case study in the South African Karoo. Biodiversity and Conservation 28 (6): 1493-1511.
- Mann, G.K., Wilkinson, A., Hayward, J., **Drouilly, M.**, O'Riain, M.J. and Parker, D.M. (2019) The effects of aridity on land use, biodiversity and dietary breadth in leopards. Mammalian Biology 98: 43-51.
- Tensen, L., **Drouilly, M.** and Jansen van Vuuren, B. (2019) First insights into the phylogeographic structure of black-backed jackal (*Canis mesomelas*) and caracal (*Caracal caracal*) in South Africa. African Journal of Wildlife Research 49 (1): 84-88.
- **Drouilly, M**.*, Tafani, M.*, Nattrass, N. and O'Riain, M.J. (2018) Spatial, temporal and attitudinal dimensions of conflict between predators and small livestock farmers in the Central Karoo. African Journal of Range & Forage Science. Karoo Special Issue: Trajectories of Change in the Anthropocene.
- Tensen, L., **Drouilly, M.** and Jansen van Vuuren, B. (2018) Genetic structure and diversity within lethally managed populations of two mesopredators in South Africa. Journal of Mammalogy 99 (6): 1411-1421.
- **Drouilly, M.***, Clark, A.*, O'Riain, M.J. (2018) Multi-species occupancy modelling of mammal and ground bird communities in rangeland in the Karoo: A case for dryland systems globally. Biological Conservation 224:16-25.
- **Drouilly, M.,** Nattrass, N., O'Riain, M.J. (2018) Dietary niche relationships among predators on farmland and a protected area. The Journal of Wildlife Management 82: 507-518.
- Atickem, A., Stenseth, N.C., **Drouilly, M.**, Bock, S., Roos, C., Zinner, D. (2018). Deep divergence among mitochondrial lineages of African jackals. Zoological Scripta 47(1): 1-8.

General non-peer reviewed articles

- **Drouilly, M.** (Décembre 2015) Le Karoo Predator Project : prédateurs, élevage et biodiversité dans le Karoo sud-africain. La Gazette des Grands Prédateurs. FERUS.
- **Drouilly, M.,** Pryce-Fitchen, K. (February 24 2015) The Karoo Predator Project – mitigating the human-wildlife conflict. Photography by Nathalie Houdin and Denis Palanque. National Geographic Voices.
- **Drouilly, M.** (Mars 2013) Action : Mieux connaître le caracal. Terre Sauvage 290.

Red List assessments (peer-reviewed)

- Taylor, A., Cowell, C., **Drouilly, M.** (2017). Pelea capreolus. The IUCN Red List of Threatened Species 2017.
- Avenant NL, **Drouilly M**, Power RJ, Thorn M, Martins Q, Neils A, du Plessis J, Do Linh San E. (2016). A conservation assessment of Caracal caracal. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, editors. The Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.
- Minnie L, Avenant NL, Kamler J, Butler H, Parker D, **Drouilly M**, du Plessis J, Do Linh San E. (2016). A conservation assessment of Canis mesomelas. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, editors. The Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.
- Wilson B, Sliwa A, **Drouilly M**. (2016). A conservation assessment of Felis nigripes. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, editors. The Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.
- Taylor A, Cowell C, **Drouilly M**, Schulze E, Avenant N, Birss C, Child MF. (2016). A conservation assessment of Pelea capreolus. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, editors. The Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.

Book chapters (peer-reviewed)

- Minnie L., Avenant NL, **Drouilly M.** & Samuels I. (2018). Biology and ecology of the black-backed jackal and the caracal. In Kerley GIH, Wilson SL, Balfour D, editors. Livestock predation and its management in South Africa: a scientific assessment. Centre for African Conservation Ecology, Nelson Mandela University, Port Elizabeth, 178-204.
- Tambling CJ, Avenant NL, **Drouilly M.** & Melville H. (2018). The Role Of Mesopredators In Ecosystems: Potential Effects Of Managing Their Populations On Ecosystem Processes And Biodiversity. In Kerley GIH, Wilson SL, Balfour D, editors. Livestock predation and its management in South Africa: a scientific assessment. Centre for African Conservation Ecology, Nelson Mandela University, Port Elizabeth, 205-227.

TABLE OF CONTENT

CHAPTER 1

Introduction

Typical landscape of a small-livestock farm (top) with sheep and some cattle (below) in the Central Karoo, South Africa © Nathalie Houdin & Denis Palanque – The Karoo Predator Project.

Impacts of livestock grazing on global biodiversity and the particular case of drylands

The human population is predicted to exceed 9 billion people by 2050 (United Nations - Department of Economic and Social Affairs - Population Division, 2015), with food demand expected to increase two- to threefold (Bongaarts, 1996; Green, 2005) due to rapidly increasing per capita consumption (Myers and Kent, 2003), especially of meat. Livestock grazing is leading to natural habitat loss and fragmentation, identified as one of the main threats to biodiversity at a global level (Butchart et al., 2012; Hilty et al., 2006; Rouget et al., 2003). Recent studies and reviews have clearly shown that agriculture (including livestock grazing) is classified as a major current and likely future threat to bird species (Balmford et al., 2005), large herbivores (Ripple et al., 2015), large carnivores (Ripple et al., 2014) and small mammals (Kuiper and Parker, 2013). This major issue is particularly high in developing countries and in arid regions, which include most parts of Africa (Darkoh, 2003). The resulting loss of biodiversity has significant implications for ecosystem health and functioning (Larsen et al., 2005; Zavaleta and Hulvey, 2004) and the provision of ecosystem services (Hooper et al., 2005; Odling-Smee, 2005; Ripple et al., 2015, 2014).

Low productivity and low biomass have resulted in ecologists and conservationists largely overlooking the biodiversity present in drylands (Davies et al., 2012), to the point that “the status of species in the drylands remains unknown, as no assessment exists to date” (UNCCD, 2012). It is therefore difficult to assess the impacts of livestock grazing on biodiversity in drylands. Yet, drylands comprise 41% of the earth’s surface (Davies, 2017) and 65% of the African continent (Darkoh, 2003). They harbour half of the world’s population (UNCCD, 2014), including “the poorest, the hungriest, the least healthy and most marginalized people in the world” (Middleton et al., 2011). They also support half of the world’s livestock and provide forage and habitat for many wildlife species (Niemeijer et al., 2005). They include approximately 20% of the primary centres of global plant diversity and more than 30% of the designated endemic bird areas (Maestre et al., 2012). According to the Millennium Ecosystem Assessment, eight out of the 25 global hotspots are in drylands (Niemeijer et al., 2005). As Darkoh (2003) highlights, there is a crucial need to evaluate the agricultural potential of drylands and to develop distinct agricultural programmes and policies to improve their sustainable utilization and the simultaneous conservation of biodiversity. Realising these changes will first require a better understanding of biodiversity occuring in drylands, of its impact on livestock farming, and on the returned impacts of both private landholders’ management practices and livestock grazing on biodiversity.

Farmer-livestock-wildlife interactions on rangeland

Range is defined by the American Society of Range Management (Jacoby, 1989) as "all land producing native forage for animal consumption, and lands that are revegetated naturally or artificially to provide a forage cover that is managed like native vegetation". Rangeland (I will use the term "farmland" interchangeably with rangeland in this thesis) is generally considered as land that is not cultivated, as it is often too dry, rocky or steep for intensive cropping cultivations (Williams et al., 1968). Approximately 47% of the world's land area is only suitable for grazing by domestic livestock and game animals and much of it lies within drylands. Rangelands are essential for watersheds, wildlife habitat, soil and water conservation, fuel and important by-products. They also support domestic animals that provide most of the world's meat, milk, hides, wool and other animal products (Williams et al., 1968). The juxtaposition of domestic livestock and wild animals does however lead to negative interactions in rangelands (Zimmermann et al., 2009), especially in Africa where many different species of wild carnivores still occur outside of protected areas (PAs) (Prins 2000; Gusset et al. 2009; Thorn et al. 2012).

Sheep (*Ovis aries*), which are small in size and lack well-developed anti-predator responses, are especially vulnerable to predation by free-ranging wild carnivores on rangelands (Glen and Dickman, 2014). Predatory attacks can result in acute and chronic stress in sheep, with long-lasting impacts on health and welfare (Clinchy et al., 2013; van Bommel and Johnson, 2017; Ward et al., 2017). In addition, the economic losses suffered by individual farmers from livestock predation can be high and are seldom compensated (Kissui, 2008). Together, these impacts can fuel negative attitudes of livestock farmers towards predators (Baker et al., 2008), leading to retaliatory and even pre-emptive killing of both target and non-target predators (McManus et al., 2014). In these instances the welfare harms to predator species may be extreme because they often include prolonged periods either within a cage trap or tethered by a foot in a gin-trap without food, water and shelter (Sharp and Saunders, 2010). Large antelope are often hunted too (Gordon et al., 2004) for meat, trophy or if they compete for grazing; or they are excluded by livestock as a result of resource depression (Ripple et al., 2015). Lethal management might also be used for small herbivores, to limit their competition with livestock on pastures (Hey, 1964; Hoogland, 2006; Pech et al., 2007). The viability of other wildlife species including smaller carnivores is also at risk by unselective lethal control methods that target predators, such as indiscriminate trapping (McManus et al., 2014) and poisoning (Ogada, 2014). Poisoning, in addition to usually being illegal, can be harmful to secondary consumers

(Berny, 2007; Eason and Spurr, 1995; Glen et al., 2007) and trigger unintended cascading effects on species assemblages (Colman et al., 2014).

Despite the often negative interactions between livestock farmers and wildlife in rangelands, the importance of farmland for maintaining biodiversity outside of PAs has been broadly recognised (Haines et al., 2006; Kiffner et al., 2015; Knight, 1999; Maestas et al., 2003; Msuha et al., 2012; Norton, 2000), including in southern Africa (Bond et al., 2004). The integration of conservation and production goals and respecting the legitimate right that private landowners have to make a living from their land, has now been endorsed by many conservationists and scientists worldwide (Brussaard et al., 2010; Harvey et al., 2008; Mitchley et al., 2006; Thrupp, 2000). Despite this, we do not have a clear understanding of the ecological processes and biodiversity present in modified ecosystems that dominate private lands. Norton (2000) suggests that this is largely because most conservation research has focused on public PAs rather than on private land, stating: "Working with remnant species in muddy fields among cows cannot match the appeal of working with a charismatic national icon in a remote wilderness area". However, it is crucial that we consider private land in the conservation process if we are to successfully protect biodiversity, limit habitat fragmentation and support the ecological needs of far-ranging species such as large carnivores.

Mesopredators on private rangeland

Most carnivores are midsized species (<15kg) called mesocarnivores (I will use the term "mesopredators" interchangeably in this thesis). They outnumber large carnivores in terms of species richness and fulfil a myriad of ecological roles (Prugh et al., 2009; Roemer et al., 2009). They are important drivers of ecosystem function, structure and dynamics and regulate prey populations that are generally not regulated by their larger counterparts, due to metabolic scaling (Carbone et al., 2007). Among their most important ecological roles, is the regulation of small vertebrates (Sinclair and Krebs, 2002), many of which are classified as pest species on farmland (Newsome, 1990). Mesopredators also disperse seeds (Kurek and Holeksa, 2015) and shape plant communities through predation on seed and plant predators (Asquith et al., 1997). They also function as facultative scavengers, removing waste (Ćirović et al., 2016) and prey that carry diseases (Levi et al., 2012), although they too can be reservoirs of diseases (Delahay et al., 2001). Despite this diversity in ecological roles, the majority of research effort and funding has been and still is directed at charismatic apex carnivores living in select ecosystems (Roemer et al., 2009).

When apex carnivores are extirpated, which is a common phenomenon in rangelands (Kamler et al., 2008; Kauffman et al., 2007a; Klare et al., 2010), the resulting relaxation of top-down control of mesopredator populations may allow them to typically increase in abundance through a process termed "mesopredator release" (Soulé et al., 1988), and to become functionally elevated to the position of top predators (Courchamp et al., 1999; Crooks and Soulé, 1999; Ritchie and Johnson, 2009). This release may result in increased mesopredator predation on prey populations (Prugh et al., 2009), including livestock and can have important consequences for ecosystem processes (Ritchie and Johnson, 2009). However, it remains a challenge to find suitable evidence to thoroughly quantify the exact roles apex carnivores play as biodiversity (including mesopredator) regulators (Allen et al., 2011, 2013b, 2017). Multiple reasons can be highlighted to explain the success of various species of mesopredators. Diverse intrinsic biological traits (Cardillo, 2003), including high reproductive rate and small body size (Roemer et al., 2009), allow some mesocarnivores to persist and even thrive in anthropogenically-modified habitats with sustained lethal management (Knowlton et al., 1999). This persistence is further facilitated by behavioural and dietary flexibility (e.g. shift in activity period in the presence of humans, Kitchen et al., 2000; Murray and St. Clair, 2015), allowing them to adapt to constantly changing environments. Together these factors have given rise to chronic levels of negative impacts (often called "conflict") between livestock owners and mesocarnivores worldwide, with livestock owners finding it progressively more difficult to control mesocarnivore predation on their farms (Berger, 2006; Minnie et al., 2016b). Examples in the Canid family include the red fox (*Vulpes vulpes*) (the most widely distributed canid species apart from domestic dogs *Canis lupus familiaris*), the coyote (*Canis latrans*), the dingo (*Canis lupus dingo*) and two jackal species (i.e. the black-backed jackal *Canis mesomelas* and the golden jackal *Canis aureus*), all of which attack and kill livestock in their natural and introduced ranges and whose depredation is rarely successfully controlled (Macdonald and Sillero-Zubiri, 2004). Amongst the felid family, it is the larger species that are typically implicated in livestock predation, with the exception of the caracal (*Caracal caracal*) and, to a lesser extent, the Eurasian lynx (*Lynx lynx*) (Inskip and Zimmermann, 2009).

The lethal control of mesopredators is widespread but with few exceptions, has had limited long-term success (Berger, 2006; Doherty and Ritchie, 2017; Knowlton et al., 1999; Minnie et al., 2016b; Minnie et al., 2018b; Woodroffe and Frank, 2005). The social transmission of behaviours combined with rapid population growth of lethally managed populations through compensatory breeding and immigration, as well as the disruption of predator social systems and specific site effects have been cited as possible reasons for the lack of efficacy of many lethal mesopredator control programs (Swan et al., 2017). Furthermore, most lethal methods are applied as a "one-size-fits-all" solution despite wide agreement among researchers that their efficacy will be both site- and species-specific and they might not therefore be either cheaper or more efficient than non-lethal alternatives (McManus et al., 2014; Smith and Appleby, 2018). In addition, it has been shown that a coordinated approach amongst farmers for entire regions is critical when using mesopredator culling as a management tool for the protection of livestock (Allen, 2015; Allen and Sparkes, 2001; Heydon and Reynolds, 2000; McLeod et al., 2010; Niemiec et al., 2017; Saunders et al., 1995), including against black-backed jackal (hereafter jackal) predation (recommended in Bingham and Purchase, 2002). Such engagement of farmers as a cooperative group in landscape-wide management decisions and actions was considered and is still advocated today by some farmers as the only effective approach to control predators in the Karoo, South Africa (Nattrass et al., 2017). Yet, nowadays this collaborative effort is not easy to achieve, especially with the global increase in the number of farms bought for leisure or for game farming that do not function as agricultural production units (Müller, 2002; Reed and Kleynhans, 2010; Smailes, 2002) and therefore do not necessarily want, or need to cull predators. Highlighting the real impact of mesopredators on livestock farming sustainability, understanding how farmers perceive predators, and which particular strategies and tools they employ to reduce predation on their livestock and why, are therefore essential first steps before implementing programmes aiming to modify farmers' behaviours.

The importance of the human dimensions of farmer-mesopredator conflict

Human-wildlife conflict is typically understood as more than mere competition between people and wildlife for space, food and other resources. It is often complex and multi-factorial (Dickman, 2010), which requires that effective management first identifies and then integrates the underpinning ecological, socio-economic, legal and environmental contexts of the conflict (Kansky et al., 2014; Nie, 2002). Addressing the human dimensions of conflict with wildlife has been recognized as critical to resolving the conflict in ways that are beneficial to both humans and wildlife (Bennett et al., 2017; Dickman, 2010; Manfredo, 2015; Redpath et al., 2013). Framing the conflicts within Social Ecological Systems (SES) (Berkes et al., 1998; Folke et al., 2004), highlights the importance of a multidisciplinary research approach that considers the interactions between ecosystems, biodiversity and people and recognises the true complexity of the problem when livestock are farmed extensively in rangelands where wildlife still occur.

Conservation conflicts, defined by Redpath et al. (2013) as "situations that occur when two or more parties with strongly held opinions clash over conservation objectives and when one party is perceived to assert its interests at the expense of another" are an important component of the generally termed human-wildlife conflicts. Conservation conflicts are essentially conflicts between stakeholders over how to manage wildlife. It is essential to understand the rival points of view and interests involved in those conflicts to minimize their negative impacts on biodiversity, human livelihoods and resource sustainability (Redpath et al., 2013). Conservation conflicts have for example been reported between urban and rural communities, or between the authorities and local people (Ericsson and Heberlein, 2003), with diverse stakeholders attaching different values to biodiversity conservation and animal welfare (Howley et al., 2014; Te Velde et al., 2002). In the case of livestock farming, policy-makers and the general public are increasingly pushing for farmers, as custodians of wildlife on their land, to manage their farms in a manner that supports both biodiversity conservation and promotes the welfare of domestic and wild animals (Broom, 2010; Hall et al., 2004).

Private landholders are clearly critical to promoting and developing landscape-level conservation strategies that will allow for the attainment of global biodiversity goals. Convincing farmers that this objective is in their interests remains a massive challenge and one that is unlikely to be realised within existing stakeholders' forums where open hostility and a lack of trust often prevent the collaborative pursuit of mutually beneficial outcomes (Nattrass and Conradie, 2015). Therefore, as a first step, it is essential to understand farmers' attitudes towards wildlife in general and predators of livestock in particular and to explore what influences their attitudes. Simultaneously, we need to understand the drivers of reported livestock losses and how they are influenced by economic, political and societal changes. From this discussion, it is evident that a multidisciplinary research approach needs to be adopted as a starting point for developing a new strategy to a pervasive and seemingly intractable conflict between livestock, predators, farmers, wildlife managers, conservationists and animal rightists.

Small-livestock farmer – mesopredator conflict: South Africa and the Central Karoo as a case study

The livestock industry is a crucial component of the agricultural sector in South Africa, contributing 44% of the sector's gross income (KPMG Services (Pty) Ltd, 2012) and representing a significant source of employment in rural areas. Sheep farming in particular has a long history in the country, with the Khoikhoi herding sheep prior to the first settlers' arrival in the Cape in 1652 (Nattrass et al., 2017). Early Cape governments subsequently placed bounties on livestock predators, then on animals that damaged fences (e.g. aardwolves *Proteles cristata*) or competed with livestock for grazing (e.g. rock hyrax *Procavia capensis*) (Hey, 1967).

The transition to democracy in South Africa in 1994, meant the end of the economic and political support that had been provided to white farmers for predator control and fencing (Nattrass et al., 2017). This, coupled with environmental (e.g. droughts, predation) and development (i.e. shale gas exploration) threats, has exacerbated the already precarious economic status of many farmers in the Karoo (Conradie and Piesse, 2016). Despite centuries of both intensive and extensive lethal control of livestock predators (van Sittert, 1998), few farming areas in the Karoo are today experiencing acceptable levels of reported livestock losses to predators and it is now recognised that the problem of livestock depredation is extensive and has social, economic, ecological, ethical and legal drivers and consequences (Kerley et al., 2018).

In South Africa, 68.6% (839 281 km^2) of the land is estimated to be used for domestic livestock farming and game ranching (Thorn et al., 2012). Sheep farming is practiced throughout the country but predominantly in the more arid regions of the Northern, Western and Eastern Cape, the Free State and Mpumalanga. There are an estimated 28.8 million sheep, owned by 8000 commercial and 5800 communal farmers in South Africa (Department of Agriculture Forestry and Fisheries, 2012). South Africa is also ranked as the third most biologically diverse country in the world and is thus of major importance for global biodiversity conservation goals (Convention on Biological Diversity-Republic of South Africa, 2014).

In the semi-arid landscape of the Karoo, which covers almost 33% of the land mass of South Africa (i.e. 400 000 km^2), most of the land is used for sheep farming. The low carrying capacity of this region means that 99% of the land is farmed extensively with, on average, only one small-stock unit per 3-6 ha (Hoffman et al., 1999). Semi-arid areas are often considered to be economically marginal for livestock farming and the Karoo is no exception (Nel and Hill, 2008; Walker et al., 2018). The Karoo is even sometimes presented as a wasteland where farmers have presided over long-term environmental degradation and loss of biodiversity (Nel and Hill, 2008). Rather than reflecting reality, this perception was largely attributed to “an urban-based value system” (Nel and Hill, 2008). Nevertheless, the controversy regarding how to best manage the biophysical environment, particularly in terms of grazing intensity, has in more recent times extended to a debate on how to best manage predators and biodiversity on farmland. This debate has been characterised by varied opinions that all thrive on the dearth of suitable data and appropriately scaled scientific studies (Dean et al., 1995; Nattrass and Conradie, 2015). According to a review by Du Plessis et al. (2015), most of the published studies on jackal (57%, n=58) and caracal (41%, n=29) were conducted in PAs or private game reserves. Only 8% and 27% of studies on jackal and caracal respectively were conducted on rangelands, and most of this research is now outdated (published before 1990s). In an attempt to better understand the gaps in our knowledge of livestock predation and to prioritise future research directions, the South African government provided funding for an independent scientific assessment of livestock predation in South Africa (Kerley et al., 2018). The assessment included expertise from the fields of ecology, social science, economics, history, animal ethics and law (Kerley et al., 2018). It highlights how little we know about even the basic biology of jackal and caracal, in particular on private land outside of PAs. It further shows that livestock predation by both species is facilitated by their ethological and ecological plasticity, enabling them to readily recolonize new areas and rapidly establish populations that farmers then struggle to control (Minnie et al., 2018a).

Internationally, more agricultural lands are being bought for alternative uses such as game viewing, conservation and outdoor activities (Adams and Mundy, 1991; Holmes, 2006). In the Karoo, farmers are increasingly exiting the industry and many long-standing sheep farms are being incorporated into nature reserves (such as Anysberg Nature Reserve, see Chapter 2) or being bought by both “weekend” and “lifestyle” farmers. Both are terms used by commercial farmers to describe farmers who, in the case of the former (weekend farmers) typically receive their income from non-agricultural sources and often do not live permanently on the farm, and in the case of the later (lifestyle farmers), who purchase farms for their aesthetic beauty and as an antidote to the frenetic urban lifestyle (Reed and Kleynhans, 2010). The later in particular are not vested in controlling predators, while the former are perceived by commercial farmers as being poor at managing predators. When combined with an increase in the number and physical extent of PAs, these weekend and lifestyle farms are widely considered by commercial farmers to have facilitated the (re-)colonization of wildlife in general and predators in particular throughout the Karoo.

On commercial farmland in the Central Karoo, sheep mostly graze freely in extensive camps often surrounded by aging or dilapidating fences and with little to no human or other supervision. Water is freely available to both domestic livestock and wild animals within these camps. The provision of permanent water and an abundant prey source in the form of sheep may have helped both jackal and caracal to persist on farmland despite sustained attempts to remove them (Tensen et al., 2018). This perpetual cycle of provisioning predators and then persecuting them has fuelled negative reactions from environmental NGOs, who in turn influence the general public (Nattrass and Conradie, 2015). These elements of conservation conflict are all prevalent in the Central Karoo where knowledge of the ecology of both predators is poor and where the impacts of recent political and economic changes have had notable impacts on farmers' livelihoods (Nattrass et al., 2017). It is this combination of variables that makes the Central Karoo an ideal study area for an interdisciplinary study on small-livestock farmer – mesopredator (i.e. jackal and caracal) conflict on rangelands, and how this is influenced by environmental (e.g. farm ruggedness), ecological (e.g. plasticity of predator diet) and socio-economic (e.g. employment fall on farmland) factors and ultimately shapes the conflict between farmers and environmentalists.

The schematic diagram presented below (Figure 1.1) shows a conceptual version of the interactions between the different biotic components including stakeholders (urbanites, farmers (D) and farm workers (C)), livestock (E), predators (large carnivores (A) and mesopredators (B)), and medium- to large-sized mammals (F) involved in the conflict in the Central Karoo. With the support of published studies in the Karoo and worldwide, I report the general impacts of these interactions in terms of farm sustainability and in the socio-cultural and environmental contexts. A new version of this diagram will be presented in the final chapter of this thesis (see Chapter 7 – Synthesis), with changes based on the knowledge gained through the data chapters presented in Chapters 3-6.

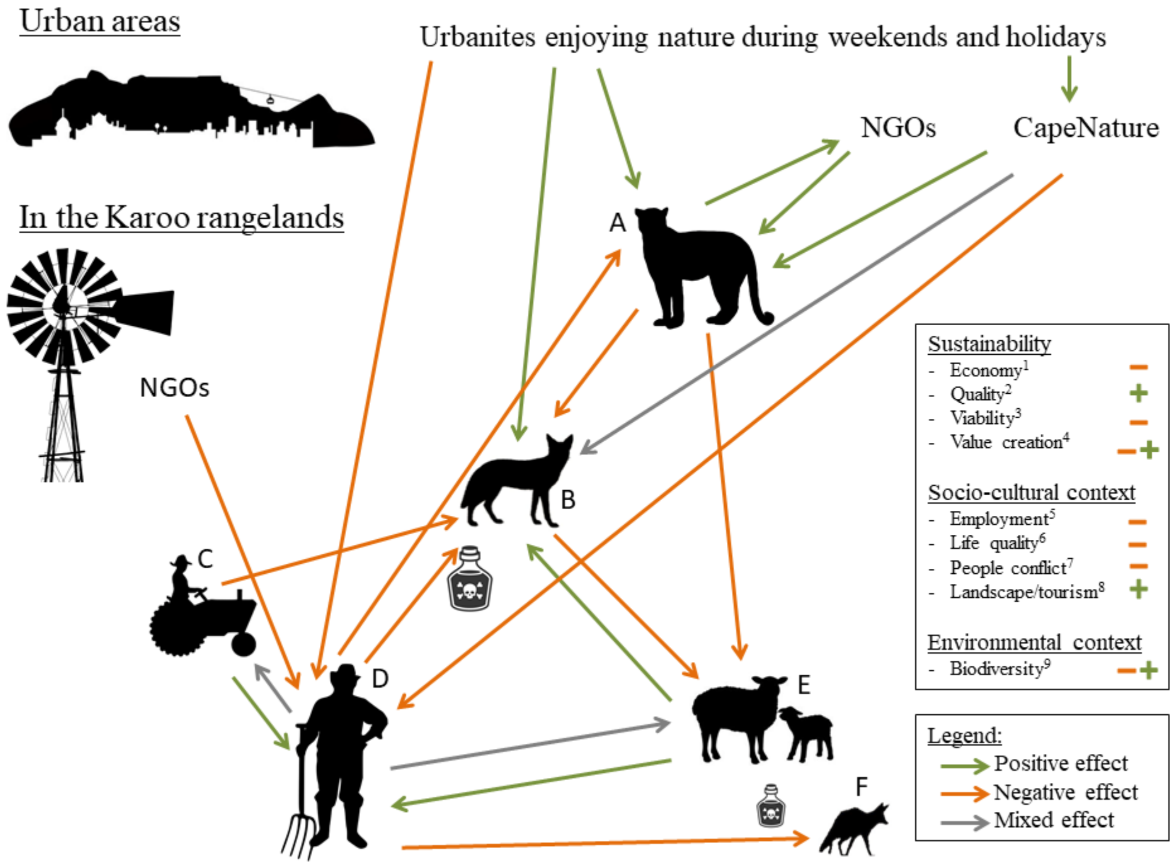


Figure 1.1. A diagram of the simplified current interactions between the principal stakeholders involved in the small-livestock farmer – mesopredator conflict in the Central Karoo. A: large carnivores, B: mesopredators, C: farm workers, D: small-livestock farmers, E: small-livestock, F: medium to large size non-predatory wildlife species. The general sustainability, socio-cultural and environmental impacts are presented in the bottom-right box. The arrows represent the effect a stakeholder has on another one, with their colour depicting whether the impact is positive (green), negative (orange) or mixed (grey). References cited in the diagram: [1]Conradie and Piesse, 2013, Conradie et al., 2013; [2]Weissnar and du Rand, 2012; [3]Conradie et al., 2015, Jordaan and Grobler, 2011; [4]http://www.karoofoundation.co.za/meatoforigin.html (accessed March 26th 2018); [5]Simbi and Aliber, 2000, Statistics South Africa, 2011; [6]de Jongh, 2002, Woolman and Bishop, 2007; [7]Nattrass and Conradie, 2015; [8]Ingle, 2010, Atkinson, 2016; [9]Joubert and Ryan, 1999, Fabricius et al., 2003, Hoffmann and Zeller, 2005, McCann et al., 2007.

Thesis outline

The main objective of this thesis is to investigate the determinants of small-livestock farmer-predator conflict on Karoo farmland in South Africa, and to use this knowledge to improve our understanding of human-wildlife conflict in dry rangelands worldwide. My general hypothesis is that ecological, environmental and socio-economic factors contribute to the conflict between predators and small-livestock farmers in the Karoo, and to the persistence of jackal and caracal in the face of severe anthropogenic mortality on farmland. To test this hypothesis, I first aim to describe variation in the occupancy and diversity of wildlife (including predators and their prey) on farmland, in addition to predator dietary ecology. I then seek to explore farmers' reported lamb losses that they attribute to predators and what they consider the drivers of predation. I further explore their attitudes towards wildlife and what might influence their tolerance towards jackal and caracal. Finally, I investigate farmers' strategies to reduce predation on their livestock and what affects their use of illegal methods such as poisoning to control mesopredators.

While there have been a few published studies on different aspects of jackal (e.g. Humphries et al., 2016, 2015a, 2015b; Kamler et al., 2012a; Minnie et al., 2018b, 2016b) and caracal (Avenant and Nel, 2002; Marker and Dickman, 2005; Ramesh et al., 2017) ecology on private small-livestock farms, none have simultaneously taken into account the ecological, socio-economic and historical factors impacting mesopredators and at a scale that incorporates landscape-level processes (e.g. prey availability, immigration, dispersal) that influence the variables of interest in this and other studies. The results obtained from single farm studies cannot be generalised to the broader region in which they are situated and are thus of limited value to understanding the determinants of farmer-mesopredator conflict on farmland.

A challenge for all previous, current and future work on private farmland and PAs is the absence of suitable baseline data for understanding how anthropogenic factors have shaped the general ecology of mesopredators and their prey in a given region. The Karoo has been subject to anthropogenic influences for thousands of years and with the arrival of Europeans, such influences have increased in both magnitude and extent (Dean and Milton, 1999). The larger terrestrial mammals have been particularly severely impacted by human activities (Boshoff et al., 2016) with the result that over the past 200-300 years, several wildlife species in the Western Cape Province of South Africa have become locally or regionally extinct (Boshoff et al., 2016; Skead, 1987). The (near) extirpation of jackals from much of the Karoo in the late 20th century was the consequence of a collective and coordinated campaign against predators. This campaign had the financial support of the government in the form of both technical assistance and equipment to build fences and drill boreholes on farms (Nattrass et al., 2017). Collectively, these human impacts greatly confound comparisons between regions and even the same area in time. How then does one interpret one's findings on farmland in relation to current management practices and biodiversity estimates? In short, there is no way of controlling for key variables of interest and this is a serious limitation when attempting to understand how land use and management are impacting wildlife and livestock. My approach to this challenge was to compare my results obtained on farmland with those using the same methods for a nearby protected area (PA: Anysberg Nature Reserve). Anysberg is close (40 km) to the farmland study site and was historically used for small-livestock grazing but there are differences in vegetation types, topography and rainfall amount (see Chapter 2) that confound direct comparisons on the impacts of land use on biodiversity and predator diet. Furthermore, Boshoff et al. (2016) warned that current distribution patterns of species in the region, including within PAs, should not become accepted as the historical norm ("shifting baseline syndrome"; Pauly, 1995) or baseline data for extant species. Despite these concerns, I think the comparison offers important insights on the impacts of extensive, sustained small-livestock farming on biodiversity patterns and predator ecology and I have made this argument repeatedly in Chapters 3 and 4 and in Drouilly et al. (2018a, 2018b).

After providing a brief description of my study area, which comprises two contrasting types of land use (i.e. a group of 22 contiguous small-livestock farms and a nearby PA) and of my principal study species (i.e. jackal and caracal) in **Chapter 2**, I have four main objectives, addressed in four data chapters.

Drylands mammals are mostly active at night, occur at low densities and are difficult to detect due to their cryptic life history strategies and the long-term impacts of sustained lethal control. This taxon is therefore particularly challenging to study in this region. In **Chapter 3**, I use camera trapping as a non-invasive network of detectors to study community-level diversity and occupancy of terrestrial vertebrates >0.5 kg in each type of land use. I hypothesize that land use and various anthropogenic and environmental factors (e.g. altitude) impact wildlife species richness and occupancy. I further hypothesize that community structure and composition will vary with land use.

Predator diet lies at the junction of carnivore ecology, predator management and human-wildlife conflict. In **Chapter 4**, I use scat analysis to quantify the diet and examine the resource partitioning patterns and dietary preference of jackal, caracal and a larger apex carnivore in the PA, the leopard (*Panthera pardus*), in response to land use and the associated change in the resource base (defined through camera trapping). I also use scat analyses to determine whether mesocarnivores in the PA feed on small-livestock present in neighbouring farmland. I hypothesize that mesopredator diet and prey preference will differ between farmland and the PA due to a different prey base and notably the presence of small-livestock on farmland.

In **Chapter 5**, I investigate the use of GPS location clusters to quantify the diet of jackal and caracal compared to the estimates obtained through scat analysis (see Chapter 4). I determine the proportion of prey that were scavenged versus depredated by both mesocarnivores, and the impact of sex and age on diet composition. I also investigate whether jackals that reside in Anysberg Nature Reserve have clusters on neighbouring farmland that contain livestock remains. I hypothesize that GPS location clusters alone are not an appropriate tool to accurately describe the diet of mesocarnivores. I further predict that both mesocarnivores will actively kill domestic livestock rather than scavenge. Finally, I hypothesize that both sex and age will have an impact on mesocarnivore diet composition and predict that the clusters on farmland, which are formed by jackals that are resident in Anysberg, will not contain livestock remains (in the light of the results presented in Chapter 4).

Finally, in **Chapter 6**, I use face-to-face interviews with Central Karoo farmers to assess the spatio-temporal distribution, the severity of and the reasons for the reported predation problems with jackal, caracal and chacma baboon (*Papio ursinus*, herafter baboon). I also investigate likely determinants of the reported percentage of lamb losses that farmers attribute to predators. I predicted that the distribution of perceived problems with the three species will have increased over time and hypothesize that the reported percentage of lamb losses will be influenced both by landscape attributes and socio-economic factors. I further explore farmers' attitudes towards wildlife and the drivers of their tolerance towards mesopredators, as well as their strategies to control predation on their farms. I predict that attitudes towards predators will be negative and hypothesize that tolerance will be influenced both by economic and cultural factors. I further predict that farmers will mostly employ lethal control methods to reduce predation because they consider non-lethal methods to be too expensive and ineffective. Finally, I draw attention to the widespread illegal use of poison – a result that requires urgent attention – and I explore some of the drivers of its use. I hypothesize that a synergy of ecological, political and socio-economic factors explains farmers' current high use of poison.

In the final chapter (**Chapter 7**), I synthetize the key findings of the four data chapters and place them into the broader context of small-livestock farmer – mesocarnivore conflict in Africa and the world. Additionally, I use the knowledge learnt throughout this thesis to re-draw the interaction diagram (Figure 1.1 above) with suggested future management options to improve farmers' livelihoods, farm sustainability and biodiversity conservation on rangelands in the Karoo.

CHAPTER 2

Study sites and study species

Black-backed jackal (top) and caracal (below) in the Central Karoo, South Africa © Nathalie Houdin & Denis Palanque – The Karoo Predator Project.

Study site: livestock farms

Creation of the Karoo Predator Project and general description of the study site

In 2012 the Centre for Social Science Research (CSSR) at the University of Cape Town obtained permission to conduct research on the productivity of 22 neighbouring farms (ca. 75 400 ha) that together are part of the Koup area (Figure 2.1). In 2013, the project grew to include both an ecological and a sociological component and became the Karoo Predator Project. The Koup falls into the Laingsburg local municipality, which is one of the three local municipalities (the other two being Prince Albert and Beaufort West) that together form the Central Karoo District Municipality (38 854 km^2) of the Western Cape Province, South Africa. The Central Karoo is the largest district in the province, making up a third of its geographical area (http://www.localgovernment.co.za/districts/view/44/Central-Karoo-District-Municipality, accessed May 20th 2017).

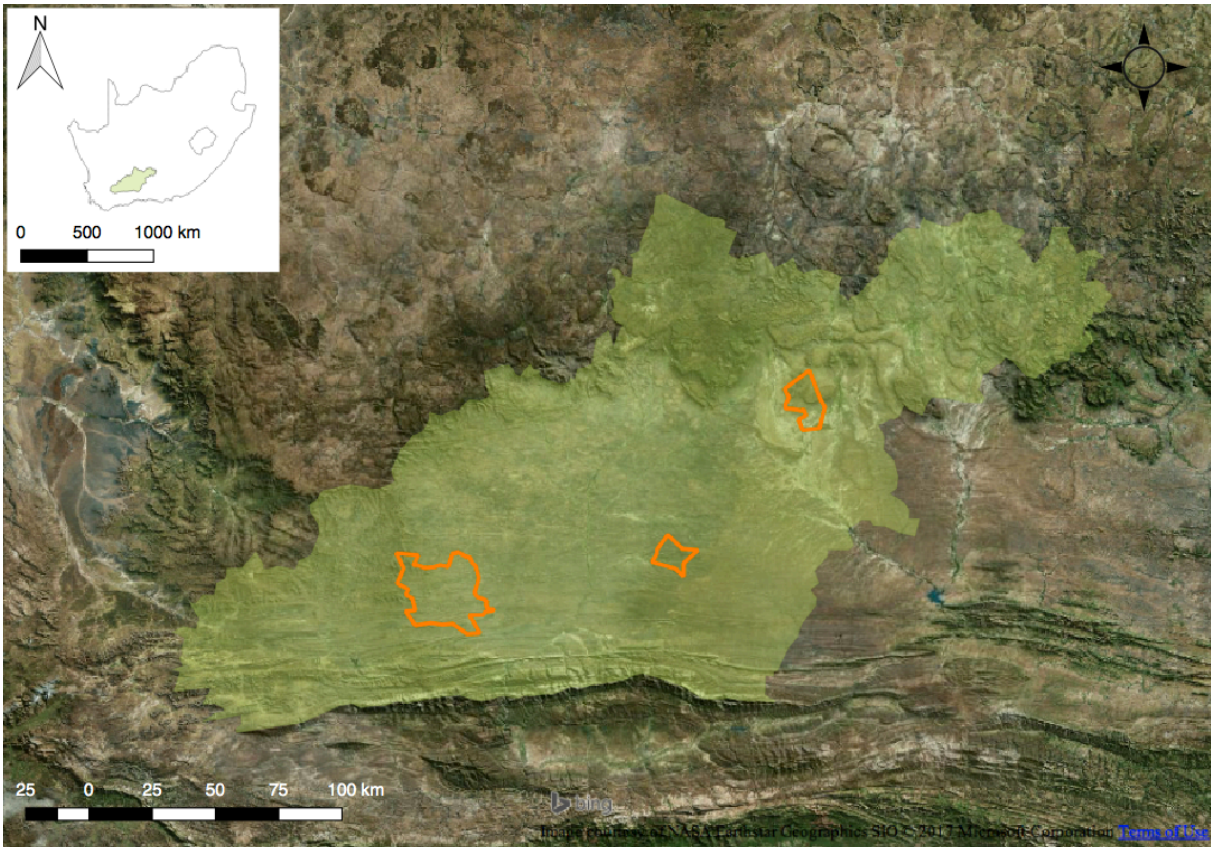


Figure 2.1. Location of the Central Karoo District Municipality in South Africa (insert and green polygon) and my study sites – the Koup, Prince Albert and Beaufort West farms (orange polygons) – within the Central Karoo District Municipality.

The main study site Koup derives its name from the railway junction (Koup) opposite which there is a turn-off to the 22 farms that together comprise the farm site. The Koup is broadly representative of the dominant land use and land management type of the Central Karoo region. Scat and GPS data were also obtained from four other farms: two of which are in the Beaufort West local municipality and two in the Prince Albert local municipality (Figure 2.1).

External farm boundaries in the Koup and Prince Albert areas are fenced with a combination of old and new predator-proof fences comprising 1.4 m high wire mesh with rocks packed at the base to discourage animal digging (Figure 2.2). Fences in the Beaufort West area include electrified wires that are activated when livestock are present in a particular camp. In 2010, the Koup farmers together with the LandCare community-based and government-supported programme initiated the "Koup jackal-proof Fence Project", which entailed re-fencing the perimeter of all 22 farms with new jackal-proof fencing and re-packing with stones. As of mid-2014, once all my ecological data were collected (see Chapters 3 and 4), a total of 238 km of refurbished and new fencing, or 86.5% of the total circumference of the Koup farms, had been completed (Nattrass et al., 2015). The goal of this fence was to limit predator movement into the Koup and hence to reduce predator losses for the collective.

Each Karoo farm is typically divided into fenced camps through which the livestock is rotated as part of a grazing management scheme. Each camp has an artificial watering point, typically in the form of a windmill which supplies a water trough and a small dam (Figure 2.2). Camps with fixed water points have replaced the traditional "shepherding-plus-kraaling" arrangements (Archer, 2000). Camps are fenced with three simple wires that avoid sheep crossing from one camp to the other but do have only a limited impact on wildlife movement and are permeable to predators. Fences separating camps on the Beaufort West farms are electrified to prevent predator and livestock movement, and so to afford better protection from predators.

In their study on performance of woollen and mutton sheep in the Laingsburg district, Conradie and Landman (2015) found flock size to vary from 187 to 1850 ewes with an average of 782 ewes. Most flocks (65%, n=60) consist of Dorper sheep with a few being a mixture of Dorper and other sheep (e.g. Merino) or Boer goats (*Capra aegagrus hircus*) (Conradie and Landman, 2015).

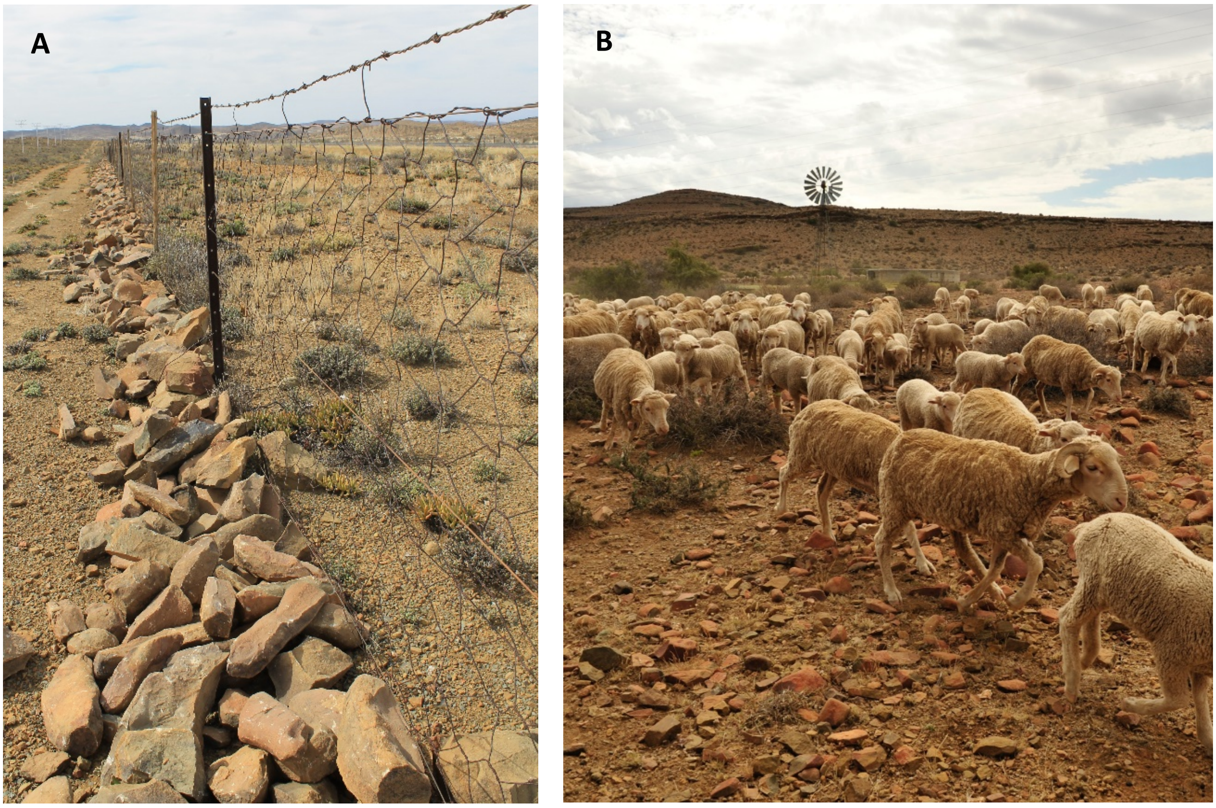


Figure 2.2. Some features found on productive farms in the Central Karoo – A: a newly-built predator-proof fence between two neighbouring farms © Nicoli Nattrass – The Karoo Predator Project; B: a flock of Merino sheep gathering around a watering point made out of a windmill, a dam (both visible in the background) and a water trough © Marine Drouilly – The Karoo Predator Project.

Lethal predator control has been widely practiced in the Karoo and continues today (Nattrass et al., 2017) with the majority of the farmers using lethal methods on a weekly or monthly basis to eliminate jackal and caracal in particular (see Chapter 6). The control methods take the form of trapping with steel jawed gin-traps, poisoning and night hunting (see Chapter 6). The latter is performed by a farmer or by professional hunters or a combination of farmers and professional hunters in block hunts.

Climate

All climatic data were obtained from the South African Weather Service, and are based on data recorded at 08:00 am at the Laingsburg and Beaufort West weather stations. The Laingsburg weather station is situated in the southwest corner of the Central Karoo and was the closest station to the Koup. The Beaufort West weather station is located in the northeastern part of the region, approximately 160 km from the Koup.

The Central Karoo is generally considered to be an arid region, where droughts are common and rainfall is both unpredictable and highly seasonal, peaking in summer between December and March (Palmer and Hoffman, 1997) (Figure 2.3). The Koup study site receives the bulk of its annual rainfall from isolated summer thundershowers with occasional cut-off low pressure systems driving heavier and sustained rainfall events often linked to major floods (Desmet and Cowling, 1999; Venter et al., 1986).

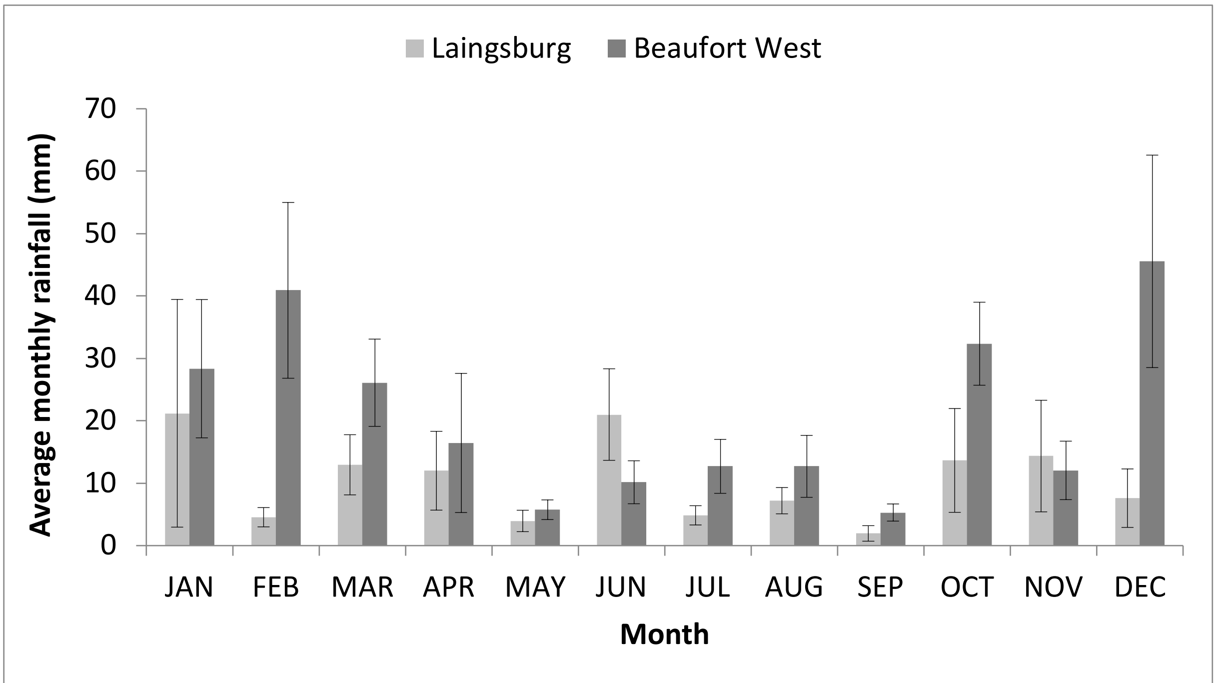


Figure 2.3. Average monthly rainfall (in mm) (± standard deviation) for Laingsburg and Beaufort West weather stations over a four-year period, from 2012 to 2015.

The mean annual rainfall for the period 2012-2015 was 125.2 (±) 16.8 mm in Laingsburg and 248.3 (±) 33.3mm in Beaufort West. The higher rainfall in Beaufort West (Figure 2.4) is attributed to its more easterly position, with rainfall in the Central Karoo generally decreasing from east to west and from north to south (Desmet and Cowling, 1999; Palmer and Hoffman, 1997).

The climate in the Karoo is considered to be harsh with marked seasonal and daily temperatures fluctuations (up to 30°C between day and night temperatures, Venter et al., 1986). In summer, average monthly maximum temperatures often exceed 32°C, while in winter average maximum temperatures are typically below 16°C (Figure 2.5). The maximum recorded average daily temperature during my study was 34.7°C (January 2015 in Beaufort West) but the temperature sensor in one of my camera traps recorded a near ground exposed temperature of 60°C at 643 m.a.s.l. on a flat plain on 18/01/2013.

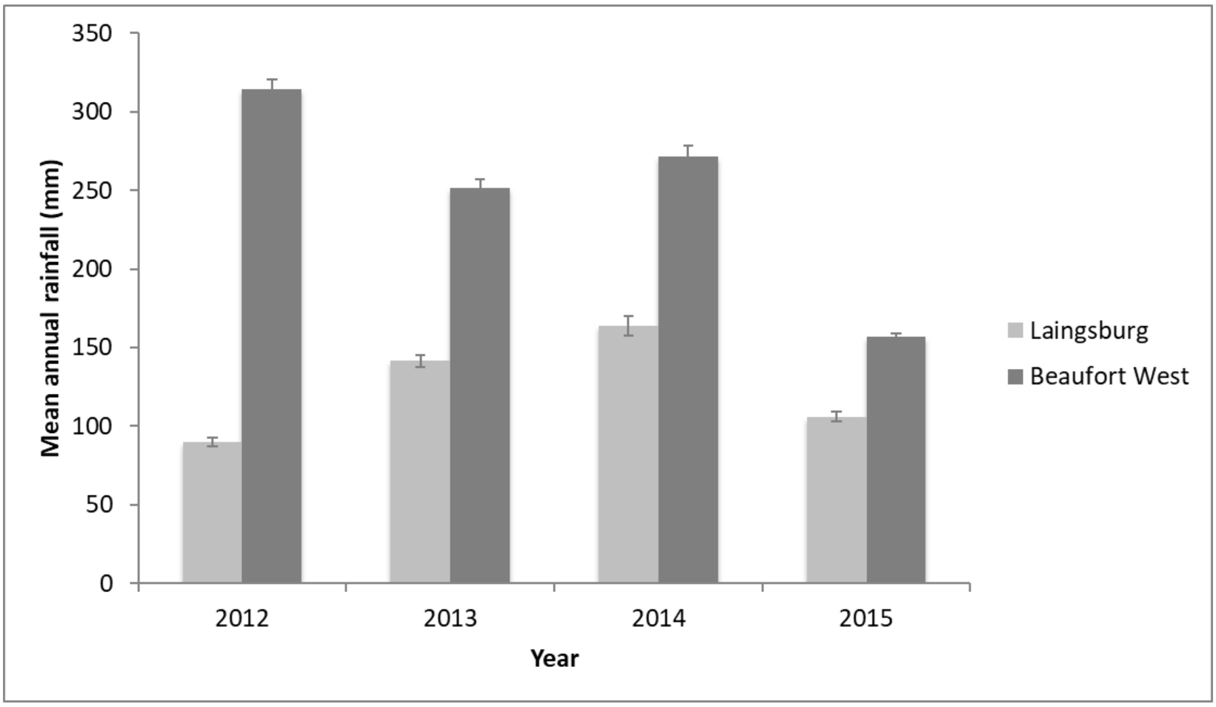


Figure 2.4. Mean annual rainfall (in mm) (± standard deviation) in Laingsburg and Beaufort West for the period 2012-2015.

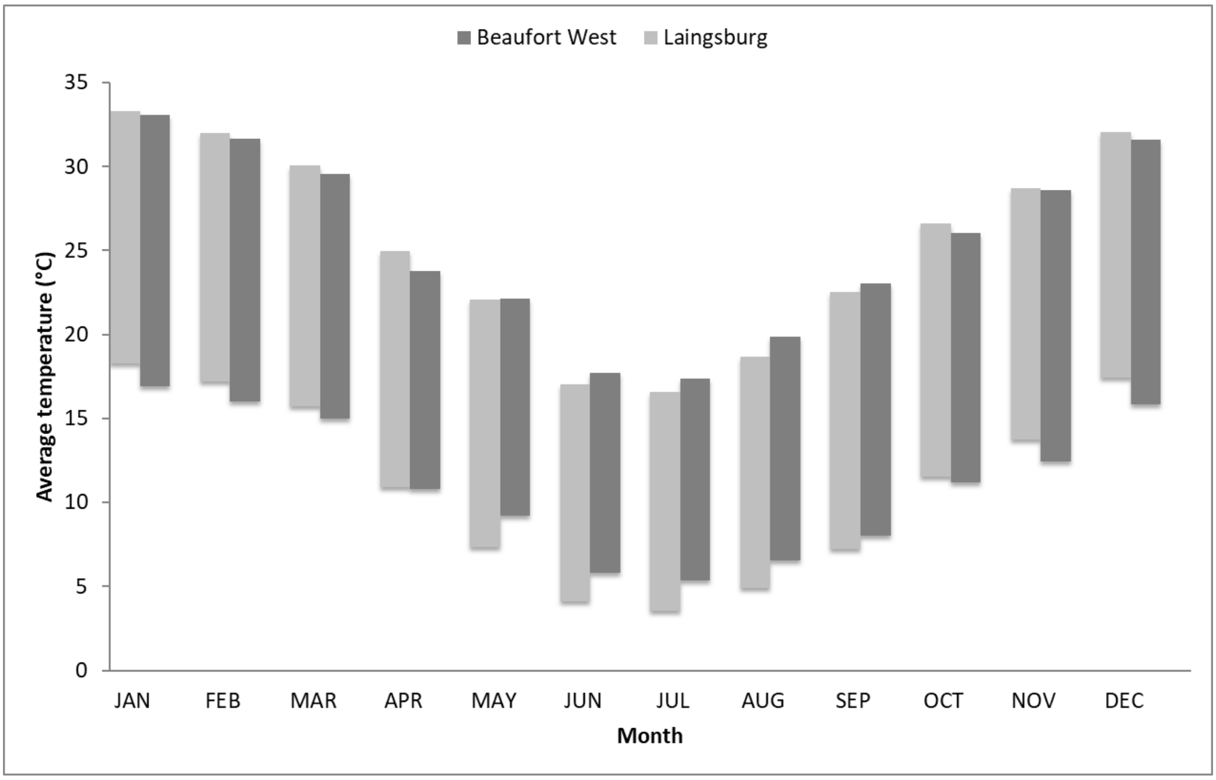


Figure 2.5. The average monthly temperature range (in °C) for Laingsburg and Beaufort West over a four-year period (2012-2015). Each bar represents the range between the average minimum and maximum temperatures for each month.

Average minimum temperatures show similar variation (Figure 2.5), ranging from 17.5°C in December (summer) to 4.1°C in June (winter) in the town of Laingsburg. The lowest recorded average daily temperature during my study was 4°C (August 2013 in Laingsburg). The lowest temperature recorded by the temperature sensor in one of my camera traps was -1°C on 29/09/2012. The camera trap was at 758 m.a.s.l. on a flat plain.

General topography and geology

The dominant type of land use in the Karoo is classified as rangeland for small-livestock grazing (Todd and Hoffman, 1999) (Figure 2.6). Farmlands are covered by shallow, weakly developed lime-rich soils that are principally underlain by sediments of the Dwyka Formation, which are covered in turn by the Ecca and Beaufort groups respectively (Watkeys, 1999).

Figure 2.6. A photograph of a "typical landscape" in the Koup farming area in the Laingsburg District Municipality, Central Karoo, Western Cape Province, South Africa. Dry riverbeds with green riverine vegetation break the monotony of flat plains and gently-sloped hills © Marine Drouilly – The Karoo Predator Project.

The Beaufort West and Prince Albert farms, along with the southern section of the Koup consist mainly of flat ground with rolling hills at low elevation (between 450 and 550 m.a.s.l.). The northern and the western sections of the Koup are more rugged, with mountains (maximum elevation of 1200 m.a.s.l.) and steeply incised valleys. Flat-topped hills found in the northern part of the Koup – called Karoo koppies – are capped by dolerite sills that are more resistant to weathering than the surrounding sandstones and shale (Watkeys, 1999). Dolerite sills are solidified lava that was forced under high pressure between the horizontal strata of the sedimentary rocks, about 180 million years ago and are typical of the Nama Karoo landscapes. The Dwyka River traverses the Koup, flowing from the northwest and joining the Gamka River – that traverses the Prince Albert farms – as a tributary at the Gamka Dam. Gullies with non-perennial rivers and streams are located throughout the study area and flow only briefly after heavy rains.

Vegetation

All the study farms lie in the Lower Karoo bioregion and are covered by the Nama-Karoo biome (Figure 2.7). In spite of being the second-largest biome in South Africa, only 1% of it falls within PAs (Barnard et al., 1998; Cowling, 1986; Roux and Theron, 1986).

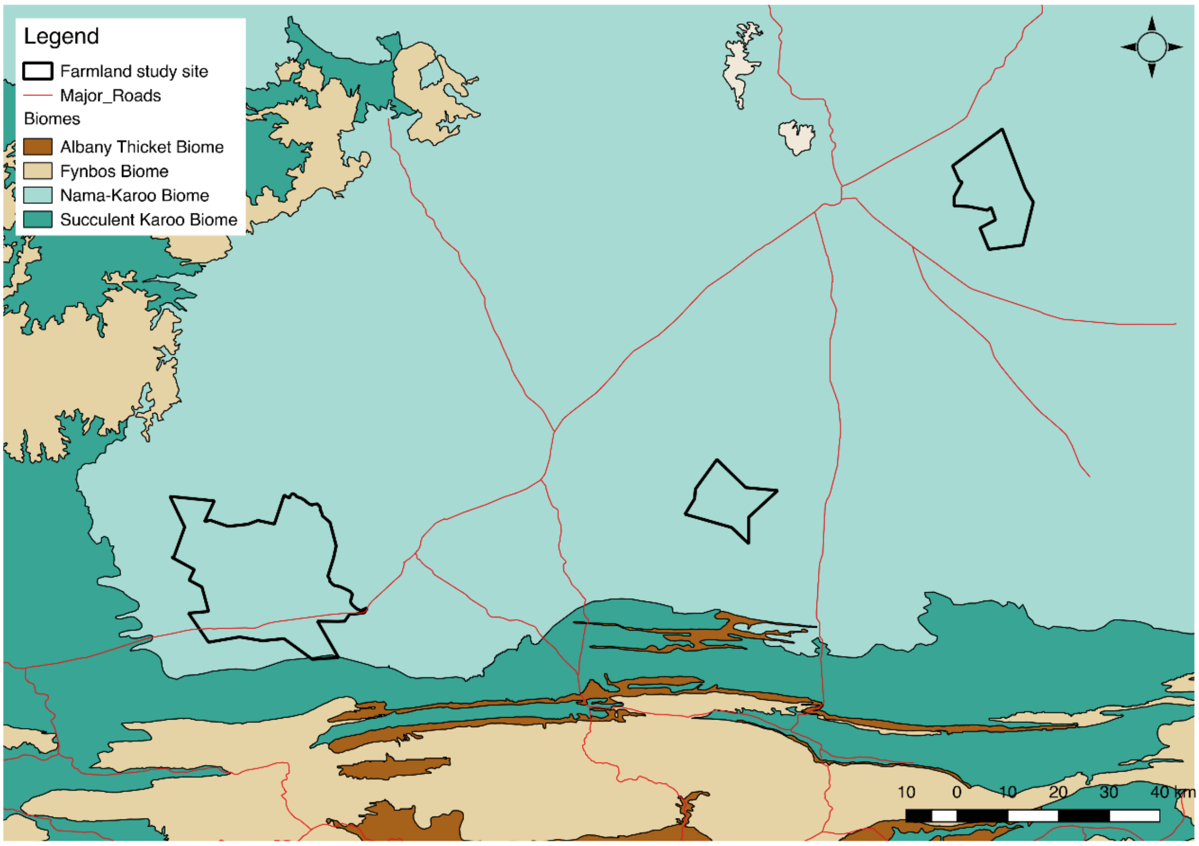


Figure 2.7. Map of the different biomes found in and around the Koup (black polygon on the left of the map) and the other farms that are part of the study site.

The vegetation of the Nama-Karoo Biome is dominated by low shrubs (chaemaphytes) and grasses (hemicryptophytes), with shrub coverage increasing with increasing aridity (Palmer and Hoffman, 1997). However, livestock overgrazing can modify this pattern by suppressing the grass component (Lovegrove, 1993). The vegetation is sparse and the xerophytes support the Merino and Dorper sheep. Most of the grasses are of the C4 type and shrubs are deciduous in response to rainfall events. Some of the most abundant shrubs include species of *Drosanthemum*, *Eriocephalus*, *Galenia*, *Pentzia*, *Pteronia*, and *Ruschia*. The principal perennial grasses are *Aristida*, *Digitaria*, *Enneapogon* and *Stipagrostis* spp. Trees and taller woody species are mostly restricted to watercourses and include *Vachellia karroo*, *Diospyros lycioides*, *Grewia robusta*, *Searsia lancea* and *Tamarix usneoides* (Palmer and Hoffman, 1997).

History and census information

In the 17th century, when the trek Boers (i.e. white pastoralist settlers) moved into the interior of the country, they decimated the wild game of the then Cape Colony, including large predators such as lions (*Panthera leo*) and brown hyenas (*Hyaena brunnea*) (Skead, 1987). The jackal – which had long since included the Khoikhoi's sheep in its prey base – soon became the apex predator throughout much of the region, and a threat to the settlers' sheep (Nattrass and Conradie, 2015). It was only during the mid-20th century that the government (represented by Sir Frederic de Waal, Administrator of the Cape from 1911 to 1925) began to assist white farmers with jackal-proof fencing, tax deductions, subsidies and state-supported predator control such as hunt clubs (Nattrass and Conradie, 2015). At that time, the government was paying out more than 60 000 jackal bounties per year (van Sittert, 1998) and between 1914 and 1923, over 300 000 jackal bounties were paid (Beinart, 2003).

Following the transition to democracy in 1994, agricultural policy was liberalised and state subsidy ceased. In addition, the number of employees per farm decreased as labour costs and fear of land claims increased (Nattrass and Conradie, 2015). Results of the most recent census from 2011 (Western Cape Government Provincial Treasury, 2013) show that the vast majority of farmland is still owned by farmers of European descent, in spite of this racial group making up only approximately 10.13% of the total population in the province, which is predominantly Coloured (76.15 %), followed by Black Africans (12.7%). Today, the sheep farming industry is still depressed (Nattrass and Conradie, 2015). Total factor productivity over the period 1952 to 2002 showed a lack of growth for the four sheep grazing districts of the Western Cape Province (Conradie et al., 2009). Sheep farmers are leaving the industry (Reed and Kleynhans, 2010; Wessels and Willemse, 2013) and the profit margins of the remaining ones are very small (Conradie and Landman, 2015).

The current population of the Central Karoo District Municipality forms only 1.21% (71 011 inhabitants with a density of 1.83 inhabitants/km^2) of the population of the Western Cape Province (Statistics South Africa 2011). The literacy rate is 73.4 %, the lowest for the Western Cape Province and the poverty rate is estimated at 32.5%, the highest for the Western Cape Province (Western Cape Government Provincial Treasury, 2013). The unemployment rate for the region is 22.7% (Western Cape Government Provincial Treasury, 2013).

Study site: Anysberg Nature Reserve

General description of the study site

The Anysberg Nature Reserve (GPS coordinates: 33° 31’ S, 020° 37’ E) served as my control, or “natural” site. Situated approximately 40 km to the southwest of the Koup area and 56 km from the town of Ladismith, it covers an area of 79 629 ha, making it one of the largest PAs in the Western Cape Province (Figures 2.8 and 2.9).

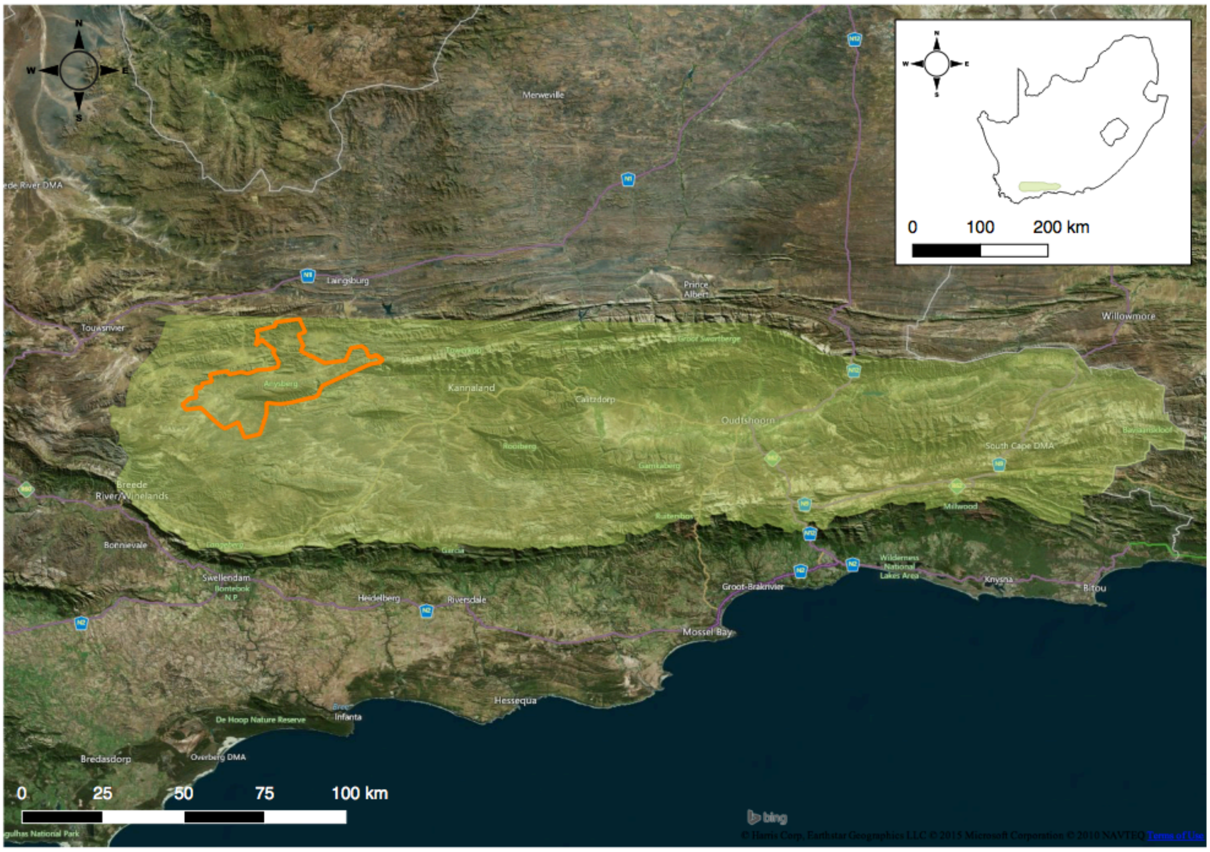


Figure 2.8. Location of the Anysberg Nature Reserve (orange polygon) within the Little Karoo (insert, and full green polygon) of South Africa.

The reserve falls within the Little or "Klein" Karoo, which covers an area of 23 500 km^2, delimited by the Witteberg-Swartberg and Baviaanskloof mountains in the north, the coastal Langeberg-Outeniqua and Tsisikamma mountains in the south and the towns of Uniondale and Montagu in the east and the west respectively (Vlok and Schutte-Vlok, 2010). The reserve is situated in the Succulent Karoo biome, an internationally recognised, predominantly winter-rainfall desert hotspot that occupies 112 000 km^2 on the fringes of South Africa's Cape Floristic Region, characterised by exceptional diversity and rarity of plant species (Cowling et al., 1999). It includes 4849 species of vascular plants (40% endemic) and is home to the richest succulent flora in the world (Hilton-Taylor, 1996). It includes state forest on top of the Anysberg Mountain, declared mountain catchment areas and land purchased by WWF-SA (Brand et al., 2018). The global significance of the Succulent Karoo as a biodiversity hotspot and its long-standing recognition as a regional conservation priority (Hilton-Taylor, 1996; Rebelo and Siegfried, 1992) suggest that it is in need of improved conservation status. Anysberg is one of the rare PAs of the region and one of the few where there has been no attempt to reintroduce large carnivores such as lions, cheetahs (*Acinonyx jubatus*) or dangerous game such as Cape buffaloes (*Syncerus caffer*) and black rhinoceroses (*Diceros bicornis*) that used to occur here.

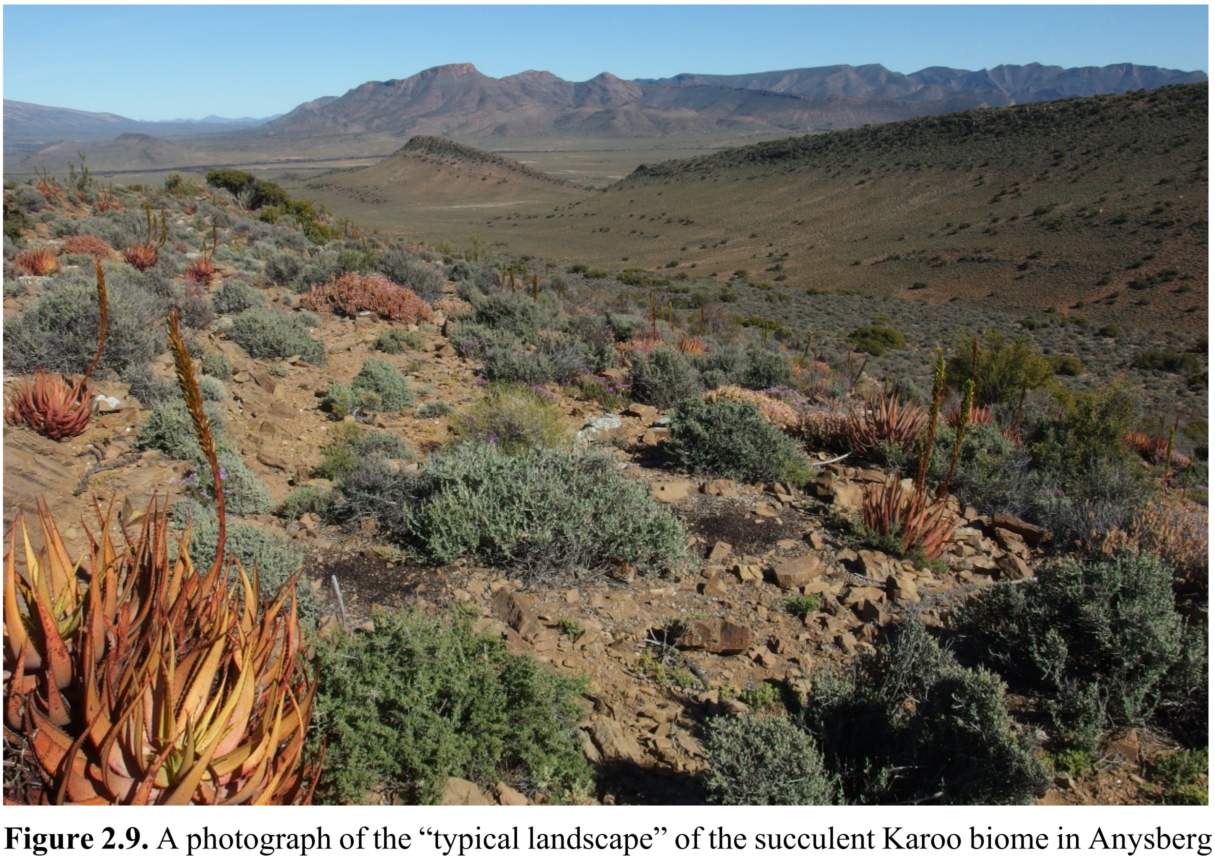


Figure 2.9. A photograph of the "typical landscape" of the succulent Karoo biome in Anysberg Nature Reserve, Little Karoo, Western Cape Province, South Africa © Marine Drouilly – The Karoo Predator Project.

Climate

All climatic data were obtained from the South African Weather Service, and are based on data recorded at 08:00 am at the Ladismith and Montagu (rainfall data only) weather stations. Rainfall data for Anysberg was obtained by averaging across the three weather stations situated in the reserve.

The climate of the Anysberg Nature Reserve is considered to be extreme (Venter et al., 1986), with a bimodal rainfall, transitional between the summer and winter rainfall regions (Brand et al., 2018). There is an important variation in rainfall topography, with the higher lying mountains in the north and south of the reserve having a higher average annual rainfall (290-330 mm) than the lower lying valleys (160-210 mm) (Brand et al., 2018). During 2012-2015, a mean annual rainfall of 247.6 (±) 21.2 mm was recorded in the reserve (i.e., approximately twice as much as on the farmland study site). In Ladismith (situated approximately 65 km east of the reserve), rainfall was 300.6 (±) 7.0 mm and 316.9 (±) 30.7 mm in Montagu (situated approximately 40 km south-west of the reserve) for the period 2012-2015 (Figure 2.10).

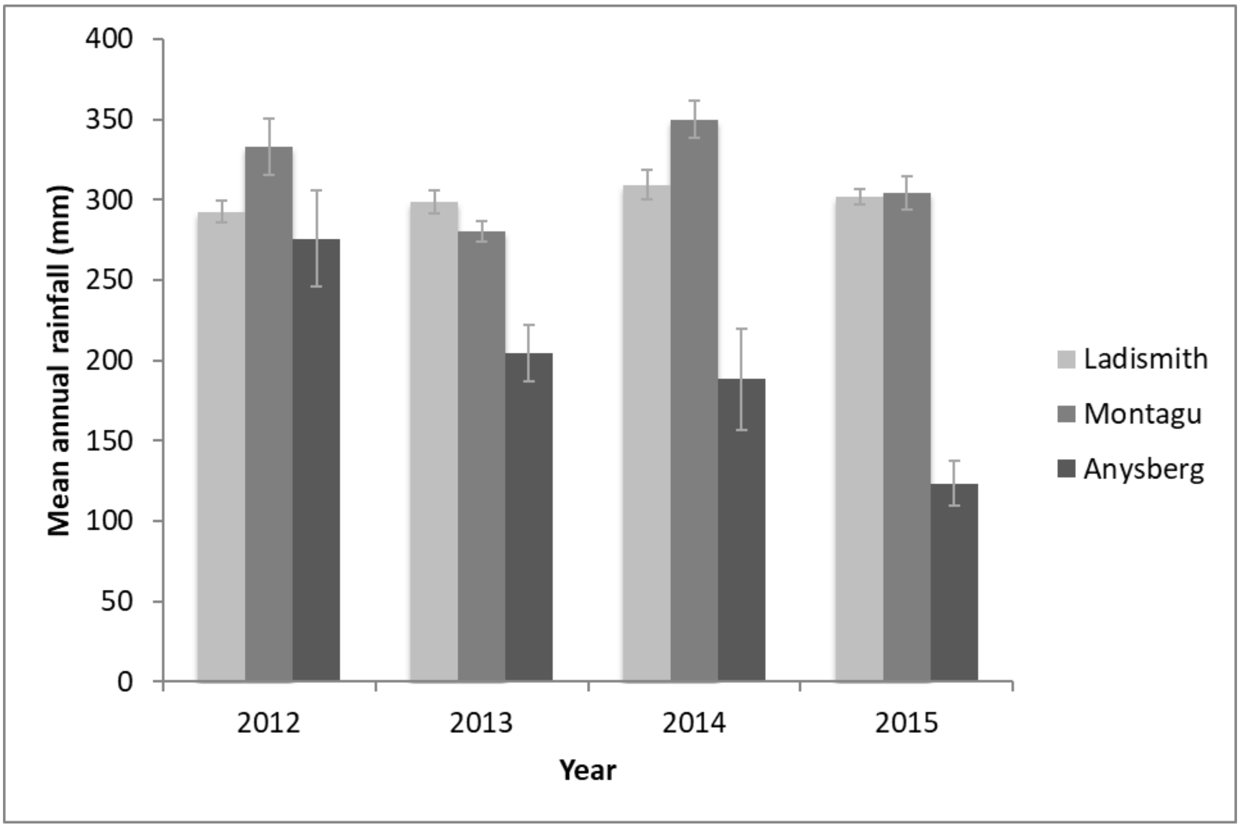


Figure 2.10. Mean annual rainfall (in mm) (± standard deviation) in Ladismith, Montagu and Anysberg Nature Reserve for the period 2012-2015.

Although Anysberg Nature Reserve falls on the border of the winter/summer rainfall line, during my fieldwork both study sites received most of their rain from summer thundershowers linked to cut-off low pressure systems (Desmet and Cowling, 1999) (Figure 2.11). Rainfall in Anysberg is likely to vary substantially with topography as mountainous areas are known to receive more orographic rainfall than low-lying areas (Desmet and Cowling, 1999; Venter et al., 1986). The annual rainfall measured by the rain meters in Anysberg Nature Reserve confirms this prediction varying from 600 mm on top of the highest peaks to only 170-200 mm on the lower plains (Brand et al., 2018).

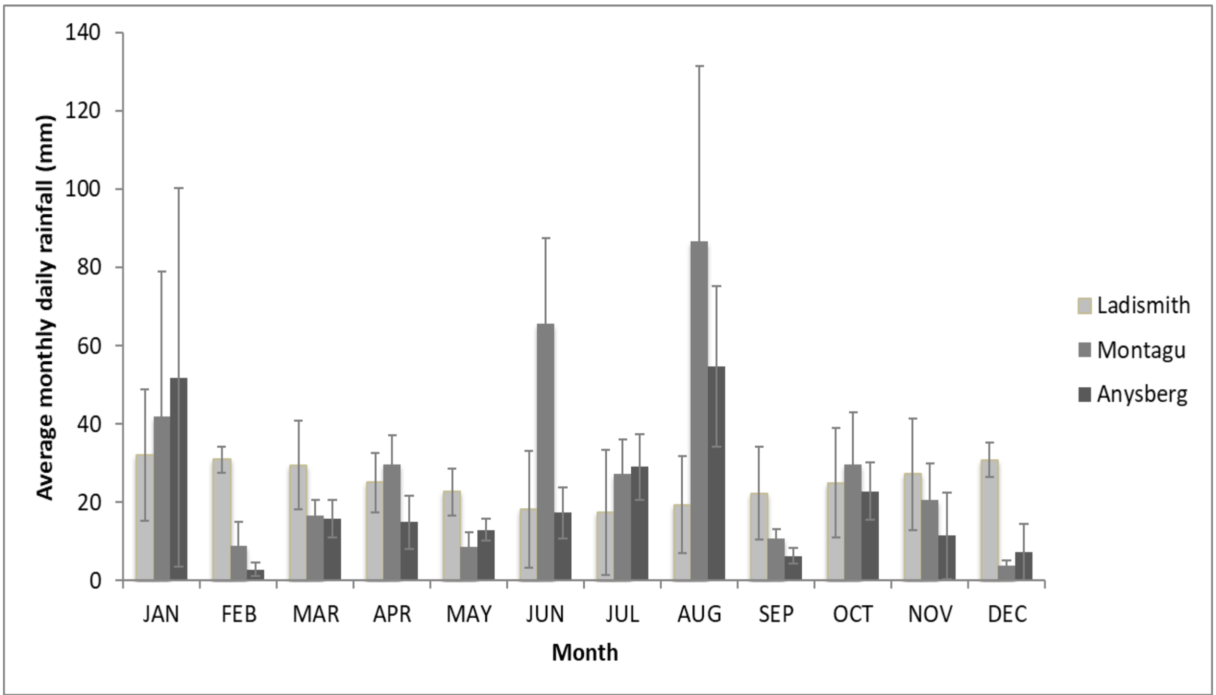


Figure 2.11. Average monthly rainfall (in mm) (± standard deviation) for Ladismith, Montagu and Anysberg Nature Reserve over a four-year period, from 2012 to 2015.

The highest maximum average daily temperature recorded during my time in the field was 33.6°C (January 2012 in Ladismith) but the temperature sensor of one of my camera traps recorded 56°C at 689 m.a.s.l. in a valley on 19/11/2013. In summer, average monthly maximum temperatures often exceed 32°C, while in winter average maximum temperatures are typically below 20°C (Figure 2.12). Average minimum temperatures show similar variation, ranging from 5.3°C in July (winter) to 16.4°C in January (summer) (Figure 2.12). The minimum average daily temperature recorded during my study was 4.2°C (July 2012 in Ladismith) but the temperature sensor of one of my camera traps recorded -4°C at 727 m.a.s.l. in a valley on 21/09/2013. No official data are available for Anysberg NR but temperatures generally range from -2°C on some of the highest peaks in winter to 45°C on the plains in summer and frost occurs in the winter months from May to September (M. Brand pers. comm., reserve manager).

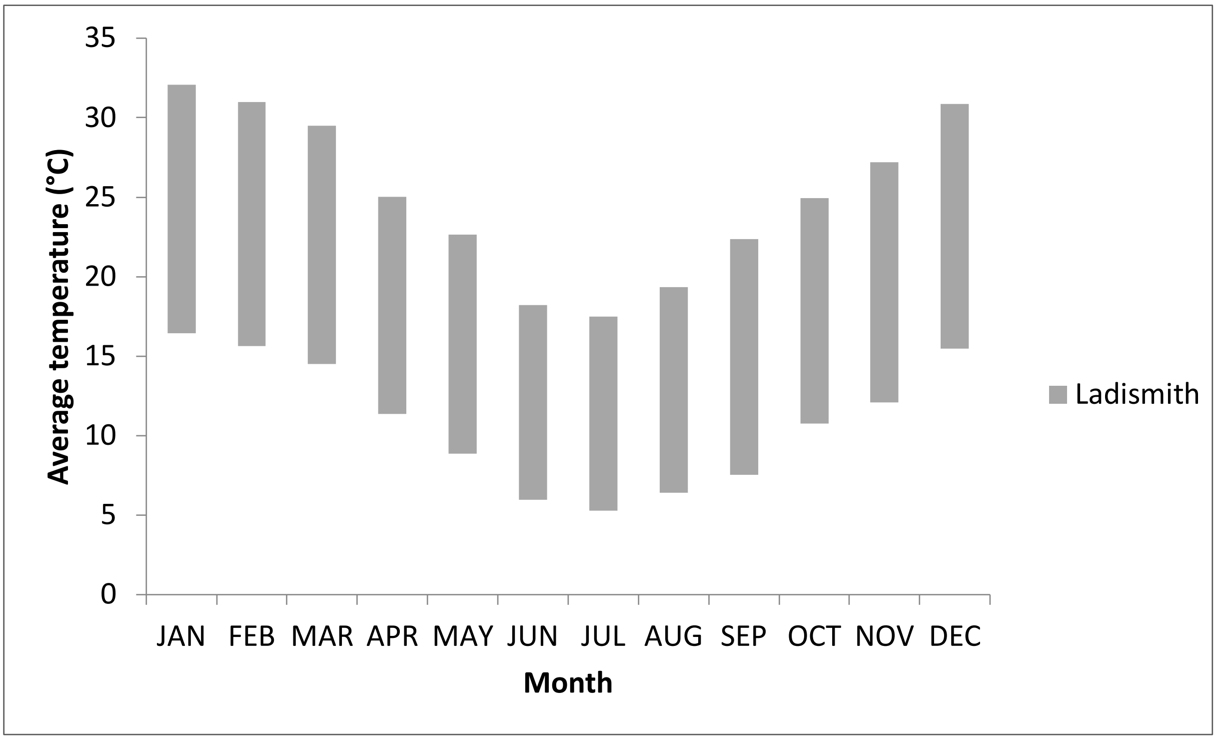


Figure 2.12. The average temperature range (in °C) for Ladismith over a four-year period (2012-2015). Each bar represents the range between the average minimum and maximum temperatures for each month. No data were available for Montagu.

General topography and geology

The Little Karoo is a mosaic of rugged, mountainous terrain with broad open valleys that can be up to 50 km wide and 200 km long (Watkeys, 1999). Anysberg Nature Reserve's southern boundary is comprised of the Anysberg range with a maximum elevation of 1621 m.a.s.l. The northern boundary includes the Suurkloof se Berg range (highest point: 1512 m.a.s.l.). Lying between these two mountain ranges, extending in an east/west direction, is a large open valley with an elevation of approximately 480 m.a.s.l. at its lowest point. Although Anysberg mountain ranges are smaller than the nearby Swartberg Mountains, they include similarly deeply incised, narrow gorges and canyons with near-vertical rocky cliffs in the southern section. The terrain in the north of the reserve is fairly rugged, characterized by low mountains and gullies, with numerous non-perennial rivers and streams. The mountains within the reserve consist predominantly of sedimentary rocks of the Cape Supergroup, of which all three elements (Witteberg Group, Bokkeveld Group and Table Mountain Group) are present (Thamm and Johnson, 2006; Visser, 1986; Watkeys, 1999). The valleys are cut into Table Mountain Group rocks, while the Witteberg sandstones are found to the north and the Bokkeveld shales underlie the Anysberg and southern inclines near the Touws River. There is a narrow infold of Bokkeveld slate along the Matjiesgoedberg (Du Toit, 1926).

Anysberg Nature Reserve lies in part of the Anysberg Mountain Catchment Area, draining into the Gouritz River System. There are several rivers running through the reserve, the major ones being the Touws, Anys, Prins and Buffels Rivers (Brand et al., 2018). Due to the low rainfall and the resulting semi-arid nature of the area most of the rivers are seasonal and in some cases, ephemeral with dry water courses (Brand et al., 2018).

Vegetation

The Little Karoo floral diversity is extremely rich with a total of 56 habitat types and 369 vegetation units (Vlok et al., 2005). The region contains elements of three global biodiversity hotspots: the Cape Floral Region, the Succulent Karoo and the Maputaland-Pondoland-Albany Thicket (Mittermeier et al., 2005; Myers et al., 2000; Vlok et al., 2005). The habitats identified by Vlok et al. (2005) belong to six distinct biomes: perennial stream, river and floodplain, subtropical thicket, succulent Karoo, renosterveld and fynbos. The fynbos biome is one of the six floral kingdoms of the world despite covering only 0.04% of the land surface of the globe; 13.6% of which only is included in PAs (Cowling and Richardson, 1995). Vegetation patterns in the Little Karoo are largely driven by rainfall, which is in turn strongly influenced by topography (Desmet and Cowling, 1999).

Anysberg Nature Reserve expands over two different bioregions, the Rainshadow Valley Karoo and the Western Fynbos-Renosterveld. The succulent Karoo and the fynbos biomes are the most represented in the reserve (Figure 2.13). Four major habitat types are found in Anysberg Nature Reserve:

- Succulent Karoo (xeric-adapted dwarf scrub belonging to the Aizoaceae, Amaranthaceae and Asteraceae families) on valleys and low hills with nutrient-rich soils and low annual rainfall (<350 mm) (Desmet and Cowling, 1999; Vlok et al., 2005).
- Renosterveld (low shrub layers from 1-2 m tall composed mainly of Ericoids) in hilly areas exposed to fire. Renosterveld may contain a large grass component (*Ehrharta* spp., *Pentameris* spp., *Pentaschistis* spp. and *Themeda triandra*), but overgrazing can lead to the grasses being completely replaced by the less palatable renosterbos (*Elytropappus rhinocerotis*) (Roux and Theron, 1986; Vlok et al., 2005).

- Montane fynbos at higher altitude (made of Proteaceae, Ericaceae and Restionaceae) and occurring on shallow, acidic, nutrient-poor sandy soils. Fire is an important disturbance element in this habitat (Vlok et al., 2005).
- Riverine and floodplain vegetation that line the mostly dry riverbeds (dominated by *Vachellia karroo, Rhus lancea and reeds Phragmitis australis*) and create a network of trees that stretch throughout the reserve's plains (Vlok and Schutte-Vlok, 2010; Vlok et al., 2005).

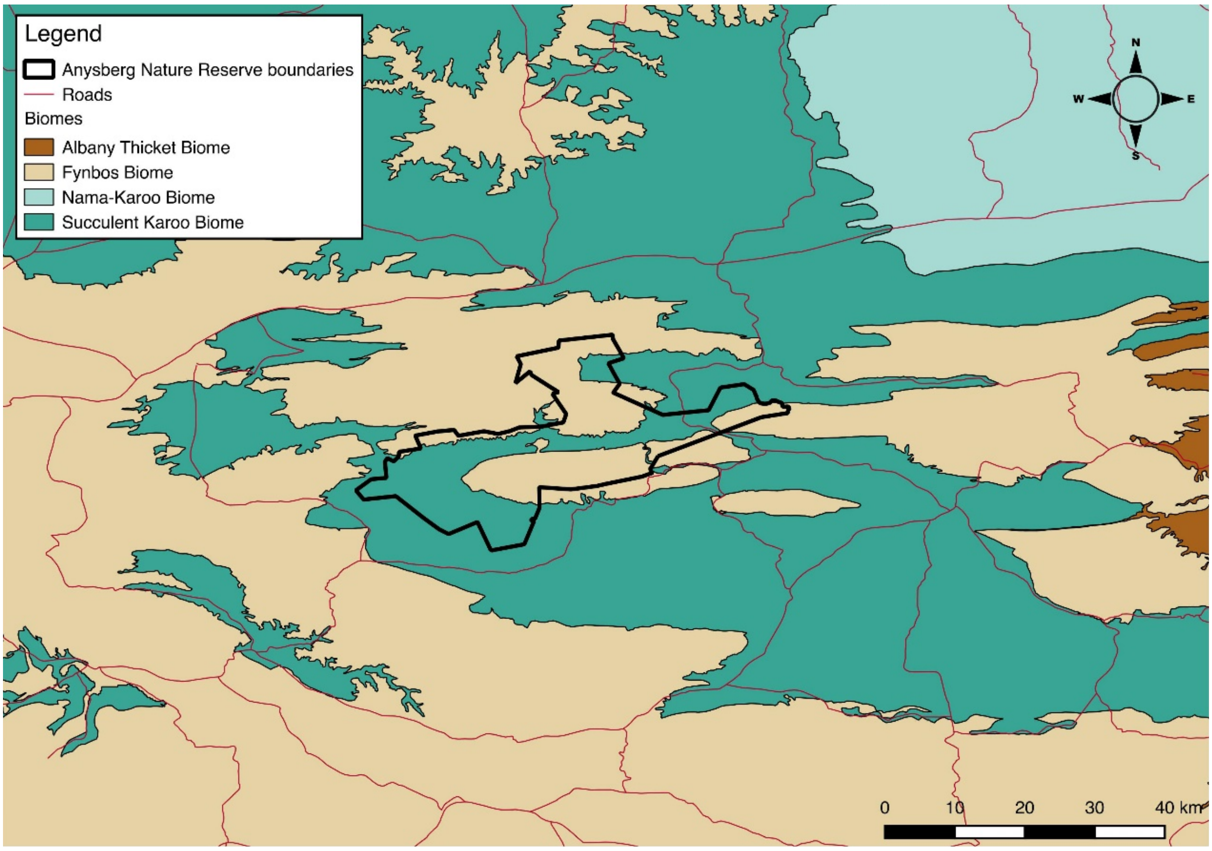


Figure 2.13. Map of the different biomes present in Anysberg Nature Reserve (black polygon) and its surroundings. Two biomes are found in the study area: the succulent Karoo biome and the fynbos biome.

More detailed information concerning the topography, geology, aquatic systems and vegetation of Anysberg NR can be found in Brand et al. (2018).

History

The first parcel of land that formed Anysberg Nature Reserve was purchased at the end of 1987 by WWF-SA under its former name "the South African Nature Foundation" for the Cape Directorate of Nature Conservation and Environmental Affairs. The reserve was proclaimed as a PA on 17 August 1990 with the goal of conserving the succulent Karoo and fynbos flora and to reintroduce animals that were historically present in this region (Brand et al., 2018).

Since 1995, as WWF-SA bought neighbouring farms, the reserve has doubled in size and expanded through agreements with surrounding landowners. In 2012, WWF-SA bought the 12 800 ha Grand Canyon farm with funding from the Leslie Hill Succulent Karoo Trust. In certain areas, vegetation rehabilitation has been underway, as most of the flat areas of the reserve were previously farmed with sheep. Thirty-six dams/boreholes remain from this time but a quarter of them are broken and only a few still supply permanent water. All the internal fences of the reserve have been taken down and only the perimeter fence has been retained (Brand et al., 2018).

The reserve was declared an Important Bird Area (IBA) in 2004 and the World Heritage Committee of UNESCO (United National Educational, Scientific and Cultural Organisation) inscribed the Anysberg Nature Reserve as an extension of the Cape Floral Region Protected Areas World Heritage Site (CFRPA WHS) on 3 July 2015 (Brand et al., 2018). It is currently managed by CapeNature, the public institution with the statutory responsibility for biodiversity conservation in the Western Cape.

Study species: black-backed jackal

Description

The black-backed jackal (Schreber, 1775) (hereafter jackal) is a mesocarnivore with a long, pointed muzzle and a dark saddle patch, marked off from brighter rufous sides that extend from the neck to the tail. Other distinguishing characters include a black-tipped and bushy tail and long triangular fox-like ears (Van der Merwe 1953; Estes 1991, Walton 2003) (Figure 2.14). Young are grey with an indistinct saddle (Estes, 1991), although by 6 months of age the black-and-white saddle becomes obvious.

There is sexual dimorphism in the species with males being larger and heavier than females (Bigalke and Rowe-Rowe, 1969; de Waal, 2017; Rowe-Rowe, 1978; Smithers, 1971). A study in KwaZulu-Natal found an average body mass of 8.4 kg for males (n = 123, range = 6.4-11.4 kg, SD = 0.8 kg) and 7.7 kg for females (n = 84, range = 5.9-10.0 kg, SD = 0.8 kg) (Rowe-Rowe 1978). The length of head and body for adult males was 746 mm (n = 4, range = 711-812 mm) and the length of tail was 321 mm (n = 4, range = 305-330 mm) while for adult females, it was 688 mm (n = 5, range = 673-711 mm) and 299 mm for the length of tail (n = 5, range = 267-318 mm) (Rowe-Rowe 1978). Shoulder height ranges from 38-48 cm (Sheldon 1992). Additional measurements are provided by Lombaard (1971), Rautenbach (1982), Stuart (1981) and de Waal (2017).

Figure 2.14. Picture of a black-backed jackal in the Karoo National Park in 2014 © Marine Drouilly – The Karoo Predator Project.

A hierarchical family group is at the basis of jackal society (Kingdon, 2015). The basic social unit is the mated pair – that can remain together for up to eight years (Moehlman, 1983) and defend mutually exclusive territories (Loveridge and Nel, 2004) – and their offspring. A stable jackal group consists of four levels of organization: the mated pair, progeny of the year, non-breeding helpers and solitary non-breeding, non-territorial individuals (Moehlman, 1979). If resources are locally abundant, other jackals may be tolerated (Hiscocks and Perrin, 1988; Jenner et al., 2011), and subordinates are accepted on the territory borders (Ferguson et al., 1983). Alloparental care is well documented (Moehlman, 1983, 1979).

In a stable social system, jackals are monogamous (Moehlman, 1983) and despite reaching sexual maturity at 11 months, typically only breed when they are ≥ 2 years of age (Moehlman 1979; Ferguson et al. 1983). Gestation lasts 60-65 days (Van der Merwe, 1953) and litter size ranges from 1 to 9 pups but is usually 3-6 (Rowe-Rowe, 1978; Walton and Joly, 2003). Pups are born blind in underground burrows and begin to open their eyes between days 8-10 (Moehlman, 1987; Van der Merwe, 1953). Pups do not emerge from underground dens until ca. 3 weeks of age, but spend most of their time in the den until ca. 7 weeks. They begin to eat regurgitated food from adults at 3 weeks and are weaned by 8-10 weeks (Lombaard, 1971; Moehlman, 1987, 1979; Van der Merwe, 1953). By 12-14 weeks, pups leave the dens and begin to forage with adults (Moehlman, 1987, 1979; Van der Merwe, 1953). Only 1-3 pups survive beyond the age of 14 weeks (Moehlman, 1987; Walton and Joly, 2003). Individuals of both sexes typically disperse from their natal ranges at around one year of age (yearlings, Ferguson et al. 1983). Gestation, litter size and dispersal are all influenced by food availability (Moehlman 1987).

Geographic range and distribution

The jackal has a disjointed distribution (Figure 2.15), occurring in two separate populations in east and southern Africa (Kingdon, 2015), separated by the Mozambique Gap (Kingdon, 2015). Two subspecies are recognized: *Canis mesomelas mesomelas* in the south from the Western Cape of South Africa northward to Angola, Zimbabwe and southern Mozambique and *Canis mesomelas schmidtii* in the north, occupying southern Ethiopia, southern Sudan, Somalia, Kenya, Uganda and northern Tanzania (Sheldon, 1992).

However, a recent study on the phylogenetic relationships between species and populations of African jackals (Atickem et al., 2018) provided evidence that these two populations might in fact correspond to two different species, but genome-wide data with adequate geographical sampling are needed to substantiate this proposal.

Habitat and ecology

Jackals are highly adaptable, opportunistic predators and scavengers (Appendix 2A Fig. S2.1) living in a wide variety of habitats, from arid coastal desert and farmland to montane grassland, arid savannah and scrubland (Loveridge and Macdonald, 2002). Jackals are generalist omnivores (Grafton, 1965; Rowe-Rowe, 1983; Sheldon, 1992), consuming insects, berries, small mammals, birds and larger prey like springbok (*Antidorcas marsupialis*) and sheep

(Bothma, 1971, see Chapter 4). Jackals have a propensity to hunt the young of antelope species that hide their offspring in vegetation (Klare et al., 2010). Dietary and behavioural flexibility are important traits facilitating the persistence of jackal populations on farmland despite concerted population reduction efforts (Grafton, 1965). However, jackals also display prey preferences (Hayward et al., 2017), notably for birds, common duiker (*Sylvicapra grimmia*), bushbuck (*Tragelaphus sylvaticus*) and springbok, and prefer to prey on species with an average body mass of 21.7 ± 3.5 kg (range: 14 – 26 kg; Hayward et al., 2017). Where water is available, jackals drink regularly, but they seem well adapted to survival without free water (Smithers, 1971; Van der Merwe, 1953).

Figure 2.15. Extant distribution of the black-backed jackal, showing the two separate populations in east and southern Africa. Data sourced from the IUCN Red List.

Jackals are most active around sunrise and sunset, but in areas where they are hunted, they can become strictly nocturnal (Ferguson et al., 1988; Fuller et al., 1989; Hiscocks and Perrin, 1988).

Black-backed jackal in the South African context

Jackals are widely considered to be the main predator of small-livestock in South Africa (Du Plessis et al., 2015) and can be legally hunted year round throughout the country (Bothma, 2012). Lethal population control efforts (e.g. hunting with dogs, poison, shooting, trapping) are used by individual farmers and cooperatives over most of the Karoo, but the species remains widespread today (Bothma, 2012; Du Plessis et al., 2015) (Figure 2.16). There is considerable contestation over why jackals persist despite sustained lethal management and it is clear that there is a need for more applied research on farmland (Bergman et al., 2013; Du Plessis et al., 2015; Minnie et al., 2018a; Tambling et al., 2018).

Figure 2.16. Picture of black-backed jackals shot during a "block hunt" (i.e. farmers and professional hunters outing to kill predators on their lands) in the Beaufort West local municipality, Central Karoo, South Africa © Marine Drouilly – The Karoo Predator Project.

Recently, jackals have also been persecuted as a result of depredation on wildlife and negative impacts in the game industry. In 2010, SANParks (South African National Parks) lethally controlled 132 jackal in the Karoo National Park and 212 in the Addo Elephant National Park due to the suspicion that they were the cause for springbok decline (Nattrass and Conradie, 2015). More detailed information on the status of jackal in South Africa can be found in the recent conservation assessment of the species (Minnie et al., 2016a) in the Red List of Mammals of South Africa, Swaziland and Lesotho (Child et al., 2016).

Study species: caracal

Description

The caracal (Schreber, 1776) is a solitary medium-sized felid with a short tail and long hind limbs that facilitate jumping to exceptional heights (3-4 meters) when attempting to catch birds (Appendix 2A Fig. S2.2). Caracals have large black-backed ears tipped with prominent tufts of hairs and tawny red fur that explains the Afrikaans name of "rooikat" or red cat. The underbelly is creamy with orange/brown spots (Mills and Hex, 1997) (Figure 2.17).

Figure 2.17. Picture of a young male caracal in the Little Karoo © Kai Fitchen – The Karoo Predator Project.

Males are bigger and heavier than females with the mean body mass for males being 12.9 kg (n = 77, range = 7.2-19 kg) and 10 kg for females (n = 63, range = 7-15.9 kg). The mean head/body length for males was found to be 868 mm (n = 98, range = 750-1080 mm) and 819 mm for females (n = 94, range = 710-1029 mm) (Stuart and Stuart, 2013).

Females reach sexual maturity between 7 and 12 months and males between 9 and 14 months (Bernard and Stuart, 1987). Females usually have 2-4 young born after a gestation period of 78 days (Bernard and Stuart, 1987). Lairs are situated under boulders, thick bushes or sometimes in disused aardvark (*Orycteropus afer*) or Cape porcupine (*Hystrix africaeaustralis*) burrows. Juveniles remain with their mother until they are about 10 months old, when they may disperse to areas up to 180 km away.

Geographic range and distribution

Caracals are widely distributed across the drier regions of Africa, Central Asia, and southwest Asia into India (Figure 2.18). The species is most abundant in southern Africa (Breitenmoser-Wursten et al., 2008). While considered to be endangered in its northern range, the caracal is regarded as a problem animal by many farmers in the more arid regions of southern Africa (Bothma, 2012; Du Plessis et al., 2015) where it is classified as Least Concern by the IUCN Red List of Mammals of South Africa, Swaziland and Lesotho (Avenant et al. 2016).

Habitat and ecology

Caracals generally prefer open habitats in wooded savannahs and rocky areas with boulders and tall shrubs. However, they are highly adaptable and may occur in diverse habitats ranging from peri-urban (Serieys et al., in press) to the arid semi-desert of the Karoo (Avenant et al., 2016). Their ability to live in anthropogenically-modified habitats with novel food sources is one of the reasons why the species still persists despite the high levels of persecution it faces across large parts of its range.

Caracals are generalist predators that typically eat small prey like rodents, rock hyraxes, hares, rabbits and birds, but they can also catch prey weighing twice their own weight, such as springboks and grey rheboks (*Pelea capreolus*) (Braczkowski et al., 2012a; Grobler, 1981; Palmer and Fairall, 1988). In the driest parts of southern Africa, caracals predominantly consume mammals (Grobler, 1981; Melville et al., 2004; Pohl, 2015), whereas in more mesic areas their consumption of alternate prey items, particularly birds increases (G. Leighton 2018 pers. comm.). Sheep and goats also often fall prey to caracals, especially in the southern part of their range (Melville et al. 2004, see Chapters 4 and 5). Caracals are mostly nocturnal but may exhibit diurnal activity (Stuart and Stuart, 2013). Their excellent camouflage and elusive nature make them difficult to detect in the wild.

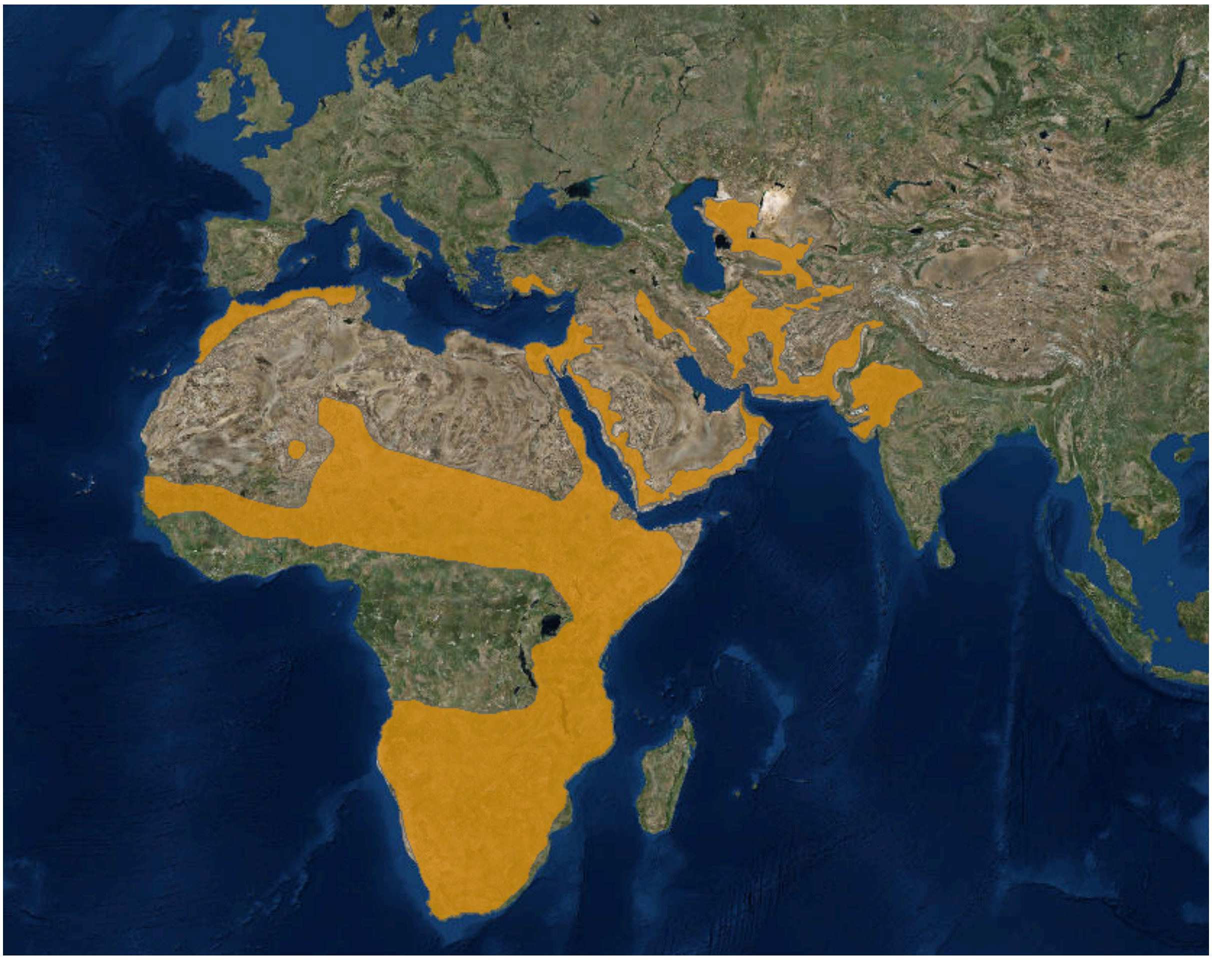


Figure 2.18. Extant distribution of the caracal. Data sourced from the IUCN Red List.

Habitat and ecology

Caracal in the South African context

Caracals are perceived to be a threat to small-livestock farmers in South Africa, second only to the jackal (Bothma, 2012). Caracals can be legally hunted throughout the year (Bothma, 2012) and between 1931 and 1952, an average of 2219 caracals were killed per year in control operations in the Karoo (Stuart, 1982). Cage traps with baits such as caracal urine, shiny devices and feathers; night hunting, day hunting with dogs and gin-traps are commonly used by farmers to control caracal on farmland (see Chapter 6; Bothma 2012; Du Plessis et al. 2015) (Figure 2.19).

Figure 2.19. Picture of a male caracal killed by a farm-worker after being caught in a gin-trap on a farm in the Central Karoo © Marine Drouilly – The Karoo Predator Project.

APPENDIX 2A

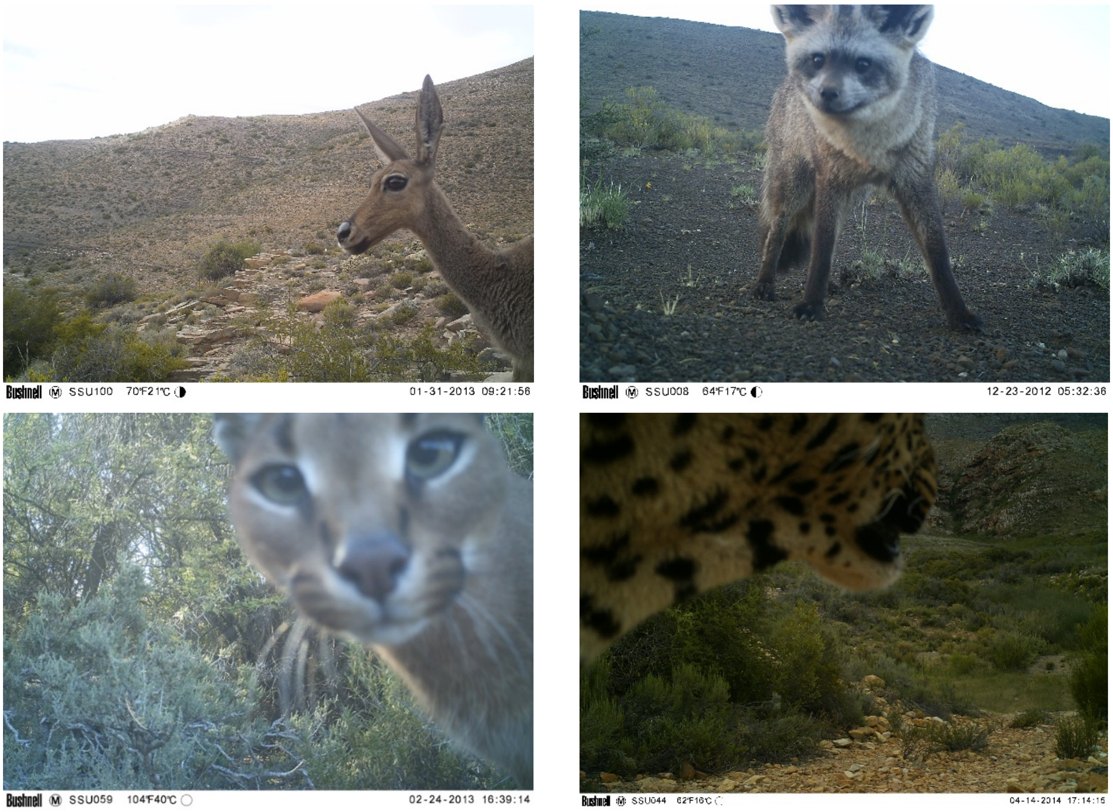
CARTOONS FROM ROHAN CHAKRAVARTY ABOUT ASPECTS OF JACKAL AND CARACAL ECOLOGY

Figure S2.1. Lessons from the (~~Indian~~) jackal dad available for non-commercial use at www.greenhumour.com

Figure S2.2. Caracals' long hind limbs facilitate their jumping to exceptional heights when attempting to catch birds, available for non-commercial use at www.greenhumour.com

CHAPTER 3

Multi-species occupancy modelling of mammal and ground bird communities living on two contrasting types of land use



Pictures taken by camera traps set on farmland and in Anysberg Nature Reserve, South Africa. From top left to bottom right: grey rhebok on farmland, bat-eared fox on farmland, caracal on farmland, leopard in Anysberg Nature Reserve.

Abstract

Land transformation is the most significant factor impacting South Africa's biodiversity today and the agricultural sector has had the most profound impact through the degradation of natural habitat. With less than 9% of land in South Africa being formally protected and approximately 79% privately owned, it is essential to understand how land use on private property affects biodiversity. In this chapter, I used a combination of camera trapping, rarefaction analyses and hierarchical multi-species occupancy modelling to determine community diversity (i.e. species richness, species diversity, evenness, dominance, functional diversity), structure and distribution of semi-desert terrestrial mammals and birds (body mass >0.5 kg) living on extensive small-livestock farmland (Koup) and a nearby protected area (Anysberg Nature Reserve). I also evaluate species-specific responses to different anthropogenic and environmental variables. I obtained more than 307 000 images and detected a total of 42 species of interest over 4035 6-day pooled trap nights across 322 sites. Both methods (rarefaction analyses and occupancy modelling) led to the same conclusion that species richness was not significantly different between the two types of land use, but there were important differences in community structure and composition. Farmland had lower entropy, functional diversity and higher dominance than the reserve. Contrary to my expectation, human disturbance did not affect individual species occupancy in either area. Community species richness in the reserve decreased with increasing elevation whereas on farmland, probability of use increased with the presence of riverine habitat. Carnivores, omnivores and medium-sized species occupancy probabilities were similar between the two areas but occupancy probabilities were higher for herbivores and large species in the reserve and for insectivores and small species on farmland. Large carnivores were absent on farmland and black-backed jackal had a higher posterior mean occupancy probability in the reserve. Detection probabilities were low in general and varied for some species in the reserve with the presence of trails and with general habitat types in both areas. Contrary to predictions, my results reveal that drylands in the South African Karoo region, including rangeland used for extensive small-livestock farming, support a diverse community of terrestrial vertebrates. Private landowners are thus important custodians of key components of biodiversity outside of protected areas, especially in low-lying areas. The multi-species approach used in this chapter facilitated inferences on even the rarest species, which is particularly applicable to drylands where species occur at low densities.

Introduction

Protected areas (PAs) – described as "a clearly defined geographical space, recognised, dedicated and managed (…) to achieve the long term conservation of nature with associated ecosystem services and cultural values" (Dudley, 2008) – play an important role in global conservation efforts by limiting anthropogenic impacts on wildlife, such as excessive hunting and habitat loss (Carrillo et al., 2008; Geldmann et al., 2013; Nagendra, 2008). PAs cover approximately 13% of the Earth's land surface and have been recognized as the most important components for the success of *in situ* conservation (Chape et al., 2005). However, throughout the world, many established PAs are threatened by illegal exploitation, overall impoverishment of their ecology, major conversion, human encroachment, degradation and isolation (Brandon et al., 2001; Carey et al., 2000; Oates, 1999). In addition, they are often too small to be sufficient for the survival of larger and more wide-ranging species (Woodroffe and Ginsberg, 1998).

Although biodiversity loss has occurred across all terrestrial ecosystems, many of its drivers are associated with the change of land use from natural to agricultural (Green, 2005; Hails, 2002). The drive for agricultural productivity explains why most PAs are located in the least productive portions of the landscape or in areas with a high disease risk for humans and/or livestock (Gallo et al., 2009; Norton, 2000; Pressey, 1994; Rouget et al., 2003; Scott et al., 2001) and often at higher elevations (Hunter and Yonzon, 2013; Joppa and Pfaff, 2009; Scott et al., 2001; Watson et al., 2014).

Despite biodiversity loss being associated with agriculture, the distribution of extant terrestrial plants and animals suggests that the greatest numbers of species are found at lower elevations, on more productive soils, often on privately owned land (Scott et al., 2001). Consequently, significant elements of biodiversity are underrepresented in PAs. For example, in the United States, >90% of threatened and endangered species occur on private lands, with 66% having >60% of their total existing area on private lands (Groves et al., 2000; Scott et al., 2001). Similarly in New Zealand, the upland-lowland imbalance resulted in some ecosystem types being almost lost from the country, such as the area of lowland alluvial forests in the Hokitika Ecological District in the southwest of the country, which has declined by 99.7% since 1840 (Norton, 2000). As a consequence, species preferring such environments have to persist in highly fragmented or marginal habitats where their ability to respond to environmental change may be limited (Scott et al., 2001). Africa is no different to the global pattern, with only 8.5 % of the land designated as PA (Bonkoungou, 2001). In Namibia, unprotected rangelands comprise 86% of the land surface and contain up to 90% of the populations of some large mammal species (Richardson, 1998). In South Africa, PAs are mostly situated in less productive mountainous or arid regions of the country (Gallo et al., 2009; Hoffman et al., 1999) and many of them are too small to be sufficient for the survival of larger and more wide-ranging species (Baeza and Estades, 2010; Woodroffe and Ginsberg, 1998).

The limited extent and growing threats to existing PAs demands that we include the unprotected surrounding private lands in the biodiversity conservation process if we are to protect the full range of species and conserve different – and sometimes more endangered – habitats than those found in PAs (Gallo et al., 2009; Groves et al., 2000; Knight, 1999). Yet without information on what species are found on private lands compared to PAs and how wildlife communities respond to various environmental factors and anthropogenic practices, it is difficult to develop stewardship programmes and other management strategies that incentivise landowners to contribute to global and local biodiversity conservation goals.

Although the literature has shown that areas outside of PAs can hold significant populations of various wildlife species (Kiffner et al., 2015; Moore et al., 2016; Msuha et al., 2012; Ogutu et al., 2017; Rannestad et al., 2006; Western et al., 2009), most studies have demonstrated that increased intensity of land use reduces habitat diversity, resulting in a decrease in species diversity (Du Toit and Cumming, 1999; Maitima et al., 2009; Wretenberg et al., 2010). In particular, compared to pristine lands, rangelands used for livestock farming have shifted from wild herbivore multi-species guilds differentiating their foraging in space and time (Mcnaughton and Georgiadis, 1986), to few-species guilds (commonly sheep, goats and cattle), which can have adverse impacts on vegetation diversity and plant palatability (Todd, 2006). Intensification of land use has also been shown to negatively impact large-bodied mammal diversity and distribution (Kinnaird and O'Brien, 2012; Stephens et al., 2001), including carnivores (Kauffman et al., 2007a; Zimmermann et al., 2009) that occur at lower densities and have larger home ranges and greater food requirements (Duncan et al., 2015; Jetz et al., 2004) than other species.

Studying terrestrial mammal and large ground bird biodiversity on different types of land use requires collecting valuable information on multiple species simultaneously. In the case of non-identifiable species or when capture and marking of most animals is not possible, occupancy analyses are a useful tool for estimating species distributions and the processes driving distributional patterns. Occupancy is defined as the probability that a given site is occupied by a particular species of interest and has been used as a surrogate for abundance (MacKenzie and Bailey, 2004). Sampling to collect occupancy data can take many forms, from direct observations of the animals (Fleishman et al., 2003; Kiffner et al., 2013) to some indirect detection indices (scent station, scat, tracking plate, tracking tube, song, hair snare, camera trap surveys – Royle and Nichols, 2003; Stanley and Royle, 2005). Sensitivity to animal welfare (Long et al., 2008) and the need to reduce time, effort and costs associated with data collection have together prioritized non-invasive methodologies.

In semi-arid regions such as the Karoo rangeland, wild mammals are mostly nocturnal, occur at low densities and are difficult to capture and detect due to their cryptic life history strategies. In addition, most predators are persecuted and large antelope often hunted, possibly reducing detection probabilities – defined as the likelihood of detecting an individual, or species, during a sampling occasion (O'Connell et al., 2011). In such scenarios, non-invasive sampling methods that can correct for detection bias are particularly well suited to sampling medium and large mammals and ground birds. Camera trapping is a powerful, easily replicable tool for sampling wary animals that might react to sampling methods that require human presence. Furthermore, cameras can be left in the field for extended periods of time and operate continuously under any weather conditions. Camera trapping has been used worldwide and recently, there has been a rapid increase of large-scale camera trap studies that aim to make inferences at the community level (Ahumada et al., 2011; Meyer et al., 2015; Pettorelli et al., 2010; Steenweg et al., 2017; Swanson et al., 2015; Tobler et al., 2008). In addition to occupancy analyses, camera trap surveys can bring valuable information on species richness and community diversity (through the computation of diversity indices), as well as the identity of species present, termed community composition (rare versus common species), along with the distribution of their absolute or relative abundances termed community structure.

I chose to focus on medium- to large-sized terrestrial mammals and ground birds weighing more than 0.5 kg (Cusack et al., 2015; O'Brien et al., 2010) because micromammals, reptiles, insects and passerine birds would probably not be reliably detected on camera traps, partly because of their velocity (the camera traps I used are triggered by motion sensors) but also because some species are semi-terrestrial, and even if they are present, they may not be detected due to vertical habitat gradients (O'Brien et al., 2010). Another advantage of focusing on larger species of mammal and bird is that they are often more vulnerable to exploitation and persecution than species from lower trophic levels (Laliberté and Ripple, 2004; Ripple et al., 2015). They may thus provide a good indicator for maintenance of species at lower trophic levels on rangelands.

Currently, mammalian and ground bird diversity within most of South Africa, including the Karoo is restricted to local, general or historical species lists that do not provide accurate data for species richness, distribution, abundance estimates and community structure and composition. Such data are essential to understand how land use, especially on private property, affects medium- to large-bodied animal communities, and for the management of wildlife and predators in general (Roberts, 2011; Silveira et al., 2003; Tobler et al., 2008). In the absence of the possibility to collect data before and after the change in land use from natural to farming, I assessed community structure, diversity and distribution of medium- to large-sized mammal and ground bird species in the region by using landscape camera trapping on both a PA (the Anysberg Nature Reserve) and the Koup farming region (see Chapter 2 for study sites description). Hone (2007) classified this type of study design as a "quasi-experiment" type III, which, even if it is limited to a comparison of one site to the other with their differences (e.g. habitat type and rainfall), is still an important part of the adaptive process of distinguishing credible from incredible patterns in nature (Holling and Allen, 2002) and is a commonly-used approach in ecology (Allen et al. 2013b). I also argue that the close proximity of the two study areas (approximately 40 km away) ensures that most medium and large vertebrates can move between both study sites, and further that the effects of land use are far greater than the subtler changes in rainfall and vegetation that are apparent between the two study sites (see Chapter 2). I tested the hypotheses that land use in the semi-arid region of the Karoo would affect the species richness (H1), community diversity (H2), composition and structure (H3), as well as the species distribution and mean probability of use (i.e. occupancy) (H4) by terrestrial vertebrates >0.5 kg. I further hypothesized that environmental and anthropogenic variables related to the probability of use would be unique to each species (H5), and that life-history traits such as body mass and trophic guild would impact the probability of use by mammals in the two areas (H6).

I predicted that the wildlife community on farmland would present lower wildlife species richness (prediction 1, P1), lower diversity (P2), higher dominance (P3) and lower mean probability of use (P4) than the community in the reserve (Du Toit and Cumming, 1999; Kinnaird and O'Brien, 2012; Msuha et al., 2012). I also predicted that the presence and probability of use by large mammals would be more affected than the presence and probability of use by small mammals on farmland (Kinnaird and O'Brien, 2012), with large carnivores being prone to extirpation on farmland (P5). I further predicted that there would be a lower relative abundance of and mean probability of use by known livestock predators on farmland compared to the reserve (P6) and that in general, human disturbance would negatively impact probability of use by wildlife on rangeland (Kinnaird and O'Brien, 2012; Lenth et al., 2008; Stephens et al., 2001; Williams et al., 2018).

Methods

Study design and camera trap placement

My camera trapping surveys were carried out in the Western Cape Province of South Africa, and were nested within two different types of land use: the group of 22 neighbouring extensive small-livestock farms in the Laingsburg district of the Central Karoo and the Anysberg Nature Reserve situated in the Little Karoo presented in Chapter 2 of this thesis (Figure 3.1).

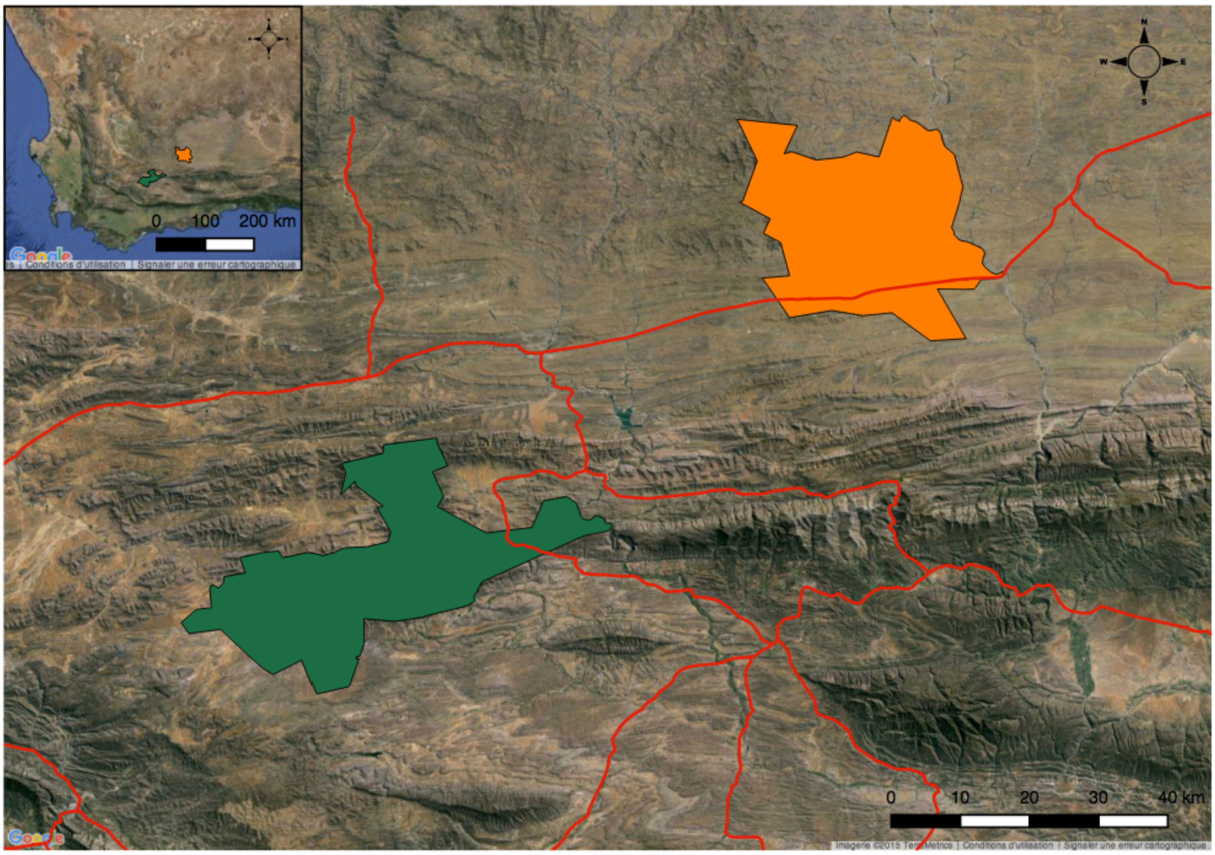


Figure 3.1. Location of the two study sites – Anysberg Nature Reserve (green polygon) and the farmland (orange polygon) in the Western Cape Province, South Africa (insert).

I deployed Bushnell Trophy CAM HD (Bushnell Outdoor Products, Overland Park, Kansas, USA) camera traps at 176 locations on farmland between the end of September 2012 and March 2013, and at 156 locations in the reserve between the end of September 2013 and May 2014. This model of camera trap uses a highly sensitive Passive Infra-Red (PIR) motion sensor that detects movement. The cameras are equipped with built-in infrared LEDs that function as a flash and allow night pictures, but the pictures are in black and white. This technology allows avoiding the use of a real flash, known to influence the detectability of some species (Larrucea et al., 2007; Séquin et al., 2003; Wegge et al., 2004).

Due to my study design and the camera trap density required, I did not have enough cameras to cover the whole farming area or the PA at once. I therefore divided both study sites in two equal halves for survey (south and north for the farms, and east and west for the PA) and rotated my cameras in two phases to facilitate a greater spatial coverage. The surveys in each type of land use occurred one year out of synchrony because I did not have sufficient cameras to cover both study sites simultaneously. However, I would argue that year is unlikely to have had much effect as community change in both plants and medium and large animals is slow in arid regions such as the Karoo (Dean and Milton, 1999; Noy-Meir, 1973) and no fire or unusual events occurred in the reserve or on farmland during the sampling periods. I used a systematic placement design with a randomized starting point and orientation, with my cameras deployed at regular intervals on a grid pattern with a 2 km inter-camera distance (Kinnaird and O'Brien, 2012; Meek et al., 2014; O'Brien et al., 2003) (Figures 3.2 and 3.3). Thus, particular features such as trails were sampled in proportion to their occurrence in the landscape (Cusack et al., 2015; Rowcliffe et al., 2013). This randomisation allows a wider variety of landscape features to be sampled. When considering multi-species surveys, selecting optimal camera placement for increased capture probability of specific species may result in biased placement for the detection of other species (Cusack et al., 2015; Harmsen et al., 2010; Larrucea et al., 2007; Mann et al., 2015). In my study, 27.8% and 32.7% of the cameras were positioned on trails/roads on farmland and in the PA respectively.

Altitude at each camera location was recorded using a handheld GPS device and ranged from 468 m.a.s.l. to 1177 m.a.s.l. (mean = 676.2 m.a.s.l.; SD = 147.9 m.a.s.l.) on farmland and from 535 m.a.s.l. to 1486 m.a.s.l. (mean = 823.3 m.a.s.l.; SD = 191.1 m.a.s.l.) in the PA. The choice of the coverage was also a compromise between the time required to trap a large number of sites, the cost of camera traps and deployment in the field and the large areas to be sampled, and followed the recommendations of O'Brien et al. (2010) for the Wildlife Picture Index. Cameras were programmed to take 3 pictures each time they were triggered, with a 1-minute delay between triggers. Sensitivity of the infrared sensor was set to high.

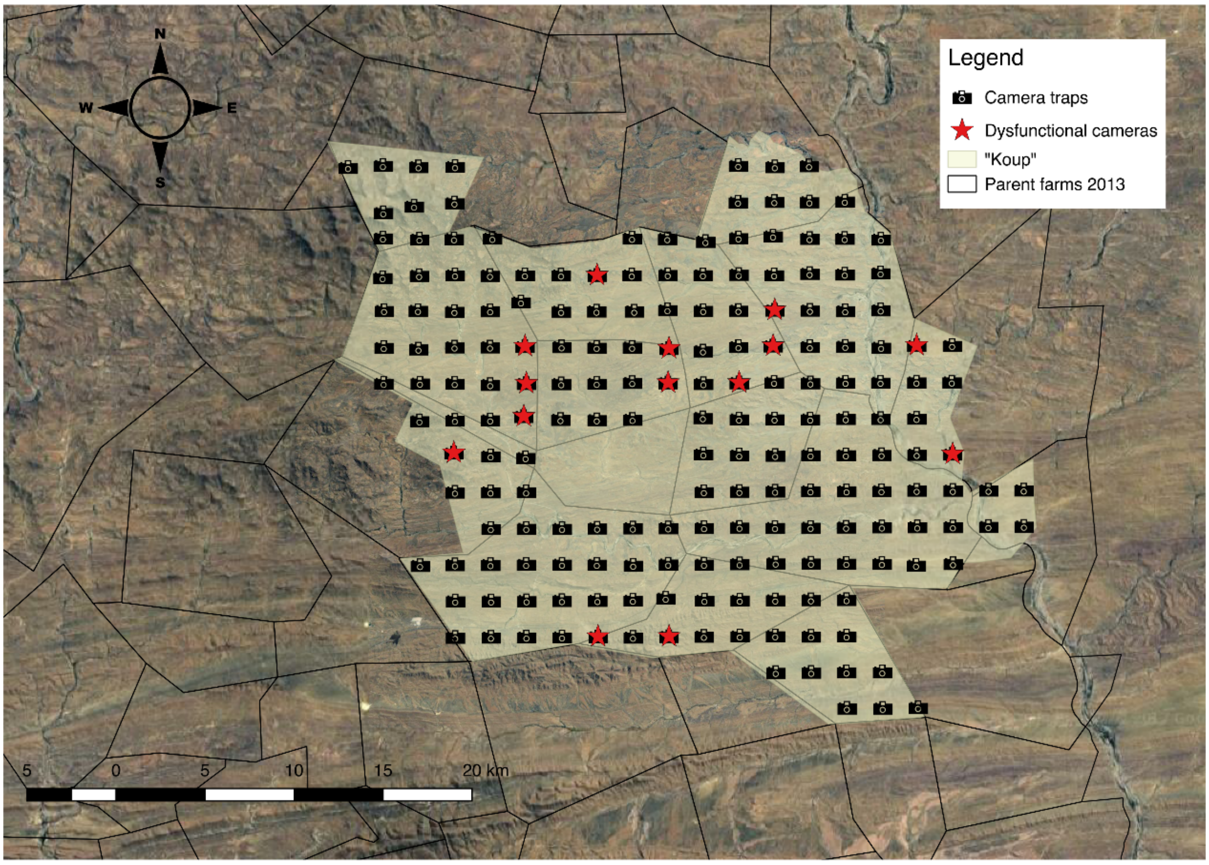


Figure 3.2. Location of the camera traps (black camera symbols) on the 2km-grid inside the 22 farms in the Laingsburg district, Central Karoo, South Africa. The red stars symbolized the faulty cameras (no data collected). The area inside the polygon with no cameras belongs to two farmers who did not allow access on their land for camera trapping.

I used ArcView 3.2 (ESRI, Redlands, CA, USA) to locate sample unit centroids and placed cameras within 50 m (but up to 200 m in three cases due to topographical barriers) of the centroid, choosing a microplacement where different species' tracks or signs were abundant, to give the highest probability of obtaining photographs of a wide range of species (Colyn et al., 2018; O'Brien et al., 2010).

In their paper, Larrucea et al. (2007) showed that juvenile coyotes – an ecologically similar species to the jackal – were more likely to be photographed by cameras placed away from man-made objects, and that an average of 14 days was necessary before the first adult photograph was captured at a camera station. I thus never used man-made objects as supports for my cameras, but rather used large rocks from the natural environment as posts for setting the cameras approximately 35-40 cm off the ground. Still following Larrucea et al. (2007), I did not visit the cameras until the end of the surveys to avoid leaving my scent and disturbing wildlife in the area, especially neophobic species such as jackal on farmland. The downside to that was that some cameras experienced premature battery deficiency leading to a loss of data (see below).

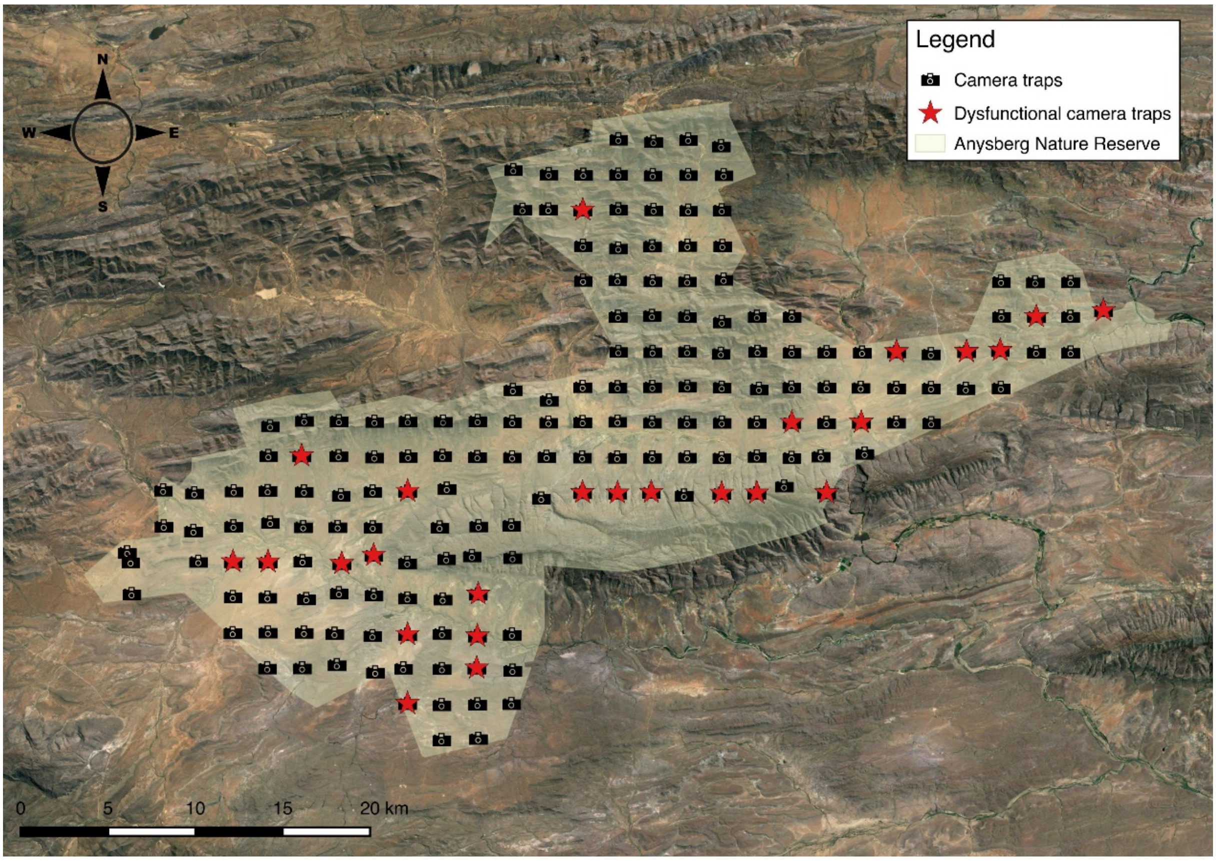


Figure 3.3. Location of the camera traps (black camera symbols) on the 2km-grid inside Anysberg Nature Reserve in the Klein Karoo. The red stars symbolized the faulty cameras (no data collected). Areas inside the polygon with no cameras are cliffs, rivers or gorges that I could not access on foot or with a vehicle.

On farms, sites were sampled 54-63 days (mean = 58.0; SD = 3.1) during the first survey in the south and 86-103 days (mean = 89.0; SD = 18.9) during the second survey in the north between the end of September 2012 and the beginning of March 2013. In the PA, sites were sampled 54-62 days (mean = 55.2; SD =11.3) during the first survey in the east and 90-110 days (mean = 82.5 due to camera failure; SD = 33.3) during the second survey in the west between the end of September 2013 and May 2014.

Eighteen and 34 camera traps experienced extensive data loss on farms and in the PA respectively, for various reasons (Figure 3.4), resulting in less trapping nights than expected. I omitted those cameras from analyses, resulting in a total data loss of 1094 and 1966 camera trap nights (7.8% and 15.6%) on farms and in the PA respectively. At the end of each survey, cameras were collected and deployed to their new locations as quickly as possible.

Figure 3.4. Reasons for camera trap failure on farmland and in the PA – A: disturbance and displacement of cameras by chacma baboons, severe weather conditions such as B: hail storms, C: mud flows, D: flash floods © Marine Drouilly – The Karoo Predator Project.

To limit auto-correlation in my data, I grouped photographic events following the recommendations of O'Brien et al. (2003) and Rich et al. (2016), with consecutive photographs of individuals of the same species being considered independent captures only if taken more than 30 minutes apart. I cleaned my database by deleting all the blank pictures (i.e., that did not contain any subject), such as the ones with moving grass (Meek et al., 2014). For some pictures taken at night, it was difficult to identify the species. I therefore discarded those few pictures too to avoid including false detections in my models (MacKenzie et al., 2002). I kept all the pictures of domestic animals (sheep, goat, cattle, dog, cat, horse) and human activities (people, vehicles) to use as a disturbance index. An event was defined as a trap night (except when stated differently) – because most of the Karoo wildlife is nocturnal – and represented a 24 hour timeframe starting at 00:00 and ending at 23:59 (Meek et al., 2014).

For each type of land use, I first computed the naïve occupancy of each species (i.e. the proportion of sampled camera locations at which the species was detected) and the landuse-level species-specific detection frequency, also called relative abundance index (RAI), which is the total number of independent captures of a species at the land use level, divided by the total number of nights the cameras were active for and multiplied by 100 (i.e. number of captures of a particular species per 100 camera trap nights; Carbone et al., 2001; Cusack et al., 2015; Rovero and Marshall, 2009). This calculation does not take into account the variation in detection probabilities between species, but different studies highlighted a strong linear relationship between trapping rates and independent density estimations in various species, including African mammals (Carbone et al., 2001; Kinnaird and O'Brien, 2012; O'Brien et al., 2003; Rovero and Marshall, 2009). In addition, camera trapping rates or RAI have been shown to reach satisfactory precision when trapping effort amounts to 250-300 camera trap days or nights (Rovero and Marshall, 2009), which is far below what my effort was (i.e. more than 10 000 trap nights per area). I therefore initially calculated RAIs for comparison with published studies and for computing community indices, before applying the multi-species occupancy model to my data, taking into account imperfect detection. I also recorded the number of farms where each species was detected, species body mass and trophic guild (Tables 3.7 and 3.8). I compared the mean number of wild species recorded per camera trap between the farmland and the reserve with a t-test.

Community diversity and structure

a) Wildlife species richness and diversity analyses

Relative species richness is the most fundamental concept of diversity (Peet, 1974) and is defined as the proportion of a regional pool of species represented at a site (i.e., α diversity / γ diversity). I used rarefaction analyses (both with camera trap nights and cumulative monitoring nights) to generate the species-effort relationship (Colwell et al., 2004; Gotelli and Colwell, 2011), to compare species richness between the farmland and the reserve, and to assess if data collection was adequate to capture the total number of species in each land use (i.e. if the species accumulation curves reached an asymptote). For each type of land use, the curves were compared for the same levels of sampling effort using 95% confidence intervals drawn from 1000 randomisations performed with replacement (Colwell et al., 2004). Species accumulation curves, although ignoring imperfect detection of individual species and therefore presenting limitations in communities that contain many rare species or in communities of species that are common but difficult to detect, are useful for comparison with other studies. To account for undetected species, I computed non-parametric species richness estimators (i.e. Chao 1, first-order Jackknife (Jack 1) and bootstrap) (Colyn et al., 2018; Tobler et al., 2008) for each land use, under the assumption that community composition remained the same during each survey. The Jackknife estimator also assumes no temporal variation in capture probability for all species (Burnham and Overton, 1979; Chao et al., 2004). Because my surveys were of short duration and because fences enclosed both systems – even if those were partially porous – I considered these assumptions to be met.

I then computed wildlife species diversity and evenness (i.e. a measure of the relative abundance of the different species making up the richness in each type of land use) for the communities in each land use by calculating Shannon's diversity index (*H*) (Shannon, 1948) and Shannon's equitability index or evenness (E_H), as follow:

$$H = -\sum_{i=1}^{S}(p_i \ln p_i)$$

where p_i is the proportion of species *i* relative to the total number of species in the community (richness).

$$E_H = \frac{H}{H_{max}} = \frac{H}{\ln S}$$

where *S* is the total number of species in the community (richness).

Equitability ranges from 0 to 1 (complete evenness, all the species range in equal proportions).

For each site, I also calculated dominance (*D*) (i.e. the degree to which a species is more numerous than the others in a community) with the Berger-Parker index (Berger and Parker, 1970), using the formula:

$$D = N_{max}/N$$

where N_{max} is the number of pictures for the most abundant species (according to RAIs) and *N* is the total number of wildlife pictures in the considered land use.

However, entropies such as the Shannon diversity index (*H*) are not themselves diversities. And they must be converted into an Effective Number of Species (ENS), which represents the number of equally-common species in a community, to enable interpretation (Jost, 2006). The true diversity of a community is therefore given by:

$$ENS = \exp(H)$$

where H is the Shannon's diversity index.

b) Community composition and structure

I used the Jaccard Similarity Index (S_J) (Jaccard, 1912) and its representation in terms of dissimilarity to quantify compositional differences between the observed communities in the two types of land use. This index was developed to compare regional floras and uses presence/absence data. It is defined by the size of the intersection (in terms of species detected in this case) divided by the size of the union of the sample set A (corresponding to the farms) and B (corresponding to the reserve).

$$S_{J(A,B)} = \frac{|A \cap B|}{|A \cup B|} = \frac{|A \cap B|}{|A|+|B|-|A \cap B|}$$

where:

$|A \cap B|$ is the number of species detected in both types of land use,

$|A|$ is the number of species detected in the farms only,

$|B|$ is the number of species detected in the reserve only.

S_J can range from 0 (the areas are completely dissimilar in terms of species composition) to 1 (the areas are identical in terms of species composition). S_J can then be multiplied by 100 to express the result as a percentage and can be represented in terms of percentage of dissimilarity or distance (i.e. $D_J = 100 - S_J$).

I then investigated the structure of each observed community in terms of its rank abundance distribution (RAD). To do so, I only considered species that were detected at both sites (27/42 species). I fitted null, pre-emption, lognormal, Zipf and Zipf-Mandelbrot models to rank abundance distributions (Cusack et al., 2015; Wilson, 1991) from the RAIs of selected species in each study site to check whether the structure of each community differs. I used the deviance criterion defined as the minimisation of the sum of squares of deviations from predicted and observed values (Cusack et al., 2015; Wilson, 1991) to select the model that best fitted the data. The relative rank each species occupies within the observed communities, named rank shifts and constructed from their RAIs, was calculated using the mean absolute rank shift (MARS) from the reserve to the farm survey using the following formula:

$$MARS = \sum_{i=1}^{n}(|R_{i,farms} - R_{i,reserve}|)/n$$

where n is the number of species considered and R_i is the relative rank of species i on farms and in the reserve. I tested the hypothesis that the MARS was not significantly different from 0 using a Wilcoxon rank sum test (Cusack et al., 2015).

c) Functional diversity

Functional diversity quantifies a range of species' functional traits (that define a species' ecological role in a community) within multidimensional niche space (Petchey and Gaston, 2002; Villéger et al., 2008). I analysed whether the functional diversity of the mammal community differed between land use types (Ahumada et al., 2011; Kiffner et al., 2015). To do so, I used two functional traits considered to be attributes of resilience to land use change (following Msuha et al., 2012): body mass and trophic category (carnivore, herbivore, insectivore or omnivore; Brashares, 2003; Cromsigt et al., 2009). I graphically represented the data for each land use separately in a functional space (Ahumada et al., 2011; Kinnaird and O'Brien, 2012) and added livestock species in the farmland graph. At the land use level, I calculated the functional dispersion index (FDis; Laliberte and Legendre, 2010), which is the weighted (by RAIs) mean distance in the multidimensional trait space of individual mammal species to the centroid of all species (as defined in Ahumada et al., 2011; Laliberte and Legendre, 2010), and compared it between the two study sites.

To investigate the effect of body mass and trophic category on species presence between the two types of land use, I used a General Linear Model (GLM) to model the binomial response variable "species presence", in which the species was detected (1) or not (0), as a function of land use (i.e. farmland or reserve), log-ransformed body mass and trophic category. For each mammal species, I calculated the mean body mass for males and females obtained from the literature (Apps, 2012; Table 3.3), except for livestock (I took the mean body mass recorded from farmers during interviews – see Chapter 6).

Finally, I compared the RAIs of the region's main small-livestock predators (i.e. jackal, caracal and baboon) between land use types using one-tailed unpaired two-sample Wilcoxon tests to test the null hypothesis that the species' RAI in the reserve was greater than on farmland where they are persecuted (Jenks et al., 2011).

Species accumulation curves were plotted using the packages iNEXT (Hsieh et al., 2016) and vegan (Oksanen et al., 2017), which was also used to calculate diversity indices and conduct analyses of community composition and structure. Analyses of functional diversity were conducted with the package FD (Laliberté et al., 2015). I used R version 3.0.3 (R Development Core Team, 2016).

Single-season multi-species occupancy model

a) Covariates

I hypothesized that wildlife occupancy would be influenced by variation in human disturbance (Caro, 1999) and livestock presence (Kinnaird and O'Brien, 2012; Williams et al., 2018), general habitat type, elevation (Karanth et al., 2009) and vegetation (Table 3.1). I used a soil-adjusted vegetation index that seeks to address some of the limitation of the Normalized Vegetation Index (NDVI) when applied to areas with a high degree of exposed soil surface, as in my study areas (Rondeaux et al., 1996). The NDVI is a measure of vegetation productivity (Pettorelli, 2013) and has been linked to occurrence patterns for many wildlife species (Mueller et al., 2008; Oindo, 2002; Oindo and Skidmore, 2002; Pettorelli et al., 2011) including carnivores (Carroll et al., 2001; Wiegand et al., 2008). In rangeland conditions, light from the soil surface can influence NDVI values, because arid and semi-arid environments tend to have a higher proportion of bare ground cover than other habitat types (Rondeaux et al., 1996). The soil surface impact on NDVI values is greatest in areas with between 45% and 70% vegetation cover (Huete and Jackson, 1988). I therefore used a soil-adjusted vegetation index that seeks to address some of the limitation of NDVI when applied to areas with a high degree of exposed soil surface, like in our study areas, to measure vegetation greenness. I used the modified soil-adjusted index (MSAVI2) (Qi et al., 1994), which has been used in a number of rangeland studies (e.g. Chen and Gillieson, 2009; Liu et al., 2005), with the following formula:

$$MSAVI2=((2\times NIR+1-\sqrt{((2\times NIR+1)^2-8\times(NIR-RED))}))/2$$

where NIR is the near infrared band reflectance and RED is the red band reflectance from the Moderate-Resolution Imaging Spectroradiometer (MODIS) sensor (Global MOD13Q1 product from the Terra satellite, 16-day composite image at 250 m spatial resolution, downloaded from http://reverb.echo.nasa.gov/) (Didan, 2015).

My modelling approach also accounted for heterogeneity in wildlife detection probability through the addition of site-specific covariates (Table 3.1). I hypothesized that general habitat type and presence of trail/road (Cusack et al., 2015) would affect the detection probability of different species. I extracted detection – non-detection data for all species targeted in this study and calculated the values of the covariates at each camera trap site in each type of land use. I scaled the covariates to have a mean of 0 and variance of 1. Covariates were checked for correlation using Pearson correlation tests. None of the variables were highly correlated (i.e. r > 0.6, sensu Van der Weyde et al., 2018).

b) Modelling framework

I adopted the hierarchical formulation of a community occupancy model as described by Dorazio et al. (2006), with data augmentation to estimate species richness (N) as a function of model-based estimators of species occurrence (i.e. the probability species i occurred within the area sampled by a camera trap during our survey period). I included detectability (i.e. the probability of detecting species i at a camera site when it has been detected at least once on the grid) at each camera site for each type of land use separately. Species richness in each land use was therefore the average estimated species richness across all sites in that particular land use. I interpreted the occupancy parameter (ψ) as the proportion of area used rather than the proportion of area occupied by a species (Mackenzie and Royle, 2005). The species of interest were from related communities in two different but spatially linked types of land use. I therefore analysed the two types of land use separately because I argue that they are two different management systems and hence, it is possible that the relationship between species richness/occupancy and predictor variables differs between the two types of land use.

A sampling occasion of 6 days was used to avoid having too many non-detections during the surveys (Mackenzie and Royle, 2005; Tobler et al., 2015). I constructed and fitted four separate models and used the deviance information criterion (DIC; Appendix 3A) to select the candidate model with the smallest DIC (Claeskens and Hjort, 2008), in the same spirit as model selection conducted with the Akaike's Information Criterion (AIC).

Table 3.1. Variables hypothesized to influence patterns of terrestrial vertebrates' occupancy (probability of use) and detection in two contrasting types of land use in the Karoo, with the corresponding index used and the predicted direction of effect (i.e. negative or positive influence or both) on probability of use and on probability of detection, and the source of data.

Variable	Index	Influence on	Predicted effect	Source
Human disturbance	Relative abundance index (RAI; number of records per trap effort) of humans, vehicles and pets	ψ	-	Camera trap pictures
Livestock relative abundance	RAI of livestock	ψ	+/-	Camera trap pictures
General habitat type	Plain, mountain or riverine habitat	ψ, p	+/-	Classification was made in the field
MSAVI2	16-day composite MSAVI2 value most closely matched to the period over which a given camera station was active in the field; average of multiple composite values for cameras in the field for more than 16 days or over a period split across two or more composite time frames	ψ	+/-	MODIS sensor
Elevation	Elevation in m.a.s.l.	ψ	+/-	Recorded at each site with a handheld GPS unit (Garmin GPSMAP® 64s, Garmin International Inc. Olathe, Kansas, USA)
Presence of trail/road	1 (on a trail/road) or 0 (off-trail/road)	p	+/-	Direct observation when setting up the cameras

For each land use, I assumed that there exists a super-population of species (S) that consists of the observed species (n) and of additional unseen species (S-n). The observed data Y_n consisted of an n x J matrix of observed counts associated with the i^{th} species at camera site j and is denoted as $[y_{i,j}]$ for $i = 1, \ldots, n$ (the number of observed species) and $j = 1, \ldots, J$ (the number of camera sites). Since N was unknown, an (S-n) x J matrix of zeroes was introduced, which represented the counts associated with the unobserved species for each type of land use (Dorazio et al., 2006). I introduced a latent indicator variable w_i, which was given the value 1 if species i in the super-population occurred in the land use under investigation and 0 if it did not. From the above discussion $w_i = 1$ for $i = 1, \ldots, n$ and $N = \sum_{i=1}^{S} w_i$. The latent variable $z_{i,j}$ representing occurrence took on the value 1 if species i used the range covered by camera station j and 0 otherwise. The w_i indicator was modelled as a Bernoulli random variable with success probability Ω. The detection process (conditional on $w_i = 1$) was modelled using a binomial distribution such that:

$$p(y_{i,j}|z_{i,j} = 1, p_{ij}) = \binom{K_j}{y_{i,j}} \theta_{i,j}^{y_{i,j}} (1 - \theta_{i,j})^{K_j - y_{ij}}$$

$$p(y_{i,j}|z_{i,j} = 0, p_{ij}) = 1$$

The occupancy and detection probabilities were modelled using a logit link function, which relates the occupancy and detection probabilities to covariates. Using the above description, I formulated the model as a hierarchical mixed effects model (Table 3.2) where I included species-specific random effects (u_i and v_i), site-specific random effects (β_j and α_j), as well as site-level covariate effects in the occupancy and detection process. In this community model formulation, the detection of all species informs the detection of an individual species and allows estimates of rare and cryptic species that would otherwise not be possible, as coefficients are modelled through community-level parameters, rather than independently for each species.

In Table 3.2, I denoted $x_{j,k}$ and $w_{j,k}$ as the covariate values associated with the j^{th} camera site and the k^{th} occupancy and detection covariate respectively. One model was suggested for each type of land use and we expected species diversity, occupancy and detection to be affected by various environmental and anthropogenic variables. To investigate these variables, I followed the procedure of Zipkin et al. (2009) and developed an *a priori* model based on biological hypotheses on how terrestrial vertebrate (>0.5 kg) diversity, occupancy and detection could be influenced by these variables on drylands. I used generalized linear mixed models to incorporate the corresponding site-level covariates in the models. The hierarchical prior distributions used to undertake the analysis are presented in Table 3.4. Results are reported using posterior means and standard deviations, 95% credible intervals (CI) as well as 95% highest density posterior intervals (HDPI), which in Bayesian statistics are the shortest intervals on a posterior density (Turkkan and Pham-gia, 1993). I considered coefficients as having strong inference values when their 95% HDPI did not include 0.

Table 3.2. Species richness hierarchical specification.

Super-population process	$w_i \sim \text{Bern}(\Omega), \forall_i = 1, \ldots, S$
State process (occurrence)	$(z_{i,j} \mid w_i, \psi_{i,j}) \sim \text{Bern}(w_i\, \psi_{i,j})$, $\forall_i = 1, \ldots, S; \forall_j = 1, \ldots, J$
Observation process (detection)	$(y_{i,j} \mid z_{ij}, p_{i,j}) \sim \text{Bin}(K_j, z_{i,j}\, p_{i,j})$
Species effect	$u_i \sim N(0; \tau_u)$
Site specific effect	$v_i \sim N(0; \tau_v)$
Species heterogeneity – occupancy parameters, where $\psi_{i,j}$ is the probability that species *i* occurred at camera station *j*.	$\text{logit}(\psi_{i,j}) = \bar{\beta} + u_i + \sum_{k=1} \beta_{i,k} x_{j,k}$
Species heterogeneity – detection parameters, where $p_{i,j}$ is the probability that species *i* was detected at camera station *j*, conditional on $\psi_{i,j} = 1$	$\text{logit}(p_{i,j}) = \bar{\alpha} + v_i + \alpha_j \sum_{k=1} \alpha_{i,k} w_{j,k}$

Table 3.3. Body mass and trophic guild for all mammal species recorded in the two study sites in the Karoo, South Africa.

Family *Genus species*	Common name	Body mass	Trophic guild
Canidae			
Canis mesomelas	Black-backed jackal	7.75	Carnivore
Vulpes chama	Cape fox	2.8	Carnivore
Otocyon megalotis	Bat-eared fox	3.6	Insectivore
Felidae			
Caracal caracal	Caracal	11.75	Carnivore
Felis sylvestris	African wildcat	4.35	Carnivore
Panthera pardus	Leopard	35	Carnivore
Herpestidae			
Herpestes pulverulentus	Cape grey mongoose	0.768	Carnivore
Cynictis penicillata	Yellow mongoose	0.83	Insectivore
Atilax paludinosus	Water mongoose	3.2	Carnivore
Suricata suricatta	Meerkat	0.73	Insectivore
Hyaenidae			
Proteles cristata	Aardwolf	7.5	Insectivore
Parahyaena brunnea	Brown hyena	39	Carnivore
Mustelidae			
Mellivora capensis	Honey badger	12	Carnivore
Ictonyx striatus	Striped polecat	0.828	Carnivore
Aonyx capensis	Cape clawless otter	14	Carnivore
Viverridae			
Genetta sp.	Genet	1.85	Omnivore
Cercopithecidae			
Chlorocebus pygerythrus	Vervet monkey	4.8	Omnivore
Papio ursinus	Chacma baboon	25	Omnivore
Leporidae			
Lepus spp.	Hare	2.42	Herbivore
Pronolagus rupestris	Smith's red rock rabbit	1.6	Herbivore
Hystricidae			
Hystrix africaeaustralis	Cape porcupine	15.4	Omnivore
Orycteropodidae			
Orycteropus afer	Aardvark	53	Insectivore
Equidae			
Equus zebra zebra	Cape mountain zebra	244.5	Herbivore
Bovidae			
Sylvicapra grimmia	Common duiker	19.7	Herbivore
Raphicerus campestris	Steenbok	11.1	Herbivore
Damaliscus pygargus	Blesbok	61	Herbivore
Oreotragus oreotragus	Klipspringer	11.9	Herbivore
Oryx gazella	Oryx	225	Herbivore
Tragelaphus strepsiceros	Greater kudu	193.5	Herbivore
Antidorcas marsupialis	Springbok	39	Herbivore
Pelea capreolus	Grey rhebuck	20	Herbivore
Alcelaphus buselaphus caama	Red hartebeest	136	Herbivore
Taurotragus oryx	Cape eland	530	Herbivore
Cervidae			
Dama dama	Fallow deer	50	Herbivore
Procaviidae			
Procavia capensis	Rock hyrax	3.55	Herbivore
Suidae			
Potamochoerus larvatus	Bushpig	60.5	Omnivore

Similar to the presence data presented earlier (paragraph on community diversity and structure, c), I hypothesized that the probability of use by mammals would be different in each type of land use depending on their body size and their trophic guild. Thus, for each type of land use, I divided the mammal species into body size groups based on mean body mass for adult males and females of those species (Apps, 2012) and on trophic guilds. Body size groups included 0.5 kg <small ≤5 kg, 5 kg <medium ≤20 kg and large >20 kg, whereas trophic groups include carnivores, herbivores, omnivores and insectivores (Table 3.3).

Table 3.4. Hierarchical prior distributions used to undertake the multi-species occupancy analyses. I assumed that species-specific parameters were random effects derived from a normally distributed, community-level hyper-parameter. Hyper-parameters specify the mean response and variation among species within the community to a covariate.

$\bar{\beta} \sim N(\mu_b; \tau_b)$	$\bar{\alpha} \sim N(\mu_a; \tau_a)$
$\mu_b \sim N(0; 0.01)$	$\mu_a \sim N(0; 0.01)$
$\tau_b = 1 / \sigma_b^2$	$\tau_a = 1 / \sigma_a^2$
$\sigma_b \sim U(0; 5)$	$\sigma_a \sim U(0; 5)$
$u_i \sim N(0; \tau_u), \forall_i$	$v_i \sim N(0; \tau_v), \forall_i$
$\tau_u = 1 / \sigma_u^2$	$\tau_v = 1 / \sigma_v^2$
$\sigma_u \sim U(0; 5)$	$\sigma_v \sim U(0; 5)$
$\beta_{i,k} \sim N(\mu_{\beta,k}; \tau_{b,k}), \forall_i, k$	$\alpha_{i,k} \sim N(\mu_{\alpha,k}; \tau_{a,k}), \forall_i, k$
$\mu_{\beta,k} \sim N(0; 0.01)$	$\mu_{\alpha,k} \sim N(0; 0.01)$
$\tau_{b,k} = 1 / \sigma_{b,k}^2$	$\tau_{a,k} = 1 / \sigma_{a,k}^2$
$\sigma_{\beta,k} \sim U(0; 5)$	$\sigma_{\alpha,k} \sim U(0; 5)$

The models were run using the R package jagsUI 1.4.4 (Kellner, 2017) in combination with JAGS 4.3.0 (Plummer, 2017). The posterior distributions of the model parameters were obtained using three chains of 500 000 iterations, discarding a burn-in sample of 200 000 iterations. The chains were thinned by retaining every 100 sampled values in order to reduce the size of the final results file (Link and Eaton, 2012). I assessed convergence using the Gelman-Rubin statistic, with values <1.1 indicating convergence (Gelman et al., 2004).

Results

Descriptive statistics

The complete dataset included a total survey effort of 23 796 camera trap nights (12 934 on farmland and 10 598 in the PA) for 332 camera trap locations (Table 3.5). The sampling effort was calculated based on the number of nights that camera traps operated for (or until the last photo was taken if the camera stopped working before the end of the survey for various reasons, see Figure 3.4). A total of 307 901 photographs were collected (178 223 on farmland and 129 678 in the PA), of which 291 850 were non-blank pictures. Eighteen and 34 camera traps experienced extensive data loss (1094 (7.8%) and 1966 (15.6%) camera trap nights) on farmland and in the reserve respectively, due to disturbance (mostly by baboons) or extreme weather conditions (e.g. hail storm). No cameras were stolen by people.

Table 3.5. An overview of the extent and effort of the four camera trapping surveys conducted on farmland in the Central Karoo and in Anysberg Nature Reserve in the Little Karoo.

Survey	Area size (Km^2)	Number of working camera traps	Effort (trap nights)	Sampling period	Camera failure (%)
Farm South	357	87	5043	Sept-Nov 2012	4.4
Farm North	397	89	7891	Nov-March 2012-2013	11.9
Anysberg East	431	82	4492	Oct-Dec 2013	15.5
Anysberg West	371	74	6106	Feb-June 2014	11.9
Total	**1556**	**332**	**23796**		**10.9**

I recorded a total of 36 species of wild mammals (>0.5 kg, of which 3 were extra-limital species: red hartebeest (*Alcelaphus buselaphus caama*), oryx (*Oryx gazella*) and blesbok (*Damaliscus pygargus*), and two were introduced: fallow deer (*Dama dama*) and Cape mountain zebra (*Equus zebra zebra*)) and 6 species of ground birds (>0.5 kg) in my two study areas (Table 3.6). The mean number of wild species recorded per camera trap was significantly higher ($t = 2.14$, $P = 0.033$) on farmland (mean = 5.76 ± 2.98, with an associated range of 0-14 species) than in the PA (mean = 5.07 ± 2.88, with an associated range of 1-14 species). Surveyed mammal and bird species spanned a large array of body sizes: average mammal body mass (between male and female) ranged from 0.73 kg for the meerkat (*Suricata suricatta*) to 530 kg for the Cape eland (*Taurotragus oryx*) (median = 11.95 kg), and average bird body mass (between male and female) varied from 0.75 kg for the Cape spurfowl (*Pternistis capensis*) to 8.40 kg for the Kori bustard (*Ardeotis kori*) (median=5.78 kg).

The overall trapping rate for wildlife (i.e. the number of wildlife photographs divided by the total number of trap nights for each area) was 0.28 on farmlands whereas it was 0.32 in the PA. The total number of detections per species was very heterogeneous and varied from 1 for the southern black korhaan (*Afrotis afra*) to 957 for the common duiker for the 12 934-night pooled data on farms (Table 3.7), and from 1 for the water mongoose (*Atilax paludinosus*), the striped polecat (*Ictonyx striatus*) and the clawless otter (*Aonyx capensis*) to 537 for the baboon for the 10 598-night pooled data in Anysberg Nature Reserve (Table 3.8).

Table 3.6. Number of independent wildlife photography events, species of mammal and ground bird detected during the four camera trapping surveys conducted on farmlands and in Anysberg Nature Reserve.

Type of land use	Number of independent wildlife images	Number of species of mammal detected	Number of species of ground bird detected
Farmland	3609	28	5
PA	3415	31	4
Total	**7024**	**36**	**6**

On farms, Bovidae (n=2048), Leporidae (n=586) and Canidae (n=341) were the most frequently detected families (Table 3.7) whereas in the PA it was Bovidae (n=1503), Cercopithecidae (n=556) and Leporidae (n=240) (Table 3.8). Steenbok (*Raphicerus campestris*) were detected at more sampling sites (a naïve measure of occupancy without accounting for detectability) than any other species, followed by hares (both *Lepus capensis* and *Lepus saxatilis* were pooled because they were not distinguishable from the photographs) and common duikers, whereas red hartebeests and southern black korhaans were detected at the fewest sites on farmland (Table 3.7). In the PA, chacma baboons were detected at the greatest proportion of sampling sites, followed by oryx (*Oryx gazella*) and common duikers, whereas bat-eared foxes (*Otocyon* *megalotis*), water mongooses, striped polecats and Cape clawless otters were detected at the fewest sites in the PA (Table 3.8).

Five domestic species (not included in the analyses, except if mentioned otherwise) were detected on farmland: cats (2 photographs), horses (3 photographs), cattle (38 photographs), goats (266 photographs) and sheep, with sheep having the highest number of detections (2836 photographs) and being detected at more than 60% of the sampling sites on farmland. Only cats were also detected in the PA (1 photograph).

Wildlife species richness and community diversity

After 5000 camera trap nights, the species accumulation curve for the south of the farm site levelled off but detected the least species of all surveys (Sobs = 27) (Figure 3.5A), whereas the survey in the north of the farm site detected 33 species and the curve did not reach an asymptote (Figure 3.5B) for the same effort. In the reserve, 28 species would have been detected in the east (Figure 3.5C) for the same effort while 32 species were detected in the west. (Figure 3.5D).

Table 3.9. Observed diversity (N_{obs}), asymptotic estimates, estimated bootstrap standard errors (SE) and 95% confidence intervals for Hill number with q = 0 (i.e. species richness).

Sites	N_{obs}	Asymptotic estimate ± estimated bootstrap SE	95% confidence intervals
Farmland south	27	27.17 ± 0.54	27.00 - 30.53
Farmland north	33	36.00 ± 4.60	33.35 - 58.91
Reserve east	28	30.00 ± 3.74	28.18 - 50.12
Reserve west	32	34.25 ± 3.39	32.27 - 51.04

The species accumulation curves for the two pooled surveys on farms and the two pooled surveys in the reserve had very similar shapes (Figure 3.6), with a steep initial slope showing both communities had a high proportion of abundant species. Neither of the curves had completely levelled off by the end of the surveys but most of the species had been detected, with the curves reaching a plateau (Figure 3.6). The reserve survey detected one more species (Sobs = 35) than the farmland survey (Sobs = 34), but the overlapping confidence intervals preclude stating that the communities differed significantly in their richness.

Table 3.7. General results of the camera trapping surveys conducted on farmland, presented per family and species. Shaded in grey, the species/families that are absent or have not been detected by the surveys. The naïve occupancy[1] is the proportion of sampled locations at which the species was detected. The detection frequency[2] or relative abundance index (RAI) is the camera trapping rate and corresponds to the number of captures per 100 trap nights. It is also referred to as capture success.

Family Species	**Number of independent records**	**Number of cameras where the species was detected**	**Number of farms where the species was detected**	**Naive occupancy[1]**	**Detection frequency (RAI)[2]**
Canidae	**341**	**72**	**19**	**0.409**	**2.636**
Black-backed jackal *Canis mesomelas*	107	34	16	0.193	0.827
Cape fox *Vulpes chama*	16	11	8	0.062	0.124
Bat-eared fox *Otocyon megalotis*	218	41	17	0.233	1.685
Felidae	**33**	**27**	**12**	**0.153**	**0.255**
Caracal *Caracal caracal*	23	18	9	0.102	0.178
African wildcat *Felis sylvestris*	10	10	8	0.057	0.077
Leopard *Panthera pardus*	0	0	0	0	0
Herpestidae	**56**	**38**	**18**	**0.216**	**0.433**
Cape grey mongoose *Herpestes pulverulentus*	37	27	14	0.153	0.286
Yellow mongoose *Cynictis penicillate*	16	12	9	0.068	0.124
Water mongoose *Atilax paludinosus*	0	0	0	0	0
Meerkat *Suricata suricatta*	3	3	2	0.017	0.023
Hyaenidae	**100**	**48**	**17**	**0.273**	**0.773**
Aardwolf *Proteles cristata*	100	48	17	0.273	0.773
Brown hyena *Parahyaena brunnea*	0	0	0	0	0
Mustelidae	**36**	**25**	**16**	**0.142**	**0.278**
Honey badger *Mellivora capensis*	0	0	0	0	0
Striped polecat *Ictonyx striatus*	36	25	16	0.142	0.278
Cape clawless otter *Aonyx capensis*	0	0	0	0	0
Viverridae	**42**	**24**	**14**	**0.136**	**0.325**

Family Species	**Number of independent records**	**Number of cameras where the species was detected**	**Number of farms where the species was detected**	**Naive occupancy[1]**	**Detection frequency (RAI)[2]**
Genet *Genetta sp.*	42	24	14	0.136	0.325
Cercopithecidae	**103**	**32**	**10**	**0.182**	**0.796**
Vervet monkey *Chlorocebus pygerythrus*	8	6	5	0.034	0.062
Chacma baboon *Papio ursinus*	95	28	9	0.159	0.734
Leporidae	**586**	**116**	**22**	**0.659**	**4.531**
Hare *Lepus spp*.	556	115	23	0.653	4.299
Smith's red rock rabbit *Pronolagus rupestris*	30	2	2	0.011	0.232
Hystricidae	**65**	**37**	**15**	**0.210**	**0.503**
Cape porcupine *Hystrix africaeaustralis*	65	37	15	0.210	0.503
Orycteropodidae	**43**	**24**	**14**	**0.136**	**0.332**
Aardvark *Orycteropus afe*r	43	24	14	0.136	0.332
Equidae	**0**	**0**	**0**	**0**	**0**
Cape mountain zebra *Equus zebra zebra*	0	0	0	0	0
Bovidae	**2048**	**149**	**22**	**0.847**	**15.835**
Common duiker *Sylvicapra grimmia*	957	107	19	0.608	7.399
Steenbok *Raphicerus campestris*	702	116	23	0.659	5.428
Blesbok *Damaliscus pygargus*	27	10	4	0.057	0.209
Klipspringer *Oreotragus oreotragus*	51	15	11	0.085	0.394
Gemsbok *Oryx gazelle*	20	3	2	0.017	0.156
Greater kudu *Tragelaphus strepsiceros*	134	27	10	0.153	1.036
Springbok *Antidorcas marsupialis*	86	14	8	0.079	0.665
Grey rhebuck *Pelea capreolus*	69	20	8	0.114	0.533
Red hartebeest *Alcelaphus buselaphus caama*	2	1	1	0.006	0.015
Cape eland *Taurotragus oryx*	0	0	0	0	0
Cervidae	**18**	**4**	**3**	**0.023**	**0.139**
Fallow deer *Dama dama*	18	4	3	0.023	0.139
Procaviidae	**14**	**6**	**4**	**0.034**	**0.108**

Family Species	**Number of independent records**	**Number of cameras where the species was detected**	**Number of farms where the species was detected**	**Naive occupancy**[1]	**Detection frequency (RAI)**[2]
Rock hyrax *Procavia capensis*	14	6	4	0.034	0.108
Suidae	**0**	**0**	**0**	**0**	**0**
Bushpig *Potamochoerus larvatus*	0	0	0	0	0
Otididae	**90**	**149**	**22**	**0.847**	**0.696**
Kori bustard *Ardeotis kori*	30	23	12	0.131	0.232
Ludwig's bustard *Neotis ludwigii*	14	11	8	0.062	0.108
Karoo korhaan *Eupodotis vigorsii*	45	22	13	0.125	0.348
Southern black korhaan *Afrotis afra*	1	1	1	0.006	0.008
Phasianidae	**22**	**7**	**5**	**0.040**	**0.170**
Cape spurfowl *Pternistis capensis*	22	6	4	0.034	0.170
Grey-winged francolin Scleroptila afra	1	1	1	0.006	0.008

Table 3.8. General results of the camera trapping surveys conducted in Anysberg Nature Reserve, presented per family and species. Shaded in grey, the species/families that are absent or have not been detected by the surveys. The naïve occupancy[1] is the proportion of sampled locations at which the species was detected. The detection frequency[2] or relative abundance index (RAI) is our camera trapping rate and corresponds to the number of captures per 100 trap nights. It is also referred to as capture success.

Family Species	**Number of independent records**	**Number of cameras where the species was detected**	**Naive occupancy[1]**	**Detection frequency (RAI)[2]**
Canidae	**244**	**45**	**0.288**	**2.302**
Black-backed jackal *Canis mesomelas*	237	45	0.288	2.236
Cape fox *Vulpes chama*	0	0	0	0
Bat-eared fox *Otocyon megalotis*	7	1	0.006	0.066
Felidae	**129**	**55**	**0.353**	**1.217**
Caracal *Caracal caracal*	9	5	0.032	0.085
African wildcat *Felis sylvestris*	97	44	0.282	0.915
Leopard *Panthera pardus*	23	15	0.096	0.217
Herpestidae	**50**	**22**	**0.141**	**0.471**
Cape grey mongoose *Herpestes pulverulentus*	49	21	0.135	0.462
Yellow mongoose *Cynictis penicillata*	0	0	0	0
Water mongoose *Atilax paludinosus*	1	1	0.006	0.009
Meerkat *Suricata suricatta*	0	0	0	0
Hyaenidae	**38**	**21**	**0.135**	**0.358**
Aardwolf *Proteles cristata*	23	16	0.103	0.217
Brown hyena *Parahyaena brunnea*	15	9	0.058	0.141
Mustelidae	**19**	**10**	**0.064**	**0.178**
Honey badger *Mellivora capensis*	17	9	0.058	0.160
Striped polecat *Ictonyx striatus*	1	1	0.006	0.009
Cape clawless otter *Aonyx capensis*	1	1	0.006	0.009
Viverridae	**18**	**13**	**0.083**	**0.170**
Genet *Genetta sp.*	18	13	0.083	0.170
Cercopithecidae	**553**	**114**	**0.731**	**5.218**

Family Species	**Number of independent records**	**Number of cameras where the species was detected**	**Naive occupancy[1]**	**Detection frequency (RAI)[2]**
Vervet monkey *Chlorocebus pygerythrus*	16	5	0.032	0.151
Chacma baboon *Papio ursinus*	537	113	0.724	5.067
Leporidae	**238**	**53**	**0.340**	**2.246**
Hare *Lepus spp*.	138	25	0.160	1.302
Smith's red rock rabbit *Pronolagus rupestris*	100	29	0.186	0.944
Hystricidae	**112**	**36**	**0.231**	**1.057**
Cape porcupine *Hystrix africaeaustralis*	112	36	0.231	1.057
Orycteropodidae	**28**	**23**	**0.147**	**0.264**
Aardvark *Orycteropus afe*r	28	23	0.147	0.264
Equidae	**20**	**10**	**0.064**	**0.189**
Cape mountain zebra *Equus zebra zebra*	20	10	0.064	0.189
Bovidae	**1506**	**146**	**0.936**	**14.210**
Common duiker *Sylvicapra grimmia*	320	63	0.404	3.019
Steenbok *Raphicerus campestris*	108	36	0.231	1.019
Blesbok *Damaliscus pygargus*	0	0	0	0
Klipspringer *Oreotragus oreotragus*	211	52	0.333	1.991
Gemsbok *Oryx gazella*	444	68	0.436	4.189
Greater kudu *Tragelaphus strepsiceros*	80	18	0.115	0.755
Springbok *Antidorcas marsupialis*	91	22	0.141	0.859
Grey rhebuck *Pelea capreolus*	73	19	0.122	0.689
Red hartebeest *Alcelaphus buselaphus caama*	115	19	0.122	1.085
Cape eland *Taurotragus oryx*	64	25	0.160	0.604
Cervidae	**0**	**0**	**0**	**0**
Fallow deer *Dama dama*	0	0	0	0
Procaviidae	**45**	**5**	**0.032**	**0.425**
Rock hyrax *Procavia capensis*	45	5	0.032	0.425
Suidae	**4**	**4**	**0.026**	**0.038**
Bushpig *Potamochoerus larvatus*	4	4	0.026	0.038

Family Species	**Number of independent records**	**Number of cameras where the species was detected**	**Naive occupancy[1]**	**Detection frequency (RAI)[2]**
Otididae	**129**	**12**	**0.077**	**1.217**
Kori bustard *Ardeotis kori*	0	0	0	0
Ludwig's bustard *Neotis ludwigii*	0	0	0	0
Karoo korhaan *Eupodotis vigorsii*	17	7	0.045	0.160
Southern black korhaan *Afrotis afra*	112	5	0.032	1.057
Phasianidae	**24**	**5**	**0.032**	**0.283**
Cape spurfowl *Pternistis capensis*	24	2	0.013	0.226
Grey-winged francolin Scleroptila afra	6	3	0.019	0.057

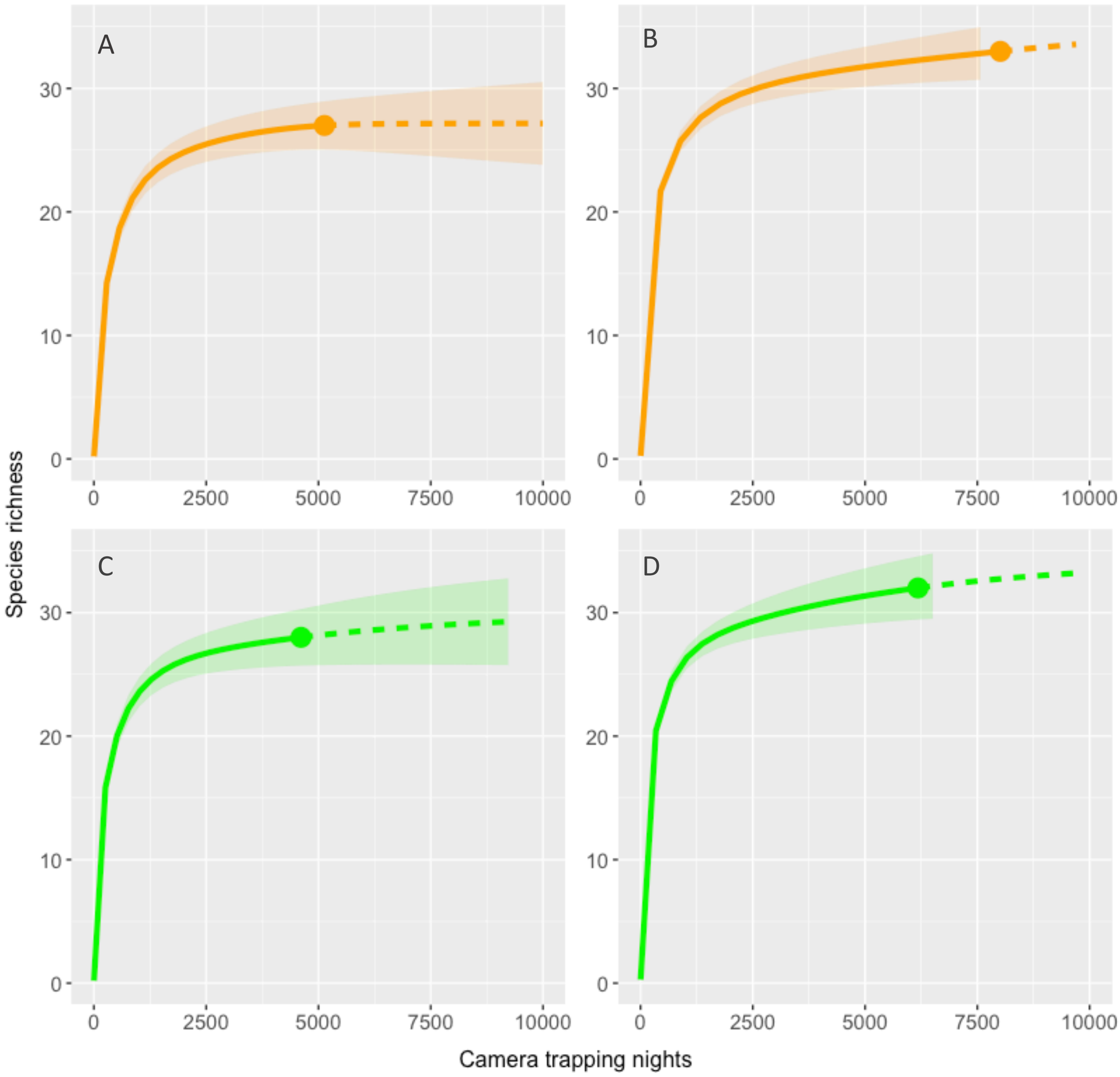


Figure 3.5. Sample-based species accumulation curves describing the medium to large ground bird and mammal species richness on farmland (orange lines, A: south of the Koup, B: north of the Koup) and in Anysberg Nature reserve (green lines, C: east of the reserve, D: west of the reserve), South Africa. Shaded polygons represent the 95% confidence intervals drawn from 1000 randomisations performed with replacement.

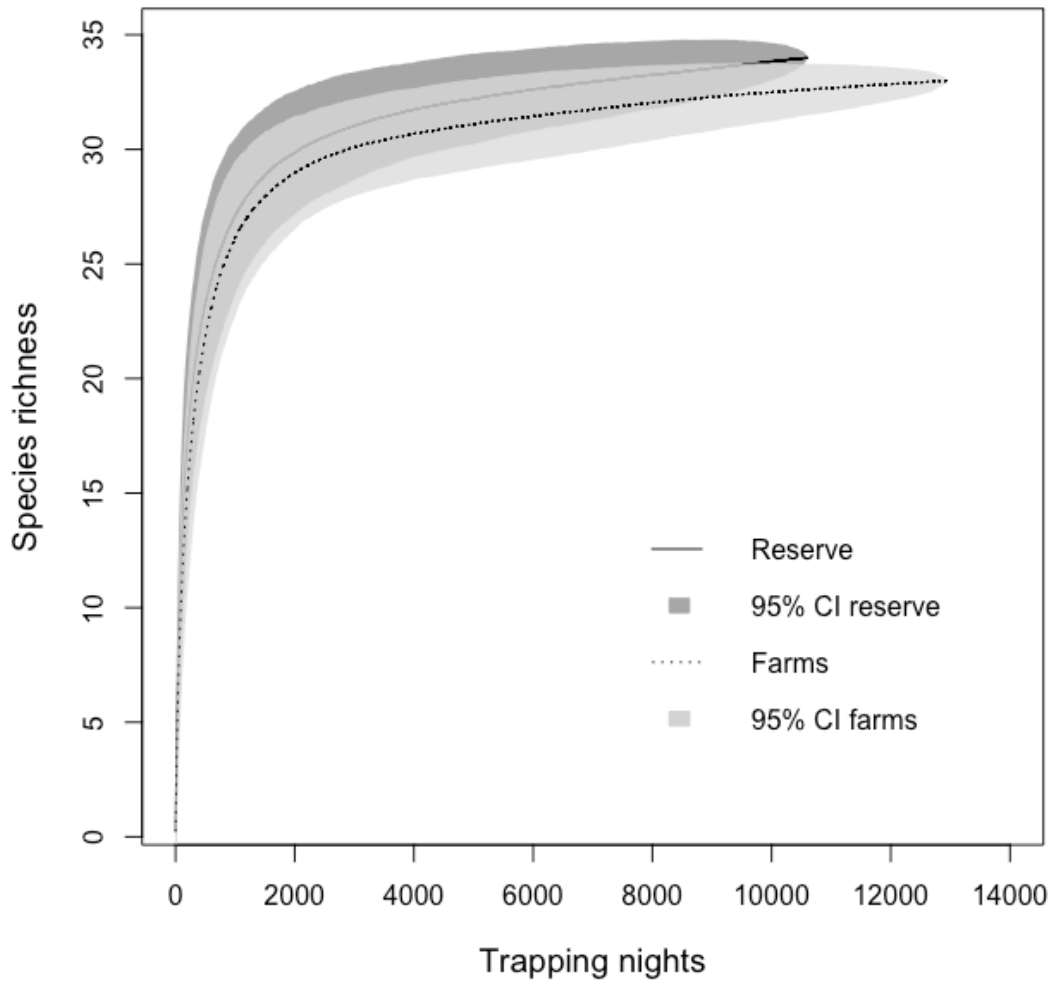


Figure 3.6. Rarefaction curves for Anysberg Nature Reserve and the farms expressed over sampling effort calculated as the number of camera trap nights. Shaded polygons represent 95% confidence intervals drawn from 1000 randomisations performed with replacement.

Table 3.10. Observed and estimated (± SE) species richness for medium- to large-sized mammal and ground bird species on farmland and in the reserve, with the total number of camera trap nights (n) conducted in each land use. Non-parametric estimators include Chao 1, first order Jackkniffe (Jack 1) and bootstrap.

Survey	N_{obs}	Chao 1	Jack1	Bootstrap	n
Farmland	33	35.00 ± 3.74	35.00 ± 1.41	33.92 ± 0.79	12 934
Reserve	34	37.00 ± 4.60	37.00 ± 1.73	35.14 ± 0.85	10 598

All non-parametric richness estimators produced species richness values higher than the observed number of species for both types of land use (Table 3.10).

The community in the reserve ($H_{reserve}$ = 2.84) was 1.4 times as diverse as the one on farmland ($H_{farmland}$ = 2.47), with an effective number of species (*ENS*) of 17 and 12 respectively. Evenness (*EH*) was high on both land use types ($EH_{farmland}$ = 0.70, $EH_{reserve}$ = 0.79) although it was higher in the reserve, showing that the individuals in this community were distributed more equitably among the species considered than on farmland.

Community composition and structure

The farmland community had slightly higher dominance (*D* = 0.27) than the reserve community (*D* = 0.21) when considering wildlife species only. However, when considering livestock, the farmland community had a far higher dominance (D = 0.79), with sheep dominating the community. The two types of land use had a Jaccard Similarity Index of S_J = 0.75, showing relatively important compositional differences, with a quarter of the species detected overall only detected in one of the land use type (D_J = 24.5%).

Seven species were only detected on farmland (Cape fox (*Vulpes chama*), yellow mongoose (*Cynictis penicillate*), meerkat, blesbok, fallow deer, Ludwig's bustard (*Neotis ludwigii*) and Kori bustard) and eight species were only detected in the reserve (leopard, water mongoose, brown hyena, honey badger (*Mellivora capensis*), Cape mountain zebra, Cape eland, bushpig (*Potamochoerus larvatus*) and Cape clawless otter). No wildlife was considered rare on farmland or in the reserve (i.e., with a detection rate less than 1/1000 trap nights; O'Brien et al., 2010).

Twenty-seven species of the 42 detected occurred on both land use types and were thus considered in the analysis of community structure. This included five carnivores, 11 herbivores, five omnivores, two insectivores and four birds. Based on the deviance criteria, the Zipf-Mandelbrot distribution and the lognormal distribution provided the best fit (i.e. lowest deviance) for observed rank abundance distributions of species resulting from farmland and the reserve respectively, thus indicating dissimilar overall community structures (Table 3.11, Figure 3.7). Additionally, the MARS for both types of land use was significantly different from 0 ($V=378$, $N=27$, $P < 0.001$), indicating that species occupied different ranks within the observed communities (Figure 3.8).

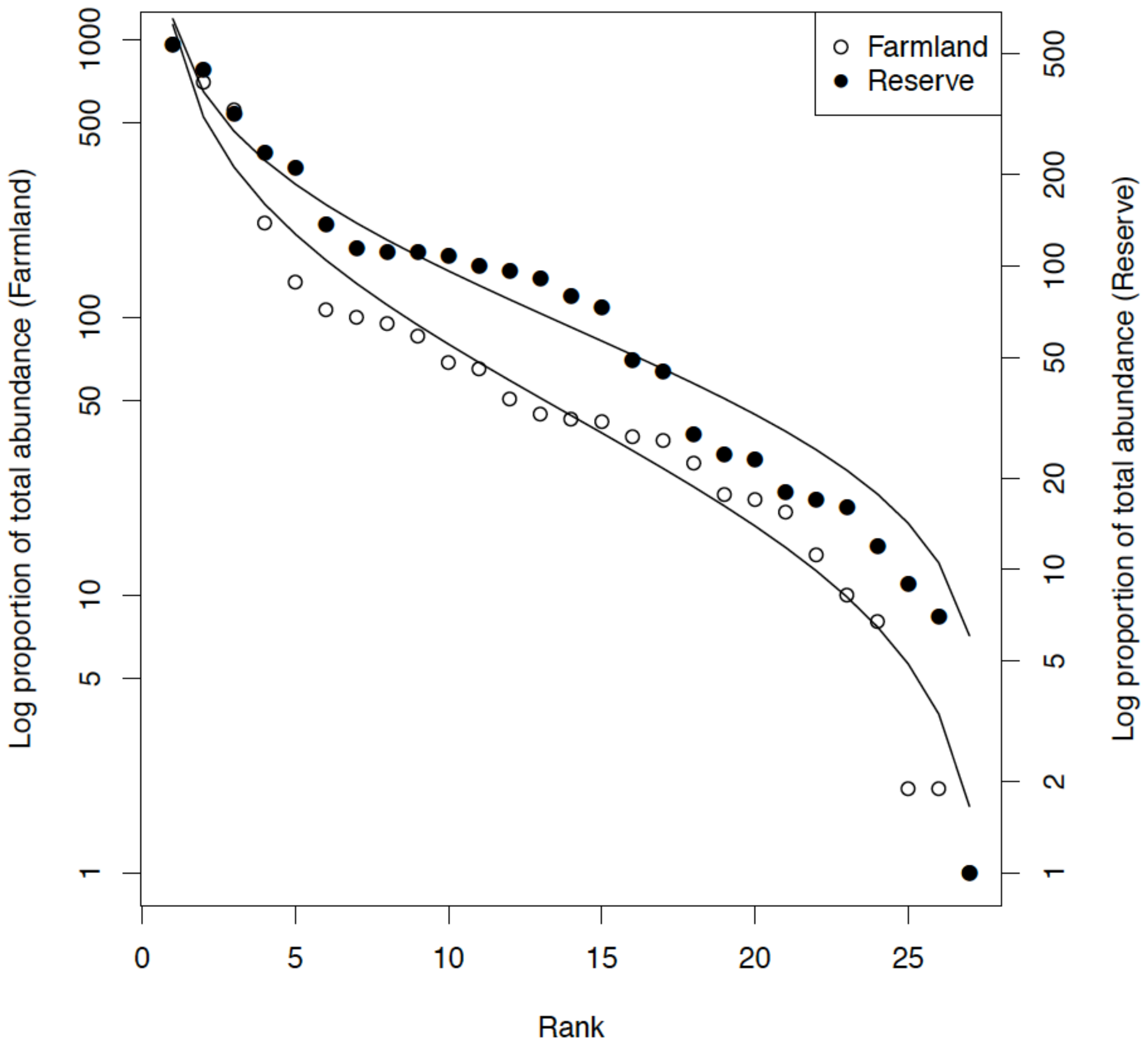


Figure 3.7. Zipf-Mandelbrot and lognormal distributions fitted to observed rank abundance distribution constructed from the survey-level RAIs of selected species on farmland and Anysberg Nature Reserve respectively.

Table 3.11. Deviance criteria for the five types of model fitted to rank abundance distributions (RAD) of medium- to large-sized wildlife species detected by camera traps during surveys on farmland and in Anysberg Nature Reserve.

Survey	Deviance criterion by model				
	Null	Pre-emption	Lognormal	Zipf	Zipf-Mandelbrot
Farmland	1331.64	534.77	264.07	420.20	192.57
Reserve	169.85	137.60	107.82	369.20	120.27

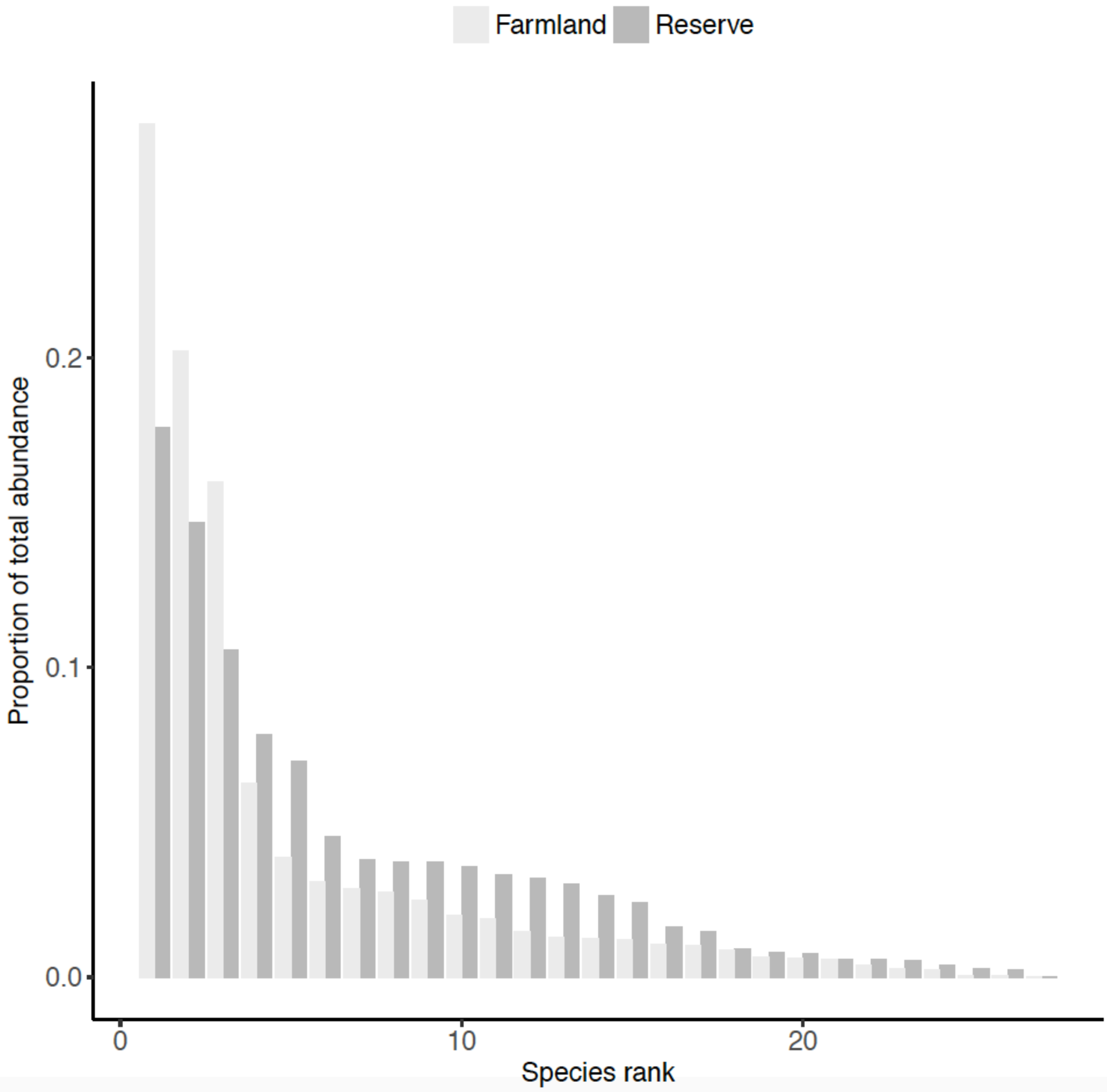


Figure 3.8. Rank abundance distributions for the farmland (pale grey) and Anysberg Nature Reserve (dark grey) for the set of 27 species considered in the comparison. Species are ranked from 1 to 27 on the x-axis according to decreasing proportion of total relative abundance, with ranks based on RAIs measured at the survey level in each type of land use.

Functional diversity

Figure 3.9 shows differences in functional structure of mammal communities between the two types of land use (A: farmland, B: reserve). Within trophic levels, functional diversity of the community (the area of two-dimensional trait space occupied by the community) and average body mass declined from the reserve to farmland. No functional groups were missing on farmland. Regarding livestock predators (black silhouettes on Fig. 3.9), I could not reject the null hypothesis that jackal (W = 11640, P = 0.999) and baboon (W = 5298.5, P = 1) RAIs were higher in the reserve than on farmland. However, I rejected the null hypothesis that caracal RAI in the reserve was greater than on farmland (W = 14748, P = 0.0046). Large carnivores were not detected on farmland. Overall on farmland, relative abundance and diversity of carnivores was lower compared to the reserve and the size distribution shifted to smaller species. The relative abundance of herbivores was more evenly distributed across the log of body mass in the reserve than on farmland where sheep dominate. Insectivores were more diverse and abundant on farmland. In general, wild mammal communities in the reserve filled the functional space more completely than on farmland (Fig. 3.9). The functional diversity of the community (the area of two-dimensional trait space occupied by the community of wildlife species) on farmland was significantly lower (FDis = 0.189) than in the reserve (FDis = 0.224) (t = 11.465, P = 0.05).

Overall, body size groups included 11 small, 14 medium and 11 large mammal species. Trophic guilds included 15 herbivores, 11 carnivores, five omnivores and five insectivores in total between the two study sites. The results of the GLM (Table 3.12) statistically confirmed the graphical results of the functional space represented in Figure 3.9. In particular, I found a significant (z = 0.998, P = 0.029) relationship between wild mammal presence and the log of their body mass in interaction with land use. Species were more likely to be present in the reserve than on farmland when their log of body mass increased (Table 3.12).

Table 3.12. Summary statistics of the binomial logistic regression for the effect of body mass (BM), trophic guild and land use (i.e. reserve, farmland) on the dependent variable medium- to large-sized mammal species presence (coded 1) / absence (coded 0) (N = 36).

Variable	Estimate	SE	Z value	P ($>|z|$)
Intercept	2.7194	1.1113	2.447	**0.0144 ***
Herbivore - carnivore	1.9172	0.9964	1.924	**0.0543 .**
Insectivore - carnivore	0.3906	0.9886	0.395	0.6928
Omnivore - carnivore	1.5388	1.2192	1.262	0.2069
Reserve	-2.0237	1.3517	-1.497	0.1343
Log (BM)	-0.8307	0.3444	-2.412	**0.0159 ***
Reserve x log (BM)	0.9985	0.4565	2.187	**0.0287 ***

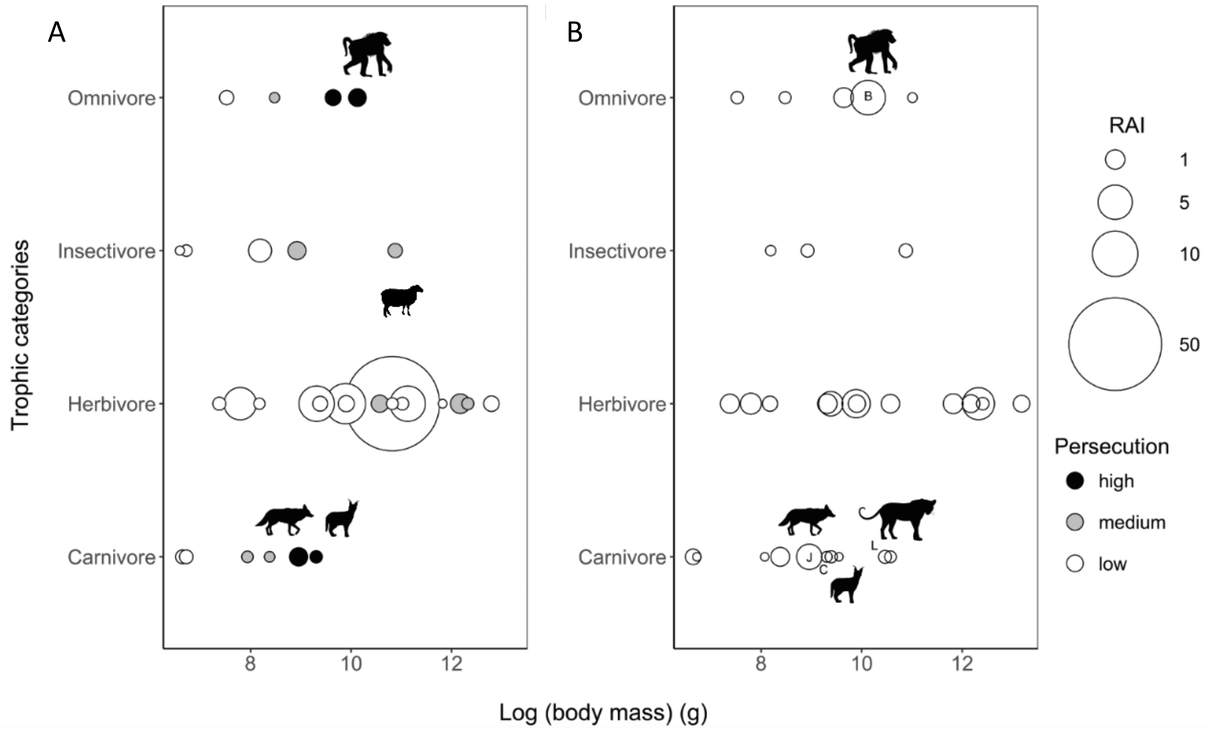


Figure 3.9. Distribution of mammal species on farmland (A) and in Anysberg Nature Reserve (B), along two functional traits: trophic category and body mass (expressed in a log scale). Each circle in the figure represents a species in functional space, with the size of the circle proportional to the relative abundance index (RAI) of that species in each land use and the colour of the circle representing the level of persecution of that species on farmland in the Karoo. The silhouettes of sheep and its main predators are represented in each graph for comparison purposes. In graph (B), letters representing predators (B: baboon, J: jackal, C: caracal, L: leopard) are situated in or close to their respective circles for more clarity.

Single-season multi-species occupancy model to estimate species richness

a) Species richness and group-level summaries

After pooling my data by 6 days, I recorded a total of 4185 detections of the species of interest for this study. Species richness was not significantly different (95% HDPI of the difference between farmland and Anysberg Nature Reserve includes zero: [-9, 6]) between farmland (95% CI = [34, 43]) and the reserve (95% CI = [35, 45]). Elevation in the reserve had the most influence on probability of use and community-level species richness of all covariates included in the model, with probability of use and richness decreasing with increasing elevation (Table 3.13, Figure 3.10). On farmland, probability of use increased with the presence of riverine habitat (Table 3.13). None of our other variables significantly impacted species richness or probability of use in either study site.

Table 3.13. Mean ($\bar{x}$) and 95% credible interval (95% CI) estimates of the community-level hyper-parameters hypothesized to influence the probability of use by 42 terrestrial vertebrate species >0.5 kg on farmland and Anysberg Nature Reserve.

	Farmland			Anysberg Nature Reserve		
Community-level hyper-parameter	$\bar{x}$	95% CI		$\bar{x}$	95% CI	
Habitat (plain)	0.46	-0.32	1.23	0.20	-0.59	1.05
Habitat (riverine)	0.70	0.07	1.33	0.01	-0.88	0.81
Elevation	0.28	-0.06	0.64	-0.49	-0.93	-0.03
MSAVI2	0.11	-0.09	0.34	0.19	-0.05	0.42
Human presence	-0.06	-0.30	0.17	0.13	-0.04	0.31
Livestock presence	0.24	-0.12	0.61			

There was a significant effect of body size on the mean site probability of use by mammals, with small species displaying a higher probability of use on farmland than in the reserve and large species displaying a higher probability of use in the reserve (95% HDPI of their difference overlaps 0 in both cases, Table 3.14, Appendix 3C Figure S3.1).

There was no significant difference in the mean site probability of use by carnivores and omnivores between the two types of land use (95% HDPI of their difference overlapped 0, Appendix 3C Figure S3.2). Conversely, there was a higher mean site probability of use by herbivores in the reserve than on farmland (95% HDPI: [-0.08, -0.02]) and a lower mean site probability of use by insectivores in the reserve (95% HDPI: [0.06, 0.30]) (Table 3.14, Appendix 3C Figure S3.2). Gelman-Rubin statistics indicated convergence for all parameters.

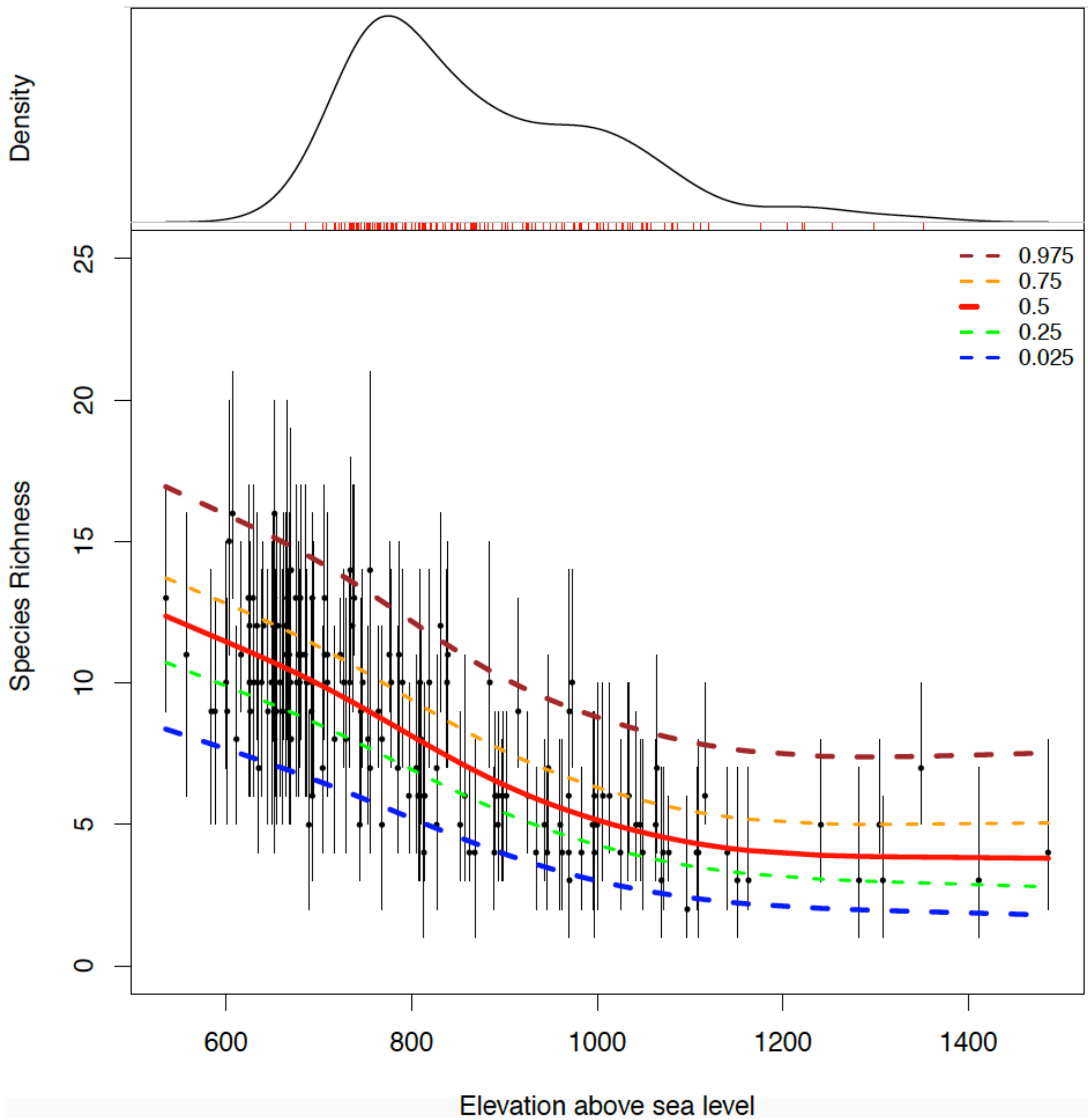


Figure 3.10. Non-parametric density estimate of the elevations in Anysberg Nature Reserve and 95% credibility interval of the community-level species richness estimate at the sample elevation values (vertical lines) within the reserve. Cubic spline fits (line plots) that relate community-level species richness to elevation for five quantiles (0.025, 0.25, 0.5, 0.75 and 0.975) of community-level species richness are displayed.

Table 3.14. Posterior mean ($\bar{x}$) site occupancy of four trophic guilds (carnivores, herbivores, omnivores and insectivores) and three body size groups (0.5 kg <small ≤5 kg, 5 <medium ≤20 kg and large >20 kg) comprising the 36 species of terrestrial mammals detected on farmland and in Anysberg Nature Reserve by the camera traps in the semi-arid region of the Karoo. The last column represents the 95% HDPI of the difference in the mean occupancy between the farmland and the reserve for each trophic guild and body size group.

		Farmland				Anysberg Nature Reserve				Difference
		$\bar{x}$	2.5%	50%	97.5%	$\bar{x}$	2.5%	50%	97.5%	
Trophic guild	Carnivore	0.25	0.19	0.25	0.31	0.25	0.19	0.25	0.32	[-0.09, 0.09]
	Herbivore	0.18	0.17	0.18	0.20	0.23	0.21	0.23	0.26	[-0.08, -0.02]
	Omnivore	0.28	0.21	0.21	0.41	0.35	0.26	0.34	0.46	[-0.20, 0.09]
	Insectivore	0.33	0.26	0.32	0.44	0.16	0.10	0.16	0.24	[0.06, 0.30]
Body size	Small	0.32	0.26	0.32	0.40	0.17	0.12	0.16	0.23	[0.06, 0.24]
	Medium	0.38	0.33	0.38	0.45	0.31	0.27	0.31	0.36	[-0.01, 0.14]
	Large	0.13	0.09	0.13	0.18	0.34	0.27	0.34	0.43	[-0.31, -0.12]

b) Species-level summaries

The mean probability of use across all species and camera sites was 0.28 (95% CI = [0.25, 0.32]) on farmland and 0.26 (95% CI = [0.22, 0.30]) in the reserve, with 81.8% and 91.2% of species having a probability of use <0.5 respectively. The 95% HDPI of the difference in the mean probabilities of use between the farmland and the reserve overlapped zero [-0.02, 0.08], showing there was no significant difference between the two types of land use. Mean probabilities of use were very heterogeneous among species, ranging from 0.02 for bat-eared fox to 0.75 for baboon in the reserve (Figure 3.11A) and from 0.02 for Smith's red rock rabbit (*Pronolagus rupestris*) and for oryx, to 0.77 for steenbok on farmland (Figure 3.11B). The mean probability of use by caracal was significantly higher on farmland ($\bar{x}$ = 0.48 ± 0.22) than in the reserve ($\bar{x}$ = 0.08 ± 0.11; 95% HDPI of the difference = [0.28, 0.52]). Conversely, there was no significant difference in the mean probability of use by jackal between farmland ($\bar{x}$ = 0.36 ± 0.23) and the reserve ($\bar{x}$ = 0.40 ± 0.34; 95% HDPI: [-0.19, 0.12]).

Mean species detection probabilities showed high levels of heterogeneity in both types of land use, ranging from r = 0.02 for the brown hyena, the honey badger and the bushpig to r = 0.26 for the rock hyrax in the reserve (Figure 3.11A), and from r = 0.01 for the African wildcat (*Felis sylvestris*) to r = 0.43 for the oryx on farmland (Figure 3.11B). Detailed species-specific probabilities of use and detection probabilities in each type of land use are presented in Appendix 3B.

The probability of use of the 42 species photographed was not significantly impacted by human disturbance (i.e. humans, dogs and vehicles trapping rate; Appendix 3B) on either land use. On farmland, livestock trapping rate had a strong positive effect (i.e. 95% CI did not overlap zero) on three wildlife species (i.e., grey rhebok, oryx and bat-eared fox, Appendix 3B). MSAVI2 only had an effect on the probability of use by species in the reserve (three species positively impacted; Figure 3.13). Elevation affected seven species positively and one negatively on farmland (Figure 3.12) and strongly affected probability of use in the reserve (11 species negatively and three positively, Figure 3.13).

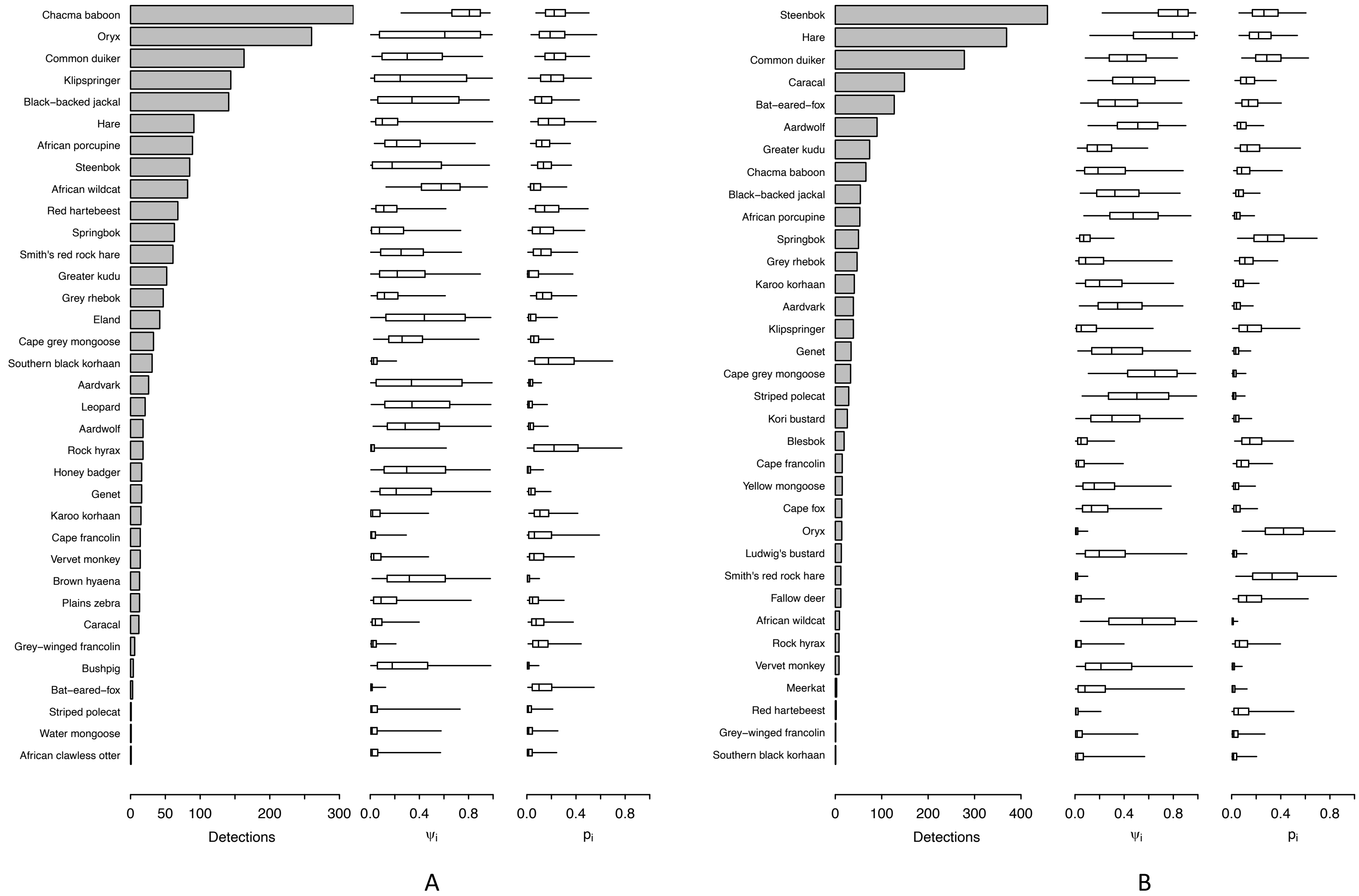


Figure 3.11. Distribution of the total number of detections per species for the 6-day pooled data, the occupancy (Ψ_i) and detection probabilities (p_i) in Anysberg Nature Reserve (A) and on farmland (B). Occupancy and detection probabilities were estimated under a hierarchical multi-species occupancy model and values shown are the posterior means across all camera trap sites in Anysberg Nature Reserve (A), and on farmland (B).

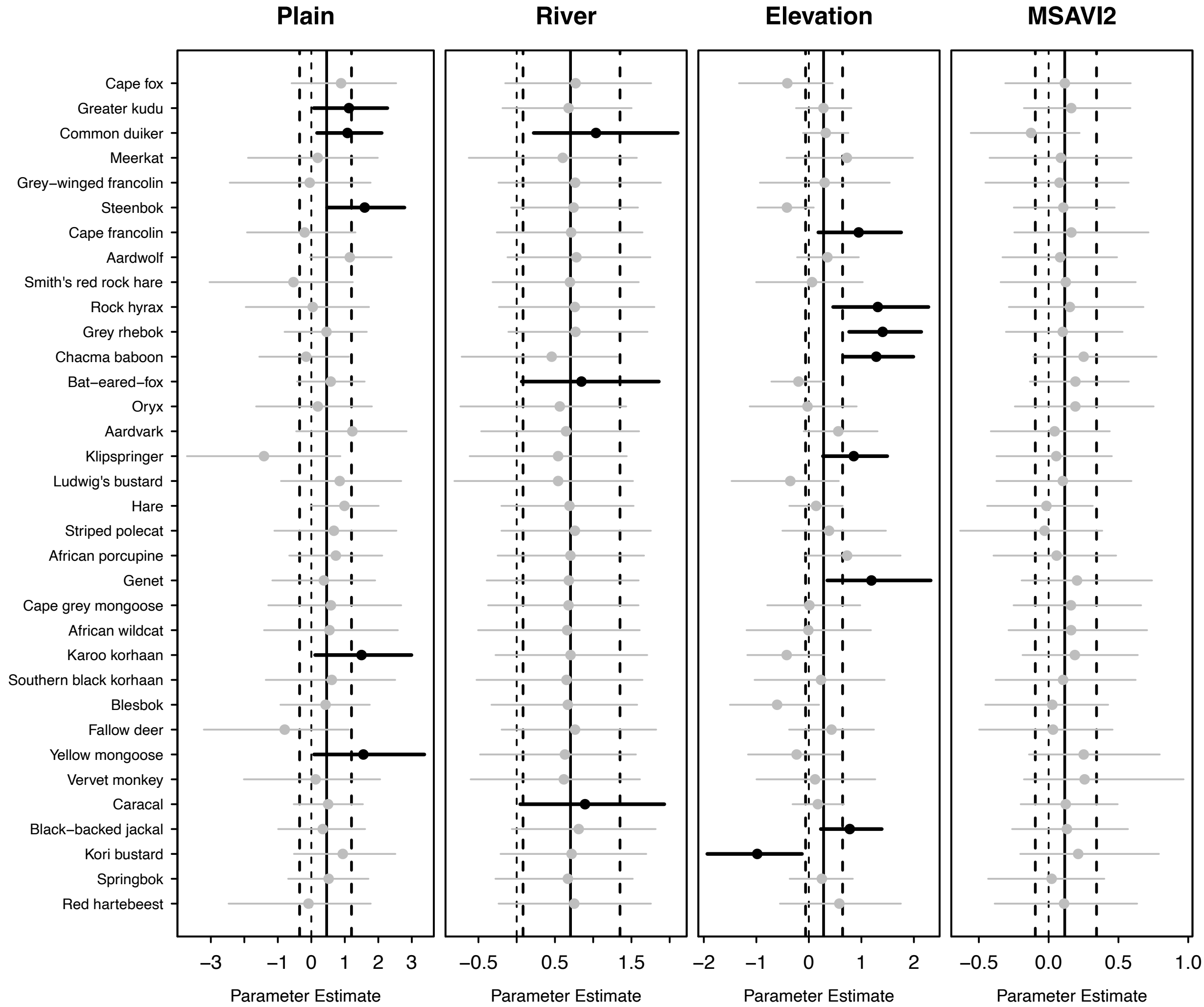


Figure 3.12. Caterpillar plots showing the standardized beta coefficients and 95% credible intervals for the influence of habitat type (plain, riverine), elevation and MSAVI2 on the probability each species used farmland between September 2012 and March 2014. Confidence intervals in bold do not overlap 0. The thick dashed lines indicate the 95% CI for the mean community response to each variable.

Regarding potential livestock predators, caracal probability of use was higher in riverine habitat on farmland (Figure 3.12) but none of my chosen environmental covariates significantly impacted their occupancy in the reserve (Figure 3.13). Jackals used plains and areas with higher MSAVI2 values in the reserve (Figure 3.13). They also favoured higher elevations on farmland, while choosing lower grounds in the reserve, similarly to baboons (Figure 3.13).

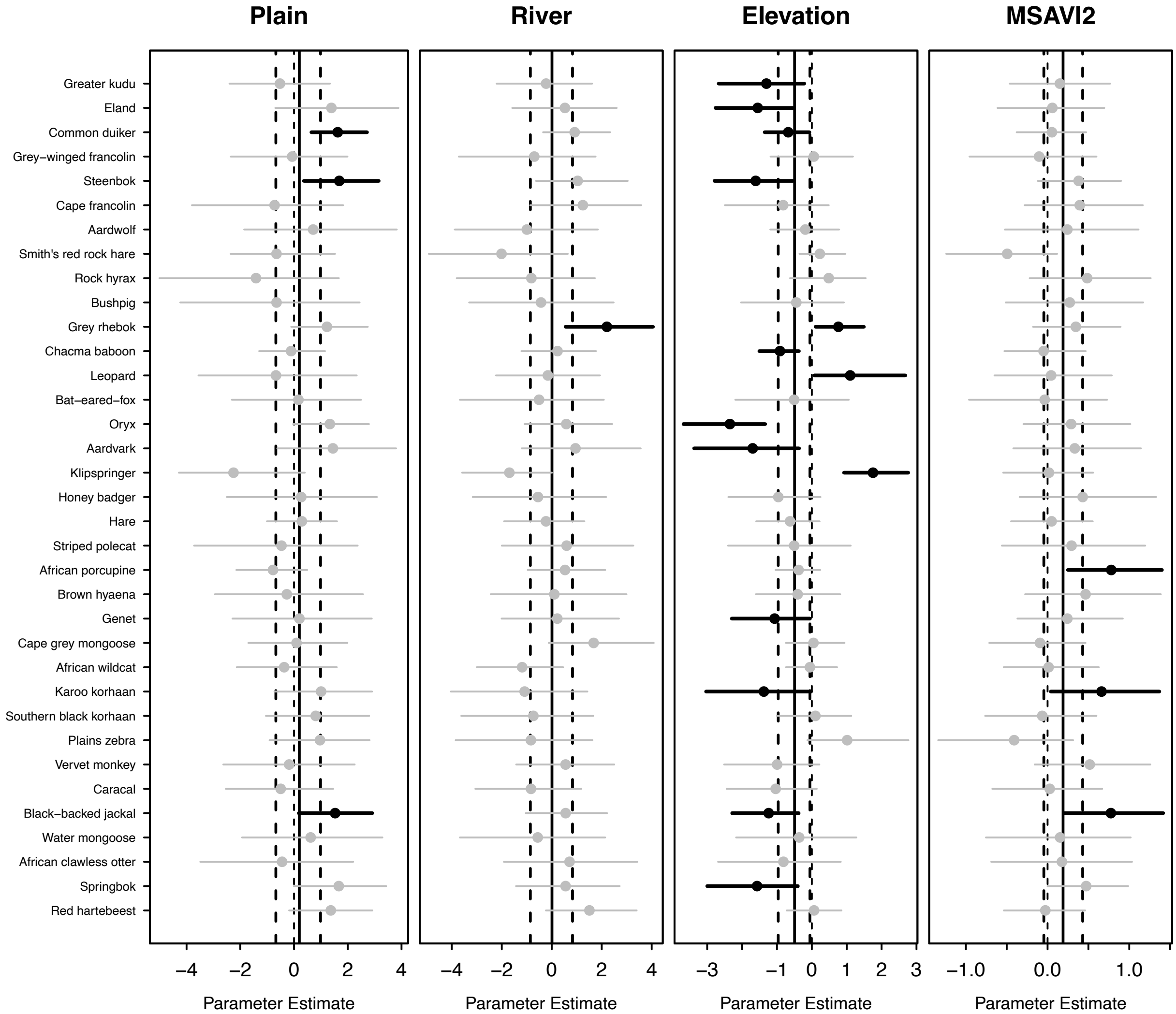


Figure 3.13. Caterpillar plots showing the standardized beta coefficients and 95% credible intervals for the influence of habitat type (plain, riverine), elevation and MSAVI2 on the probability each species used Anysberg Nature Reserve between September 2013 and May 2014. Confidence intervals in bold do not overlap 0. The thick dashed lines indicate the 95% CI for the mean community response to each variable.

Out of 42 species, the detection of 12 species was strongly (i.e. 95% CI did not include zero) related to the presence of an animal trail or a road (three positively and nine negatively) in the reserve (Figure 3.15, Appendix 3B). By contrast, this covariate had no significant impact on the detection of species on farmland (Figure 3.14, Appendix 3B). On farmland, the detection of seven species was strongly and positively related to general habitat types (Figure 3.14, Appendix 3B) whereas the detection of nine species was positively affected by general habitat type in the reserve (two by riverine, five by plain and two by riverine and plain habitats) (Figure 3.15, Appendix 3B).

Regarding potential livestock predators, none of my chosen covariates significantly impacted caracal detection probability on farmland (Figure 3.14) or in the reserve (Figure 3.15). Jackals had higher detection probabilities on plains and off-trail in the reserve (Figure 3.15), while baboons had higher detection probabilities in riverine habitat both on farmland (Figure 3.14) and in the reserve (Figure 3.15).

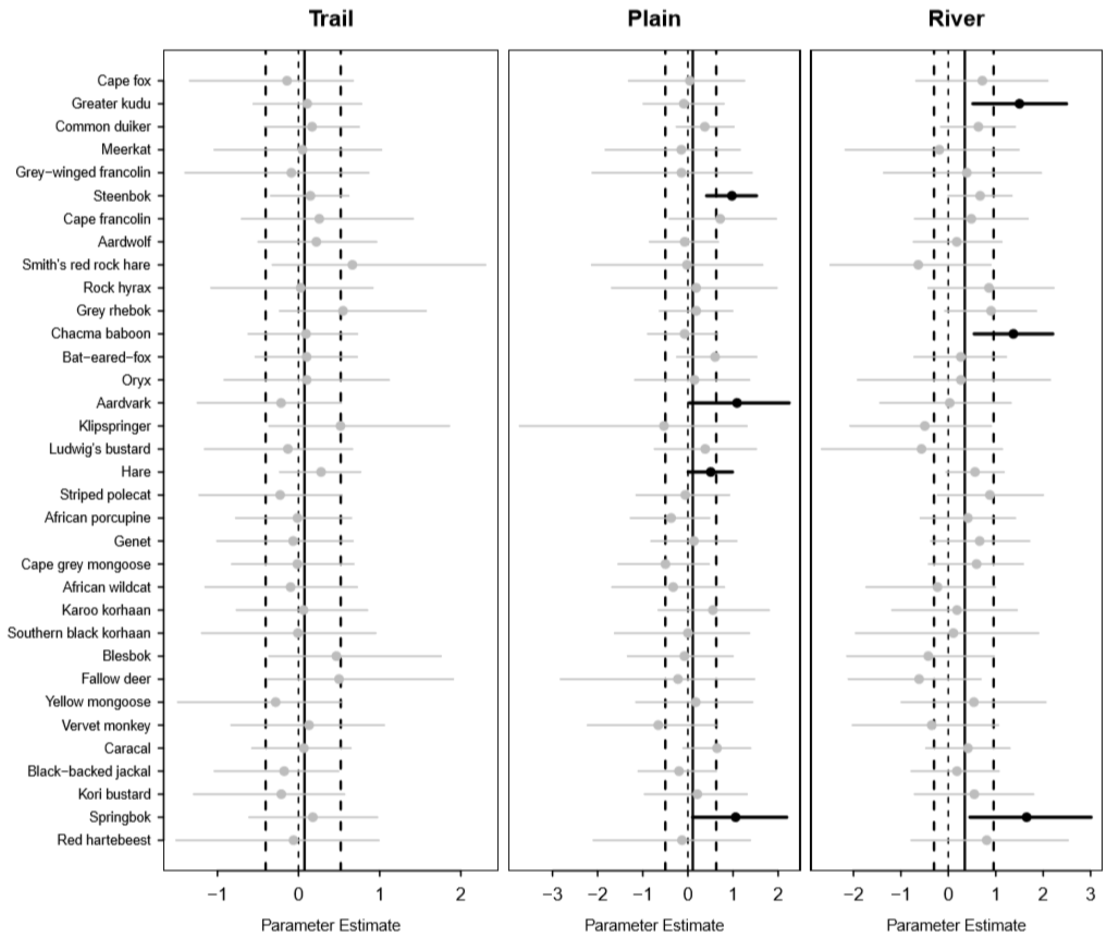


Figure 3.14. Caterpillar plots showing the standardized beta coefficients and 95% credible intervals for the influence of trail/road and habitat type (plain, riverine), on the probability of detection for each species on farmland between September 2012 and March 2014. Confidence intervals in bold do not overlap 0. The thick dashed lines indicate the 95% CI for the mean community response to each variable.

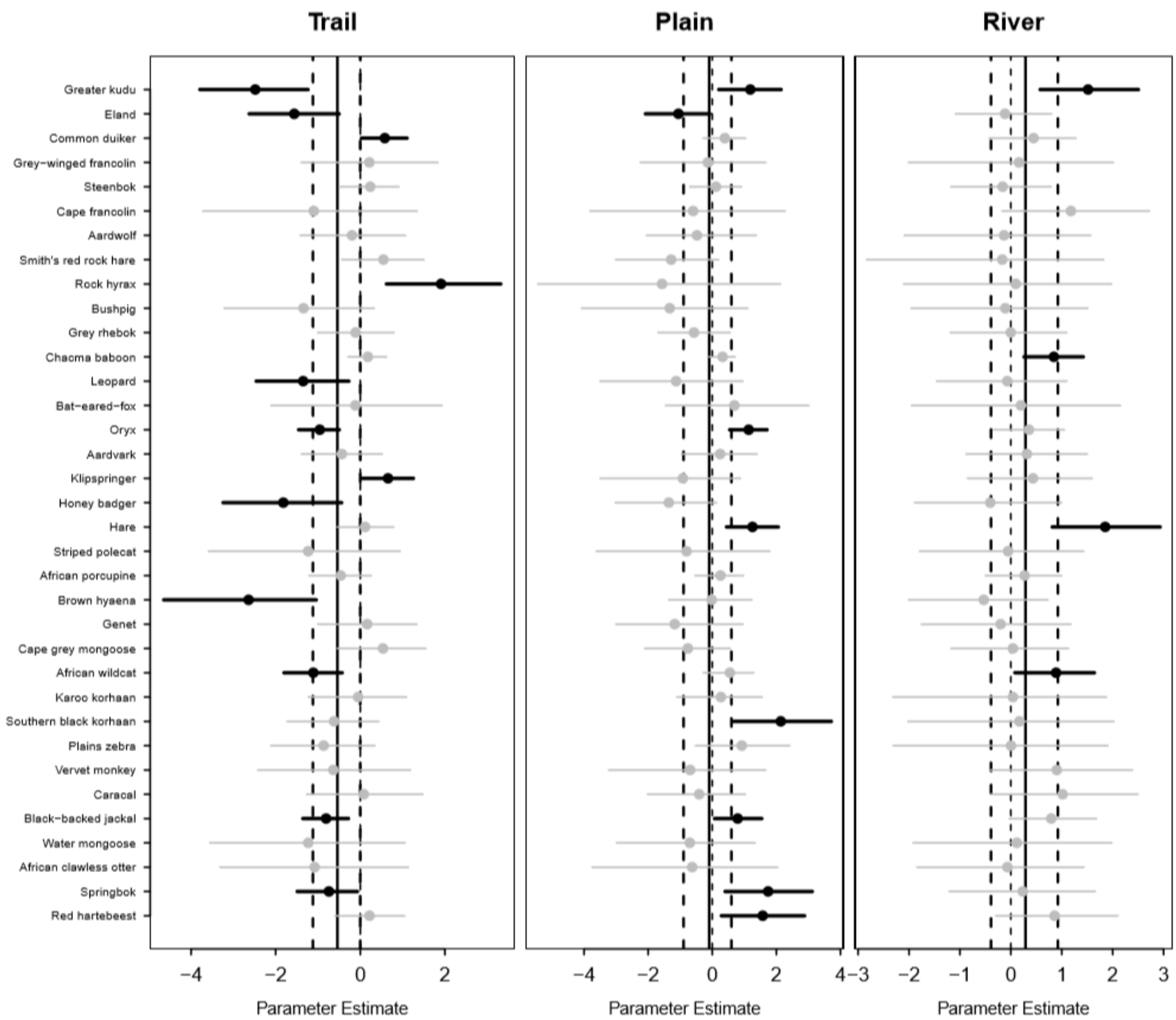


Figure 3.15. Caterpillar plots showing the standardized beta coefficients and 95% credible intervals for the influence of trail/road and habitat type (plain, riverine), on the probability of detection for each species in Anysberg Nature Reserve between September 2012 and March 2014. Confidence intervals in bold do not overlap 0. The thick dashed lines indicate the 95% CI for the mean community response to each variable.

Discussion

My results only partly supported my main hypotheses that wildlife species richness, community diversity, composition and structure, as well as species distribution and probability of use would vary between the two types of land use. The hierarchical multi-species occupancy model was able to estimate species richness from a large and unknown pool of species for each type of land use and gave similar results to the rarefaction analyses, namely, that species richness was not significantly different between farmland and the reserve.

Impact of land use and covariates on species richness and community occupancy

My results do not support my first and fourth hypotheses (H1, H4), as I found that there was no significant difference in species richness and community mean probability of use (i.e. occupancy) between farmland and the reserve. This result is similar to what some researchers have found in other African rangelands, where small-livestock farming was shown to be compatible with wildlife presence (Kiffner et al., 2015; Kinnaird and O'Brien, 2012; Msuha et al., 2012; Rannestad et al., 2006). Kiffner et al. (2015) and Msuha et al. (2012) evoked the intermediate disturbance hypothesis to explain their findings (i.e. diversity is higher when levels of disturbances are intermediate in terms of frequency and intensity (Connell, 1978; Huston, 1979)), a theory that has recently been challenged (Fox, 2013). Mann (2014) found species richness to be similar between livestock farms, game farms and PAs in the Western Cape Province, which he attributed to the minimal impact of sparsely stocked cattle grazing on wildlife.

The Karoo ecosystem has had a long association with both medium- and large-sized indigenous herbivores, creating intermediate levels of disturbance (Dean and Milton, 1999). It may consequently be more resilient to extensive small-livestock grazing impacts than other ecosystems (Todd, 2006), partly explaining why species richness is not significantly different between the two types of land use. It has even been suggested that rangelands might be an optimal habitat for some species that benefit from the routine grazing by sheep at an intermediate intensity (Arsenault and Owen-Smith, 2002; Williams et al., 2018). Thus for example, Blaum et al. (2007) found that yellow mongoose, bat-eared fox and small-spotted genet (*Genetta genetta*) in the Kalahari reached maximum abundance when shrub encroachment was constrained (10-18%) by intermediate livestock grazing intensity. Similarly, Kurberg (2005) found that medium-intensity grazing by sheep favoured bat-eared fox abundance. Both authors justify their results by invoking the resource availability hypothesis, with an increase in shrub cover resulting in a decrease in the availability of preferred prey (e.g. beetles, grasshoppers). Both of these studies are supported by the findings presented in this chapter, with bat-eared fox, yellow mongoose, genets and Cape fox (which distributional ranges overlap with the reserve) all having higher RAIs and probability of use on farmland, characterized by medium intensity livestock grazing and different types of rotational graze-rest systems (Saayman et al., 2016). Therefore, it is not too surprising that livestock presence had a positive influence on the probability of use by grey rhebok, oryx and bat-eared fox in my study site, and did not significantly impact other individual species negatively (Appendix 3B).

Another possible explanation is that the different biomes in which the farmland and the PA are situated might have had a more significant effect on small carnivores RAIs and probability of use than what I was able to show with my study design. For example, the vegetation forming the biome in the PA might not be optimal for small carnivores compared to farmland.

In the reserve, both species richness and mean probability of occupancy were greater at lower elevation (Table 3.13 and Figure 3.10). Despite biodiversity loss being associated with agriculture, the distribution of extant terrestrial plants and animals suggests that the greatest numbers of species are found at lower elevations, on more productive soils, often on privately owned land (Gallo et al., 2009), a pattern my findings seem to be in accordance with. My results therefore highlight the importance of low-lying areas in maintaining biodiversity levels in drylands. On farmland, none of the environmental covariates significantly affected community species richness but mean occupancy probability was greater in riverine habitat (Table 3.13). In these dry landscapes, narrow strips of riverine vegetation represent distinctive habitat features associated with water sources and higher standing biomass. Riverine vegetation is vital for the wildlife in arid areas, providing both food and a refuge from temperature extremes and predators.

A strong presence of human activities has been shown to be detrimental to many wild species (Blom et al., 2004; Caro, 1999). Therefore, the weak to no effect of human disturbance on community-level species richness and occupancy in both of my study sites was unexpected, especially for farmland and contrary to prediction P7. Rich et al. (2016) also reported a weak effect of human/vehicle on wildlife in a PA in Botswana. The authors explain their results by the fact that tourism activities seek areas of high wildlife density and are generally restricted to daylight hours, and therefore have minimal impact on nocturnal species. The PA used in this study, Anysberg Nature Reserve, does not host high densities of charismatic large mammals and hence tourist numbers are low. Human presence is even lower on farmland, which I suggest explains the observed null effect on both species richness and probability of use at the community level in both types of land use. In addition, roaming domestic dogs and cats are extremely rare at my study sites and dogs were only rarely photographed and then with farmers. The hierarchical multi-species occupancy model (Table 3.2) and all the non-parametric richness estimators (Table 3.10) produced higher species richness than the observed number of wildlife species for both types of land use. Based on discussions during interviews with farmers (see Chapter 6), two species that are known to occur on the farms I surveyed were not detected: the water mongoose and the Cape clawless otter, which corresponds to the predicted values for species richness of both the Chao 1 and the first order Jackknife estimators. Both species are semi-aquatic carnivores known to favour riverbeds with permanent water, boulders and reed-beds (Somers and Nel, 2004), which are rare habitats in my study site. These two “missing” marginally distributed species would have needed a far greater survey effort to be detected with the random 2-km grid I used. Similarly, three species – the yellow mongoose, the African striped polecat and the Ludwig’s bustard – are known to occur in Anysberg Nature Reserve based on its species list and discussions with the manager and field rangers, but were not detected in my surveys. Yellow mongooses were also not detected in other studies in drylands where they were supposed to occur, maybe due to the thicker vegetation (Mann, 2014; Stein et al., 2008).

Species richness studies within tropical forests in South America have reached asymptotes between 500 and 1000 camera trap days (Tobler et al., 2008), whereas those within grassland and woodland habitats required 400 and 870 camera days respectively (Roberts, 2011; Silveira et al., 2003). Studies in south-central Tanzania (Rovero et al., 2014) and the Cape Floristic Kingdom of South Africa (Colyn et al., 2018) showed that a minimum of 1000 camera days would be necessary to detect most or all of the species present at a site. In my study, even 10000 trap nights were not sufficient to reach a complete asymptote for species richness (Figure 3.6). This result was expected for drylands where species are often wide ranging, occur at low densities and might be difficult to detect because of their elusiveness, especially on farmland where they are hunted. This highlights the benefit of using Bayesian multi-species modelling in arid environments, because the detection of all species informs the detection of an individual species and allows estimates for rare and cryptic species that would otherwise not be possible.

Community composition and structure

Predictions (P2) and (P3) were supported, with diversity being lower on farmland and dominance higher than in the reserve. A quarter of all species detected were unique to either site. Seven species were only detected on farmland, including Kori bustards (near threatened) and Ludwig’s bustards (endangered) (Shaw et al., 2018). In the case of bustards though, it was not possible to disentangle whether the driver of their non-detection in the PA was land-use or seasonal differences in their use of biomes. Over half of Ludwig’s bustards’ global population is thought to occur in the Karoo. My results suggest however that neither the PA or the farmland constantly provides all the resources and habitats required for all species to persist, as some species are doing badly on farmland and others in the reserve. Consequently, relying solely on PAs in this region of the Karoo for the protection of medium- to large-sized mammal and ground bird diversity is unlikely to be successful and some species will need to be conserved on private farmland where the biome is also different than that of most PA in the region. Owen-Smith et al. (2017) reached a similar conclusion by revealing that PAs in Kwazulu-Natal may not be able to retain all the species that previously occurred within their boundaries, in particular smaller ungulates with locally patchy distributions.

Community dissimilarity (D_J) between the two types of land use was primarily due to the detection/non-detection of large carnivore (e.g. leopard) and large herbivore species (e.g. eland), habitat-specialists (e.g. water mongoose), species at the limit of their distributional range (e.g. meerkat) and species introduced by humans (e.g. fallow deer) (Figures 3.7 and 3.8). Leopards were never detected on small-livestock farms, as found by Msuha et al. (2012) and in accordance with the results of Chapter 4. The non-detection of large carnivores on farmland was predicted (P5) given their historical and continued lethal control throughout the livestock farming regions of the Western Cape (van Sittert, 2016, 1998). Although most of the differences in community composition and structure are likely to be attributed to the difference in land use that we observe between the reserve and the farmland, land use might not be the only variable driving species presence on the two sites. Differences in topography, biomes, habitat types, grazing intensity and rainfall amount (see Chapter 2) could also have played a role and influenced species occurrence and detection rates at both sites. However, a recent study covering 120 000 km^2 in the Karoo showed that neither topography (terrain roughness), average annual precipitation nor NDVI were significant predictors of species richness at the landscape level in the region. Rather, longitude (that is negligible between my two study sites) emerged as the best predictor to explain the variation in the effective number of species in the area (Woodgate et al., 2018). I would thus argue that the difference in community composition and structure observed between our two sites is likely to be driven mostly by land use, even if other variables such as biome may also play a role.

Functional diversity

Similar to the findings of Kiffner et al. (2015) in the Tarangire-Manyara ecosystem in Tanzania, all functional trophic guilds except top-order carnivores were still present on farmland. However, the relative abundance, body mass and diversity of carnivores were all lower than in the reserve (Figure 3.9), and within trophic levels, body mass was lower on farmland (Table

3.12). Kauffman et al. (2007a) also found large carnivores to be absent from the Namibian farmlands they studied. Body size is a functional trait that might predispose some species to respond differentially to a change in land use as it is positively correlated with home range and density (Lindstedt et al., 1986). My fifth prediction (P5) was supported, with large mammal occupancy being more adversely affected by small-livestock farming than medium-sized mammal occupancy (Tables 3.12), a result in agreement with other African studies (Kinnaird and O'Brien, 2012; Rich et al., 2016). In addition, trophic guild (Appendix 3C Figure S3.2) was an important life-history trait affecting mammal occupancy in the two study sites (in agreement with my sixth hypothesis (H6)), with the occupancy probability of omnivores and insectivores being unaffected or positively affected by farmland compared to the reserve, results that were also partly found by Rich et al., (2016) and Van der Weyde et al. (2018).

Finally, (P6) was only partially supported in spite of sustained control efforts to reduce livestock predators on farmland (Nattrass et al., 2017, see Chapter 6). Only jackal and baboon presented lower RAIs on farmland compared to the PA, but then, the probability of use by jackal was not significantly different between the two types of land use. This difference in results is likely due to the lower detection probability of jackal on farmland (0.07) compared to the PA (0.15), resulting in the apparent lower RAI of jackal on farmland. Caracal had both a higher RAI and probability of use on farmland than in the reserve. A similar result was obtained for fenced ranches relative to a national park in Kenya (Kinnaird and O'Brien, 2012) and for livestock farms relative to PAs in the Klein Karoo (Mann, 2014). In small-livestock farms and many other modified landscapes, the removal of apex carnivores may have facilitated increased mesocarnivore abundance (Ritchie and Johnson, 2009) and it is possible that caracals are more sensitive than jackals to the presence of large carnivores found in the reserve (such as leopards).

Effects of covariates on species-level detection and occupancy probabilities

In accordance with my fifth hypothesis (H5), the impacts of environmental factors varied between species, which was expected given the diversity of species considered in this study, and they also varied with land use (Figures 3.12 and 3.13). Interestingly, probability of use by jackal increased with elevation on farmland but decreased with elevation in the reserve. This result corresponds to farmers' perceptions obtained during interviews (see Chapter 6) that jackals choose high grounds to look for sheep and watch their surroundings. The GPS collar data (some of which is presented in Chapter 5) also show that jackals often rest on high grounds in farmland. In the reserve, jackals might favour lower grounds because leopards have a higher probability of use at higher elevations (Figure 3.14).

Interestingly and contrary to the literature for tropical forest and savannah ecosystems (e.g. Cusack et al., 2015; Harmsen et al., 2010), the presence of trail did not have a significant influence on the detection of species in farmland. In the reserve, I showed that many species had a higher probability of detection off-trail, including carnivores such as leopard, brown hyena, honey badger, jackal and African wildcat. In the reserve, the presence of apex predators may lead smaller predators such as jackals to avoid roads/trails, as was shown in other studies (Hayward and Marlow, 2014; Mann et al., 2015). This finding contradicts results found in more densely vegetated areas (Harmsen et al., 2010; Tobler et al., 2015) and suggests that the generally open habitat in the semi-arid Karoo allows predators to move freely off paths where prey species generally have a higher probability of occurrence (Mann et al., 2015). This finding stresses the importance of not restricting camera placement to trails and roads within drylands, as is the norm in other more mesic ecosystems, densely vegetated areas (e.g. Kauffman et al., 2007; Rich et al., 2016; Van der Weyde et al., 2018). This recommendation holds even if there is to be a focus on single carnivore species or guild within a dryland ecosystem.

Conclusion

My results highlight the importance of low-lying unprotected rangeland for complementing PAs in maintaining medium to large terrestrial vertebrate biodiversity in the extensive Karoo drylands. They also support regional conservation initiatives that aim at including private landowners in the conservation process through stewardship programmes (CapeNature, 2016). However, in the Karoo like in many other livestock regions of the world, livestock owners have few incentives to keep wildlife on their properties (Kinnaird and O'Brien, 2012). Rather, farmers complain that they bear the full cost of livestock depredation and receive neither compensation nor assistance in managing predators from either provincial or national wildlife authorities. Consequently, there has been a devaluation of wildlife in general on farmland and of carnivores in particular, which are often seen as pests that need eradication rather than integral components of functional ecosystems. Despite these concerns and widespread lethal management practices (see Chapter 6), wildlife persists on farmland. As most PAs are rarely connected, it is crucial to recognise that conservation cannot be land-use specific and that effective protection of all species will need to occur in a multi-use landscape, integrating areas used by people with those set aside specifically for wildlife (Glennon and Didier, 2010).

APPENDIX 3A
SINGLE-SEASON MULTI-SPECIES OCCUPANCY MODELS AND MODEL SELECTION RESULTS USED FOR THE ESTIMATION OF SPECIES RICHNESS ON FARMLAND AND IN ANYSBERG NATURE RESERVE

Model 1: The model includes an intercept term, a species-specific random effect, as well as site-specific covariates as fixed effects.

logit $(\psi_{i,j}) = \bar{\beta} + u_i + \sum_{k=1} \beta_{i,k} \cdot x_{j,k}$ Occupancy

logit $(p_{i,j}) = \bar{\alpha} + v_i + \sum_{k=1} \alpha_{i,k} \cdot w_{j,k}$ Detection

Model 2: The model that was selected for my study, based on the DIC (Table S1) and that includes an intercept term, a species- and a site-specific random effect, as well as covariates as fixed effects.

logit $(\psi_{i,j}) = \bar{\beta} + u_i + \beta_j + \sum_{k=1} \beta_{i,k} \cdot x_{j,k}$ Occupancy

logit $(p_{i,j}) = \bar{\alpha} + v_i + \alpha_j + \sum_{k=1} \alpha_{i,k} \cdot w_{j,k}$ Detection

Model 3: The model includes an intercept term as well as a site-specific random effect.

logit $(\psi_{i,j}) = \bar{\beta} + u_i$ Occupancy

logit $(p_{i,j}) = \bar{\alpha} + v_i$ Detection

Model 4: The model includes an intercept term, a species- and a site-specific random effect.

logit $(\psi_{i,j}) = \bar{\beta} + u_i + \beta_j$ Occupancy

logit $(p_{i,j}) = \bar{\alpha} + v_i + \alpha_j$ Detection

Table S3.1. Bayesian model selection conducted using the deviance information criterion (DIC) for the 4 models fitted for each type of land use. Model 2 exhibited the smallest DIC for each type of land use and was therefore chosen to conduct the multi-species occupancy analyses.

	DIC farmland	DIC protected area
Model 1	7028.624	6206.575
Model 2	**6585.518**	**6001.347**
Model 3	7318.710	6968.389
Model 4	6814.238	6731.367

APPENDIX 3B

SPECIES-SPECIFIC OCCUPANCY AND DETECTION PROBABILITIES AND COVARIATE EFFECTS FOR EACH TYPE OF LAND USE

Supplementary data can be found online in Appendix C in the form of an Excel sheet at: https://doi.org/10.1016/j.biocon.2018.05.013.

APPENDIX 3C

DIFFERENCES IN OCCUPANCY PROBABILITIES FOR THE DIFFERENT GROUPS OF BODY SIZE AND TROPHIC GUILDS BETWEEN FARMLAND AND ANYSBERG NATURE RESERVE

Figure S3.1. Differences in mean site occupancy probabilities for different body size groups (i.e. small, medium and large) between farmland and the reserve. The posterior densities not overlapping zero show a significant difference in their mean site occupancy probability.

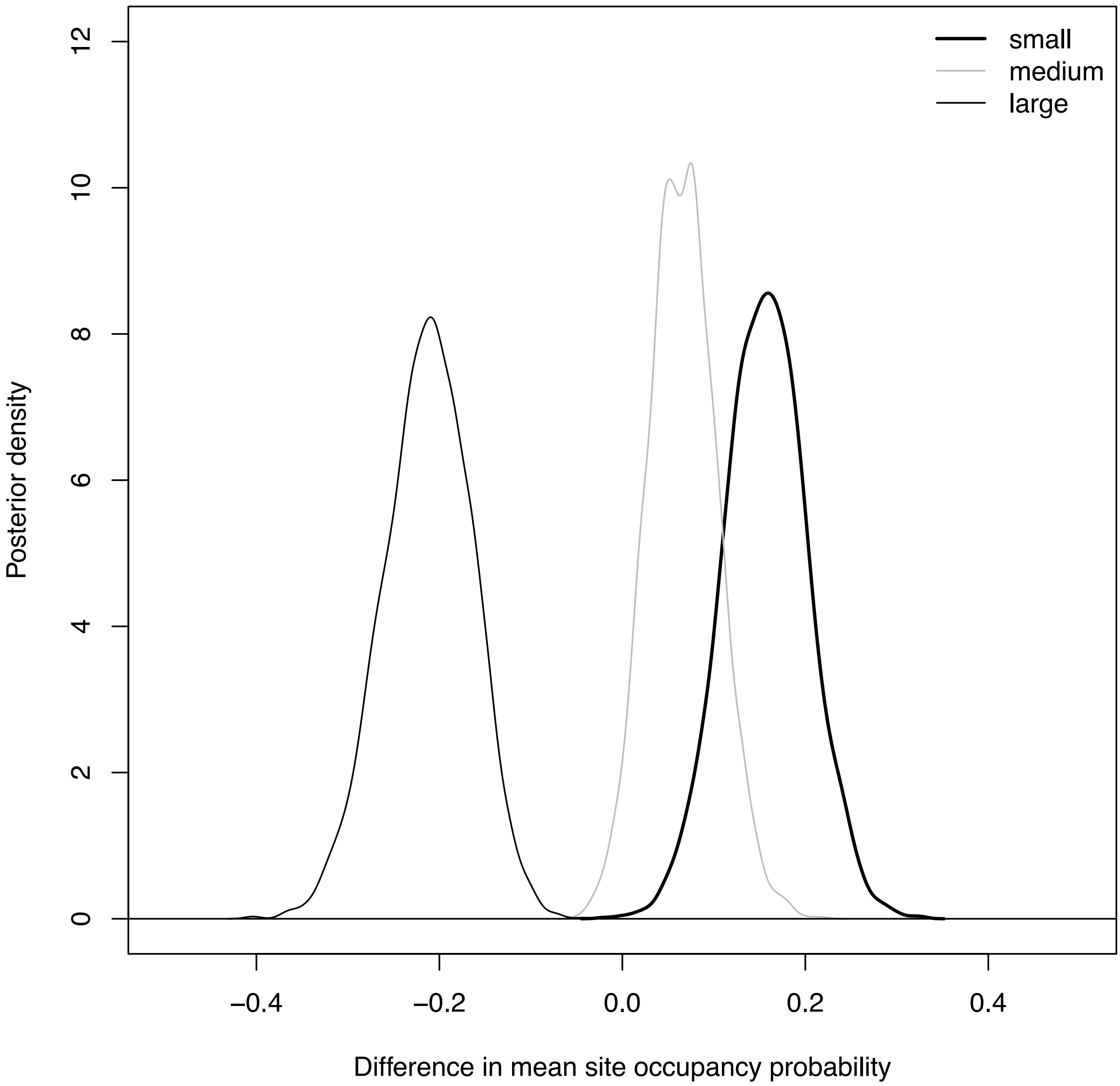
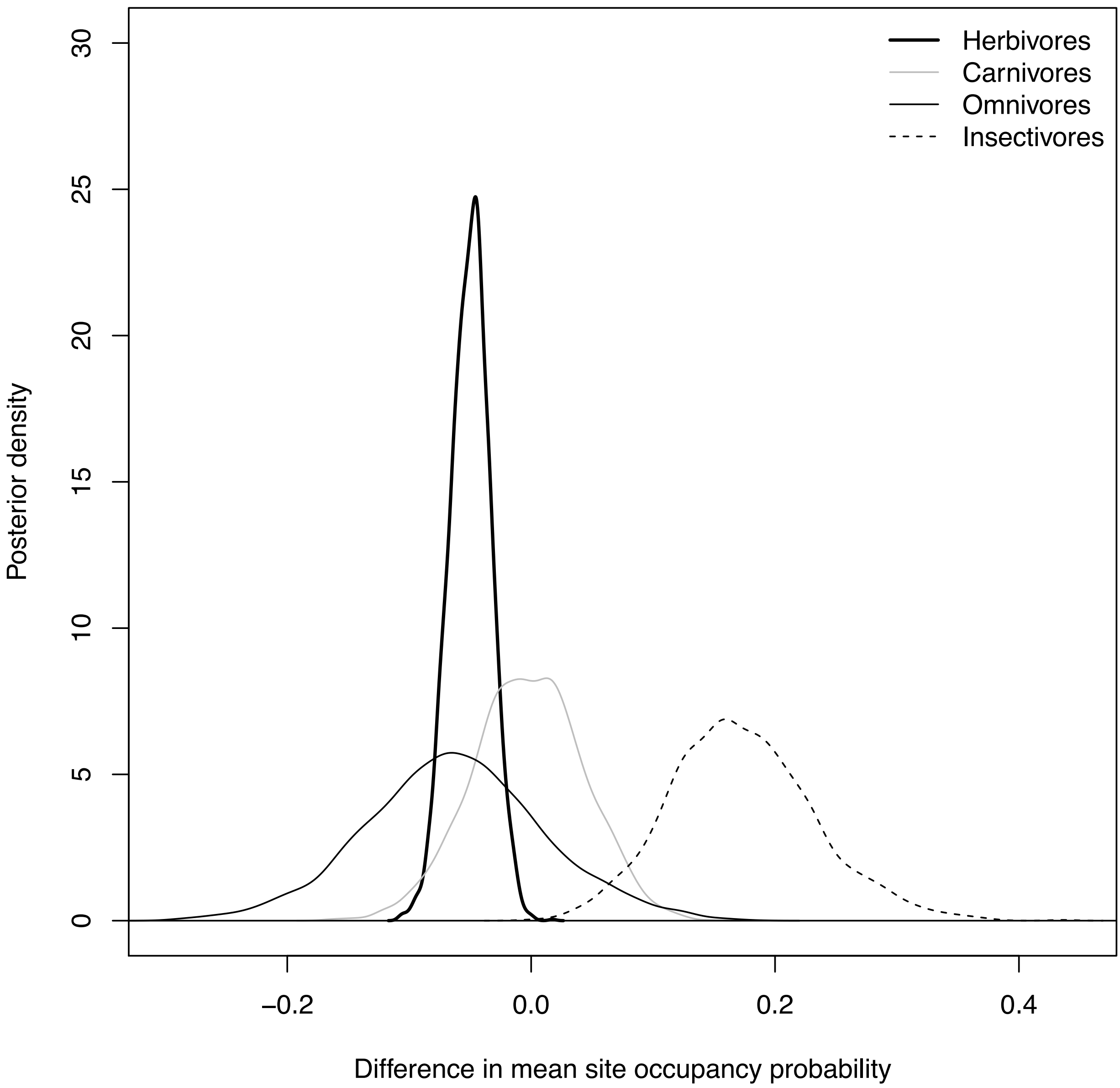


Figure S3.2. Differences in mean site occupancy probabilities for different trophic guilds (i.e. herbivores, carnivores, omnivores and insectivores) between farmland and the reserve. The posterior densities not overlapping zero show a significant difference in their mean site occupancy probability.



CHAPTER 4

Diet, prey preference and dietary niche relationships among sympatric predators on farmland and a protected area

Top picture: A black-backed jackal scat deposited on top of a succulent bush in Anysberg Nature Reserve, South Africa © Scott N Ramsay. Bottom picture: Drying and sorting out individual predator scats from the Central Karoo, South Africa © Marine Drouilly – The Karoo Predator Project.

Abstract

The use of natural habitat for pastoralism is often associated with a reduction in the diversity and abundance of wildlife and considered a major driver of conflict between farmers and predators worldwide. In this chapter, I explored how the differences in diversity and relative abundance of medium- to large-sized terrestrial vertebrates highlighted in the previous chapter between farmland and the reserve; affect prey consumption by the three main sympatric carnivores of the Karoo – the black-backed jackal, the caracal and the leopard. All three predators, but especially jackals and caracals, are a source of conflict with small-livestock farmers, many of whom believe that predators use Anysberg Nature Reserve as a base for raiding farmland. I determined predator diets using 657 scats collected on both types of land use in subsequent years. As shown in the previous chapter, domestic ungulates dominated the farming landscape. Unsurprisingly, livestock comprised the bulk of prey in the scats of jackals and caracals as determined by the frequency of occurrence (42% and 25% respectively), percent volume (47% and 32% respectively) and ingested biomass. By contrast, jackals and caracals in the reserve fed primarily on fruits and micromammals respectively, with a lower ingested biomass of mammalian prey. No trace of domestic sheep was found in any of the scats in the reserve, contradicting farmers' belief that predators use Anysberg as a base for raiding farmlands. I did not find leopard scats on farmland, reinforcing the results of my occupancy model. Dietary niche breadth and overlap were higher on farmland than in the reserve and attributed to the high consumption of domestic livestock by both mesopredators. Dietary overlap between mesopredators and leopard was small. Caracals on farmland and both mesopredators in the reserve showed strong prey preference for wild mammals, while jackals on farmland showed prey preference for goats and sheep over similar-sized wild mammals. Leopards showed preference for bushpig and mountain-dwelling antelopes but consumed baboons according to availability. Together these results fill a gap in our knowledge about mesopredator diets on farmland and dietary niche relationships between a large apex carnivore and two sympatric smaller counterparts, all potentially in conflict with small-livestock farmers in the semi-arid regions of South Africa. In terms of management, my results show that mesopredators' trophic flexibility is likely to be an advantage in a human-transformed landscape and that it is crucial for farmers to protect their livestock, even on farms where wild prey are available because of jackal's preference for small-livestock over similar-sized wild mammals.

Introduction

The occurrence and persistence of terrestrial carnivore populations in a given ecosystem are linked to a multitude of physical and ecological variables including resource availability and abundance (Carbone and Gittleman, 2002; Fuller and Sievert, 2001), particularly for water (Kluever and Gese, 2016), food (Singh et al., 2014) and resting sites (Pépin and Angibault, 2007). Competition for critical resources (Larkin, 1955; Ritchie and Johnson, 2009), especially between sympatric species occupying a similar trophic level may result in niche differentiation (Hayward and Kerley, 2008; Jones and Barmuta, 2000) and resource partitioning (Fedriani et al., 2000; Kamler et al., 2012b; Pianka, 1969). Together, these mechanisms serve to reduce dietary overlap (Azevedo et al., 2006; Carvalho and Gomes, 2004) and are considered important for their coexistence (Lodé, 1993; Schmidt et al., 2009).

Analysis of carnivore diets through dietary choices and prey preferences can bring valuable information on various aspects of their ecology. Such information include their role in the ecosystem (Ćirović et al., 2016; Ripple et al., 2014; Roemer et al., 2009), their potential competition or niche overlap with sympatric carnivores (Caro and Stoner, 2003; Fedriani et al., 1999; Lanszki et al., 2006; Loveridge and Macdonald, 2003; Volmer and Hertler, 2016; Wang, 2002) and their impacts on prey populations (Głowaciński and Profus, 1997; Klare et al., 2010), including livestock (Banerjee et al., 2013; Kamler et al., 2012a).

The diet of free ranging carnivores and predation on livestock have mostly been studied indirectly through stomach contents and scat analysis because direct observations of feeding events are rare (Bothma et al., 1984; Braczkowski et al., 2012a; Meriggi et al., 1996; Mukherjee et al., 2004). Gut content analysis is particularly invasive, requiring the death of the animal, but enables an easier identification of food remains and provides a more accurate measure of the relative volume of each item (Cavallini and Volpi, 1996). Scat analysis is non-invasive but because the food has been digested, the extrapolation to the amount of ingested prey biomass varies with the method used (Klare et al., 2011). Variance in the surface to volume ratio of prey of different sizes and differences in digestibility of particular food constituents may also influence the percentage of the items to the overall diet (Klare et al., 2011; Zabala and Zuberogoitia, 2003). To counteract these limitations, biomass models have been developed, but they are very often limited to mammalian prey and typically require feeding trials for the studied species to provide correction factors for each prey type or build linear regression models (Klare et al., 2011; Rühe et al., 2008). Consequently, these limitations render the simultaneous use of qualitative and quantitative methods critical when using scats to obtain more reliable estimates of diet composition.

When natural food resources are limited by human activities such as farming or by aridity; predators may switch their diet to include introduced domestic species (Beckmann and Berger, 2003; Farias and Kittlein, 2008; Morehouse and Boyce, 2011; Valeix et al., 2012). In South Africa, approximately 80% of the land is suitable for extensive livestock farming, with cattle, sheep and goat farming comprising about 53% of all agricultural land in the country (i.e. approximately 590 000 km^2) (Ilvkhulhv, 2016). The National Wool Growers Association reported that more than 500 000 wool sheep were caught annually by jackals and caracals, accounting for an estimated loss of USD 29.3 millions in 2005 in the wool industry alone (Avenant and Du Plessis, 2008), while in 2007, a study estimated that the livestock industry incurred losses attributed to predators to the value of USD 22 million annually (Statistics South Africa, 2011). Van Niekerk (2010) estimated the annual cost of predation by jackal and caracal to be even higher: USD 171 million for the whole country, of which more than USD 8.5 million was recorded in the Central Karoo districts of the Western Cape. Whereas it is difficult to quantify the total costs of depredation damage, livestock losses to predators in South Africa are perceived as a growing threat to the financial sustainability of the small-livestock industry (Bergman et al., 2013; Kerley et al., 2018; Nattrass and Conradie, 2015; Thorn et al., 2012). Results of diet analysis, coupled with predation data (see Chapter 5), may therefore have a strong influence on the management of the species involved, especially when the latter have an important economic impact on human societies.

Jackal, caracal and to a lesser extent leopard, are considered to be responsible for most of the small-livestock losses in South Africa (Avenant and Du Plessis, 2008; PMF, 2016), and more recently to impact adversely on the growing game farming industry (Du Plessis et al., 2015). Small-livestock farmers often blame PAs for being a source of predators, particularly jackals, and many suspect that those with territories in reserves regularly cross into farmland to prey on their livestock. There is some (but limited) evidence for such cross-boundary foraging in other parts of South Africa (Bothma, 1971a; Melville et al., 2004). Suspicion that similar dynamics might be at work in the Karoo has resulted in significant tension between farmers and wildlife managers in the region, especially with regards to reserves without lions and where fences are correspondingly less secure, such as Anysberg Nature Reserve.

Jackals are facultative scavengers and predators with a broad opportunistic diet including rodents, small and large antelopes, fruits, birds, insects and even Cape fur seals (Table 6.2; see Chapter 2). Caracals and leopards are obligate carnivores. In natural areas, caracals feed mostly on rodents and small antelopes (Table 6.1; see Chapter 2) and in the Western Cape, leopards predominantly feed on rock hyraxes and small antelopes (Norton et al. 1986). Both species of mesopredators have been shown to kill and eat livestock in farming areas (Tables 6.1, 6.2), but it is difficult to determine the proportion of livestock that are killed versus scavenged when relying on indirect methods such as scat or stomach content analysis.

The diets of both jackal and caracal have been more intensely studied than any other aspects of their ecology (jackal = 44% of the publications, n = 58; caracal = 37% of the publications, n = 29; Du Plessis et al., 2015), due to the relative ease of data collection (i.e., scats or stomach contents from carcasses of predators killed during control operations). However, nearly all the research conducted on the diet of both species was carried out in areas where wild species are the dominant prey available. In addition, dietary information is scarce in the most important small-livestock farming areas of southern Africa, such as the Karoo (but see Kamler et al., 2012a) and no published studies have been conducted at the landscape level while accounting for prey availability. At the time of writing this thesis, in the Succulent Karoo and Nama Karoo biomes where human-mesopredator conflicts are the most severe due to the type of land use (Du Plessis et al., 2015), only a single study has been performed on jackal diet and two on caracal diet respectively (Du Plessis et al., 2015). In the Succulent Karoo biome, the study on jackal diet was from the less productive coastal area (Nel et al., 1997) where no sheep are present (Table 6.2), therefore not being representative of this important small-livestock farming region (Du Plessis et al., 2015). In the Nama Karoo biome, the studies on caracal diet conducted outside PAs (Stuart, 1982; Stuart and Hickman, 1991) showed that even if domestic livestock was consumed, it was not the principal food item of the mesopredator. In their paper on the seasonal diet and prey selection of jackal on a single small-livestock farm in the Free State Province of South Africa, Kamler et al. (2012a) found that the mesopredator selectively consumed various food items throughout the year and that wild prey were consistently selected over sheep. However, sheep were often the main food source, comprising 25-48% of the biomass consumed by jackal across seasons, with a peak in consumption during the lambing seasons (Kamler et al., 2012a).

The primary goal of this chapter was therefore to contribute to our limited knowledge on the diet of mesopredators on small-livestock farmland in the major sheep-farming region of South Africa and to determine whether livestock are preferred prey relative to similar-sized wild species. In addition, I compared these data with the diet of sympatric mesopredators and leopard in Anysberg Nature Reserve (see Chapter 2 for characteristics of the study sites) to determine: (1) whether predators that live within the PA feed on livestock and thus contribute to depredation on farmland; and (2) whether predators in the PA show a preference for wild prey similar in size to domestic livestock on farmland. I expected some livestock consumption in the scats of predators living in the PA because there is some evidence for such cross-boundary foraging in other parts of South Africa (Bothma, 1971a; Melville et al., 2004). I also predicted that jackal and caracal would show preference for wild prey over domestic livestock, as was previously shown for jackal (Kamler et al., 2012a). I further examined the resource partitioning patterns for predators on farmland and in the PA using measures of dietary niche breadth and overlap. I expected dietary niche breadth to be larger for jackal than for caracal or leopard because of the more specialized dentition of felids to eat meat (Kok and Nel, 2004). I also expected a larger amount of dietary overlap between predators on farmland than in the PA because sheep consumption by both mesopredators would likely be high on farmland.

Table 4.1. Data from other studies[1] regarding caracal diet, including characteristics of the study area, methods and sources used to determine the diet, most common type of prey consumed, whether livestock was detected in the diet and references of the corresponding papers.

Study area	Country	Protected area?	Method(s) of diet determination	Sources of diet determination	Major prey species or family	Presence of livestock in diet?	Reference(s)
- George region - Fransmanshoek Conservancy	South Africa	No Yes	- Frequency occurrence - Relative occurrence - Corrected frequency occurrence	- Scat (n=142)	- Rodentia (vlei rat) - Rodentia (vlei rat) - Rodentia (vlei rat)	No No	Braczkowski et al., 2012a
- Abbasabad Naein Reserve	Iran	Yes	- Direct observations - Macroscopic analysis of scat (presence-absence)	- Scat (n=N.C.) - Direct observations (n=20)	- Rodentia	Yes	Farhadinia et al., 2007
- Kgalagadi Transfrontier Park	Along the South African – Namibian border	Yes	- Percentage occurrence - Percentage of total number of prey units - Percentage occurrence	- Scat (n=116) - Spoor-tracking of attempted hunts (n=327)	- Rodentia (springhare) - Rodentia (springhare)	Yes No	Melville et al., 2004

- [1] Three international databases (Web of Science, Scopus and Google Scholar) were accessed and searched using the following terms: Caracal OR rooikat. I also visually searched the bibliography of all the articles I found in these databases to find new articles on caracals. I manually selected the ones that dealt with caracal diet, keeping the others as references for my other chapters.

Study area	Country	Protected area?	Method(s) of diet determination	Sources of diet determination	Major prey species or family	Presence of livestock in diet?	Reference(s)
- Free State Province	South Africa	No	- Frequency occurrence - Dry mass	- Stomach contents (n=57)	- Mammals (sheep) - Mammals (sheep)	Yes	Kok and Nel, 2004
- Sariska Tiger Reserve	India	Yes	- Percentage occurrence - Biomass - Percentage of the predator daily energy requirement	- Scats (n=25)	- Rodentia (flat-haired mouse)	No	Mukherjee et al., 2004
- West Coast National Park (WCNP) - Adjacent farms	South Africa	Yes No	- Percentage occurrence - Relative percentage occurrence - Percent volume - Importance value (I) = relative percentage occurrence in scats x estimated mass eaten	- Scat (n=391)	- Rodentia (Cricetidae and Muridae) - Rodentia (Cricetidae and Muridae)	No Yes	Avenant and Nel, 2002
- Harrat al-Harrah Reserve	Saudi Arabia	Yes	- Macroscopic analysis (presence-absence) - Direct observations	- Scat (n=nc) - Kill sites (=6)	- Rodentia (Lybian jird) - Artiodactyla (baby camel)	No	van Heezik and Seddon, 1998

Study area	Country	Protected area?	Method(s) of diet determination	Sources of diet determination	Major prey species or family	Presence of livestock in diet?	References
- West Coast National Park	South Africa	Yes	- Percentage occurrence - Relative percentage occurrence	- Scat (n=202)	- Rodentia (*Otomys unisulcatus*)	No	Avenant and Nel, 1997
- Karoo National Park	South Africa	Yes	- Percentage occurrence	- Scat (n=100)	- Rodentia (Natal multimammate mouse)	No	Palmer and Fairall, 1988
- Cape Province	South Africa	No	- Percentage occurrence	- Scat (n=248) - Kill sites (n=30) - Stomach contents (n=394)	- Rodentia (bush vlei rat) - Artiodactyla (grysbok, grey duiker) - Wild mammal (grysbok)	Yes	CT Stuart, 1982
- Mountain Zebra National Park	South Africa	Yes	- Identification of species killed - Percentage occurrence - Relative percentage occurrence - Percentage biomass	- Kill sites (n=21) - Scat (n=200)	- Artiodactyla (mountain reedbuck) - Hyracoidea (Cape hyrax) - Artiodactyla (mountain reedbuck)	No	Grobler, 1981

Study area	Country	Protected area?	Method(s) of diet determination	Sources of diet determination	Major prey species or family	Presence of livestock in diet?	References
- Farming area in the Bedford district	South Africa	No	- Percentage of stomachs containing particular prey species	- Stomach contents (n=103)	- Sheep and goats	Yes	Pringle and Pringle, 1979
- Farm Goraas, Cape Province	South Africa	No	- Identification of species killed	- Kill sites (n=2) - Stomach contents (n=3)	- Sheep	Yes	Skinner, 1979

Table 4.2. Data from other studies[2] regarding black-backed jackal diet, including characteristics of the study area, methods and sources used to determine the diet, most common type of prey consumed, whether livestock was detected in the diet and references of the corresponding papers.

Study area	Country	Protected area?	Method(s) of diet determination	Sources of diet determination	Major prey species or family	Presence of livestock in diet?	References
- Nottingham Road/Mooi River agricultural areas, KZN	South Africa	No	- Percentage occurrence - Relative percentage occurrence	- Scat (n=154)	- Rodentia (southern African vlei rat, mesic four-striped grass rat)	Yes	Humphries et al., 2015b
- Samara Private Game Reserve	South Africa	Yes	- Frequency occurrence - Percentage ingested biomass	- Scat (n=240)	- Ungulates - Small ungulates	No	Van de Ven et al., 2013
- Pilanesberg National Park and Mankwe Wildlife Reserve	South Africa	Yes	- Frequency occurrence - Relative frequency of occurrence	- Scat (n=100)	- Large mammals	No	Yarnell et al., 2013
- Private small-livestock farm in the Free State Province	South Africa	No	- Percentage ingested biomass - Percentage of scat volume - Frequency occurrence	- Scat (n=143)	- Ungulates (sheep, springbok)	Yes	Kamler et al., 2012a

[2] Three international databases (Web of Science, Scopus and Google Scholar) were accessed and searched using the following terms: Black-backed jackal OR Canis mesomelas. I also visually searched the bibliography of all the articles I found in these databases to find new articles on black-backed jackals. I manually selected the ones that dealt with diet, keeping the others as references for my other chapters.

Study area	Country	Protected area?	Method(s) of diet determination	Sources of diet determination	Major prey species or family	Presence of livestock in diet?	References
- Great Fish River Reserve - Kwande Private Game Reserve	South Africa	Yes Yes	- Percentage occurrence	- Scat (n=496)	- Artiodactyla (bushbuck) - Artiodactyla (bushbuck)	No No	Brassine and Parker, 2012
- Reserves - Farms	South Africa	Yes No	- Percentage frequency of occurrence - Relative percentage frequency of occurrence	- Scat (n=453) - Scat (n=89)	- Artiodactyla (bushbuck) - Artiodactyla (bushbuck and Dorper sheep)	Yes Yes	Forbes, 2011
- National West Coast Recreation Area (Cape Cross Seal Reserve)	Namibia	Yes	- Observation of feeding behaviour	- Direct observation (n=N.C.)	- Fur seal (carcasses and young individuals)	No	Jenner et al., 2011
- Namib Desert	Namibia	Yes	- Frequency occurrence - Relative dry mass - Proportion of biomass consumed	- Scat (n=200)	- Insect (giant longhorn beetle) - Insect (giant longhorn beetle) - Mammal (Rodentia and ungulates)	Yes	Goldenberg et al., 2010

Study area	Country	Protected area?	Method(s) of diet determination	Sources of diet determination	Major prey species or family	Presence of livestock in diet?	References
- Benfontein Game Farm - Rooiport Nature Reserve	South Africa	No No	- Frequency occurrence - Ingested biomass - Percent of scat volume - Frequency occurrence - Ingested biomass - Percent of scat volume	- Scat (n=313) - Scat (n=522)	- Mammal (springbok) - Mammal (springbok) - Mammal (hare) - Plant - Plant - Plant	Yes Yes	Klare et al., 2010
- Great Fish River Reserve	South Africa	Yes	- Percentage occurrence - Relative percentage occurrence - Percent volume	- Scat (n=109)	- Fruits and arthropods - Arthropods and other mammals (warthog) - Arthropods and other mammals (warthog)	No	Do Linh San et al., 2009
- Moremi Game Reserve	Botswana	Yes	- Observation of hunting behaviour	- Direct observation (n=1)	- Impala	No	Kamler et al., 2010
- Protected areas - Game/cattle farms	South Africa	Yes No	- Percentage occurrence - Relative percentage occurrence	- Scat (n=9) - Scat (n=34)	- Small mammals - Small mammals	No No	Merwe et al., 2009

Study area	Country	Protected area?	Method(s) of diet determination	Sources of diet determination	Major prey species or family	Presence of livestock in diet?	References
- Etosha National Park	Namibia	Yes	- Observation of hunting behaviour	- Direct observation (n=1)	- Springbok	No	Krofel, 2008
- Free State Province	South Africa	No	- Frequency occurrence - Dry mass	- Stomach contents (n=293)	- Mammals (sheep)	Yes	Kok and Nel, 2004
- Mokolodi Nature Reserve	Botswana	Yes	- Percentage occurrence	- Scat (n=237)	- Mammals (Rodentia)	Yes	Kaunda and Skinner, 2003
- Private wildlife estate	Zimbabwe	No	- Percentage occurrence - Percentage frequency occurrence - Percentage ingested biomass	- Scat (n=397)	- Arthropods - Springhare	No	Loveridge and Macdonald, 2003
- Van Reenen Bay	Namibia	No	- Number of kills and scavenging events on the Cape fur seal colony	- Direct observations (13 hours a day for 29 days±5, for 13 years)	- Cape fur seal pups	No	Oosthuizen et al., 1997

Study area	Country	Protected area?	Method(s) of diet determination	Sources of diet determination	Major prey species or family	Presence of livestock in diet?	References
- Namib Desert Coast - South African coast	Namibia and South Africa	No	- Frequency occurrence - Relative frequency occurrence	- Scat (n=nc)	- Great cormorant and Cape fur seal - Insects	No	Nel et al., 1997
- Skeleton Coast Park	Namibia	Yes	- Percentage occurrence	- Remains of prey at middens (n=13)	- Birds (great cormorant)	No	Avery et al., 1987
- Cape Cross Seal Reserve	Namibia	Yes	- Percentage occurrence - Direct observations	- Scat (n=47) - Feeding sites (n=102)	- Mammals (Cape fur seal) - Birds (Cape cormorant)	No	Hiscocks and Perrin, 1987
- Namib Desert	Namibia	Yes	- Percentage occurrence	- Scat (n=46)	- Plant material - Insects	No	Bothma et al., 1984
- Giant's Castle Game Reserve	South Africa	Yes	- Relative percentage occurrence	- Scat (n=477)	- Small mammals (southern African vlei rat)	Yes	Rowe-Rowe, 1983
- Addo Elephant National Park	South Africa	Yes	- Percent volume	- Stomach contents (n=5)	- Insect (Coleoptera and Lepidoptera)	No	Hall-Martin and Botha, 1980
- Serengeti	Tanzania	Yes	- Frequency occurrence	- Scat	- Rodentia or Insect	No	Lamprecht, 1978

Study area	Country	Protected area?	Method(s) of diet determination	Sources of diet determination	Major prey species or family	Presence of livestock in diet?	References
- Namib Desert Park	Namibia	Yes	- Percentage occurrence - Percent volume	- Scat (n=772)	- Birds and *Euclea* fruits and seeds	No	Stuart, 1976
- Farmlands - Nature, game and forestry reserves in Western Natal	South Africa	No Yes	- Percent volume - Percentage frequency occurrence	- Stomach contents (n=72)	- Antelopes and carrion in reserves - Sheep on farms	Yes	Rowe-Rowe, 1976
- Agricultural areas - Game reserves	South Africa	No	- Percent volume - Percentage frequency occurrence	- Stomach contents (n=201 from Grafton 1965 + 378)	- Carrion and domestic ungulates - Insects and rodents	Yes Yes	Bothma, 1971b
- Sheep/crop and fruit farms, cattle ranches, mixed-farming areas and Nature Reserves across the country	South Africa	Yes and No	- Percentage occurrence - Percent volume	- Stomach contents (n=201)	- Mammals (Rodentia) - Mammals (sheep)	Yes	Grafton, 1965
- Kalahari Gemsbok Park	South Africa	Yes	- Percent volume	- Stomach contents (n=11)	- Insect (locusts)	No	Bothma, 1966

Methods

Scat collection

I collected jackal and caracal scats on farmland, mostly in the Koup. I collected jackal, caracal and leopard scats in Anysberg Nature Reserve (Figure 4.1). Collection mostly occurred while walking and driving both sites (see Chapter 2 for sites descriptions) to establish and remove my extensive camera trap grids (see Chapter 3). Camera traps were placed on a grid pattern with a 2 km inter-camera distance throughout both sites, ensuring an even spatial sampling effort for scat detection (see Chapter 3).

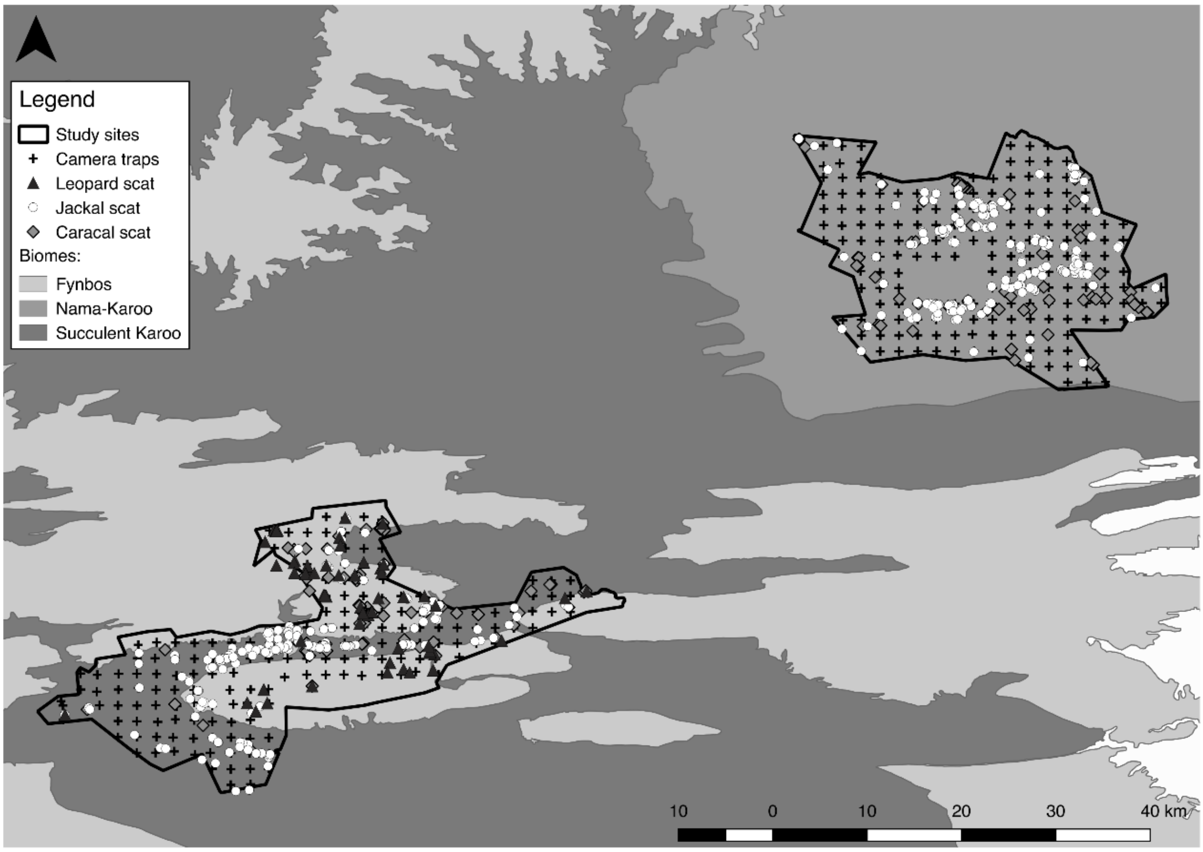


Figure 4.1. Map of the two study sites (Anysberg Nature Reserve on the left and the farmland on the right) on a background layer representing the different biomes of the area. The locations of the camera traps (black crosses) and site of collection of the different predator scats are denoted as white solid circles (jackals), grey diamonds (caracals) and black triangles (leopards).

Scats were also detected and collected opportunistically along roads and dry riverbeds as these landscape features tend to be used preferentially by carnivores to travel (Dillon and Kelly, 2007; Larrucea et al., 2007; Mann et al., 2015) and defecate (Farhadinia et al., 2009; Hayward and Hayward, 2010; Ramakrishnan et al., 1999; Stuart, 1982) and by jackals for territorial signalling (Hayward and Hayward, 2010), thus increasing the chance of encountering scats from different individuals (sexes and age classes). I ensured that at least 2 weeks elapsed between collection periods in the same area and only collected fresh or semi-fresh scats. Together, this approach reduced the probability of sampling the same prey item in multiple scats from the same individual (i.e. pseudoreplication) given that a single consumed item may appear in up to seven sequential scats (mean=2.8, n=7) (Bowland and Bowland, 1991).

Table 4.3. Scat characteristics used to identify the species of carnivore responsible for the scats collected.

Species	Shape	Length and breadth	Colour
Black-backed jackal (*Canis mesomelas*)	Cylindrical, generally tapered at both ends, not segmented	74 x 10-20 mm	Variable
Caracal (*Caracal caracal*)	Cylindrical, sausage-shaped with round ends and well-defined segments	55 x 20-22 mm	Variable
Leopard (*Panthera pardus*)	Cylindrical with round ends and well-defined segments	> 22 mm and up to 35 mm	Variable but often white due to high calcium content as a consequence of bone ingestion or very dark due to the great amount of blood ingested

Scats were identified by their shape, size, diameter, colour and macroscopic content (Table 4.3, Appendix 4A Tables S4.1 and S4.2) (Braczkowski et al., 2012a, 2012b; Chame, 2003; Do Linh San et al., 2009; Norton et al., 1986; Ott et al., 2007), as well as by the presence of associated field signs such as spoor in their surroundings. The location of each scat was recorded with a handheld GPS unit (Garmin GPSMAP® 64s, Garmin International Inc. Olathe, Kansas, USA), along with the date, the area, the altitude, the defecation site and the substrate on which the scat was found. Collected faecal samples were placed in paper envelopes and air-dried at ambient temperature in the field station before being transported to the laboratory for further processing.

Adult jackals scent mark with urine or faeces (Figure 4.2A), often on conspicuous objects like grass tufts or rocks (Ferguson et al., 1983; Hayward and Hayward, 2010). Jackals spoors are easy to identify with front and hind feet having 5 and 4 digits respectively, and with claws measuring 15 mm on average along the curve (Apps, 2012). Caracal scats were recognised by their greater diameter (between 20 and 22 mm) and their more round, segmented appearance (Figure 4.2B). They also contained smaller bone shards than those present in leopard scats. Caracal tracks are much smaller than those of leopards, with a rounder aspect (Walker, 1996).

Figure 4.2. A: Typical adult black-backed jackal scat deposited on top of a bush in the Central Karoo, and B: Typical caracal scat with rodent skull in the Central Karoo.

Leopard scats were identified by their segmented appearance (Figure 4.3) and greater diameter. Only those scats larger than 22 mm in diameter were collected as leopard scat to reduce the probability of overlap with caracal scats, which are similar in appearance. Leopard tracks are both bigger and more elongated than caracal's (Walker, 1996). When not sure about the species responsible for a scat, it was not collected.

In the laboratory, jackal (Kaunda and Skinner, 2003), caracal (Braczkowski et al., 2012a) and leopard (Norton et al., 1986) scats were further positively identified by the presence of hair from the focal predator as a result of self-grooming (Boast et al., 2016; Breuer, 2005; Klare et al., 2010). I discarded a few scats (n=6) where the species that produced it could not be inferred with certainty.

Figure 4.3. A: Typical leopard scats © Utsuk Shah and the Cape Leopard Trust.

Scat analysis

a) Scat preparation and cross-sections of hairs

Once in the laboratory, the scats were weighed and I followed the methods of Klare et al. (2011) in preparing them, with minor modifications. Each scat was inserted into a section of nylon stocking that was then tied at both ends before being immersed in warm water for 48 hours to soften the contents. I then opened the stockings and sieved (1mm mesh) the contents under running water before leaving them to air-dry for at least three days on plastic sorting trays. Once washed and dried, I re-weighed the scats to obtain a dry mass after which I visually separated the major components of each scat (i.e. bones, teeth, hooves and hairs).

The hairs of prey species have characteristic shapes, lengths, colours, scale patterns and cross sections (Keogh, 1983; Lawes et al., 1999; Perrin and Campbell, 1979). Various methods have been described for taking cross-sections of hairs (see Douglas (1989) for a review). In this study, I used tweezers to pick-out a sub-sample of approximately 20 hairs representative of each hair type found in the scat (by macroscopic observation) for subsequent cross-sectioning. Hairs were then inserted into the end of a thin, disposable plastic Pasteur pipette and a small amount of hot paraffin wax (Paraplast Plus, Sherwood Medical Co., St Louis, Missouri, USA) was sucked up into the pipette. The pipettes were then placed into a beaker of ice to enhance cooling and the solidifying of the wax. Once the wax had set, the pipette was sliced (~0.2 mm sections) using a sharp razor blade and the sections were mounted onto glass slides with a drop of wax to secure the cross-sections (Douglas, 1989). The cross-sections were then observed under a LEICA Galen III microscope (at 40x magnification) and hair samples were identified to species-level by comparing them to known samples and keys (Keogh, 1985, 1983; Perrin and Campbell, 1979) and to the mammalian reference collection held in the Wildlife and Reserve Management Research Group laboratory at Rhodes University, South Africa. Hairs that were too damaged or otherwise unidentifiable were recorded as "unidentified mammal".

b) Identification of prey items

The overall diet of predators was determined by macroscopically identifying the scat contents and separating the fragments into 18 broad categories: invertebrates, squamates, tortoises, birds, small rodents, shrews, carnivores, wild ungulates, domestic ungulates, Cape porcupines, hyraxes, hares, unidentified mammals, other mammals (that would vary between carnivores and represent rare events, such as bushpig), grass and leaves, fruits and seeds, anthropogenic items (i.e., items of human origin such as plastic or rubber) and non-food items (e.g., grass) (Herbst and Mills, 2010; Kaunda and Skinner, 2003; Klare et al., 2010; van der Merwe et al., 2009). I refer to small rodents and shrews as micromammals in the rest of this chapter.

When possible, all the remains were identified to species level, weighed and their percent volume in each sample was estimated. Plant matter (other than fruits and seeds), birds and reptiles were not classified to finer taxonomic levels as remains in the scats were too fragmented to allow for identification (Grafton, 1965; Klare et al., 2011). Invertebrates were recognized by the presence of exoskeletons. Fruits were identified down to species by comparison with reference material collected in the study areas and with the help of the Anysberg Nature Reserve manager, Marius Brand. Non-food items such as gravel, sand, insects found on the surface of the scats during collection and hairs from the species of origin presumably ingested when self-grooming were recorded but not included in the analysis (Klare et al., 2011). Two trained observers identified all the remains independently to avoid bias (Spaulding et al., 1973).

Macroscopic remains present in the scats such as teeth, bones and hooves were used as corroborative material, particularly when identification by hair alone was difficult (Kaunda and Skinner, 2003), to corroborate my identifications. Micromammals were identified to species level by using jaws and teeth by Dr. Margaret Avery from the Iziko Museums of South Africa, using an established key (Avery, 1979) and comparative material (Figure 4.4).

Figure 4.4. A: Photograph of micromammal bones, jaws and teeth separated by predator species and by sample number for a later identification by Dr. Margaret Avery. B: Preserved rodent specimens with identification tags lying face down on a white tray, stored at the University of Cape Town and used to complete the Rhodes University hair reference library.

c) Data analysis

I plotted species accumulation curves with the number of scats analysed for the three predators in both study sites. I used the R package "vegan" (Oksanen et al., 2017) and the function "specpool" to generate the Chao 1 non-parametric species richness estimator associated with each curve (Gotelli and Colwell, 2011).

Diet choice was calculated using five different methods. Following the review of Klare et al. (2011), I used two qualitative methods that allow for a comparison with published results, and three quantitative methods that provide the best approximations of the true diet of mesocarnivores. Quantitative methods are preferred to frequency methods when determining the importance of different food components in the diet because the latter tend to overestimate the importance of small food items (Weaver, 1993). However, qualitative methods are important to detect rare food items or very small prey items frequently consumed but negligible in terms of ingested biomass (Kamler et al., 2012a), and to understand the ecological role of predators as specialists or opportunists (Klare et al., 2011). I used:

- The frequency of occurrence per scat, expressed as the percentage of scats containing a particular food item (Breuer, 2005; Do Linh San et al., 2009).
- The relative frequency of occurrence, which is the number of identified prey items divided by the total number of all prey items found and expressed as a percentage (Do

Linh San et al., 2009). For this method, I removed the categories grass/leaves and non-food items from the analysis because they are often omitted in other studies.

- The percent volume that is calculated by adding all the volumes (estimated visually by two independent observers to the nearest 5%) of each prey item in all the scats analysed and dividing this value by the total number of scats analysed (Capitani et al., 2004; McDonald and Fuller, 2005).
- The percent mass in scats, which is the dry mass of remains for each food item in the scats, in relation to the total mass of all the prey remains in all the scats analysed and expressed as a percentage (Forman, 2005).
- The percentage of mammalian biomass ingested (Bio), calculated in two ways. For jackal, I used the Goszczyński (1974) biomass calculation model initially developed for European red foxes, based on correction factors for the different prey items consumed. I used correction factors from Jędrzejewska and Jędrzejewski (1998) for the species not included in the Goszczyński's (1974) paper. The model converts the dry mass of the undigested remnants of prey in the scats into the biomass ingested of the different prey species (Goszczyński, 1974; Jędrzejewska and Jędrzejewski, 1998; Klare et al., 2011). The prey spectrum used by Goszczyński (1974) is similar to that of jackal in our study sites and because both species belong to the same family, I applied the same correction factors for digestion in jackal, as in Kamler et al. (2012a). For caracal and leopard, I used the model recently developed for obligate carnivores by Chakrabarti et al. (2016): $Y = (0{,}033 - 0{,}025 \exp^{(-4{,}284(X/P))})*P$, where Y is the mass of prey consumed per collectable scat, X is the prey body mass, and P is the predator body mass.

Biomass calculations are essential because biomass ingested to excrete a scat differs across prey sizes (Floyd et al., 1978) with larger prey having lower surface area-to-volume ratio resulting in more digestible matter per unit biomass (i.e. flesh over skin, bones and hide). Therefore, fewer scats are produced when eating a large prey than a small one. They are also the ecologically most relevant calculations. For the biomass calculations with the Chakrabarti et al. (2016) formula, I used the mean body mass of adult males and females of each prey species provided in Apps (2012). The only exceptions were for greater kudu (*Tragelaphus strepsiceros*), oryx and red hartebeest where I used juvenile mass (adult mass multiplied by 0,3) (Mann, 2014; Radloff and Du Toit, 2004) as adults are generally too large to be captured by caracal (Braczkowski et al., 2012a; Melville et al., 2004) or leopard (Hayward et al., 2006).

To compare the diets of mesopredators in the two types of land use in terms of frequency of occurrence, I used Chi-square analysis and Fisher's exact tests when expected values of frequency of occurrence were <5%. Results were assessed at $\alpha = 0.05$.

I used the 18 prey categories identified above (but excluding the unidentified mammals, as in Kamler et al. (2012a) to perform the following analyses:

- I calculated diet specialization using Levins (1968) measure of niche breadth (B): $B = 1/\sum p_i^2$ where p_i is the relative frequency of the item *i*. I used this index to measure diet specialization for the three species in both study sites. B ranges from 1 to *n*, where *n* is the total number of possible items in the diet (here, *n*=17). B is maximal when the species does not appear to discriminate among the resource states, and thus has the broadest possible dietary niche, whereas B is minimal when only one dietary item is used (dietary specialist).
- Niche overlap was investigated by calculating a pair-wise degree of dietary niche overlap amongst the three carnivores and the study sites using Pianka (1973) (O) and between each mesopredator and leopards in the reserve. The index is calculated as follow:

$$\hat{O}_{jk} = \frac{\sum_i^n \hat{p}_{ij}\hat{p}_{ik}}{\sqrt{\sum_i^n \hat{p}_{ij}^{\,2} \sum_i^n \hat{p}_{ik}^{\,2}}}$$

where:

O_{jk} is Pianka's measure of niche overlap between species *j* and species *k*,

p_{ij} is the proportion dietary category *i* is of the total dietary categories consumed by species *j*,

p_{ik} is the proportion dietary category *i* is of the total dietary categories used by species *k*,

n is the total number of dietary categories.

This measure of overlap ranges from 0 (no prey consumed in common) to 1 (complete dietary overlap).

I also calculated the Renkonen index (Krebs, 1999), which gives the percentage overlap from the previous equation, as:

$$\hat{P}_{jk} = \left[\sum_{i=1}^{n} (minimum\ \hat{p}_{ij,}\, \hat{p}_{ik}\right] 100$$

Mammalian prey availability through camera trapping

I used data from the extensive camera trapping surveys performed in both types of land use (see Chapter 3) to estimate the medium- to large-sized mammalian prey available to predators (Braczkowski et al., 2012a; Jenks et al., 2011; O'Brien et al., 2003). Medium-sized mammalian prey were defined as being at least the size of a Smith's red rock hare (*Pronolagus rupestris*), while the largest mammalian prey available was the Cape eland. Despite micromammals being an important part of mesopredator diet, I was not able to assess their availability at the extensive spatial scale (ca. 160 000 ha) I considered appropriate for the primary aims of this study. Consequently, I restricted my assessment of prey availability to medium and large species that can be reliably recorded using camera traps (Carbone et al., 2001; Kinnaird and O'Brien, 2012; O'Brien et al., 2003; Rovero and Marshall, 2009).

Most of the prey species consumed by the three predators are not individually identifiable, thus limiting my analysis to relative abundance indices (RAIs) for each prey species (Figure 4.6). This method has been criticized (Jennelle et al., 2002) because it does not consider the difference in probability of detection between diverse species, or the differences in movement rates in the trapping rate. However, different studies highlighted significant positive correlations between trapping rates and independent density estimations in various species (Carbone et al., 2001; Kinnaird and O'Brien, 2012; O'Brien et al., 2003) and it was suggested that under a standardized sampling design as in my study (that is in addition occurring in a very open landscape), trapping rates could be used as RAIs (Oliveira-Santos et al., 2010). RAIs of prey species were calculated based on 176 camera traps on farms and 156 in the reserve. The RAI for a particular species was given by the total number of photographs of that species per 100 trap nights (see Chapter 3 for more details and sampling information) (Balme et al., 2010; Jenks et al., 2011; O'Brien et al., 2003). I considered two photographs of the same species in the same location as being independent when at least 30 minutes elapsed between them (Kinnaird and O'Brien, 2012). Both camera trapping surveys overlapped with scat collection time at each site.

I calculated Ivlev's electivity index *D* (modified by Jacobs, 1974) using biomass data for the three carnivores in each site in which they occur. This index has already been used to measure prey preference in jackal (Klare et al., 2010), but also in larger carnivores such as lions (Hayward and Kerley, 2005; Valeix et al., 2012), tigers (*Panthera tigris*) (Hayward et al., 2012), wolves (*Canis lupus*) (Hosseini-Zavarei et al., 2013; Wagner et al., 2012) and leopards

(Braczkowski et al., 2012b; Rautenbach, 2010). It provides a measure of prey preference, defined as using a prey more than expected given the prey's relative abundance (Jacobs, 1974). Jacobs' index has the following equation: $D = (r_i - p_i)/(r_i + p_i - 2r_ip_i)$; where r_i is the proportion of all scats containing species i, extracted from the results of the biomass models, and p_i is the relative abundance of species i, as determined by the camera trap-based relative abundance index. The resulting values range from 1 (complete preference) to -1 (complete avoidance) with $-0.2<D<0.2$ indicating that prey was used according to its availability (Jacobs, 1974).

I only calculated *D* for the species that occurred in at least 1% of the predator scats or the species that were not considered rare (i.e. species with a detection rate > 1/1000 trap nights; O'Brien et al., 2010), because *D*-values of rare species are often biased, with detection in one scat leading to *D*-value of +1 and no detection to *D*-value of -1 (Klare et al., 2010).

Results

Overall diet of predators

In total for both types of land use, I collected 670 predator scats and included 657 scats in the analyses (jackal: n=417, caracal: n=182, leopard: n=58) after excluding those in which the hairs had disintegrated and there were no other identifiable remains (Table 4.4).

Table 4.4. Table showing the number of scats analysed, the total number of scats collected and the Chao estimator for number of dietary categories consumed per species and type of land use.

	Farmland		Reserve	
	Number of scats analysed	Chao 1 estimator (±SE)	Number of scats analysed	Chao 1 estimator (±SE)
Jackal	216	18.48 ± 7.16	201	14.98 ± 4.50
Caracal	102	13.49 ± 1.31	80	14.96 ± 4.46
Leopard	0	NA	58	20.86 ± 11.47

Accumulation curves for each species in both study sites (Figure 4.5) suggest that I was close to reach asymptotes for the mesopredators. The non-parametric Chao 1 estimators of species richness (Table 4.4) associated with the species accumulation curves (Figure 4.7) indicate that 81% and 80% of all dietary categories were detected for jackals on farmland and in the reserve respectively. For caracal, species accumulation curves almost reached an asymptote on farmland (96% of all dietary categories detected) and 80% of all dietary categories were detected in the reserve. For leopards, 72% of all dietary categories were detected. (Table 4.4). Between the scats of the three predators, 32 different mammalian prey types were found (Table 4.5) and most of the scats collected had two prey items in them but never more than 4 for mesopredators and 5 for leopards (Table 4.6).

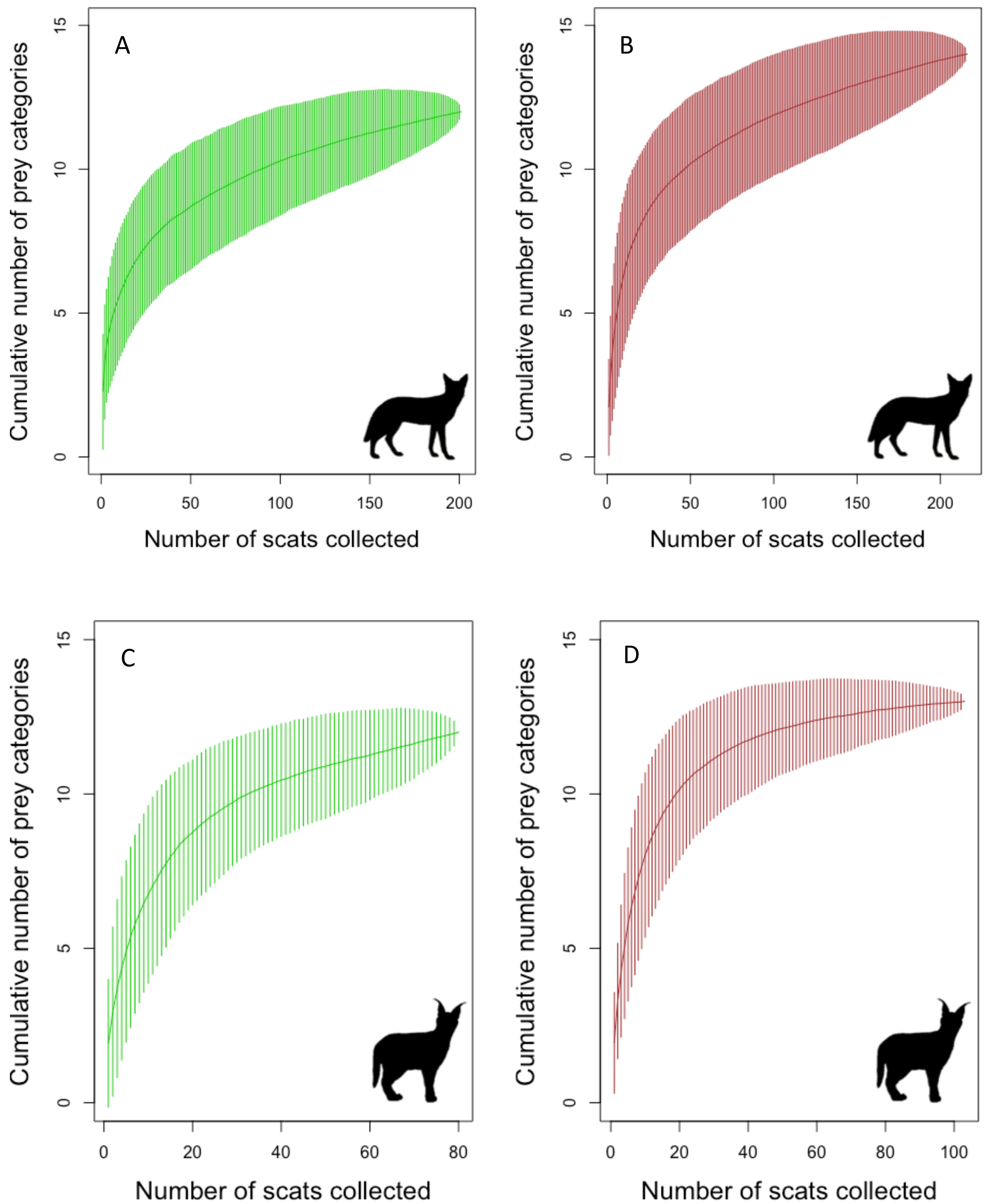
Table 4.5. Table showing the number of individual prey items, mammalian prey items and mammalian prey types in the scats of the three carnivores collected on farmland and in Anysberg Nature Reserve in the Karoo.

	Number of individual prey items in scats	Number of mammalian prey items in scats	Number of mammalian prey types in scats
Jackal	993	405	24
Caracal	412	221	22
Leopard	135	66	16
Total	**1540**	**692**	**32**

Table 4.6. Table showing the number of scats of each predator with one, two, and three or more prey items respectively, and in parenthesis the maximum number of prey items found in the scat for each carnivore on farmland and in Anysberg Nature Reserve in the Karoo.

	Number of scats with one prey item	Number of scats with two prey items	Number of scats with three or more prey items
Jackal	122	194	101 (max. = 4)
Caracal	59	82	41 (max. = 4)
Leopard	13	32	13 (max. = 5)
Total	**194**	**308**	**155**

Anysberg Nature Reserve **Farmlands**



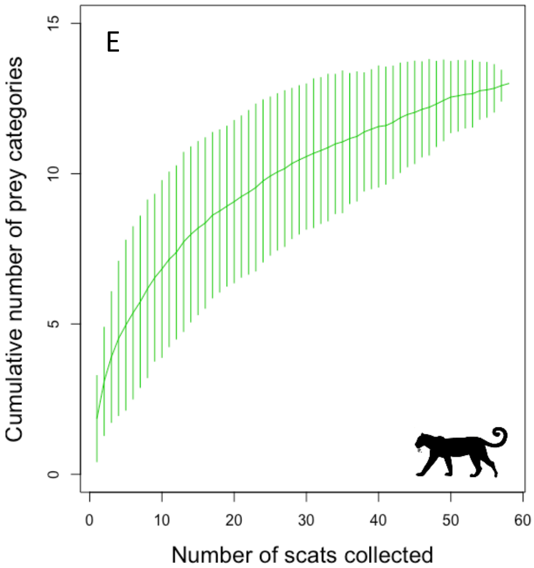


Figure 4.5. Species accumulation curves with 95% confidence intervals for A: 12 prey groups recorded in 201 black-backed jackal scat samples collected in the reserve; B: 15 prey groups recorded in 216 black-backed jackal scat samples collected on farmland; C: 12 prey groups recorded in 80 caracal scat samples collected in the reserve; D: 13 prey groups recorded in 102 caracal scat samples collected on farmland; and E: 15 prey groups recorded in 58 leopard scat samples collected in the reserve.

There were clear dietary differences between mesopredators within and between the two sites (Tables 4.7 and 4.8). On farmland, domestic ungulates dominated the scats of both jackals and caracals in terms of frequency of occurrence (57% and 24% respectively), RFO, percent volume, percent mass and ingested biomass. Within the reserve, micromammals for caracal (Table 4.7) and fruit for jackal (Table 4.8) were most prevalent in terms of frequency of occurrence, RFO, percent volume, percent mass and ingested biomass. Leopard scats were dominated by mountain-dwelling ungulates in terms of frequency of occurrence, RFO, percent volume, percent mass and ingested biomass (Table 4.9).

Domestic ungulates (25%, incl. sheep 16%), micromammals (14%, incl. Karoo bush rat (*Otomys unisulcatus*): 6%) and both wild ungulates (12%, incl. common duiker: 10%) and invertebrates (12%) were the most frequently found prey items in caracal scats on farms, while micromammals (58%, incl. Karoo bush rat: 26%), invertebrates (13%) and both birds (5%) and wild ungulates (5%, incl. common duiker: 5%) were most frequently found in caracal scats in the reserve (Table 4.7). Micromammals occurred in caracal scats more often in the reserve than on the farmland (χ^2= 23.432, P ≤ 0.001). On the other hand, there was no significant difference in the occurrence of invertebrates and wild ungulates between the reserve and farmland (χ^2= 0.157, P = 0.265, and χ^2= 1.270, P = 0.196, respectively).

For jackals on farmland, domestic ungulates (42%, incl. sheep: 25%) were the most frequently detected prey, followed by invertebrates (11%) and micromammals (10%, incl. Karoo bush rat: 5%), while fruits and seeds (41%, incl. common guarri *Euclea undulata*: 99%), micromammals (36%, incl. Karoo bush rat: 22%) and invertebrates (8%) were the most frequently recorded prey items in jackal scats in the reserve (Table 4.8). There was a significantly higher relative frequency of occurrence of micromammals in the scats collected in the reserve compared with farmland (χ^2= 11.357, P ≤ 0.001). Similarly, fruits were significantly more prevalent in the scats in the reserve than on farmland (χ^2= 17.165, P ≤ 0.001). Despite the frequency of occurrence of invertebrate and wild ungulate remains in the scats being higher on farmland than in the reserve, there was no statistically significant difference between the two types of land use for these two prey types (χ^2= 0.15747, P = 0.803 and χ^2= 0.1631, P = 0.288 respectively).

Leopards consumed wild ungulates most frequently (41%, incl. grey rhebok: 16%), followed by micromammals (16%, incl. Karoo bush rat: 8%) and invertebrates (15%) (Table 4.9).

Table 4.7. Dietary items recorded in caracal scats on farmland (in orange, n=102) and in the reserve (in grey, n=80). Number of occurrences shows the number of scats in which each prey item was found. Relative frequency of occurrence is the percentage of each prey item relative to the total number of prey items identified in the scat pool once grass and leaves and non-food items have been removed. The percentage volume is the percent volume a particular item represents divided by the total number of scats. The percentage mass is the percent mass a particular item represents relative to the total mass. Total biomass consumed represents the amount of mammalian prey consumed converted using the calculation of Chakrabarti et al. (2016).

Dietary categories	Number of occurrences (n=214) (n= 198)		Frequency of occurrence per scat (FO, %)		Relative frequency of occurrence (RFO, %)		% Volume		% Mass		Total biomass consumed (kg) (Chakrabarti et al. 2016)	
Invertebrates	17	19	16.67	23.75	12.06	12.75	1.76	0.88	1.70	0.14	-	-
Squamates	0	4	0.00	5.00	0.00	2.68	0.00	0.19	0.00	0.10	-	-
Tortoises	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-	-
Birds (Aves)	6	8	5.88	10.00	4.26	5.37	2.50	2.00	1.33	1.81	-	-
Mammals	109	112	96.08	100.00	77.30	75.17	91.45	96.56	94.38	97.70	-	-
- Small rodents	20	86	15.69	80.00	14.18	57.72	15.25	75.6	15.98	68.54	-	-
Southern African Vlei Rat *Otomys irroratus*	3	6	2.94	7.50	2.13	4.03	2.79	6.81	2.42	4.44	0.33	0.65
Karoo Bush Rat *Otomys unisulcatus*	9	39	8.82	48.75	6.38	26.17	8.24	40.45	8.58	38.62	0.96	4.17

Dietary categories	Number of occurrences (n=214)	(n= 198)	Frequency of occurrence per scat (FO, %)		Relative frequency of occurrence (RFO, %)		% Volume		% Mass		Total biomass consumed (kg) (Chakrabarti et al. 2016)	
Grant's Rock Rat *Aethomys granti*	1	1	0.98	1.25	0.71	0.67	0.49	0.25	0.80	0.26	0.11	0.11
Hairy-Footed Gerbil *Gerbillurus paeba*	2	5	1.96	6.2	1.42	3.36	0.82	1.46	1.14	2.34	0.19	0.48
Namaqua Rock Rat *Aethomys namaquensis*	3	29	2.94	36.25	2.13	19.46	1.51	22.10	1.23	20.33	0.30	2.87
Four-Striped Grass Mouse *Rhabdomys pumilio*	2	6	1.96	7.50	1.42	4.03	1.31	4.48	1.82	2.55	0.20	0.59
- Shrews	1	5	0.98	6.25	0.71	3.36	0.33	2.73	0.20	3.18	-	-
Karoo Round-Eared Sengi *Macroscelides proboscideus*	0	5	0.00	6.25	0.00	3.36	0.00	2.73	0.00	3.18	0.10	0.49
Reddish-Gray Musk Shrew *Crocidura cyanea*	1	0	0.98	0.00	0.71	0.00	0.33	0.00	0.20	0.00	0.00	0.00
- Carnivores	8	1	7.84	1.25	5.67	0.67	7.40	1.25	9.70	5.26	-	-
Southern African Wildcat *Felis sylvestris cafra*	1	0	0.98	0.00	0.71	0.00	0.88	0.00	0.58	0.00	0.33	0.00
Cape Grey Mongoose *Herpestes pulverulentus*	4	1	3.92	1.25	2.84	0.67	3.87	1.25	5.27	5.26	0.66	0.17

Dietary categories	Number of occurrences (n=214) (n= 198)		Frequency of occurrence per scat (FO, %)		Relative frequency of occurrence (RFO, %)		% Volume		% Mass		Total biomass consumed (kg) (Chakrabarti et al. 2016)	
Common Genet *Genetta genetta*	1	0	0.98	0.00	0.71	0.00	0.98	0.00	1.38	0.00	0.24	0.00
Bat-Eared Fox *Otocyon megalotis*	2	0	1.96	0.00	1.42	0.00	1.67	0.00	2.47	0.00	0.62	0.00
- Wild ungulates	17	8	16.67	10.00	12.06	5.37	12.60	9.25	12.29	13.09	-	-
Common Duiker *Sylvicapra grimmia*	14	4	13.73	5.00	9.93	2.68	9.80	4.94	8.60	4.41	5.43	1.55
Springbok *Antidorcas marsupialis*	2	0	1.96	0.00	1.42	0.00	1.91	0.00	3.35	0.00	0.78	0.00
Greater Kudu *Tragelaphus strepsiceros*	1	0	0.98	0.00	0.71	0.00	0.88	0.00	0.34	0.00	0.39	0.00
Gemsbok *Oryx gazella*	0	1	0.00	1.25	0.00	0.67	0.00	1.25	0.00	4.54	0.00	0.39
Steenbok *Raphicerus campestris*	0	2	0.00	2.50	0.00	1.34	0.00	1.81	0.00	2.11	0.00	0.77
Klipspringer *Oreotragus oreotragus*	0	1	0.00	1.25	0.00	0.67	0.00	1.25	0.00	2.84	0.00	0.38
- Domestic ungulates	35	1	34.31	1.25	24.82	0.67	31.72	0.13	33.66	0.03	-	-
Sheep	23	0	22.55	0.00	16.31	0.00	20.74	0.00	20.43	0.00	8.92	0.00

Dietary categories	Number of occurrences (n=214)	(n= 198)	Frequency of occurrence per scat (FO, %)		Relative frequency of occurrence (RFO, %)		% Volume		% Mass		Total biomass consumed (kg) (Chakrabarti et al. 2016)	
Goat	12	1	11.76	1.25	8.51	0.67	10.98	0.13	13.23	0.03	4.26	0.35
- Cape Porcupine *Hystrix africaeaustralis*	2	0	1.96	0.00	1.42	0.00	0.98	0.00	0.79	0.00	0.77	0.00
- Rock hyrax *Procavia capensis*	10	1	9.80	1.25	7.09	0.67	9.29	0.47	8.93	0.45	3.07	0.31
- Hares spp.	11	7	10.78	8.75	7.80	4.70	9.02	4.75	10.71	5.71	2.93	1.86
- Unidentified mammals	5	3	4.90	3.75	3.55	2.01	4.80	2.44	2.14	1.43	-	-
- Grass and leaves	65	29	63.73	36.25	-	-	3.84	0.13	1.03	0.10	-	-
- Fruit and seeds	4	6	3.92	7.50	2.84	4.03	0.34	0.25	1.53	0.15	-	-
- Anthropogenic food	5	0	4.90	0.00	3.55	0.00	0.10	0.00	0.04	0.00	-	-
- Non-food items	8	20	7.84	25.00	-	-	-	-	-	-	-	-
Niche breadth	-	-	-	-	6.68	4.24	6.08	1.69	5.38	2.03	-	-

Table 4.8. Dietary items recorded in black-backed jackal scats on farmland (in orange, n=216) and in the reserve (in grey, n=201). Number of occurrences shows the number of scats in which each prey item was found. Relative frequency of occurrence is the percentage of each prey item relative to the total number of prey items identified in the scat pool once grass and leaves and non-food items have been removed. The percentage volume is the percent volume a particular item represents divided by the total number of scats. The percentage mass is the percent mass a particular item represents relative to the total mass. The percentage of ingested biomass is the percentage each prey represents in the diet of black-backed jackal based on correction factors of Goszczyński (1974) and Jedrzejewska & Jedrzejewski, 1998.

Dietary categories	Number of occurrences (n=478)	(n=515)	Frequency of occurrence per scat (FO, %)		Relative frequency of occurrence (RFO, %)		% Volume		% Mass		% ingested biomass (Goszczyński 1974, Jedrzejewska & Jedrzejewski, 1998)	
Invertebrates	33	28	15.28	13.93	10.89	7.71	1.66	0.42	1.03	0.18	0.07	0.05
Squamates	1	0	0.46	0.00	0.33	0.00	0.02	0.00	0.03	0.00	0.01	0.00
Tortoises	1	1	0.46	0.50	0.33	0.28	0.05	0.00	0.02	0.00	0.00	0.00
Birds (Aves)	7	13	3.24	6.47	2.31	3.58	0.76	0.77	0.16	0.08	0.07	0.16
Mammals	232	173	100.00	77.61	78.22	47.66	82.64	51.08	84.63	30.33	95.35	40.89
- Small rodents	31	130	12.96	62.19	10.23	35.81	10.07	40.25	13.45	24.46	3.81	32.97
Southern African Vlei Rat *Otomys irroratus*	7	19	3.24	9.45	2.31	5.23	2.13	5.69	2.34	3.38	0.66	4.56
Hairy-Footed Gerbil *Gerbillurus paeba*	3	1	1.39	0.50	0.99	0.28	0.73	0.01	0.95	0.01	0.27	0.00
Karoo Bush Rat *Otomys unisulcatus*	16	80	7.41	39.80	5.28	22.04	5.44	26.84	7.71	15.23	2.19	20.53

Dietary categories	Number of occurrences (n=478) (n=515)		Frequency of occurrence per scat (FO, %)		Relative frequency of occurrence (RFO, %)		% Volume		% Mass		% ingested biomass (Goszczyński 1974, Jedrzejewska & Jedrzejewski, 1998)	
Namaqua Rock Rat *Aethomys namaquensis*	5	17	2.31	8.46	1.65	4.68	1.77	4.71	2.45	2.71	0.69	3.65
Four-Striped Grass Mouse *Rhabdomys pumilio*	0	13	0.00	6.47	0.00	3.58	0.00	3.00	0.00	3.13	0.00	4.23
- Shrews	1	3	0.46	1.49	0.33	0.83	0.15	0.66	0.19	0.30	0.05	0.41
Karoo Round-Eared Sengi *Macroscelides proboscideus*	0	1	0.46	0.50	0.33	0.28	0.15	0.16	0.19	0.13	0.05	0.17
Greater Red Musk Shrew *Crocidura flavescens*	0	1	0.00	0.50	0.00	0.28	0.00	0.25	0.00	0.07	0.00	0.10
Reddish-Gray Musk Shrew *Crocidura cyanea*	0	1	0.00	0.50	0.00	0.28	0.00	0.25	0.00	0.10	0.00	0.14
- Carnivores	5	0	2.31	0.00	1.65	0.00	2.22	0.00	3.18	0.00	1.96	0.00
Cape Grey Mongoose *Herpestes pulverulentus*	3	0	1.39	0.00	0.99	0.00	1.30	0.00	1.11	0.00	0.68	0.00
Common Genet *Genetta genetta*	1	0	0.46	0.00	0.33	0.00	0.46	0.00	1.20	0.00	0.74	0.00
Bat-Eared Fox *Otocyon megalotis*	1	0	0.46	0.00	0.33	0.00	0.46	0.00	0.87	0.00	0.54	0.00
- Wild ungulates	29	17	12.96	8.46	9.57	4.68	8.94	5.39	6.37	2.84	9.26	19.66

Dietary categories	Number of occurrences (n=478) (n=515)		Frequency of occurrence per scat (FO, %)		Relative frequency of occurrence (RFO, %)		% Volume		% Mass		% ingested biomass (Goszczyński 1974, Jedrzejewska & Jedrzejewski, 1998)	
Common Duiker *Sylvicapra grimmia*	14	3	6.48	1.49	4.62	0.83	5.05	0.97	3.65	0.44	5.31	3.01
Red Hartebeest *Alcelaphus buselaphus*	0	3	0.00	1.49	0.00	0.83	0.00	0.27	0.00	0.43	0.00	2.95
Greater Kudu *Tragelaphus strepsiceros*	1	5	0.46	2.49	0.33	1.38	0.23	1.97	0.14	0.85	0.20	5.88
Steenbok *Raphicerus campestris*	8	0	3.70	0.00	2.64	0.00	1.99	0.00	1.97	0.00	2.87	0.00
Springbok *Antidorcas marsupialis*	0	2	0.00	1.00	0.00	0.55	0.00	0.55	0.00	0.42	0.00	2.93
Gemsbok *Oryx gazella*	0	1	0.00	0.50	0.00	0.28	0.00	0.21	0.00	0.12	0.00	0.81
Klipspringer *Oreotragus oreotragus*	6	3	2.78	1.49	1.98	0.83	1.67	1.42	0.60	0.59	0.88	4.07
- Domestic ungulates	125	1	56.94	0.50	41.58	0.28	46.86	0.10	50.55	0.02	73.54	0.11
Sheep	77	0	35.65	0.00	25.41	0.00	26.82	0.00	32.71	0.00	47.58	0.00
Goat	48	1	22.22	0.50	16.17	0.28	20.03	0.10	17.85	0.02	25.96	0.11
- Cape Porcupine ***Hystrix africaeaustralis***	3	4	1.39	1.99	0.99	1.10	0.65	0.25	0.92	0.26	0.57	0.75

Dietary categories	Number of occurrences (n=478) (n=515)		Frequency of occurrence per scat (FO, %)		Relative frequency of occurrence (RFO, %)		% Volume		% Mass		% ingested biomass (Goszczyński 1974, Jedrzejewska & Jedrzejewski, 1998)	
- Rock hyrax ***Procavia capensis***	0	1	0.00	0.50	0.00	0.28	0.00	0.50	0.00	0.12	0.00	0.36
- Hares spp.	13	4	6.02	1.99	4.29	1.10	5.39	1.76	5.97	1.45	3.68	4.25
- Chacma Baboon ***Papio ursinus***	2	0	0.93	0.00	0.66	0.00	0.56	0.00	2.08	0.00	1.28	0.00
- Unidentified mammals	27	13	12.50	6.47	8.91	3.58	7.79	2.18	1.94	0.88	1.19	2.58
- Grass and leaves	108	107	50.00	53.23	-	-	7.13	3.17	2.18	2.83	0.38	2.32
- Fruit and seeds	23	148	10.65	73.63	7.59	40.77	7.72	43.86	11.88	66.58	4.01	56.58
- Anthropogenic food	1	0	0.46	0.00	0.33	0.00	0.02	0.00	0.07	0.00	0.12	0.00
- Non-food items	72	45	33.33	22.39	-	-	-	-	-	-	-	-
Niche breadth	-	-	-	-	6.41	4.95	3.95	2.78	6.85	1.96	-	-

Table 4.9. Dietary items recorded in leopard scats in the reserve (n=58). Number of occurrences shows the number of scats in which each prey item was found. Relative frequency of occurrence is the percentage of each prey item relative to the total number of prey items identified in the scat pool once grass and leaves and non-food items have been removed. The percentage volume is the percent volume a particular item represents divided by the total number of scats. The percentage mass is the percent mass a particular item represents relative to the total mass. Total biomass consumed represents the amount of mammalian prey consumed converted using the calculation of Chakrabarti et al. (2016).

Dietary categories	Number of occurrences (n=162)	Frequency of occurrence per scat (FO, %)	Relative frequency of occurrence (RFO%)	% Volume	% Mass	Mammalian biomass consumed (kg) (Chakrabarti et al. 2016)
Invertebrates	12	20.69	14.63	2.41	1.46	-
Squamates	3	5.17	3.66	0.34	0.10	-
Tortoises	0	0.00	0.00	0.00	0.00	-
Birds (Aves)	1	1.72	1.22	0.69	0.23	-
Mammals	66	100.00	80.49	93.19	97.40	-
- Small rodents	13	18.97	15.85	16.16	8.53	-
Saunder's Vlei Rat *Otomys saundersiae*	1	1.72	1.22	1.21	1.00	0.29
Karoo Bush Rat *Otomys unisulcatus*	7	12.07	8.54	8.81	5.15	2.04
Namaqua Rock Rat *Aethomys namaquensis*	4	6.90	4.88	4.50	1.86	1.14
Four-Striped Grass Mouse *Rhabdomys pumilio*	1	1.72	1.22	1.64	0.53	0.28

Dietary categories	Number of occurrences (n=162)	Frequency of occurrence per scat (FO, %)	Relative frequency of occurrence (RFO, %)	% Volume	% Mass	Mammalian biomass consumed (kg) (Chakrabarti et al. 2016)
- Shrews	1	1.72	1.22	0.43	0.33	-
Forest Shrew *Myosorex varius*	1	1.72	1.22	0.43	0.33	0.28
- Carnivores	3	5.17	3.66	4.31	3.55	-
Leopard *Panthera pardus*	1	1.72	1.22	1.03	0.10	1.09
Southern African Wildcat *Felis sylvestris cafra*	2	3.45	2.44	3.28	3.44	1.20
- Wild ungulates	34	55.17	41.46	46.08	58.92	-
Common Duiker *Sylvicapra grimmia*	12	20.69	14.63	18.19	26.86	13.03
Grey Rhebok *Pelea capreolus*	13	22.41	15.85	18.43	26.44	14.03
Greater Kudu *Tragelaphus strepsiceros*	1	1.72	1.22	1.64	0.95	1.15
Steenbok *Raphicerus campestris*	1	1.72	1.22	0.09	0.01	0.94
Klipspringer *Oreotragus oreotragus*	7	12.07	8.54	7.74	4.66	6.87

Dietary categories	Number of occurrences (n=162)	Frequency of occurrence per scat (FO, %)	Relative frequency of occurrence (RFO, %)	% Volume	% Mass	Mammalian biomass consumed (kg) (Chakrabarti et al. 2016)
- Domestic ungulates	1	1.72	1.22	1.64	0.42	-
Sheep	0	0.00	0.00	0.00	0.00	0.00
Goat	1	1.72	1.22	1.64	0.42	1.15
- Cape Porcupine ***Hystrix africaeaustralis***	5	8.62	6.10	6.29	6.38	5.11
- Rock hyrax Procavia capensis	1	1.72	1.22	1.72	2.72	0.58
- Hares spp.	2	3.45	2.44	2.41	0.6	1.10
- Chacma Baboon ***Papio ursinus***	3	5.17	3.66	4.83	12.61	3.09
- Bushpig ***Potamochoerus larvatus***	2	3.45	2.44	3.19	2.88	2.31
- Unidentified mammals	1	1.72	1.22	6.12	0.47	-
- Grass and leaves	40	68.97	-	3.28	0.75	-
- Fruit and seeds	3	5.17	-	0.09	0.05	-
- Anthropogenic food	0	0.00	0.00	0.00	0.00	-
- Non-food items	10	17.24	-	-	-	-
Niche breadth	-	-	5.60	4.04	2.76	-

According to the biomass models, the total mammalian biomass consumed by caracals on farmland over the entire study period was 30.6 kg while it was 15.2 kg in the reserve (Table 4.7), compared to 55.7 kg for leopards in the reserve (Table 4.9). For jackals, the total biomass of all dietary items consumed on farmland over the entire study period was 59.1 kg (incl. 56.4 kg of mammalian dietary items) while it was 38.9 kg (incl. 15.9 kg of mammalian dietary items and 22.0 kg of fruit) in the reserve (Table 4.8).

Caracals on farmland mostly consumed domestic ungulates (Figure 4.6). They consumed 8.9 kg of sheep (29% biomass), 5.4 kg of common duiker (18% biomass) and 4.3 kg of goat (14% biomass) over the entire study period, while in the reserve they mostly consumed micromammals (Figure 4.6), in particular 4.2 kg of Karoo bush rat (27% biomass), 2.9 kg of Namaqua Rock Rat *Micaelamys namaquensis* (19% biomass), and 1.9 kg of hares (12% biomass) (Table 4.7).

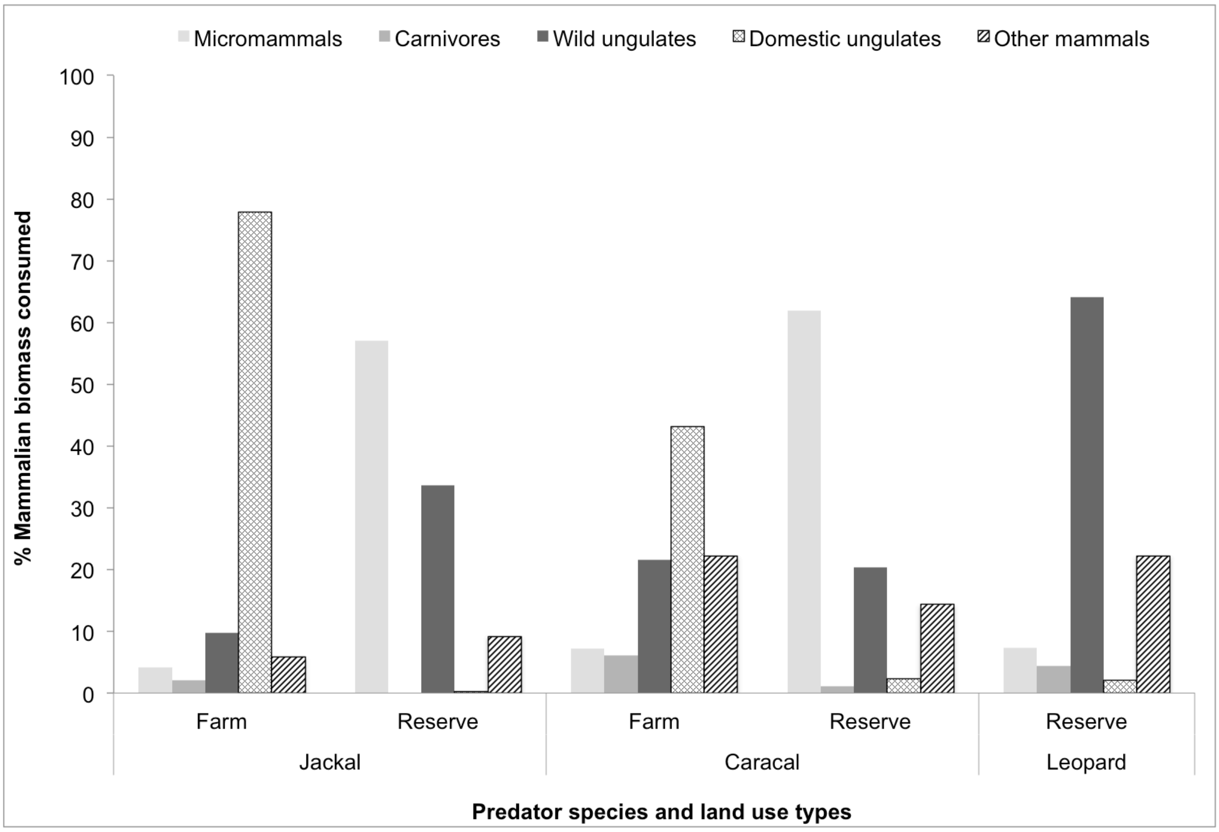


Figure 4.6. Percentage of mammalian prey biomass consumed for the five main mammalian food groups in the diet of black-backed jackal and caracal on small-livestock farms and in Anysberg Nature Reserve in South Africa, September 2012 to May 2015. The category "Other mammals" includes all the mammals not fitting in the other categories, including hares, rock hyrax and Cape porcupine.

Jackals on farmland mostly consumed domestic ungulates too (Figure 4.6). They consumed 28.1 kg of sheep (48% biomass), 15.3 kg of goat (26% biomass) and 3.1 kg of common duiker (5% biomass), while in the reserve, they consumed 22.0 kg of fruit (56.6% biomass), 8 kg of Karoo bush rat (20% biomass) and 2.3 kg of greater kudu (6% biomass) (Table 4.8) over the entire study period. Leopards mostly consumed wild ungulates (Figure 4.6), in particular 14.0 kg of grey rhebok (25% biomass), 12.9 kg of common duiker (23% biomass), and 6.7 kg of klipspringer *Oreotragus oreotragus* (12% biomass) over the entire study period (Table 4.9).

Birds were recorded at a relatively low frequency on farms (caracal: 6%; jackal: 3%) and in the reserve (caracal: 10%; jackal: 6%; leopard: 2%) and they never represented more than 1% of the biomass ingested by any of the three predators. Invertebrates occurred in a range from 14 to 24% of the scats (jackal in the reserve and caracal in the reserve respectively) but were negligible in terms of percent mass for all three predators. Fruit represented a very low percent mass in the diets of caracal and leopard, as expected. However, they represented an important percentage of the ingested biomass for jackals in the reserve (56.6%), but not on farms (4.0%). In the reserve, 99% of the fruits consumed were the common guarri while on farms, 79% of the fruits consumed were from the bluebush (Tables 4.7, 4.8 and 4.9).

I infrequently found remains of small carnivores in the diets of mesopredators and they mostly occurred on farms. They included Cape grey mongoose, bat-eared fox, small-spotted genet and African wildcat (Tables 4.7 and 4.8). I did not find any evidence of intraguild predation – an extreme case of interference competition (Polis et al., 1989) – between jackal, caracal and leopard, but I did find one event of intra-species predation (or scavenging) in one leopard scat (very large amount of leopard hairs with some still attached to the skin, presence of large bone fragments and absence of hairs from other prey species).

Only tortoises were not recorded in any of the two sites in caracal scats. Squamates were also not recorded in caracal scats coming from farms. Rock hyraxes were not recorded in jackal scats coming from farms and squamates, carnivores and anthropogenic food were not recorded in jackal scats coming from the reserve. In the category "other mammal", chacma baboons were recorded in the scats of jackals coming from farms and in the scats of leopards, along with bushpigs. Goats, not found in the reserve and not detected by my intensive camera trap surveys, occurred rarely in the three carnivore diets in the reserve (1 occurrence each time) and likely originated from adjacent farms.

Dietary breadth and niche overlap

I calculated Levin's measure of niche breadth (B) with the frequency of occurrence, percent volume and percent mass results. When the 17 food categories were considered (I removed the "unidentified mammals" category) and regardless of the method used, B values varied both between species and study sites. B was higher on average on farmland than in the reserve and highest for caracal on farmland (Tables 4.7 to 4.9).

Estimates of dietary niche overlap varied markedly with the method used to assess the diet (i.e. from O=0.1 to O=0.6 for leopards and jackals in the reserve; Figure 4.7) and was also higher when calculated using qualitative methods versus quantitative methods. The highest dietary overlap was between mesopredators on farmland (O=0.7 to O=0.9; Figure 4.7), and to a lesser extent within the reserve (O=0.3 to O=0.8; Figure 4.7). There was limited dietary overlap for either jackals or caracals between sites, and dietary overlap between leopards and both mesopredators in the reserve was low (Figure 4.7).

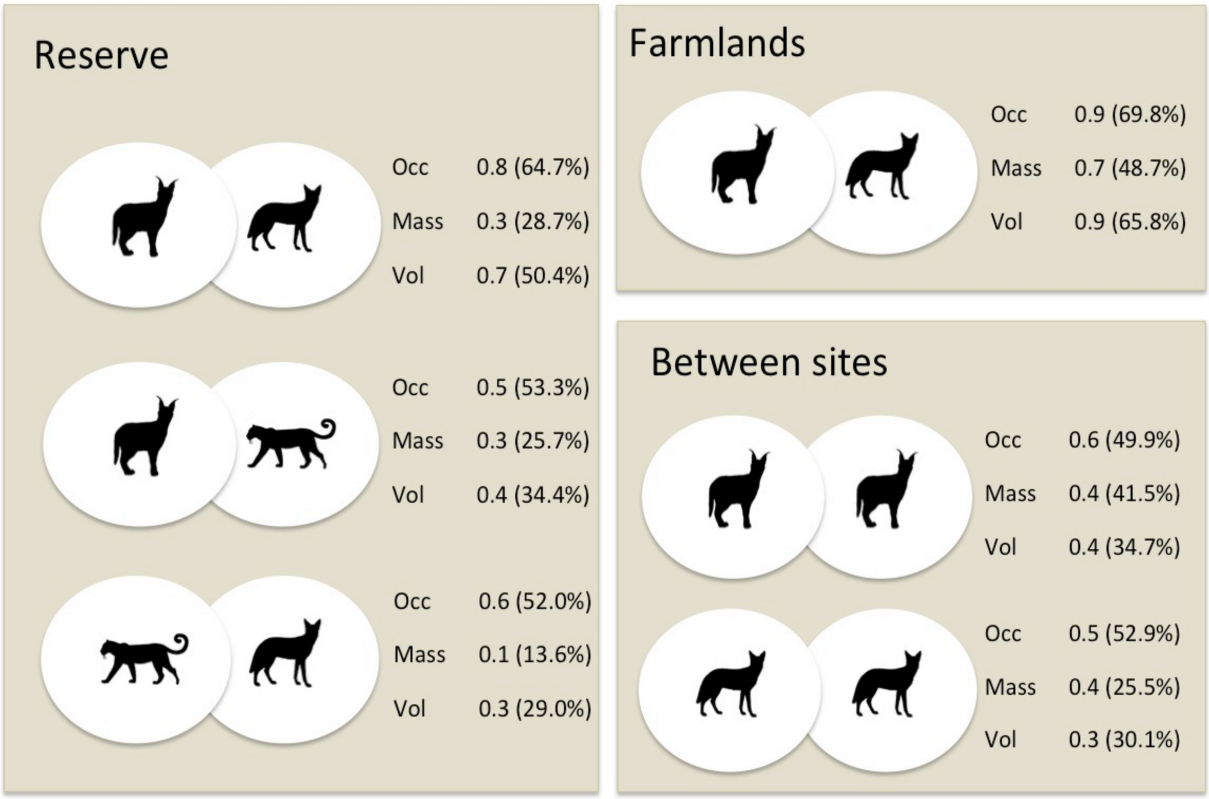


Figure 4.7. Diagrams representing the different values for the Pianka's index of dietary overlap and the percentage of overlap (in parenthesis) for three different methods: Occ=Frequency of occurrence, Mass=Percentage mass, and Vol=Percentage volume, between the three predators in the reserve, on farmlands and between sites.

Prey preference

Dietary preference varied between the types of land use and between jackal, caracal and leopard (Tables 4.10 and 4.11). Regarding livestock, jackals (*D* = 0.90) and caracals (*D* = 0.77) consumed goats more than expected given goats' relative abundance on farmland, and jackals showed preference for sheep (*D* = 0.57) (Figure 4.8), while caracals consumed them in accordance with their availability (*D* = 0.19) (Table 4.10, Figure 4.9). Leopards consumed more mountain-specialists (i.e., grey rheboks and klipspringers) than expected given their relative abundance.

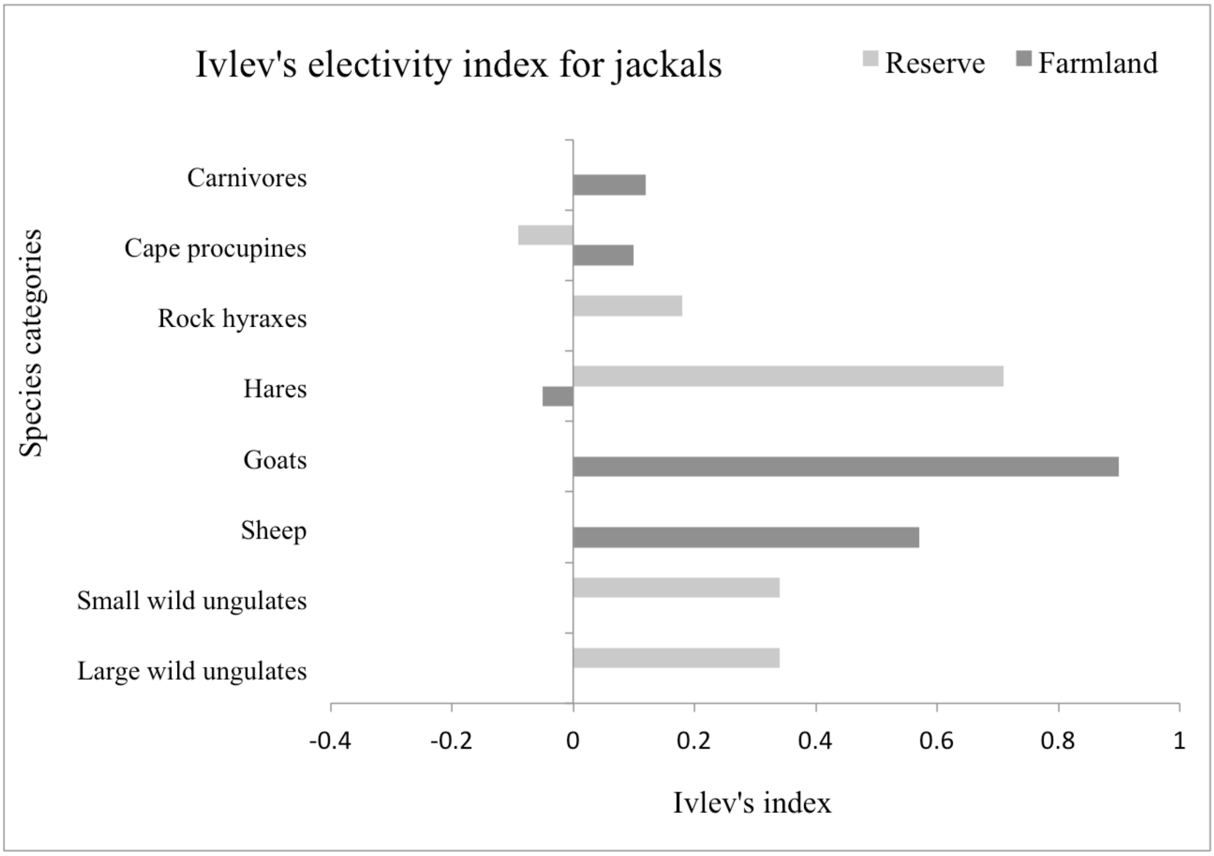


Figure 4.8. Ivlev's electivity indices (*D*) for eight mammalian species categories for black-backed jackals, in the reserve and on farmland, South Africa, September 2012 to May 2015.

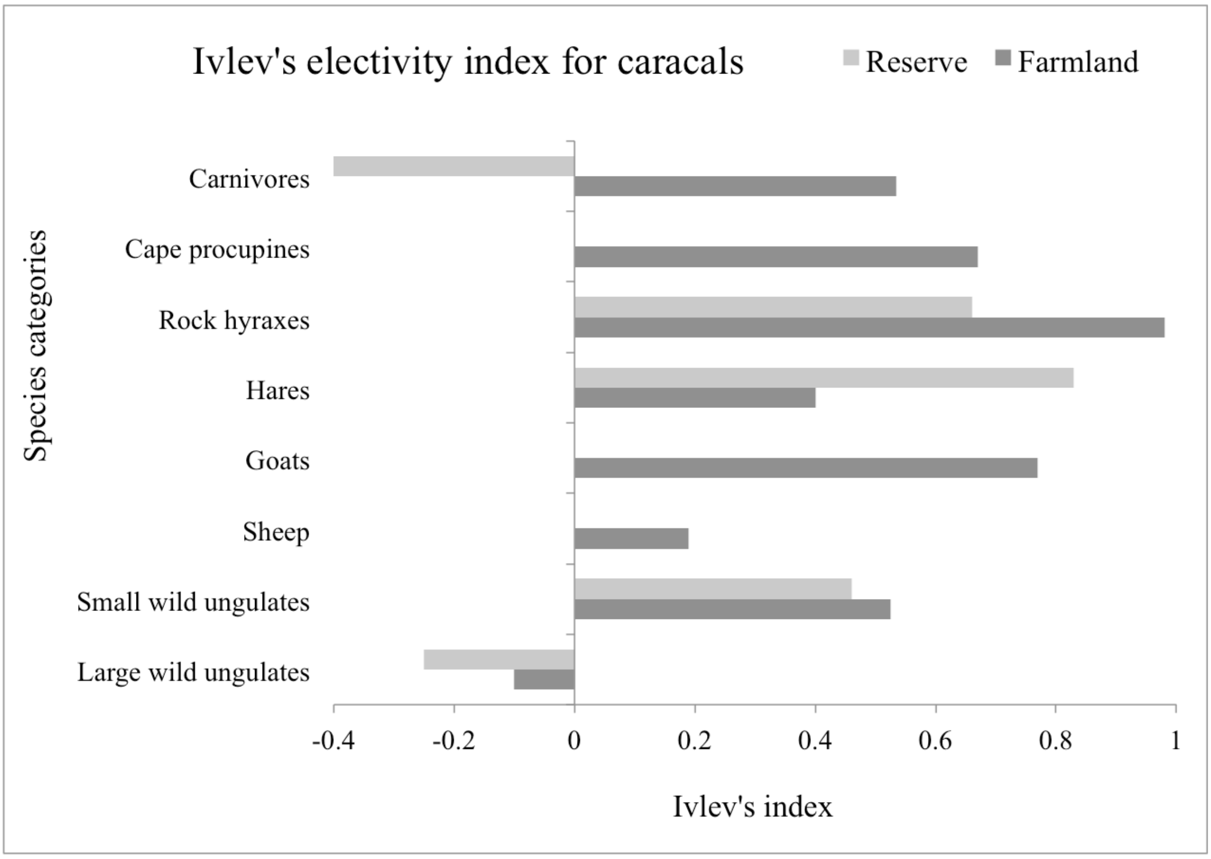


Figure 4.9. Ivlev's electivity indices (*D*) for eight mammalian species categories for caracals, in the reserve and on farmland, South Africa, September 2012 to May 2015.

Table 4.10. Summary of the number of independent photographs of each prey species taken on farmland by 176 camera traps, and their relative abundance indices (RAI). Jacobs' indices for both mesopredators were calculated based on the biomass model values for mammalian prey species.

Prey species	Number of photos	RAI	Scat biomass caracal	Jacobs' index caracal	Scat biomass jackal	Jacobs' index jackal
Bat-eared fox	218	1.7	0.02	0.09	0.01	-0.50
African wildcat	10	0.1	0.01	0.87	0.00	NA
Cape grey mongoose	37	0.3	0.02	0.77	0.01	0.43
Small-spotted genet	42	0.3	0.01	0.41	0.01	0.42
Chacma baboon	95	0.7	0.00	NA	0.01	0.30
Hare	556	4.3	0.10	0.40	0.04	-0.05
Cape porcupine	65	0.5	0.03	0.67	0.01	0.10
Common duiker	957	7.4	0.18	0.46	0.06	-0.14
Steenbok	702	5.4	0.00	NA	0.03	-0.29
Klipspringer	51	0.4	0.00	NA	0.01	0.41
Greater kudu	134	1.0	0.01	-0.10	0.00	NA
Springbok	86	0.7	0.03	0.59	0.00	NA
Rock hyrax	14	0.1	0.10	0.98	0.00	NA
Sheep	2836	21.9	0.29	0.19	0.51	0.57
Goat	266	2.1	0.14	0.77	0.28	0.90

Table 4.11. Summary of the number of independent photographs of each potential prey species taken in Anysberg Nature Reserve by 156 camera traps, and their relative abundance indices (RAI). Jacobs' indices for both mesopredators and leopard were calculated based on the biomass model values for mammalian prey species.

Prey species	Number of photos	RAI	Scat biomass caracal	Jacobs' index caracal	Scat biomass jackal	Jacobs' index jackal	Scat biomass leopard	Jacobs' index leopard
African wildcat	97	0.9	0.00	NA	0.00	NA	0.02	0.44
Cape grey mongoose	49	0.5	0.01	-0.41	0.00	NA	0.00	NA
Chacma baboon	537	5.1	0.00	NA	0.00	NA	0.06	0.09
Hare spp.	138	1.3	0.12	0.83	0.07	0.71	0.02	0.17
Cape porcupine	112	1.1	0.00	NA	0.01	-0.09	0.09	0.81
Common duiker	320	3.0	0.10	0.57	0.05	-0.27	0.23	0.81
Steenbok	108	1.0	0.05	0.68	0.00	NA	0.02	-0.25
Klipspringer	211	2.0	0.03	0.12	0.07	0.57	0.12	0.74
Oryx	441	4.2	0.03	-0.25	0.01	-0.51	0.00	NA
Greater kudu	80	0.8	0.00	NA	0.10	0.87	0.02	-0.47
Springbok	91	0.9	0.00	NA	0.05	0.72	0.00	NA
Grey rhebuck	73	0.7	0.00	NA	0.00	NA	0.25	0.96
Red hartebeest	115	1.1	0.00	NA	0.05	0.66	0.00	NA
Rock hyrax	45	0.4	0.02	0.66	0.01	0.18	0.01	-0.43
Bushpig	4	0.0	0.00	NA	0.00	NA	0.04	0.98

Discussion

Overall diet of predators

In this chapter I explored the diet of two sympatric mesocarnivores, the jackal and the caracal, living within two different types of land use under semi-arid conditions. Diet varied markedly both between species and for each species in different types of land use, suggesting both niche partitioning and dietary flexibility. These findings are similar to those from previously published studies (Tables 4.1, 4.2) and largely attributed to both species being dietary generalists and capable of adapting to human-modified habitats with divergent prey bases.

In Anysberg Nature Reserve, jackals mostly ate fruit and micromammals, which is similar to what has been found in other PAs (Grafton, 1965; Kaunda and Skinner, 2003; Kok and Nel, 2004; Loveridge and Macdonald, 2003; Rowe-Rowe, 1983; van der Merwe et al., 2009). I was not able to assess fruit availability in the reserve, but the common guarri made up 99% of the fruit found in jackal scats (RFO: 41%). Guarri fruits were found on bushes from April to September (Coates Palgrave and Coates Palgrave, 2002) and jackals continued to feed on ground-fallen and dried fruit for a further two months (pers. obs.).

On farmland, jackals fed predominantly on domestic ungulates (RFO: 41.6%), especially sheep (RFO: 25.4%). This result is similar to other studies recording livestock feeding in jackals, with RFO ranging from 3.4% to 48.1% with a mean of 21.6 % (Bothma, 1971a; Grafton, 1965; Kamler et al., 2012a; Kok and Nel, 2004; Rowe-Rowe, 1983). In this study, the higher levels of consumption of domestic ungulates on farms by jackals – and to a lesser extent by caracals – may be explained by the higher RAI of this prey category relative to natural prey items in this arid environment (see Chapter 3). Within the livestock dietary category, goats were consumed less than sheep, which may be explained both by their lower RAI and different husbandry, with goats often being kept closer to farmhouses and managed more intensively than sheep (Kamler et al., 2012a; pers. obs). Dietary studies for jackals living on game farms in the Nama-Karoo reveal a much higher RFO of wild ungulates, with Klare et al. (2010) reporting values of >50% of the diet, compared to <10% in my study. Similarly, Van de Ven et al. (2013) recorded that large wild ungulates comprised an important part of the jackal diet in a private game reserve in the East of the Great Karoo. The latter being similar to what Kamler et al. (2012a) found in a private small-livestock farm in the Free State Province. The detection of baboon hairs in jackal scats almost certainly represents opportunistic scavenging of baboon carcasses that are discarded on farms that routinely cage-capture and cull baboons (see Chapter 6).

At both study sites, caracals caught and consumed a wide range of prey taxa and prey sizes, a finding supported by previous work on this species (Avenant and Nel, 2002; Skinner and Chimimba, 2005; van Heezik and Seddon, 1998). Caracals in the reserve fed primarily on micromammals, especially the Karoo bush rat, and invertebrates, results that are also supported by previous studies in PAs (Avenant and Nel, 1997; Melville et al., 2004; Mukherjee et al., 2004; Palmer and Fairall, 1988). On farmland, there was a high incidence of domestic livestock predation, which is similar to the findings of Pringle and Pringle (1979) and Stuart (1982) for the same type of land use type. Caracals on farmland rarely consumed antelopes, which differs from the findings of Stuart (1982) and Mukherjee et al. (2004) who analysed stomach contents and scats respectively. Invertebrates had a higher RFO than for caracals in more mesic areas of South Africa, suggesting that when preferred prey (e.g. rock hyrax) are limited they may use invertebrates as fall-back foods (Kok and Nel, 2004), that are rarely consumed in most other conditions (Palmer and Fairall, 1988).

Evidence for greater carnivory in caracal than jackal was absent on farmland, despite caracal dentition being more specialized for eating meat (Kok and Nel, 2004). I found a low number of birds in the diet of caracal at both sites, which has also been reported in other studies conducted in the Karoo (Grobler, 1981; Palmer and Fairall, 1988). This may be explained by the sparse vegetation cover on farms, limiting the opportunities for caracals to stalk their prey and/or by a low density of avian species, neither of which was quantified in this study (but see RAIs and occupancy probabilities of ground bird species on farmland in Chapter 3, which are low). Furthermore, studies based on stomach contents generally report a higher percentage of bird remains than those based on faeces (Cavallini and Volpi, 1996). Contrary to Palmer and Fairall (1988), who found that caracals had a strong preference for hyrax in the Karoo National Park, scat analysis in my study showed that caracals rarely consumed them, probably because of a low abundance of the species on farmland and in the reserve (RAI of 0.1 and 0.4 respectively) and low occupancy probabilities in both types of land use (see Chapter 3).

Despite my limited collection period (Sep–Mars or May), I would argue that my general results are not temporally constrained to the period of collection regarding small-livestock predation because farmers in this area were either lambing throughout the year or in April, May, or

September, resulting in lambs being available throughout the year at the landscape level (see Chapter 6). The availability of micromammals might have been different during the 3–4 months I did not sample because of varying rainfall (Avery et al., 2005), but there is evidence that for the Karoo, the diet of jackal remains stable across all seasons in terms of biomass consumed (Van de Ven et al., 2013).

Despite the 12 934 camera trap nights conducted on farmland, no leopard was photographed (see Chapter 3) and no scat was found on farmland, which I expected due to the historical control of the species in the area (van Sittert, 2016), the negative attitudes towards leopard and the current high level of lethal control in the region (see Chapter 6). Similar to previous studies in the Western Cape Province (Martins et al., 2011; Norton et al., 1986; Rautenbach, 2010; Stuart, 1982), leopards in Anysberg Nature Reserve fed mostly on wild ungulates typically associated with mountainous areas. Studies from the Western Cape mountains found hyrax to be a common prey item for leopards (Martins et al., 2011; Norton et al., 1986). However, similar to the finding for caracal scats, rock hyraxes seldom occurred in the scats of Anysberg leopards. Micromammals were the second most consumed mammalian group for leopards in Anysberg – a finding similar to other studies conducted in the Western Cape mountains, especially when hyraxes were not often detected (Braczkowski et al., 2012b; Norton et al., 1986; Ott et al., 2007).

Dietary niche breadth and overlap

Mesopredators on farmland consumed a broader spectrum of dietary items than their counterparts and leopard in the reserve, with caracal on farmland having a broader dietary niche than jackal. The latter finding is contrary to other studies showing that felids in general include fewer food categories in their diet than canids (Kruuk, 1986). Predators with a larger niche breadth are known to be more successful in adapting to changing land use because more prey is available to them and they are less vulnerable to dietary competition and prey fluctuation (Hayward and Kerley, 2008). This large niche breadth for the species, along with the absence of larger cat species on farmland, could partly explain why caracal seems to be doing well in that land use (i.e. higher RAI and probability of use on farmland than in the reserve compared to jackal, see Chapter 3), on fenced ranches relative to a national park in Kenya (Kinnaird and O'Brien, 2012) and on livestock farms relative to PAs in the Klein Karoo (Mann, 2014). My results for the Levin's measure of niche breadth for jackal were similar to those found by Klare et al. (2011).

In this study, dietary niche overlap between jackal and caracal on farmland was higher (0.88) than has been shown for morphologically similar species from the same family. For example, Loveridge and Macdonald (2002) reported a value of 0.84 between black-backed and side-striped jackals, which is the same value that Andheria et al. (2007) found between tiger and leopard in India, and similar to the average value of 0.92 between dingo and red fox (Cupples et al., 2011). The only other study to find such a high dietary overlap between a canid and a felid (0.96) was between red fox and wild cat (Carvalho and Gomes, 2001), both very adaptable species with large dietary niche breadth. More typically, the dietary overlap between species belonging to different families is less, with for example Andheria et al. (2007) reporting a dietary overlap of 0.75 between tiger and dhole, whereas Thornton et al. (2004) provided a value of 0.49 between coyote and bobcat.

I suggest that it is the mutual reliance on domestic ungulates by both mesopredators on farms that explains the higher interspecific dietary niche overlap compared to the reserve. Sympatric species can coexist with high trophic niche overlap (e.g. Lanszki et al. (2006) for golden jackal and red fox) as long as food resources are abundant. I would argue that food was not a limiting factor on farms because livestock were not typically guarded and occurred in large fenced camps with artificial water sources (Archer, 2000) allowing them to persist at higher densities than natural prey would be expected to achieve under ambient conditions. Many farmers also do not remove carcasses of dead animals on their farms, creating scavenging opportunities for the predators (pers. obs.). Thus, exploitative competition between the two mesopredators on farms is unlikely to be severe. Nevertheless, Donadio and Buskirk (2006) argued that carnivores that have high dietary overlap are likely to have more frequent encounters as they seek similar prey. Farming may exacerbate this scenario as livestock are rotated between camps and hence, they are spatially clumped in the landscape attracting predators to particular areas. These competitive encounters can result in interspecific aggression or killing over the contested resource. Even if no evidence of intraguild predation (Polis et al., 1989) between jackal, caracal and leopard was found during my study, farmers in the region frequently report that jackal and caracal prey on each other's young (see Chapter 6). Interspecific killing has been reported between the two mesopredators (Do Linh San et al., 2009; Grobler, 1981; Kok and Nel, 2004; Melville et al., 2004), and in one account, a caracal treed by two jackals leapt on one and killed it (Davies, 1997). It was also recorded between leopard and jackal (https://www.youtube.com/watch?v=VAFBVbS4rlc; https://www.youtube.com/watch?v=sD0U_zzjaSI, accessed October 12th 2016), with leopards occasionally specializing on jackals (Kingdon, 2015) and between leopard and caracal (http://africageographic.com/blog/cat-fight-leopard-vs-caracal/, accessed October 12th 2016), and is common in terrestrial carnivores (Palomares and Caro, 1999).

Scat analysis cannot confirm if a prey item was actively hunted or scavenged. However, given that in my study sites, jackals rarely ate prey too large for them to have killed themselves (>springbok size), this is perhaps suggestive that leopards were not facilitating facultative scavenging by jackals, which is also in accordance with the fact that jackals and leopards do not use the PA in the same way (i.e. jackals favour lower grounds and plains with high MSAVI2 values whereas leopards' probability of use increased with elevation and with lower MSAVI2 values, see Chapter 3). In cases where the hairs of large ungulates were detected in jackal scats, it typically included large volumes, which I attributed to feeding on neonates of the species rather than scavenging, which seldom results in large volumes of hair in the scat (pers. obs. when inspecting GPS cluster kill sites and finding both the carcass of the prey and scat from the predator). Moreover, jackals are omnivorous (Kamler et al., 2012a), whereas leopards are obligate carnivores (Chakrabarti et al., 2016), which can explain the different prey choices between these species and the resulting low dietary overlap between them (range: 0.1-0.6). Jackals had a more flexible diet in the reserve where they mostly consumed berries, micromammals and invertebrates, resulting in decreased dietary overlap with caracals as well compared to farmland. The dietary overlap between caracal and leopard in the reserve was low. The size difference between the two cat species, with caracal weighing on average 12 kg and leopards 35 kg in the area, could explain the different prey choices (Kok and Nel, 2004).

Prey preference

Within the mammal group, wild prey were always selected over domestic ungulates by caracal on farmland but not by jackal. Neonates of wild ungulates that display the hider maternal care strategy (e.g. springbok, klipspringer, common duiker, greater kudu) are more vulnerable to wide-ranging opportunistic predators (Carl and Robbins, 1988), which might explain why they were consumed by both predators, whereas young of species classified as "followers" (e.g. mountain zebra, blesbok) were never consumed at either site. These findings are similar to those reported by Klare et al. (2010) on two game ranches in South Africa. Inside the "hider" category, common duiker was the most commonly consumed wild ungulate but springbok – an economically important species in game farms in the region – was preferred by mesopredators.

In their study, Kamler et al. (2012a) showed that jackals selectively consumed whichever group of ungulates (wild or domestic) was producing offspring and preferred wild ungulates <50 kg over sheep if both were birthing. In my study on farmland, I rarely found wild ungulates in jackal scats (<RFO 10%). The apparent preference of jackals for domestic over similar-sized wild ungulates is an unusual finding and suggests that in my study area, jackals tend to specialize on goats and sheep, perhaps because they are more profitable prey than similar-sized wild animals (minimal food acquisition time and maximal net energy gain).

In Anysberg Nature Reserve, jackals' preference for small ungulates such as steenbok and duiker could have been reinforced by the higher probability of use by these two species of plains and lower elevation ground, similarly to jackals (see Chapter 3), possibly favouring encounters. Leopards showed preference for mountain-dwelling antelopes, probably as a consequence of the greater availability of this resource in the mountains (i.e. higher elevation) that leopards mostly use in the Western Cape (Norton et al., 1986) and in Anysberg in particular (see Chapter 3). Baboons were consumed in accordance with their availability, which is similar to previous studies recording low levels of primate predation in the Western Cape (Braczkowski et al., 2012b; Martins et al., 2011; Norton et al., 1986; Rautenbach, 2010). Together, my results confirm that dietary differences were higher between sites than between predators at either site. This reflects the marked impact of land use on prey composition and availability, as shown in Chapter 3, and the ability of mesopredators to adapt their diet to include domestic livestock and persist on farmland despite continuous lethal control.

Conclusion

My results confirm an established picture of jackal and caracal as highly adaptable predators with flexible, opportunistic diets. I found that both jackal and caracal consumed small-livestock on farmland, but that no trace of sheep remains was evident in scat collected in the PA (n = 1 scat with goat remains for each mesopredator). This result suggests that there is no evidence for the widely held belief amongst farmers in the area that these predators leave the PA to predate sheep on farmland. This information could potentially help mitigate the conflict between small-livestock farmers and wildlife managers, although it is still likely that the PA provides a source of dispersing predators to recolonize territories rendered vacant on farmland by culling efforts (see Minnie et al., 2018b; Tensen et al., 2018). High relative abundance of livestock on farmland, together with my finding that jackals prefer livestock over similar-sized wild prey, suggest that reducing depredation will require that farmers reduce the availability of their livestock to predators by actively protecting them, even when wild prey is available.

APPENDIX 4A
PREDATOR SCAT CHARACTERISTICS

Table S4.1. Percentage of predator scats found in Anysberg Nature Reserve and on farmland, per species and colour category.

Colour of predator scats (% per category)			
	Jackal N=417	Caracal N=182	Leopard N=58
Black	39.7	6.0	7.8
White	18.7	31.3	39.1
Brown	14.8	10	21.9
Pale brown	13.4	7.1	10.9
Grey	11.4	45.6	20.3
Red	1.5	0	0
Yellow	0.5	0	0

Table S4.2. Percentage of predator scats found in Anysberg Nature Reserve and on farmland, per species and shape category.

Shape of predator scats (% per category)			
	Jackal N=417	Caracal N=182	Leopard N=58
Blunt ends	37.5	89.2	93.7
Pointed ends	53	8.1	6.3
Indeterminate ends	9.5	2.7	0
Segmented	3.1	75.3	78.1
Not segmented	95.9	21.5	21.9
Indeterminate	1	3.2	0

CHAPTER 5

Global Positioning System location clusters to study mesocarnivore predation on farmland? A comparison of dietary estimates with scat analysis

Using the GPS cluster method to locate a kill site (lamb) from a collared black-backed jackal on a farm in the Central Karoo, South Africa. © Nathalie Houdin & Denis Palanque – The Karoo Predator Project.

Abstract

Studying the feeding ecology of mesopredators in conflict with livestock farmers is important because it allows for an independent assessment of the livestock losses reported by farmers. However, obtaining data on direct predation is difficult and assessing diet through scat analysis only cannot confirm whether prey was actively hunted or scavenged (see Chapter 5). In this chapter I used Global Positioning System (GPS) clusters obtained from GPS collars to inspect potential feeding sites and prey remains from 11 collared caracals on farmland (n=107 cluster locations) and nine collared jackals (n=105 cluster locations) on farmland and in Anysberg Nature Reserve. I further investigated the proportion of livestock prey that were scavenged versus depredated and whether jackals that reside in Anysberg Nature Reserve had clusters on neighbouring farmland that contained livestock remains. In addition, these data allowed me to explore the impacts of sex and age differences in the predation of livestock and wild prey species within small, medium and large size categories. The success rate of finding a kill site when investigating GPS location clusters was significantly higher for caracal than for jackal. Most clusters for both species were classified as predation events, with only 16.2% and 4.7% classified as scavenging events for jackal and caracal respectively. Both species were more likely to kill from dusk to dawn (between 18:00 and 6:00 hr). On farmland, most jackal (63%) and caracal (32%) predation was on livestock whereas in the reserve, all jackal feeding sites were scavenging events. No clusters formed on farmland by Anysberg resident jackals contained livestock remains. GPS clusters provided a much higher estimation of sheep biomass consumed than scats (see Chapter 4). Caracal clusters revealed prey ranging in size from small to large whereas jackal clusters only had medium and large prey categories. For caracal, there was no significant difference between sexes in the consumption of prey within small, medium and large size categories, but subadults consumed small prey more frequently than adults and livestock less frequently. Adult male caracals depredated significantly more on livestock than any other sex and age category. Similar to previous studies on a range of larger carnivores, GPS clusters and scats produced very different estimates of diet composition. While scats provide a less invasive and generally more complete picture of mesopredator diet, GPS clusters can provide spatio-temporal and individual predator characteristics associated with predation, as well as important information on the frequency of livestock predation versus scavenging, a hotly contested subject of debate amongst farmers and environmentalists.

Introduction

Human-wildlife conflict can arise when resources are limited and wildlife's needs come into conflict with people's interests (Madden, 2004; Woodroffe et al., 2005). The use of rangelands for livestock production epitomizes conservation conflicts between wildlife preservation and socio-economic activities (Baldi et al., 2001; Saberwal, 1996; Chapter 1). Low levels of human intervention, extensive rotating camps or paddocks, harsh climatic conditions and complex and dynamic interactions between livestock and wild species, especially carnivores, characterize livestock production on rangelands (Gáspero et al., 2018; Nattrass et al., 2017; Zimmermann et al., 2009).

Attacks on domestic animals are recognized as the main source of conflict between carnivores (medium-sized or large) and humans (Berger, 2006; Macdonald and Loveridge, 2010; Macdonald and Sillero-Zubiri, 2004; Mazzolli et al., 2002; Torres et al., 2018). In a global survey, livestock losses represented 40% of the most frequently cited reasons for conflicts involving carnivores (Sillero-Zubiri and Laurenson, 2001), which is particularly relevant in southern Africa where numerous species of carnivores still occur on private land used for farming (Gusset et al., 2009; Prins, 2000b; Thorn et al., 2012, see Chapter 3). However, the elusive behaviour of many predator species often makes predation difficult to study through direct observation and hence many studies rely on indirect measures such as scat analysis (see Chapter 4). This difficulty in observing predation confounds reliable estimates of livestock loss to predators on farmland, with farmers potentially conflating other causes of livestock loss to predation (Jethva and Jhala, 2004; Polisar et al., 2003; Rosas-Rosas et al., 2008; Treves et al., 2002). Livestock can die of many different causes that are not easily identified, especially in extensive farmland with areas of rugged and brushy terrain (Henne, 1975) such as the Karoo. When remains are found, they have often been partly eaten by scavengers, which prevents an accurate evaluation of the actual cause of death (Rosas-Rosas et al., 2008), and often results in predator misidentification by farmers (Cozza et al., 1996; Montag, 2003).

In Chapter 4, I showed how scats could be used to understand the diet of three potential predators of livestock in two contrasting types of land use and reported that jackal and caracal scats contained what could be proof of heavy predation on small-livestock. Scat analysis is a non-invasive, cost effective method for understanding the diet of carnivores. However, it is also time-consuming to collect and process and the method presents some obvious biases, including overestimating the significance of smaller prey items and underestimating the biomass of large prey consumed (see Chapter 4). More importantly in the case of human-wildlife conflict, scat analysis does not allow for an assessment of the proportion of the diet that was obtained through predation versus scavenging, notably because faecal remnants of killed and scavenged prey are nearly identical (DeVault et al., 2003). Differentiating between predation and scavenging, and locating kill sites in space (Creel and Christianson, 2008; Hebblewhite et al., 2005; Kauffman et al., 2007b) and time (Anderson and Lindzey, 2003; Martins et al., 2011) are important for assessing the severity of the conflict and the potential risks for domestic ungulates.

Previous approaches for locating large carnivore kill sites included aerial or ground monitoring of animals that may or may not be radio-collared. These approaches are constrained by the need for suitable tracking conditions such as snow (Hebblewhite et al., 2005) or sand (Bothma and le Riche, 1994; Melville et al., 2004), in addition to open terrain for detecting carcasses (Dale et al., 1994; Messier and Crête, 1985) and roads to provide quick access when covering large distances. These conditions are rarely all met in extensive rangelands such as the Karoo, making the monitoring of predators and their feeding habits financially and logistically challenging. More recently, Global Positioning System (GPS) collars have been used to collect high resolution spatio-temporal data that allow for the detection of kill sites made by collared predators. This is achieved by post-hoc inspection of the GPS data on a map (e.g. in South Africa, Tambling et al., 2010). When a GPS collar records positions at a fixed interval, then clusters of points in one location reveal a period of residency at a site and may indicate where a medium- to large-sized prey item has been killed and consumed (Knopff et al., 2009). Visitation of GPS clusters that contain a kill provides information on the habitat in which the kill was made (Pitman et al., 2012) and if the prey remains are still intact, may provide information on the physical condition (Husseman et al., 2003) and the sex-age structure of prey (Mills and Shenk, 1992). When these data are combined with the known attributes of the collared individual then the influence of age and sex parameters on diet can be explored (Martins et al., 2011). These data are not obtainable using traditional scat analysis (note however that molecular genetic allows for the identification of individuals and their sex but remains challenging to put in place; Waits and Paetkau, 2005).

On its own or in conjunction with scat analysis, GPS cluster analysis has been increasingly used by ecologists studying the diet of large predators such as grey wolves (Demma et al., 2007; Franke et al., 2006; Sand et al., 2008; Webb et al., 2008), cougars (Anderson and Lindzey, 2003; Bacon et al., 2011; Knopff et al., 2009), jaguars (*Panthera onca*) (Cavalcanti and Gese, 2010), leopards (Martins et al., 2011; Pitman et al., 2014) and lions (Tambling et al., 2012, 2010) and has proved to be effective at locating kill sites. On the other hand, GPS radiocollars, even if they provide researchers with a large dataset to study multiple facets of their focal species ecology by sex and age, are costly and invasive. They are also subject to failure (Hebblewhite et al., 2007) and both sampling intervals and fix rate can influence the probability of finding a kill, especially for small prey (Ruth et al., 2010; Webb et al., 2008). In addition, for researchers using a combination of scats and GPS-located kills, it is evident that the latter method generally biases the diet towards larger prey species that contain more food and require longer handling times, thus underestimating the importance of smaller prey (Bacon et al., 2011; Swanepoel, 2008; Tambling et al., 2012). Nevertheless, two South African studies on leopard found very similar results in terms of frequency of occurrence of prey (Martins et al., 2011) and frequency of occurrence and biomass intake of prey (Pitman et al., 2014) when comparing the two methods. Similar results are unlikely to be obtained for smaller predators such as mesocarnivores whose diet includes more small species, such as micromammals (Ritchie and Johnson, 2009; see Chapter 4). Locating kill sites from mesopredators is therefore particularly difficult, with only one study having used GPS clusters to identify bobcat kill sites (Svoboda et al., 2013). However, the study restricted its search to larger prey (i.e. white-tailed deer *Odocoileus virginianus*) and thus the method has yet to be applied to mesopredator diet more broadly.

In this chapter, I made the first attempt to investigate the kill sites of jackal and caracal using GPS location clusters obtained from collared individuals on farmland and in Anysberg Nature Reserve for jackal. I compared these results with those obtained in Chapter 4 of this thesis using scats to explore mesopredator diet in the two types of land use. More specifically, I aimed to:

(1) Compare the composition, frequency of occurrence and biomass of prey items consumed at feeding sites found using GPS location clusters, to dietary components in scats (see Chapter 4). This comparison will reveal whether GPS clusters are a reliable method for studying mesopredator diet in general or whether it should be restricted to discerning the proportion of livestock that are depredated versus scavenged. I predicted that GPS clusters would not accurately detect the small prey category for either mesocarnivore (Bacon et al., 2011; Swanepoel, 2008; Tambling et al., 2012) but that they would allow for the differentiation of kill versus scavenging sites.
(2) Investigate whether there are differences in the diet profiles of individuals of different sex and age classes for both mesopredators. I hypothesized that sex and age would have

an impact on the diet profiles of jackal and caracal (Martins et al., 2011), and predicted that adult males would consume both larger prey and more livestock than adult females or subadults of either sex (Linnell et al., 1999).

Methods

Scat collection and analysis

Please, refer to the Methods section in Chapter 4.

GPS cluster analysis

a) Capture, handling and collaring of mesopredators

Caracals and black-backed jackals were captured, chemically immobilised and GPS radio-collared for this study. Research and animal ethics approval was provided by the University of Cape Town Science Faculty Animal Ethics Committee (SFAEC) (ethical clearance number 2013/V20/JOR) and the Government body responsible for biodiversity conservation in the Western Cape, CapeNature (permit number AAA007-00074-0056).

Suitable trap sites were determined using the results of my intensive camera trapping surveys (see Chapter 3), predator signs (e.g. scats, spoor) and local knowledge from farmers, their labourers and a jackal expert (Figure 5.1B). Traps were set in areas that were rapidly accessible by vehicle to allow for frequent checking and to ensure rapid response time. Traps were open from dusk to dawn only. Box/cage traps were used to capture caracals (n = 5; Figure 5.1A) as recommended by the American Society of Mammalogists for the capture of medium-sized felids (Sikes and Gannon, 2011), and have been successfully used in other studies for bobcats (Broman et al., 2014), Canada lynx (*Lynx canadensis* ; Vashon et al., 2008), Iberian lynx (*Lynx pardinus* ; Gastón et al., 2016) and servals (*Leptailurus serval* ; Ramesh et al., 2015). Visual and scent lures, as well as scent baits were used to attract caracals to the traps. Captured caracals were immobilized with Zoletil (Tiletamine-Zolazepam) at a dosage of 3mg/kg using a hand or pole syringe (Figure 5.1A).

Jackals do not readily enter cage traps (Fuller et al., 1989), especially on farmland where they are actively hunted (N. Viljoen, pers. comm. 2013). I therefore used padded foothold traps (Victor #1.5 Soft Catch traps, Oneida Victor® Inc. Ltd., Euclid, Ohio, Figure 5.1C) set along trail intersections and close to signs of territory markings (Figure 5.1C). I followed the recommendations of Kamler et al. (2008) and set the pan tension at 1.75 kg to safely and efficiently capture jackals while excluding lighter non-target species. Traps were covered with square tiles after the last morning check just after sunrise to prevent daytime captures. Captured jackals were immobilized with Domitor (medetomidine hydrochloride) at a dosage of 0.05-0.1mL/kg using a hand syringe after putting a thick blanket over the animal to calm it down. Antisedan was used to reverse the sedative and analgesic effects of Domitor.

Figure 5.1. A: Veterinarian Dr Bennie Grobler using a pole syringe to anaesthetize a female caracal caught in a cage trap on farmland; B: Jackal expert Niel Viljoen posing with his equipment to efficiently capture black-backed jackals in Anysberg Nature Reserve; C: Set-up of a soft-catch trap to capture a male black-backed jackal on farmland. The trap is set close to a bush where the target individual marked his territory © Nathalie Houdin & Denis Palanque – The Karoo Predator Project.

Immobilized mesopredators were constantly monitored for temperature, heart rate, breathing regularity and the amount of oxygen in the blood (Figure 5.2). All study animals were sexed and weighed to the nearest 0.1 kg. Caracals were classified as adult or subadult based on tooth wear, coloration, body size and scars. Jackals were classified as adult (≥12 months old) or yearling (9-11 months) according to tooth wear, body size and reproductive condition (*sensu* Kamler et al., 2012b). Captured mesopredators were fitted with GPS radio-collars (Followit, Tellus Satellite Ultra Light, Lindesberg, Sweden, Figures 5.2 and 5.3). All collars were equipped with a drop-off mechanism allowing me to detach the collar remotely at a pre-defined date or on command, and preventing the need to recapture the animal when the battery was low.

Figure 5.2. Collaring a female caracal on farmland in the Beaufort West District Municipality, South Africa, in presence of the farmer and his family. Veterinarian Dr. Grobler was monitoring several physiological parameters of the anaesthetized caracal © Nathalie Houdin & Denis Palanque – The Karoo Predator Project.

Figure 5.3. Night collaring of a black-backed jackal in Anysberg Nature Reserve, South Africa © Nathalie Houdin & Denis Palanque – The Karoo Predator Project.

The collars were chosen for their light mass (approximately 200 g, representing less than 3% of the animal body mass), robust built and Iridium satlink option. Iridium technology offers two-way communication with a satellite network that has a global coverage 24 hours per day. Data were received by emails approximately once a day (except when delays occurred due to collars failing to connect to satellites for data transmission) and plotted on Google map using Followit Geo^{TM} (Followit Lindesberg AB, Sweden) – a map-based web portal provided by the collar manufacturer. After receiving each email, I downloaded the data into the geographic information system QGIS (version 2.18.2-Las Palmas; © 2017 QGIS Development Team) and visually identified GPS location clusters (sensu Martins et al., 2011) to facilitate field searches of potential kill sites (Martins et al., 2011; Svoboda et al., 2013). Collars were programmed to acquire a GPS fix every hour for jackal and sub-adult caracal and every two hours for adult caracal (i.e. between 12 and 24 fixes per day).

b) GPS cluster identification

A cluster of GPS points denoting a feeding site has never been defined for jackal or caracal in the literature. I thus used the definition of Martins et al. (2011) for leopard and defined a cluster of GPS points as at least two consecutive locations within 50 m of each other or >2 locations within 100 m of each other over a minimum 4–h period. Whenever possible, I investigated GPS clusters within one month of their formation to reduce the risk ofprey remains being consumed and /or dispersed by scavengers or broken down by environmental factors. Carcasses were quickly 'mummified' in this dry climate, leaving apparent predation marks and feeding patterns, even after a few weeks had elapsed from the predation event, giving me confidence that the sampling interval of 1 month from formation to investigation was an acceptable interval under the arid conditions and the low wildlife densities found at my study sites. Logistical challenges prevented me from visiting all of the clusters from all the collared animals and hence "feeding (including predation) rates", viz. all feeding sites (including predation) made during a continuous time interval (Anderson and Lindzey, 2003; Boutin, 1992; Eberhardt et al., 2009) could not be determined. I thus randomly selected a subset of clusters to visit for each of the collared animals by numbering all the clusters from 1 to n and then using a random integer generator (between 1 and n) in R (R Development Core Team 2016) with the "sample" function to draw a subset of clusters to visit for each species.

The GPS coordinates of each cluster were programmed into a handheld GPS unit (Garmin GPSMAP® 64s, Garmin International Inc. Olathe, Kansas, USA) and each point within a cluster was visited on foot, starting at the cluster geometric centre. Together with my field assistant, we spent a maximum of 60 minutes in total (on our own) searching for prey remains (bones, hairs, feathers, horns, feet, hooves, rumen), drag marks and predator scat within a 50 m radius from each point. Prey remains were identified to species level and photographed for digital archiving (Figure 5.4). I classified a cluster as a kill site if prey remains were found that showed evidence of caracal or jackal predation (e.g. characteristic bite marks, scratch marks, wool/hair plucked, presence of either jackal or caracal scat) and if the state of decomposition matched the dates since the cluster was formed. If no evidence of predation by jackal or caracal (e.g. no typical spacing and depth of teeth puncture marks, bleeding patterns) was observed, if the decomposition stage did not match the cluster date or if the prey showed other signs of predation (e.g. feral dog, baboon), then it was assumed to have died of other causes (e.g. old age, disease, other predator). Under these circumstances, the cluster might be classified either as a scavenging site (presence of a carcass with no sign of either jackal or caracal predation – Pitman et al., 2012), a den site (if a den was present), a bed site (presence of hairs in a depression of vegetation or soil – (Podgórski et al., 2008; Svoboda et al., 2013), a berry patch for jackal (presence of fruiting berry species) or as "other". I did not investigate any cluster created within the first week of the animals capture and collaring date to avoid possible effects of the capture and immobilisation process on the predator behaviour (Svoboda et al., 2013).

Figure 5.4. Photographs of prey remains found at GPS clusters from GPS radio-collared predators – A: steenbok killed by a female caracal, B: rock monitor lizard (*Varanus albigularis*) killed by a male caracal, C: lamb killed by a male caracal, D: Karoo korhaan killed by a female black-backed jackal © Marine Drouilly – The Karoo Predator Project.

c) Data analyses

I calculated the frequency of occurrence (FO) of prey species that were either killed or scavenged at cluster sites. To convert prey frequency of occurrence to a corrected biomass consumed, I first estimated the proportion of the prey consumed and then assigned a body mass to each prey item according to its estimated age (Morehouse and Boyce, 2011; Pitman et al., 2014). When ageing was not possible, I used the mean body mass for the prey species obtained from Apps (2012) for the Karoo region or the closest possible location, or from Skinner and Chimimba (2005) – if not in Apps (2012). The corrected biomass consumed was calculated by multiplying the mass of the prey species with the proportion of prey consumed and was assumed to be attributed to the collared predator (presence of scats and tracks from one species only). It was not possible to estimate the biomass consumed by predators at scavenging sites due to the possibility of another predator and/or scavenger having fed on the carcass.

I categorized all prey data according to body mass: small (≥0.1-5 kg), medium (>5-10 kg) and large (≥10 kg). For mammals, I used the mean body mass of adult males and females in Apps (2012). I used Chi-Square tests or Fisher's exact tests (when one or more of my categories had an expected frequency smaller than five) (Zar, 1999) to compare the frequency of occurrence of categorized prey items (small, medium, large) found at GPS clusters with data obtained from scat analyses (see Chapter 4). No caracal was captured in the reserve so I only compared GPS cluster data to scat data collected on farmland for this species. For jackals, I compared both methods on both types of land use. I used Chi-Square tests to explore differences in livestock consumption on farmland between male and female for both species separately and between age classes (adult versus sub-adult) for caracals. I did not collar enough jackals in the same type of land use to allow for a comparison of sex or age classes with land use. All statistical analyses were conducted in R v. 3.3.0 (R Development Core Team, 2016) using preloaded packages.

Results

Characteristics of mesopredators feeding sites

Twelve caracals (five females and seven males) and nine jackals (three females and six males) were captured, chemically immobilised and GPS radio-collared for this study. GPS data were collected from 11 out of the 12 collared caracals (seven males, four females – Table 5.1) and from the nine jackals (six males, three females – Table 5.2). The average acquisition rate for 18 GPS collars was 92.8%. Sampling periods ranged from one month (373 locations) to approximately six months (4136 locations) for caracals (mean ± SD = 129.3 ± 13.0 days; mean ± SD = 2331.2 ± 299.4 locations), and from 18 days (142 locations) to seven months (4471 locations) for jackals (mean ± SD = 144.6 ± 18.8 days; mean ± SD = 2985.7 ± 439.7 locations). GPS clusters were investigated from June 2014 to October 2015. I investigated a total of 107 clusters for caracals (Table 5.1) and 105 for jackals (Table 5.2).

Table 5.1. The name, sex, age class and body mass of the 11 collared caracals for which I investigated GPS clusters in the Central Karoo, South Africa. Data include the number of GPS fixes and the duration in days that the animal was tracked, as well as the total number of clusters that were investigated, the number of kills found and the overall success rate in finding a kill site, expressed as the proportion of investigated clusters with a confirmed kill. F: female; M: male; A: adult; SA: sub-adult.

Caracal name	Sex	Age class	Body mass (kg)	No. GPS fixes	Study duration (days)	No. clusters investigated	No. kills found	Success rate
Freedom	M	A	12	1979	154	4	0	0
Moonshine	M	A	12	2777	133	1	0	0
Ginger	F	SA	8	2753	123	14	7	50.0
Sunshine	F	SA	7	4136	173	9	1	11.1
Bagheera	M	SA	10	2759	122	5	3	60.0
Marina	F	SA	8	2911	129	1	0	0
BigPaw	M	A	14	2716	125	3	0	0
Rooibos	M	SA	10	2112	177	9	4	44.4
Chai	F	A	16	373	31	11	8	72.7
Whisky	M	A	14.5	1997	172	21	9	42.9
Jumbo	M	A	13.5	1130	83	29	14	48.3
Total						**107**	**46**	**43.0**

The mean success rate (per collared individual) of finding a kill when investigating a GPS cluster was significantly higher for caracals (43.0% - Table 5.2) than for jackals (9.5% - Table 5.3) ($t = 2.318$, $df = 18$, $P = 0.03$). For caracals, the mean time from cluster formation to investigation was 18.1 ± 3.3 days (range: 0-251 days). The mean duration of a cluster was 7.0 (± 5.5) hours (range = 2-31), which was not significantly different ($t = -0.395$, $df = 151$, $P = 0.69$) from the mean duration of time (mean = 7.4 ± 6.3, range = 2-31) spent at a cluster where a kill was successfully detected. Most clusters (57.9%, n = 62) did not have kill remains associated with them. Scavenging activity was identified at 4.7% (n = 5) of sites, while 33.6% of cluster sites (n = 36) were classified as bed sites. The rest of the sites (19.6%, n = 21) could not be classified into one of the above categories.

Table 5.2. The name, sex, age class and body mass of the nine collared black-backed jackals for which I investigated GPS clusters both on farmland and in Anysberg Nature Reserve, South Africa. Data include the number of GPS fixes and the duration in days that the animal was tracked, as well as the total number of clusters that were investigated, the number of kills found and the overall success rate in finding a kill site, expressed as the proportion of clusters with a confirmed kill. F: female; M: male; A: adult; SA: sub-adult.

Jackal name	Gender	Age class	Body mass (kg)	No. GPS fixes	Study duration (days)	No. clusters investigated	No. kills found	Success rate
Rain*	F	SA	5.5	4471	212	14	4	28.6
Leroy*	M	SA	6.5	4035	192	12	1	8.3
MisterFox*	M	SA	5.5	2336	157	11	1	9.1
Rooky*	M	SA	5.5	2485	157	8	0	0
Forest*	M	SA	5.5	3044	132	22	4	18.2
Luna	F	A	8.5	3942	165	17	0	0
Pluto	M	A	7.8	2560	106	12	0	0
Spirit	F	A	8.5	142	18	3	0	0
Eskimo	M	A	8.3	3856	162	6	0	0
Total						**105**	**10**	**9.5**

* Jackals captured on farmland.

In the case of collared jackals and when pooling farmland with the PA, the mean time from cluster formation to investigation was 12.9 ± 1.3 days (range: 0-90 days). The mean duration of a cluster was 5.0 (± 2.9) hours (range = 2-15), which was not significantly different (t = 1.604, df = 113, P = 0.11) from the mean duration of time spent at a cluster where a kill was successfully detected (mean = 6.6 ± 4.1, range = 3-15). Most clusters (90.5%, n = 95) did not have kill remains associated with them. Scavenging activity was identified at 16.2% (n = 17) of sites, while 54.3% of cluster sites (n = 57) were bed sites and 7.6% (n = 8) were berry patches (presence of either *Euclea undulata* or *Diospyros lycioides* bushes). Two sites (1.9%) were den sites. The rest of the sites (10.5%, n = 11) had no evidence that could allow assignment to one of the above categories.

Caracals initiated clusters both during the day (i.e. from sunrise to sunset, 48.6%) and night (i.e. from sunset to sunrise, 51.4%). There was no significant difference (χ^2 = 2.755, df = 1, P = 0.09) between the percentage of clusters with a kill occurring at night (58.7%) or during the day (41.3%). Jackals initiated 61.9% of the clusters at night. There was no significant difference (χ^2 = 0.760, df = 1, P = 0.38) between the percentage of clusters with a confirmed kill occurring at night (60%) and during the day (40%). For both caracal and jackal, most predation (69.6% and 80% respectively) occurred between 18:00-06:00 hr. (Figure 5.5), that is from dusk to dawn and these results were statistically significant (caracal: χ^2 = 13.98, df = 1, P < 0.001; jackal: χ^2 = 6.840, df = 1, P = 0.09).

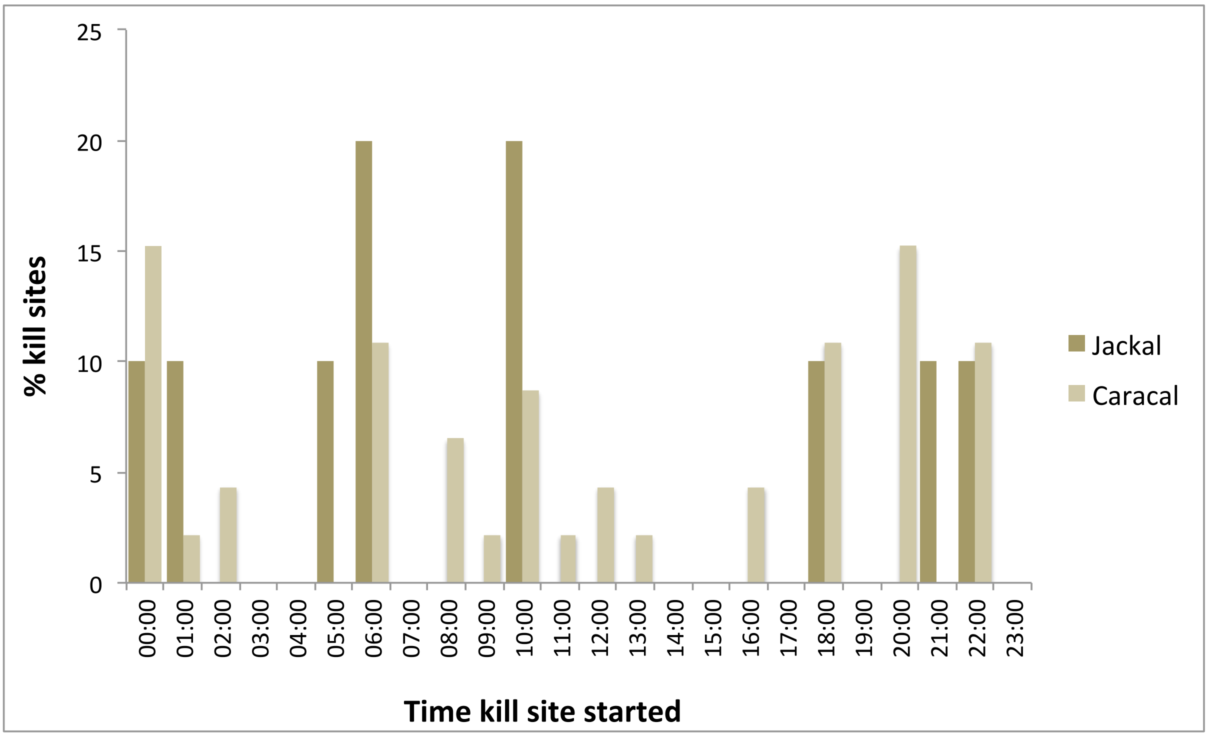


Figure 5.5. Percentage of kill sites in each hour of the day for collared black-backed jackal (n=10 kill sites, dark brown) and collared caracal (n=46 kill sites, pale brown) in the Karoo, South Africa.

Prey composition at feeding sites

Jackal and caracal consumed almost all of their prey when the body mass was <10 kg, but only partially ate larger prey. Stomach contents, skulls, hooves and horns were rarely ingested and hence provided important remnants for identifying prey remains at cluster sites. Direct observations in Anysberg Nature Reserve proved that jackals ate micromammals whole and no remains left. Twelve prey species were identified from caracal kill sites and three additional species were identified at sites where prey were scavenged (Table 5.3). Four prey species were identified from jackal kill sites on farms with none identified from clusters within the reserve. Two and three prey species were scavenged by jackals on farms and in the reserve respectively (Table 5.4 and Table 5.5). For caracals, the majority of prey items were rock hyraxes (22%, n

= 11), followed by lambs (20%, n = 10), adult sheep (12%, n = 6; scavenging: 4%, n = 2) and scrub hares (8%, n = 4) (Table 5.3). Jackals on farms mostly ate lambs (45%, n = 5), sheep (18%, n = 2) or scavenged (18%, n = 2, one sheep and one cow) (Table 5.4). In Anysberg Nature Reserve, 100% (n = 15) of cluster sites that had prey remains were scavenging sites and included domestic horse (66.7%), anthropogenic food items from the garbage dump (20%), oryx (6.7%) and baboon (6.7%) (Table 5.5).

The estimated total biomass of mammalian prey consumed by caracals on farmland was 244.31 kg, 54% of which was sheep (17.2% lamb), 12.3% rock hyrax and 6.3% Cape porcupine (Table 5.3). Jackals consumed an estimated 68.2 kg of prey, 66.2kg of which were mammalian prey. Sheep comprised 97% (32.5 % lamb) of the total prey biomass (Table 5.4). It was not possible to determine the biomass of prey scavenged on farms or in the reserve as they might have been scavenged by other carnivores as well, and most of them had little left on them at the time of detection.

Table 5.3. Characteristics of caracal prey species identified at GPS clusters on farmland. Data include the total number and percentage of clusters where each prey species was present, the age class, mean body mass of that age class, the percentage of the prey item consumed, the corrected biomass of prey consumed (= number of kills x mean prey body mass x proportion of prey consumed), the corrected biomass consumed expressed as a percentage of all the kill sites, and the range of hours spent at the feeding site. The mean body masses are extracted from Apps (2012) unless stated otherwise.

Prey Species	Number of kills	% of feeding events*	Prey age class	Mean prey body mass (kg)	Prey consumption (%)	Corrected biomass consumed (kg)	Corrected biomass consumed as % of all kill sites	Range of number of hours at feeding site
Rock hyrax	11	21.6	Unknown	3.03	90	30	12.3	2-15
Smith's red rock rabbit	1	2.0	Unknown	1.6	90	1.4	0.6	5
Hare	4	7.8	Unknown	3.2	90	11.5	4.7	3-19
Common duiker	1	2.0	Adult	19.7	60	11.8	4.8	5
Steenbok	2	3.9	Adult	11.1	60	13.3	5.4	5-15
Klipspringer	2	3.9	Young of the year	4	70 80	2.8 3.2	2.5	8-9
Cape grey mongoose	1	2.0	Adult	0.8	90	0.7	0.3	7
Aardwolf	2	3.9	Adult	7.5	80 60	6 4.5	4.3	4-13
Lamb	10	19.6	Young of the year	6.0[1]	70	42	17.2	2-31
Sheep	6	11.8					36.8	3-5

	2		Adult	60.0[1]	10	12		
	2		Adult	60.0[1]	30	36		
	1		Adult	60.0[1]	50	30		
	1		Subadult	40.0[1]	30	12		
Porcupine	2	3.9	Adult	15.4	50	15.4	6.3	2-7
Rock monitor	3	5.9	Adult	4.0[2]	90	10.8	4.4	5-19
Bird	1	2.0	Unknown	0.875[3]	90	0.8	0.3	25
Scavenging event	5	9.8		NA				2-10
- Nguni cow	1	2.0		400.0[1]				2
- Greater kudu	2	3.9		193.5				5
- Sheep	2	3.9		60.0[1]				5-10

* Feeding events include kills and scavenging events.
[1]Mean body mass for these domestic species on Central Karoo farms, measured in the field.
[2]Body mass measured from an intact fresh adult carcass, roadkill.
[3]Mean body mass of a Cape spurfowl (*Pternistis capensis*), which feathers were found at a kill site.

Table 5.4. Characteristics of black-backed jackal prey species identified at GPS clusters on farmland. Data include the total number and percentage of clusters where each prey species was present, the age class, mean body mass of that age class, the percentage of the prey item consumed, the corrected biomass of prey consumed (= number of kills x mean prey body mass x proportion of prey consumed), the corrected biomass consumed expressed as a percentage of all the kill sites, and the range of hours spent at the feeding site. The mean body masses are extracted from Apps (2012) unless stated otherwise.

Prey Species	Number of kills	% of feeding events*	Prey age class	Mean prey body mass (kg)	Prey consumption (%)	Corrected biomass consumed (kg)	Corrected biomass consumed as % of all kill sites	Range of number of hours at feeding site
Sheep	2	18.2	Adult Subadult	60.0[1] 40.0[1]	40 50	24 20	64.5	4-15
Lamb	5 3 1 1	45.4	Young of the year	6.0[1]	 90 60 40	 16.2 3.6 2.4	32.5	3-12
Karoo korhaan	1	9.1	Adult	1.3	90	1.2	1.8	9
Leopard tortoise	1	9.1	Unknown	2.0[1]	40	0.8	1.2	3
Scavenging events - Nguni cow - Sheep	2 1 1	18.2 9.1 9.1		NA 400.0[1] 60.0[1]				3-7 3 7

* Feeding events include kills and scavenging events.
[1]Mean body mass for these species on Central Karoo farms, measured in the field.

Table 5.5. Characteristics of black-backed jackal prey species that were scavenged, in Anysberg Nature Reserve. Data include the total number of clusters for each prey species (in that case, scavenging events), the range of hours spent at feeding site (in that case, scavenging site), the mean body mass of the prey scavenged, and the percentage of feeding events (in that case, scavenging events). The mean body masses are extracted from Apps (2012) unless stated otherwise.

Prey Species	Number of scavenging events	Range of number of hours at feeding site	Mean prey body mass (kg)	% of feeding events
Scavenging events	15	2-10	NA	100
- Oryx	1	2	175	7.7
- Horse	10	2-10	500[1]	76.9
- Chacma baboon	1	6	28[2]	7.7
- Garbage dump	3	2-8	NA	7.7

[1]Mean body mass for a domestic horse in the reserve.
[2]Body mass of one male baboon killed in the reserve.

Comparison of diet estimated from GPS cluster analysis versus scat analysis

Twenty-one mammal species were detected in 102 caracal scats collected on farmland (see Chapter 4), while 13 were identified from the 46 kill sites and five scavenging sites using GPS clusters in this chapter. Twenty-four mammal species were detected in 417 jackal scats collected both on farmland and in the reserve (see Chapter 4), and five species were identified at 10 kill sites and 17 scavenging sites investigated in both types of land use.

There was no significant difference in the proportion of small, medium and large prey species obtained from GPS clusters versus scats of caracal (χ^2 = 1.843, df = 2, P = 0.40; Figure 5.6). Similarly, there was no significant difference in the frequency of occurrence of livestock using either method (χ^2 = 0.018, df = 1, P = 0.89). However, no micromammal was identified at kill sites, while they occurred in almost 15% of the 102 caracal scats collected on farmland (see Chapter 4).

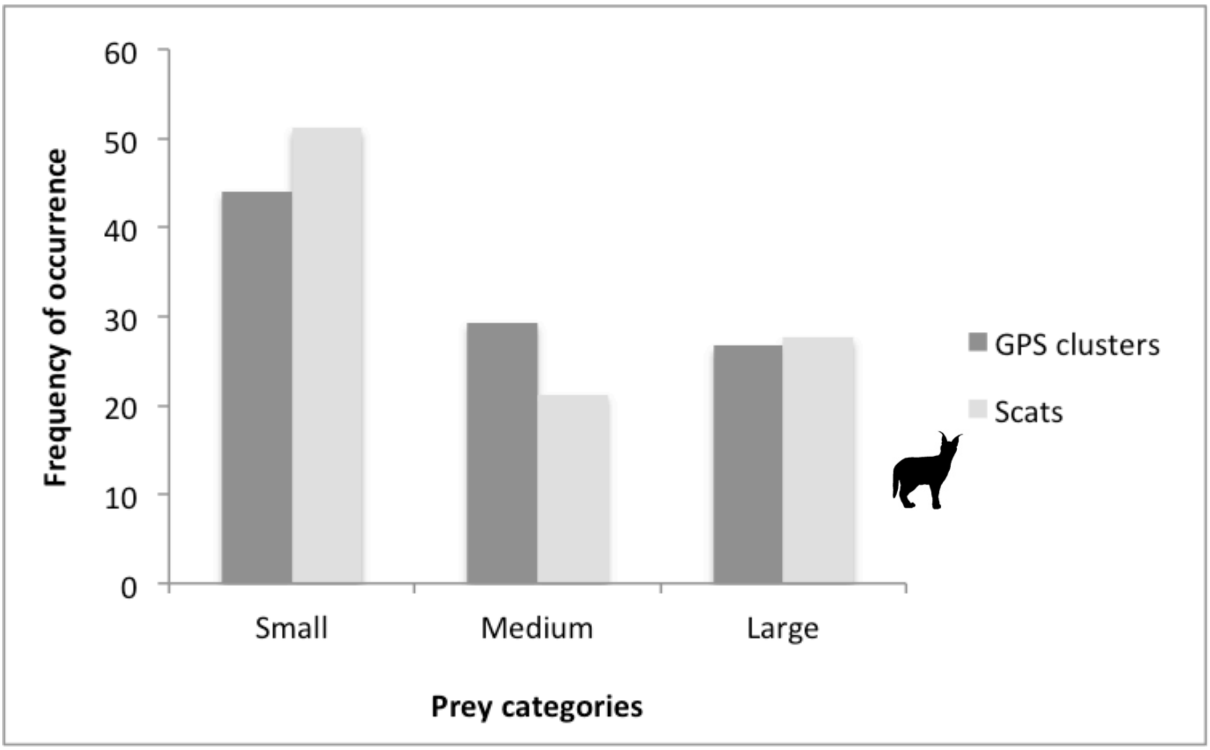


Figure 5.6. Comparison of the frequency of occurrence of different prey size classes (small, medium and large) obtained for caracal using GPS cluster analysis from seven collared caracals (n = 51 clusters) and scat analysis (n = 102 scats) from scats collected on farmland in the Central Karoo, Western Cape Province, South Africa.

There were significant differences in the proportion of small, medium and large prey obtained from GPS clusters versus scats of jackal on farmland (χ^2 = 33.40, df = 2, P < 0.001; Figure 5.7) and in the reserve (χ^2 = 242.1, df = 2, P < 0.001; Figure 5.8). These differences were largely attributable to the greater occurrence of smaller prey in scat samples and larger prey at GPS clusters. Livestock were detected more frequently at GPS clusters than in scats on farms (χ^2 = 4.034, df = 1, P = 0.04). No micromammal remains were detected at kill sites, while they occurred in almost 11% of the 216 scats collected on farmland and 36% of the 201 scats collected in the reserve (see Chapter 4).

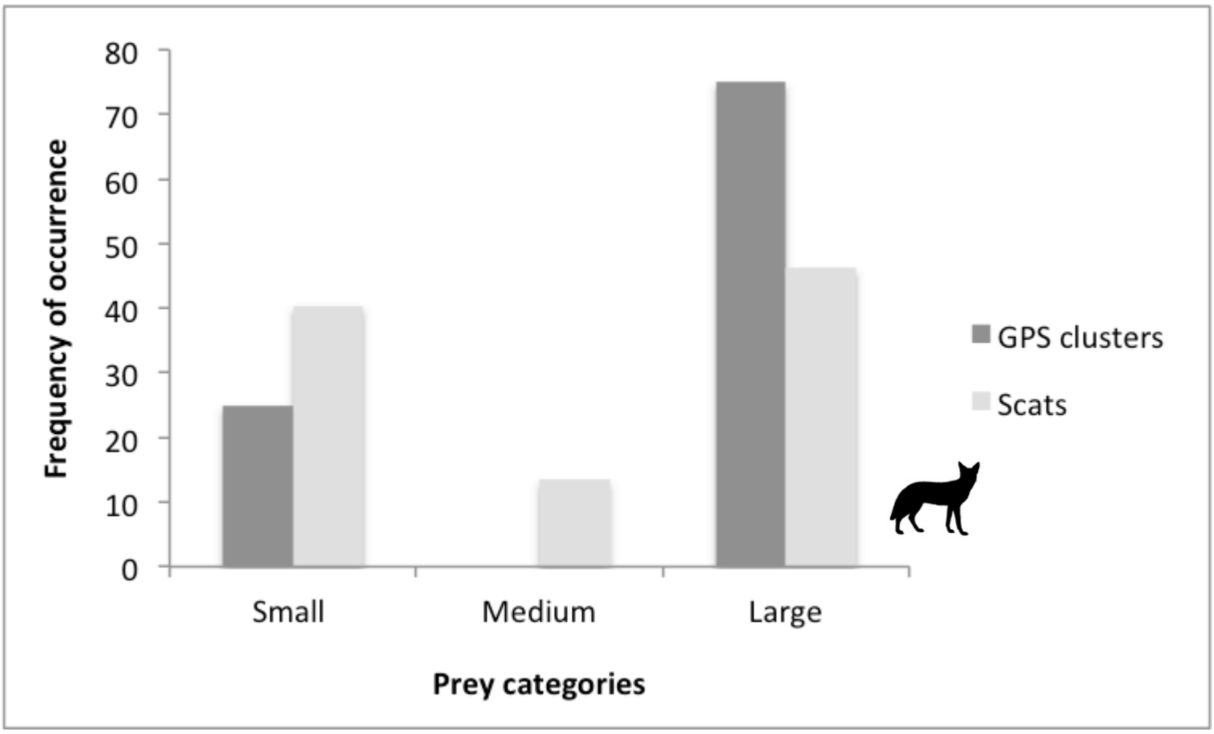


Figure 5.7. Comparison of the frequency of occurrence of different prey size classes (small, medium and large) obtained for black-backed jackal using GPS cluster analysis from four collared jackals (n = 67 clusters) and scat analysis (n = 216 scats) from scats collected on farmland in the Central Karoo, Western Cape Province, South Africa.

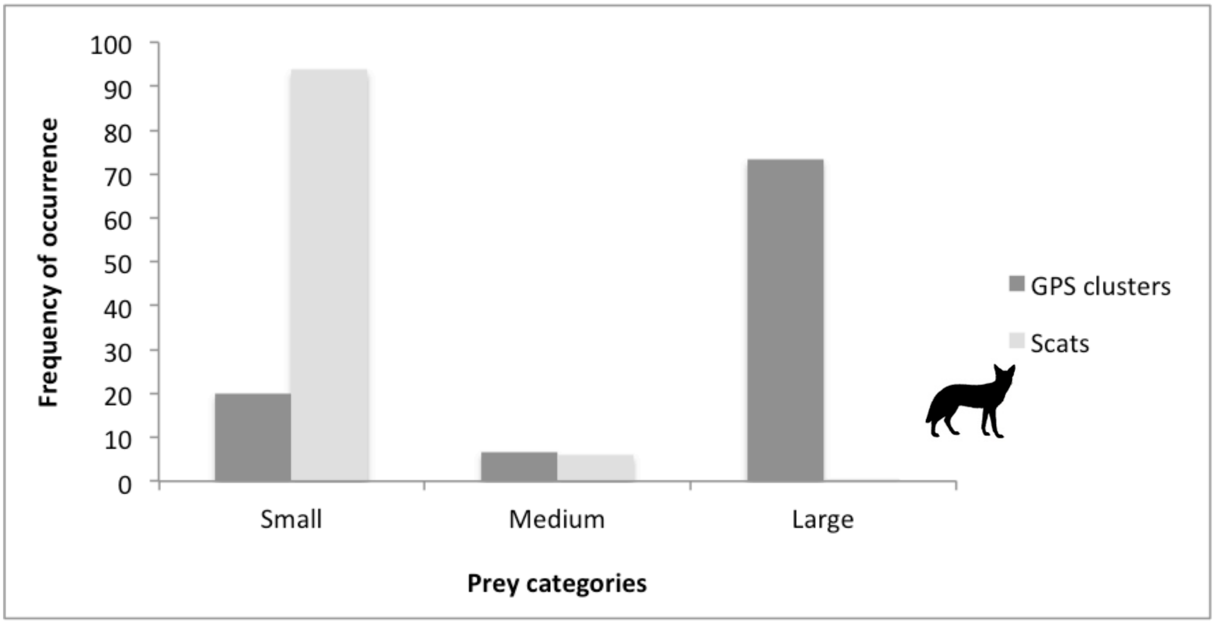


Figure 5.8. Comparison of frequency of occurrence of different prey size classes (small, medium and large) obtained for black-backed jackal using GPS cluster analysis from five collared jackals (n = 38 clusters) and scat analysis (n = 201 scats) from scats collected in Anysberg Nature Reserve in the Little Karoo, Western Cape Province, South Africa.

For caracal, the total mammalian biomass consumed ranged from 31 kg for scats to 244 kg for kill sites. Sheep represented 29% (8.9 kg) of the biomass consumed in scats, followed by 18% (5.4 kg) for common duiker and 14% (4.3 kg) for goat. At kill sites found with GPS cluster investigations, sheep represented 54% (132 kg) of the biomass consumed, followed by 12.3% for rock hyrax (30 kg) and 6.3% for Cape porcupine (15.4 kg) (Table 5.4). The estimated biomass of sheep consumed was significantly higher at kill sites than in scats (χ^2 = 6.855, df = 1, P = 0.01).

For jackal on farmland, the total biomass consumed ranged from 59 kg for scats to 68 kg for kill sites. Sheep represented the bulk of the biomass consumed (48%, 28 kg) on farmland in scats, followed by goat (26%, 15 kg) and common duiker (5%, 3.1 kg). At GPS clusters, sheep represented by far the bulk of the biomass consumed, with 66 kg consumed (97%) (Table 5.5) and it was significantly higher than in scats (χ^2 = 39.34, df = 1, P < 0.001). In the reserve, fruit and seeds (54%) and Karoo bush rat (20%) represented most of the biomass consumed in scats, while evidence of feeding on berry patches were present at 8 of the sites only and no Karoo bush rats were detected at GPS clusters (Table 5.6).

The effects of predator sex and age class on prey identified at kill sites

Caracal diet did not vary significantly between males and females (χ^2 = 5.435, df = 3, P = 0.14) when comparing prey size categories. However, there was a significant difference between adult and subadult diet (χ^2 = 10.258, df = 3, P = 0.01), with subadults consuming more small prey than adults. Adult caracals consumed significantly more sheep (RFO) than subadults (χ^2 = 6.401, df = 1, P = 0.01) and there was a significant difference (χ^2 = 8.227, df = 1, P = 0.004) in sheep consumption (RFO) between different age and sex classes, with adult males preying more frequently on livestock than any other sex and age category.

All jackals captured on farmland were subadults and consequently it was not possible to investigate the effect of age on jackal diet and their consumption of livestock. Subadult females on farmland hunted small and large prey while subadult males hunted medium prey and scavenged. Subadult males seemed to prey more frequently on sheep (RFO) than subadult females, but more data are required to perform statistical tests.

Discussion

Characteristics of mesopredators feeding sites

The success rate of finding a kill at a cluster was higher for caracal (43%, n=107) than for jackal (9.5%, n=105). The success rate for jackal is the lowest yet to be reported in the predator literature, with 15.8% being the previously lowest rate recorded for lions (Tambling et al., 2010). The higher success rate for caracal was predicted, as caracals are known to kill larger prey more often than jackal (Kok and Nel, 2004) and are more likely to make repeat visits to kill sites to feed several times from the same carcass (Bothma, 2012; PMF, 2016).

Despite the adequate mean elapsed time from cluster formation to investigation under these specific arid conditions, I did not find prey remains at most clusters (caracal: 57.9%; jackal: 90.5%). When prey remains were found, most (≥90%) of the prey was consumed if its body mass was <10kg (only the rumen, viscera, fur and tail remained), as was reported in other studies (Estes, 1991; Pringle and Pringle, 1979). This made finding depredated lambs difficult, even with the help of the GPS cluster locations. GPS location cluster analysis was thus considered suitable for distinguishing scavenging from predation for prey species ≥10 kg only. The absence of prey remains and/or resting sites at most of the clusters may reflect areas where predators have hunted and fed on small prey that are consumed whole, including micromammals, insects or fruit (for jackal). In the reserve, 7.6% of the jackal clusters had fruit bearing patches, on which jackals could have potentially been feeding (see Chapter 4; Do Linh San et al., 2009; Van de Ven et al., 2013). It is however not possible to quantify the amount of fruit consumed and the time spent feeding versus resting in the shade provided by fruit bearing bushes and trees through the investigation of GPS clusters alone.

GPS cluster visitations in the arid climate of the Karoo allowed me to investigate for both mesopredators the proportion of large prey that were likely killed by the collared animals vs. likely scavenged, following my classification method. Both species can scavenge, as was reported in previous studies (caracal: Avenant and Nel, 1997; Grobler, 1981; Stuart and Hickman, 1991 – jackal: Kok and Nel, 2004; Minnie et al., 2018a), but as expected, caracal scavenged less (4.7% of the feeding sites) than jackal (16.2% of the feeding sites). Of the five caracal scavenging events, two were on greater kudus that had died in fences. I also recorded two scavenging events on sheep, which contradicts the findings of Pohl (2015) who stated that caracals in the Free State were unlikely to scavenge on sheep. Scavenging was recorded by two males and one female, all of which appeared territorial based on their overall GPS movements. This result is also contrary to those presented by Avenant (1993) who attributed scavenging to non-territorial caracals only.

Most predation events for both predators occurred between 18:00 and 06:00 hr. (caracal: 69.6%, jackal: 80%), which corresponds to dusk, night and dawn. These results are in accordance with previous studies showing that jackal and caracal exhibit a flexible bigeminous activity pattern (crepuscular and nocturnal periods), especially when experiencing chronic levels of persecution (Avenant and Nel, 1998; Ferguson et al., 1988; Minnie et al., 2018a; Walton and Joly, 2003). Contrary to what studies on large carnivores have shown (Anderson and Lindzey, 2003; Pitman et al., 2012), there was no significant difference in the mean duration of a cluster at sites where a kill was successfully detected versus not detected. This might be the result of less time spent on kill sites because many of the prey are small in size relative to that consumed by large carnivores. Small prey necessitates shorter handling time than larger ones, resulting in a shorter time spent by the predator at the cluster (Martins et al., 2011).

Prey composition: GPS clusters versus scat analysis

A comparison of the results presented in Chapter 4 and in this chapter for jackal reveals that large prey items are over-represented when assessing diet through GPS clusters while small prey, in particular micromammals and fruit, are under-represented (both in terms of RFO and consumed biomass). This finding is in accordance with previous studies on predator diet (Bacon et al., 2011; Svoboda et al., 2013; Tambling et al., 2012), which reveal that smaller prey items are only detected in scats and seldom allow for the formation of clusters. In contrast, the relative frequency of occurrence of small, medium and large prey species in caracal diet was similar between the two methods. This suggests that caracals consume relatively fewer micromammals, with commonly consumed smaller prey such as rock hyraxes and lagomorphs being associated with cluster formation and prey remains at GPS location clusters. Analogous results regarding the similarity of both methods in detecting the relative frequency of occurrence of small, medium and large prey species were obtained for leopard by both Martins et al. (2011) and Pitman et al. (2014) in mountainous regions of South Africa.

For jackal and caracal, both GPS cluster and scat analyses indicated that the prey item with the highest relative frequency of occurrence (RFO) for caracal was sheep (32% and 16% respectively). This relationship however did not hold for the next highest ranked prey items (clusters: rock hyrax (22%) and hares (8%); scats: micromammals (14%) and common duiker (10%)). Similarly, biomass estimates based on caracal scat analysis ranked sheep (29%) and common duiker (18%) highest, while GPS clusters ranked sheep (54%) and rock hyrax (12.3%) highest. Cluster estimates of the biomass of sheep consumed were significantly higher than estimates based on scat analysis. Similar results were obtained for jackal on farms, with RFO and biomass estimates for scats and GPS clusters both ranking sheep as the most important prey item and significantly higher for clusters relative to scats. The finding that the estimated biomass of sheep consumed by both caracal and jackal are higher using clusters than scats is not unexpected though. Large prey like sheep are typically underestimated using the scat method because they include larger volumes of softer tissue that cannot be detected in scats. Furthermore, caracals are known to pluck wool from sheep and hair from antelope before eating the meat (PMF, 2016; Figure 5.9) thus reducing the volume of diagnostic tissue in the scats. By contrast, smaller prey is often consumed whole providing a high ratio of detectable material (e.g. hair) to volume consumed. A further contributing factor may relate to surplus killing by caracal, which was recorded for a single collared male caracal in this study. This phenomenon has been observed in a variety of carnivore species (Andelt et al., 1980; Fritts et al., 1992; Kruuk, 1972), including caracal (Bothma, 2012; Bothma and Walker, 1999; Skinner, 1979; Stuart and Wilson, 1988) and jackal (Estes, 1991; Hiscocks and Perrin, 1987; Kaunda, 1998; Lamprecht, 1978; Macdonald, 1976), both of which are known to catch more prey than they can eat at once and cache them for later consumption. Predators may also only be eating a small portion of the sheep they killed before moving on, as observed in the field at GPS clusters (Figure 5.9A, B). This behaviour might be a consequence of human persecution of mesopredators on farmland, with reduced time at any given location being advantageous for avoiding detection and possible negative interactions with humans. Reduced prey consumption time and increased killing rates in human-disturbed areas have been shown to occur in female cougars (Smith et al., 2015). Similarly, Amur tigers (*Panthera tigris altaica*) (Kerley et al., 2002) and grey wolves (Wilmers et al., 2003) have been shown to not return to their prey but rather to abandon it at kill sites when human disturbance or the risk thereof increased. Finally, the scavenger community might have influenced my estimation of mesocarnivore diet by overestimating biomass intake by jackal and caracal if the scavengers consumed large parts of the carcasses. However, this is unlikely for the following reasons: 1) there was a very low abundance of scavengers in my study area (see Chapter 3) with very few raptors and no vulture present; 2) small-bodied scavengers such as mongooses or Cape fox would likely have been displaced at a carcass by caracal/jackal; 3) in the Karoo, carcasses were quickly “mummified” allowing a rather easy identification of predation marks and feeding patterns, but also preventing other predators/scavengers to feed on them for more than a few days; and 4) potential scavengers only included Cape fox (very seldom detected, See Chapter 3), bat-eared fox and mongooses, all of which have very different tracks and scats compared to jackal and caracal. Thus, potential signs of their presence were easy to identify at carcass sites but were rarely detected.

GPS cluster investigation therefore confirms the high level of predation of jackal and caracal on small-livestock on farmland that was evident from scat analysis in Chapter 4. Interestingly though, and in accordance with scat analyses (see Chapter 4), none of the jackals collared in Anysberg Nature Reserve formed clusters containing small-livestock remains when they left the reserve and moved through farmland. Most of the time, it was difficult to find remains at those clusters, probably because prey consumed were too small to be detected.

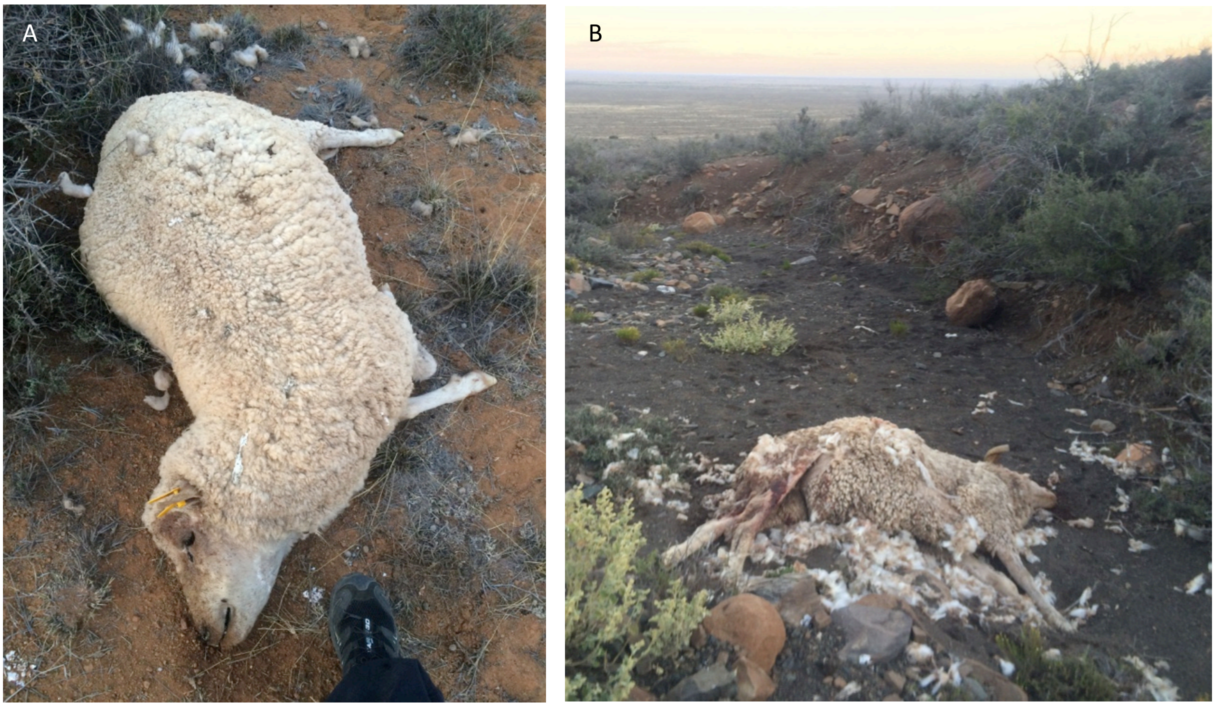


Figure 5.9. Photographs of sheep found at two GPS clusters made by two different collared male caracals. There is no evidence of feeding in (A) and only a small amount of feeding on the rump in (B), despite visiting the clusters more than a week after its initial formation. In both cases caracals have plucked the wool of the sheep to avoid ingesting it © Marine Drouilly – The Karoo Predator Project.

The effects of predator sex and age class on prey identified at kill sites

Caracal prey size did not vary significantly with sex, but subadults consumed more small prey than adults. Even if only a few studies exist on the ontogeny of hunting skills among free-ranging carnivores, it has been shown that young animals are poorer hunters than old ones, take longer to catch prey and feed on prey that are easier to kill (for cheetah see Caro, 1994; for spotted hyena (*Crocuta Crocuta*) see Holekamp et al., 1997; for polar bear (*Ursus maritimus*) see Stirling and Latour, 1978). This might explain why sub-adult caracals on farmland mostly kill small and probably easier-to-catch prey. In addition, adult caracals and particularly adult males killed significantly more sheep than any other group. Male-biased livestock killings have been reported for coyote (Blejwas et al., 2006), black bear (*Ursus americanus*) (Horstman and Gunson, 1982), and for a variety of felids including European lynx (Odden et al., 2006, 2002), cougar (Anderson, 1992; Ashman et al., 1983), jaguar (Hoogesteijn et al., 1993), leopard (Esterhuizen and Norton, 1985) and lion (Stander, 1990). Possible contributing factors to male-biased livestock predation include males being bigger, having larger territories and dispersing over larger distances than females, factors which together make them more likely to come into contact with and predate on livestock (Linnell et al., 1999; Macdonald and Loveridge, 2010).

During my study, sheep were killed by an old adult male caracal with a healed gin-trap wound on the front paw and damaged teeth (Figure 5.10A, B), by an old adult female in good health, an adult male in good health and a sub-adult male, the assumed offspring of the aforementioned old female. The literature is ambiguous about the effects of injury and age on livestock predation rates, with a few observations of old and injured snow leopards (*Panthera uncia*) being involved in depredation (Fox and Chundawat, 1988) and two studies showing that jaguars shot for livestock depredation had signs of injury (mainly old wounds from shotgun pellets) that may have affected their hunting skills and made them target easier-to-catch domestic animals (Hoogesteijn et al., 1993; Rabinowitz, 1986). Other studies have shown that livestock predators were in good health (Aune, 1991; Riley et al., 1994; reported in Linnell et al. 1999).

Interestingly, in the case of jackal, a very old male caught and collared in Anysberg Nature Reserve had almost no teeth (Figure 5.10C) and none of his GPS clusters included livestock when he crossed onto farmland, which he did a few times for a couple of weeks at a time during the time he was collared.

Figure 5.10. Photographs of (A) the healed gin-trap wound of the front paw and (B) the tooth with an abscess of an old adult male caracal on farmland in the Central Karoo; (C) the worn-down teeth of a very old male jackal in Anysberg Nature Reserve © Marine Drouilly – The Karoo Predator Project.

My sample size for jackal was too small and biased to explore the effects of sex and age on livestock predation. However, a study on coyote depredation behaviour in captivity showed that adults paired for reproduction, especially males, were more likely to kill sheep than young, unpaired or female individuals (Connolly et al., 1976). A study of free-ranging coyotes supported this conclusion (Sacks et al., 1999). I only captured sub-adults on farmland and of these, three individuals, two males and one female, killed sheep. The female and at least one of the males appeared to be preparing to pair for reproduction when the predation events occurred.

Conclusion

Over the last decade, jackal and caracal have re-established populations in former ranges and there are even signs of their distribution expanding (Bothma, 2012; Marker and Dickman, 2005; see Chapter 6). Due to their classification as damage-causing animals (DCA) by all provinces in South Africa, data on prey composition in their diet is particularly important for their management, because of the concerns over perceived and real threats to livestock. This is the first study to compare dietary estimates using scats and GPS clusters for two opportunist and generalist mesocarnivores living on farmland and in a reserve (jackal). Although my results remain preliminary due to the relatively low number of GPS clusters I was able to investigate, I provide clear evidence that mesopredators kill and consume livestock (presence of typical bite marks notably) but are also able to scavenge, albeit to a lesser extent. GPS clusters also highlighted the predatory behaviour of these heavily persecuted mesocarnivores living in a small-livestock dominated landscape, with most predation occurring during the twilight and night-time and prey seldom being entirely consumed. Together these findings suggest an avoidance of times when human presence is highest, viz. daytime, and feeding only to satiation with few repeat visits to a carcass.

In this chapter, I showed that the success of the GPS location cluster method varied between jackal and caracal and seems to only be suitable for caracals that on average consume larger prey and have a different feeding behaviour. I would therefore recommend that for mesopredators that typically consume a large number of small prey (<1 kg), the GPS location cluster method be used in conjunction with more traditional techniques, such as scat analysis (see Chapter 4) for a thorough assessment of mesocarnivore diet, and with questionnaire survey to assess socio-economic factors of importance in livestock losses attributed to predators (see Chapter 6). Scat sampling also includes samples from a larger number of different individuals at a lower cost, effort and inconvenience to the animal than GPS collaring and GPS cluster investigation, although it presents biases too (Klare et al., 2011). Both GPS cluster and scat analyses converged on the absence of livestock in the diet of jackals from the PA and improved the assessment of predation severity on farmland. My results could be used to influence both private and government approaches to reduce livestock losses and to advance knowledge in the management of both livestock (i.e. protection measures) and their predators. This is important in a farmer–predator conflict framework where indiscriminate lethal management is considered to be the main solution. Directly showing farmers the results of my research conducted on their farms was also an effective way of gaining their trust and facilitating the adoption of new behaviours.

CHAPTER 6

Farmer reported conflict with predators, their attitudes towards wildlife and strategies to reduce predation

Face-to-face interview with a sheep farmer in the Beaufort West District Municipality, Central Karoo, South Africa © Nathalie Houdin & Denis Palanque – The Karoo Predator Project.

Abstract

Conservation conflicts are increasing worldwide in both their extent and severity. Disagreement amongst stakeholders on the extent of damage that wildlife cause and the acceptable measures for preventing it have highlighted the importance of better understanding the human dimensions of conflict before attempting conflict mitigation. In the Karoo, conflict between livestock farmers and predators is pervasive, yet very little research exists on its human dimensions. I conducted 77 face-to-face interviews with small-livestock farmers in the Central Karoo, using semi-structured questionnaires to (1) assess the spatio-temporal distribution and severity of the reported predation problems with jackal, caracal and baboon, (2) identify the reasons farmers propose for the changes in predator problems, (3) highlight factors influencing the percentage of lamb losses attributed to predators, (4) determine farmers' attitudes towards wildlife in general, and jackal and caracal in particular, (5) document farmers' strategies for reducing predation, and (6) highlight key factors influencing the likelihood of using illegal poisoning to control predators. My results show that 98.7% of the respondents attributed some of their livestock losses to predators, primarily to jackal and then caracal, Cape fox and baboons. The number of farmers who reported jackal, caracal and baboons as a serious problem has increased from the 1990s to 2014 by 76%, 30% and 20% respectively. Reported percentage of lamb losses was linked to both environmental (e.g. terrain ruggedness) and socio-economic (e.g. decrease in farm labour) factors. Farmers showed positive attitudes towards non-predatory wildlife and towards emblematic predators no longer (e.g. lion) or never (e.g. tiger) previously found in the Karoo. Tolerance to jackal and caracal was best explained by their perceived aesthetic appeal, and intolerance was largely driven by the belief that they should not be present on farmland, but rather restricted to PAs. Methods currently used for reducing livestock predation were mostly lethal. Non-lethal methods were widely considered to be too expensive, unpractical and ineffective. Approximately half of the respondents reported the use of poison, with most farmers justifying its use on the basis of its efficiency. Poison use did not correlate with the level of reported livestock loss and was highest on farms that had less labour and a lower terrain ruggedness index. Farmers who used poison also listed jackal, caracal and baboons as the main predators on their farm and mentioned Cape fox as one of five predators consuming livestock. Together, these findings suggest that efforts to increase tolerance towards jackal and caracal and limit poison use on farms would best be realised by promoting the aesthetic appeal of predators, improving knowledge of their ecology and behaviour, and most of all by changing the socio-economic and political environment to promote labour on farms. All of these factors are potentially more important than those that aim solely at reducing livestock losses.

Introduction

The limited size and number of PAs means that many populations of mammals and birds must survive outside of parks and reserves, often on privately owned land (Knight, 1999; Scott et al., 2001; see Chapter 3). Predator species, in particular carnivores, differ in their ability to adapt to human-dominated landscapes (Athreya et al., 2013; Atwood, 2006; Ogutu et al., 2005; Valeix et al., 2012; see Chapter 4). Large carnivores, which require extensive areas to maintain viable populations, are particularly vulnerable to the fragmentation of natural habitat into small, unconnected patches (Crooks, 2002) and seldom persist in areas that include livestock farming activities (Kauffman et al., 2007a; Zimmermann et al., 2010; see Chapter 3). Small size, together with behavioural and ecological flexibility are important traits for persisting in anthropogenic landscapes (Cardillo et al., 2005). Predator persistence also depends on their social acceptability to communities, particularly outside of PAs (Holmern et al., 2007; Kansky et al., 2014; Linnell et al., 2001). Therefore, the attitudes (including tolerance) and perceptions of people living with wildlife are pertinent to conservation biologists, managers and policy makers (Decker and Chase, 1997), because they shape the interactions between communities and wildlife. It is now widely accepted that social sciences can contribute to conservation (Bennett et al., 2017; Dickman, 2010) by providing tools and concepts to better understand the attitudes and their drivers of communities towards wildlife. Manfredo et al. (1996) defined human dimensions as “an area of investigation which attempts to describe, predict, understand, and affect human thoughts and action”, while Decker and Lipscomb (1991) defined human dimensions of wildlife management as “identifying what people think and do regarding wildlife, understanding why, and incorporating that insight into policy and management decision-making processes and programs” (cited in Decker and Chase, 1997).

Livestock losses are one of the first causes of conflict between people and predators worldwide (Torres et al., 2018) due to their socio-economic (Holmern et al., 2007; Mishra, 1997; Wang and Macdonald, 2006), psychological (Chowdhury and Jadhav, 2012; Jadhav and Barua, 2012) and health impacts (Barua et al., 2013; Jadhav and Barua, 2012) on rural communities. Particularly, when livestock is managed extensively and when numerous species of predators still occur outside PAs, economic losses from predation can be substantial (Thorn et al., 2012; Woodroffe et al., 2005). Livestock losses are a complex issue and can be impacted by the species of predators involved (Holmern et al., 2007; Wang and Macdonald, 2006), individual predator characteristics (Sacks et al., 1999, see Chapter 5), environmental attributes (Stahl et al., 2002) and managerial factors (Ogada et al., 2003; Wang and Macdonald, 2006). In addition, losses are difficult to accurately quantify (Miller et al., 2016; see Chapter 5) and in some cases, there is evidence for a significant mismatch between the perception and actual impact predators have on livestock (Marchini, 2014). Perceived damage and risk often do exceed the number of livestock lost to predators (Ciucci and Boitani, 1973; Marchini and Macdonald, 2012; Wagner, 1988) but this is not always the case, and sometimes reality and people's perceptions of carnivore threats align (Miller et al., 2016). Surveys can therefore be an important tool for gathering information not only on farmers' reported losses, but also on the socio-economic and livestock management aspects impacting them (Gusset et al., 2009; Kabir et al., 2014; Wang and Macdonald, 2006).

Losses (or the fear thereof) and the lack of incentives to coexist with predators can make communities antagonistic and trigger negative attitudes towards wildlife in general, and predators in particular (Kinnaird and O'Brien, 2012; Schumann et al., 2008; Zimmermann et al., 2005). It is therefore important to assess the number of losses that farmers attribute to predators on their farms and how this impacts their livelihoods. In the Karoo, losses that farmers attribute to jackal and caracal are perceived as a growing threat to the financial sustainability of the small-livestock industry (Bergman et al., 2013; Kerley et al., 2018; see Chapter 4) making it a particularly important topic for regional and national economics. Livestock losses due to these two species have been reported in different regions of southern Africa (Gusset et al., 2009; Swanepoel, 2016; Thorn et al., 2012). In the Karoo, the perceived importance of jackal and caracal (and to a lesser extent baboons) as predators of livestock has fluctuated over time (Nattrass et al., 2017).

The first written records of human-predator conflict in South Africa date back to 1652 when Europeans settled in the Cape Colony. Three hundred years later, in the mid-1960s, as a resut of the bounty system introduced by the Governor of the Cape Colony (see Chapter 2), jackals were well controlled but baboons were on the increase (Hey, 1967). By 1979, the caracal had become the main predator on sheep farms in the Karoo (Pringle and Pringle, 1979) and the predator most frequently hunted in the Witzenberg Municipality District (Conradie, 2012; Conradie and Piesse, 2013) and the Eastern Cape (Bailey and Conradie, 2013). By 1994, coinciding with the onset of democratic elections in South Africa, the restructuring of local government resulted in the termination of subsidized fencing and state-supported predator control programs (Nattrass et al., 2017). The number of commercial sheep farms in the Central Karoo declined sharply from 877 in 1952 to 396 in 2002, while the mean farm size increased from 3593 to 5524 hectares (Western Cape Department of Agriculture, 2013). Both the total number of sheep and the number of sheep per farm declined, as did the number of workers per sheep. Together, these changes likely promoted what farmers perceive today as a re-emergence of the jackal as a threat to livestock (reported in Nattrass and Conradie 2015) and with that, strong negative attitudes towards the species.

The attitude concept has been a key component to predict and explain human behaviour (Fishbein and Ajzen, 2010; Heberlein, 2013) and is widely used in research on human-wildlife conflict (Kaltenborn et al., 1999; Manfredo et al., 1996; Manfredo and Zinn, 1996; Naughton-Treves et al., 2003; Romañach et al., 2007). Attitudes have been described as "dispositions or tendencies to respond with some degree of favour, or not, to a psychological object, the latter being any discernible aspects of an individual's world, including an object, a person, an issue or a behaviour" (Fishbein and Ajzen, 2010). Attitude research can provide information on stakeholders' preferences for various management strategies and for a desired population size for a species. In the case of farmers, attitudes can bring information on the quantity of damage they are willing to tolerate and the desirability of different species on farmland (Kansky and Knight, 2014). Understanding attitudes of farmers living with wildlife is thus relevant to managers, conservation practitioners and policy makers (Decker and Chase, 1997). In particular, highlighting the determinants of tolerance, which is "the proportion of individuals who have a positive attitude towards a species group despite suffering damage by that species group" (Kansky et al., 2014), can be useful to design programs to improve attitudes and alleviate the conflict.

Previous research has shown that local attitudes, perceptions, knowledge of and experience with a species are all closely interlinked (Bruskotter and Wilson, 2014; Inskip et al., 2016; Parker et al., 2018). In this respect, knowledge of, or positive experience with carnivores has often been found to create positive attitudes towards those species (Bath and Buchanan, 1989; Casey et al., 2005; Cavalcanti and Gese, 2010; Ericsson and Heberlein, 2003; Parker et al., 2014; Thornton and Quinn, 2009; Wilson and Tisdell, 2005). Conversely, the lack of knowledge on the role of predators in the ecosystems where they live can result in negative attitudes towards them (Williams et al., 2018). Age (Majić and Bath, 2010), gender (Gore and Kahler, 2012), language (Page-Nicholson et al., 2017), education, socioeconomic status, dependence upon a single livelihood (Dickman, 2010), religious beliefs (Hazzah et al., 2009), personality and emotions (Marchini and Macdonald, 2012), and aesthetic aspects of animals (Knight, 2008;

Liordos et al., 2017) have all been shown to be potentially significant drivers of local attitudes towards wildlife. In addition to these variables, the roles animals play in folklore in almost all cultures (Sax, 2017) can substantially influence attitudes (Ceríaco, 2012; Herrmann et al., 2013). In some cases, hostility over perceived social injustice and imbalances of power might also explain attitudes. For instance, rural communities often feel particularly afflicted by damage caused by protected wildlife that they perceive as being imposed by more influential urbanites (Skogen et al., 2008), which might ultimately influence people's behaviours and management strategies.

Even if it is widely assumed that negative attitudes and intolerant behaviours towards predators are motivated by retaliation for the magnitude of real and perceived losses of livelihood, experiencing damage is not always the dominant factor determining attitudes (Kansky et al., 2014) or behaviour (Thorn et al., 2012). For example, some farmers remove wildlife species despite not encountering any problems with them and others who have problems choose not to remove the species (Marker et al., 2003). Instead, recent research indicates that predator persecution is not directly related to predator problems (Graham et al., 2005; Marchini, 2014; Marchini and Macdonald, 2012), but rather to social and cultural values (e.g., peer pressure, thrill of going on a hunt, beliefs).

For most of history, humans have responded to the presence of carnivores with lethal control (Reynolds and Tapper, 1996), which is one of the most widespread forms of wildlife management (Berger, 2006). Today, wildlife perceived as "problem animals" or "damage-causing animals" are killed both legally and illegally throughout the world and in all cultures. Examples include wild dogs (*Lycaon pictus*, Woodroffe and Ginsberg, 1999), caracals (Conradie and Piesse, 2013) and jackals (Tensen et al., 2018) in Africa; dholes in Asia (Lyngdoh et al., 2014); culpeos (*Pseudalopex culpaeu*s) in South America (Novaro, 1995); dingoes in Australia (Allen and West, 2013); coyotes, wolves, red foxes, cougars, bobcats, and brown bears (*Ursus arctos*) in North America (Reynolds and Tapper, 1996); and lynx, wolverines (*Gulo gulo*), wolves, and brown bears in Europe (Breitenmoser, 1998). The most common methods to control predators include shooting, trapping and poisoning (Woodroffe et al., 2005). Predator control can be performed by individuals, informally or formally organized communities, bounty hunters, as well as by local and national governments who implement predator control initiatives at a regional or national scale (Allen et al., 2013a; Reynolds and Tapper, 1996; Woodroffe et al., 2005). In the Central Karoo, collaboration between farmers to hunt predators remains institutionalized in different forms of local associations, from farmer experimentation groups to church groups, and the management of predators is generally at the hands of ward cooperatives, in which farmers take responsibility and develop their own strategies to reach their stated aims (pers. obs.).

The United States spent $1.6 billion on carnivore removal between 1939 and 1998 (Berger, 2006) and South Africa began subsidizing predator extermination in 1889, primarily targeting the jackal (Nattrass et al., 2017). Although organized campaigns to control predators have threatened the persistence of species such as African wild dogs, and red wolves (*Canis rufus*), other canids such as foxes, coyotes, jackals, and culpeos have shown incredible resilience (Macdonald and Sillero-Zubiri, 2004). Lethal control methods are considered by some as inhumane because they cause suffering, as well as injury and mortality of non-target animals including domestic animals, protected species, and other wildlife (Naughton-Treves and Treves, 2005; Rochlitz et al., 2010). Such criticisms have raised ethical concerns and have resulted in a decrease in public support for lethal control programs (Arthur, 1981; Reiter et al., 1999; Slagle et al., 2017) and an increase in conservation conflict between stakeholders on how to best manage wildlife and predators on private land (Nattrass and Conradie, 2015). Despite the rise of ethical concerns, research on the effectiveness of non-lethal control methods to reduce predation remains scarce (Eklund et al., 2017; Treves et al., 2016). In the Karoo, predators have been controlled by small-livestock farmers over the last century, beneficiating from government support in the forms of subsidized fencing, provision of dog packs for hunting and poison (Beinart, 2003). But this support declined from the 1980s and today, sheep farmers are faced with managing predation on their own.

Among control methods, the illegal use of poison baits in urban landscapes (Riley et al., 2003), agroecosystems (Márquez et al., 2013), and even in PAs (Ntemiri et al., 2018) to kill species that predate on livestock or game, or that cause damage to food stores or crops, has been a common practice in many parts of the world, including Europe (Giorgi and Mengozzi, 2011; Graham et al., 2005), Africa (Allan, 1989; Ogada, 2014), Asia (Green et al., 2004), Australia (Allen, 2015), and North (Wobeser et al., 2004) and South America (Gáspero et al., 2018). Poisoning principally targets raptors and mammals that include scavenging as means to obtain food, but may have devastating effects on non-target wildlife through secondary poisoning (Mateo-Tomás et al., 2012). Poisoning also presents an important risk to many threatened species (Ogada et al., 2016; Santangeli et al., 2016), the environment and people (UNEP, 2016).

Despite being an illegal practice in many countries, poison remains among the most readily available methods for farmers (Mateo-Tomás et al., 2012; Santangeli et al., 2016), with a wide range of chemical substances used, including banned pesticides (e.g. carbamates, organophosphates and organochlorines) and potassium cyanide. Insecticides found on the black market, such as methomyl (in powder form) and carbofuran are commonplace (Ntemiri et al., 2018). In South Africa, the use of poison baits against predators has a long history, dating back to the 1880s, when farmers gathered into "wild animal poisoning clubs" in the Eastern Cape midlands to exterminate wild carnivores (van Sittert, 1998). The passing of the fencing act and the spread of enclosures in 1883 encouraged farmers to increase their use of poison, with devastating effects on the populations of various animals, including non-target species (van Sittert, 2016). In 1973, the Hazardous Substances Act restricted the use of sodium cyanide, 1080 and strychnine, with the result that many farmers resorted to experimenting with a variety of readily available agrochemicals as poisoning agents (Nattrass and Conradie, 2015). Given that cases of wildlife poisoning on private land are almost impossible to detect and are seldom reported, the intensity of this illegal activity and its current impact on the status of wildlife in the Karoo is largely unknown. Therefore, assessing farmers' experience with poison and uncovering some of the factors explaining its use is relevant for both guiding management strategies and informing policy (Kross et al., 2018; Treves and Karanth, 2003).

So far, most African studies interested in human-predator conflict have investigated the losses, attitudes and strategies of commercial farmers towards large carnivores (e.g., Lindsey et al., 2013; Schumann et al., 2008; Zimmermann et al., 2005). Few studies have tackled the case of common, adaptable, non-threatened mesopredators living on rangelands outside of PAs. With a mix of both qualitative (interviews, word elicitation, participant observation) and quantitative (modelling of answers) methods, this chapter aimed to better understand the topic of mesocarnivore-farmer conflict in the context of the socio-productive crisis the Karoo is experiencing, triggered by socio-political changes (Nattrass et al., 2017) and environmental events (Conradie and Piesse, 2016). In particular, I sought to document the spatio-temporal extent and severity of the reported human-wildlife conflict resulting from predation by jackal, caracal and baboons on small-livestock, and assess farmers' reasons for the perceived changes in predator numbers and predation. I predicted that (P1) the spatial extent of perceived problems with the three species would increase with time across the Central Karoo, in particular for jackal, since the transition to democracy in 1994 coincides with the restructuring of local government, as well as the termination of financial support for predator control (Nattrass et al., 2017).

Secondly, I aimed to highlight key factors influencing the reported percentage of lamb losses that farmers attribute to predators. I hypothesized that the percentage of lamb losses would be influenced by landscape attributes (Azevedo and Murray, 2007; Stahl et al., 2002; Thorn et al., 2012) and socio-economic factors (Berger, 2006; Thorn et al., 2013). In particular, I predicted that reported percentage of lambs lost would be higher on main farms: (P2a) that are managed by younger farmers because they generally have less knowledge of and experience with farming than older farmers (Berger, 2006); (P2b) with fewer farm workers because "more eyes and feet on the ground" allows for better predator control (Nattrass and Conradie, 2015) and better livestock management; (P2c) that are large (Kaartinen et al., 2009) because they are more difficult to patrol, have more border fences to check and can hold larger predator populations; (P2d) where the mean terrain ruggedness index is high because rugged terrain is favoured by baboons (Du Plessis et al., 2018) and caracals (Avenant et al., 2016); (P2e) where there is more permanent artificial water sources that sustain predators that are obligate drinkers (e.g. baboons), as well as providing a point at which livestock concentrate and could be ambushed by predators; and (P2f) where baboons are ranked as the main livestock predators because these farms will also likely be experiencing losses to caracal and jackal, and the cumulative impact of having three predators is likely to result in higher losses. Lastly, I predicted that (P2g) farms that have a high terrain ruggedness index and on which caracals are ranked as the greatest cause of lamb losses (i.e. the interaction between the two factors) should report higher losses because caracals favour rugged areas in semi-arid regions including the Karoo (Avenant et al., 2016).

I then sought to explore farmers' attitudes towards wildlife and the drivers of tolerance towards jackal and caracal. I predicted (P3) that farmers' attitudes would be negative towards predators because of the threat they pose to livestock (see Chapters 4 and 5). Tolerance has often been shown to be negatively correlated with farmers' perceptions of threats due to different predators (Andersone and Ozoliņš, 2004; Baker and Macdonald, 2000; Riley and Decker, 2000). I thus predicted (P4a) that if farmers ranked either jackal or caracal as the biggest concern for livestock losses on their farm, then they would be less tolerant towards that species. Tolerance has often been demonstrated to be negatively correlated with livestock losses (Dar et al., 2009; Mishra et al., 2003; Oli et al., 1994) even if it is not always the case as shown earlier in this chapter. For the Karoo, I predicted (P4b) that the percentage of lamb losses farmers attributed to predators would significantly impact their tolerance towards jackal/caracal. Aesthetics or physical attractiveness has been shown to be an important determinant of perceptions of endangered species and public support for their protection (Kellert, 1993; Kellert et al., 1996; Knight, 2008). I thus predicted (P4c) that farmers who perceived jackal/caracal as “physically beautiful” would be more tolerant of jackal/caracal on their farm. I further predicted (P4d) that farmers who believe that mesopredators should only occur in PAs would be less tolerant towards them on their farms; and finally (P4e) that farmers who think that jackal and caracal control each other’s populations would be more tolerant of both mesopredators in order to maintain the ecological balance on their farm. It was difficult to predict the influence age would have on tolerance. Some authors have shown that older people usually display more negative attitudes towards carnivores than younger people (Bjerke et al., 1998; Røskaft et al., 2007) but this is not always the case (Kaltenborn et al., 2006). It is possible that older men in my study area would be more intolerant of predators given past policies in favour of culling and government support to control “pest species” (Nattrass et al., 2017). Similarly, I had no clear expectation on the influence of farm size. Larger farms are more difficult to patrol with more fences to check against predators coming in, but on the other hand, having a larger farm meant that the farmer was relatively better off (i.e. could farm more sheep) and thus may have had a greater financial space to tolerate losses and to act quickly in terms of predator control if losses increased (e.g. available funds to hire a professional hunter).

Finally, I aimed to determine farmers’ control strategies against predators, and to investigate their use of illegal poisoning. I predicted (P5) that lethal methods would be preferred to non-lethal methods (Thorn et al., 2012). Regarding poison use, I predicted that farmers would be more likely to use poison (P6a) if the number of labourers had decreased since they had started farming, with the result that there was less effort on patrolling and maintaining border fences, and on active monitoring/tracking/trapping of predators and livestock husbandry; (P6b) if farmers had listed jackal, caracal and baboon as a problem for livestock on their farms, because the presence of all three predators is likely linked with higher overall losses; (P6c) if they ranked Cape fox amongst the top five main predators of livestock on their farms because they would then not have to worry about these as non-target species; (P6d) if farmers believe poison is effective at reducing livestock losses; and (P6e) if farmers reported a higher percentage of lamb losses that they attribute to predators. In northern Spain, the use of illegal poisoning increased in mountainous areas where wolves frequently depredated on livestock because rugged areas are difficult to patrol, with reduced surveillance of livestock notably by shepherds and dogs

(Mateo-Tomás et al., 2012). I thus predicted (P6f) that the likelihood of using poison would increase if farmers owned farms with a higher mean terrain ruggedness index (TRI). I also predicted (P6g) that farmers who believe in the "dominant jackal pair" narrative (i.e. that having a territorial pair of jackals on the farm prevents other jackals from coming in) would be less likely to use poison, because they might disrupt pairs and this could lead to the immigration of more jackals (Minnie et al., 2018b; Tensen et al., 2018) and higher losses; and (P6h) that farmers with more years of education would be less likely to use poison because they are more likely to be aware of the unintended ecological impacts. Once again, it was difficult to predict the influence of age or farm size on the likelihood of poison use. In their paper on the illegal poisoning of wild fauna in Spain, Mateo-Tomás et al. (2012) showed that there was no significant influence of age on the illegal use of poison. However, an economic study in the Central Karoo found that older farmers were less likely to use poison but the effect size was small (Nattrass and Conradie, 2018). It is also possible that younger men may have more motivation to hunt than poison, because they often consider hunting a form of sport and an occasion to socialize (pers. obs.). Regarding farm size, larger farms require more effort to patrol with more fences to check and maintain and hence poisoning might be more efficient than on smaller farms. On the other hand, having a larger farm may mean that the farmer is financially more secure and may thus be able to absorb more losses before resorting to the use of an illegal method.

Methods

Survey design and questionnaire administration

From July 2014 to March 2015, I conducted 77 face-to-face in-depth interviews with small-livestock farmers in the Central Karoo local districts of Laingsburg, Prince Albert and Beaufort West. I used a semi-structured questionnaire that took between 60 and 90 min to complete. Respondents were informed that the research formed part of the University of Cape Town's Karoo Predator Project and were assured that their responses were confidential. They gave their informed consent to take part in the survey. The interviews were mostly conducted in English at the domicile of the respondents, but Afrikaans and English paper versions of the questionnaire were also distributed so farmers could read the questions directly in their preferred language. Pre-testing of the questionnaire was conducted with a subset of 19 farmers in the Koup area within the Central Karoo (see Chapter 2). I selected this area as this is where a lot of my ecological fieldwork was based and hence, I already knew most of the farmers and had established a working relationship. Pre-testing was to ensure that all questions were unambiguous and could be answered by farmers (van Teijlingen and Hundley, 2001). After pre-testing, six questions were slightly reformulated and one was dropped while another one was included.

Respondents were recruited from a previous survey, which was part of the Karoo Predator Project (Conradie et al., 2015). I also approached farmers who were part of formal agricultural associations, in person at farmer meetings. Lastly, I asked the Laingsburg Animal Health Technician (working for the Department of Agriculture under the Veterinary Services) to make appointments for me with any farmer she was visiting for veterinary purposes in the district. Thereafter, I relied on referrals, which may explain why no farmers declined to be interviewed with the exception of a single individual who could neither understand nor speak English. Respondents were thus largely derived using a convenience/snowball sampling approach (Newing, 2010) rather than a probability sample. Bias in this approach is largely offset in this study by the inclusion of a large proportion of available farmers interviewed within the Central Karoo. According to the most recent farm census (2014/2015) for the Western Cape (Western Cape Department of Agriculture, 2017), there were 155 farms in the Central Karoo. The census did not report on the type of farm, but most of these would have been sheep farms and a minority would have been game, cattle and seed farms. Given that almost 39% of the farmers I interviewed own multiple farms, my survey thus includes at least 64% of the current small-livestock farmers in the Central Karoo District Municipality.

I undertook ethnographic field observations. Ethnography is defined as a process where researchers are conducting "participant-observation paired with a range of other methods, living within a community, and getting deeply involved into the rhythms, logics and complications of life as lived by a people in a place" (McGranahan, 2015). At the time of the interviews, I had been living for almost two years in the farming community, staying on a commercial small-livestock farm owned by a couple of Afrikaans-speaking sheep farmers. My presence within the community helped limit any possible mistrust or suspicion farmers may have had towards me as an "outsider" because most of them came to know me and hear of my work. During this time, I was immersed in the daily life of farmers and helped with farm duties in between setting out the first phase of my fieldwork (see Chapter 3 – camera trap biodiversity survey). To learn more about livestock farming, the farmers themselves and to gain a wider perspective on predator management on farmland, I spent the month before the interviews going into the field with some farmers. At each farm, the farmer gave me a tour of his property and explained his management system. I also attended as many social events as possible from church meetings to shooting competitions to get to know the community better. I invited farmers to join me in the field when I was deploying camera traps on their farms (see Chapter 3), and invited them to watch the collaring of jackal and caracal where possible (see Chapter 5), which was a good opportunity for them to ask me questions about my research and my personal background. Collectively, these actions increased the farmers' trust of my research motives (Constant et al., 2015; Rust and Taylor, 2016) and helped to build rapport and trust (Puri, 2010), which altogether allowed me to ask questions and obtain reliable answers concerning sensitive issues such as the illegal use of poison to manage predators. I also read newspapers, books, journal articles and farmer/professional hunter blogs relating to farmer-predator conflict in the region to gain a better understanding of the situation. Finally, I drew on farmers' narratives captured during the in-depth conversations about their interactions with wildlife and predators, and during my time with them in the field to contextualise their answers and to discuss my results. Every evening, after each interview, I mapped the respondents' farms in QGIS 2.18.2 software (QGIS Development Team, 2017) and entered and transcribed data and notes onto an Excel spread sheet to ensure the information was still fresh (Rust and Taylor, 2016).

Questionnaire instrument

Unless stated otherwise, the unit of observation in the questionnaire was an individual farmer, who might own/manage multiple properties and small-livestock types. In this chapter, I introduced the term "main farm" to denote the farm that is their main production unit and defined as a collection of neighbouring farm cadastres, which have a single exterior fence (except when the national road, the N1, runs through, effectively separating them into two farms). The main farm is also where most of the livestock activity takes place and often where the primary homestead is situated. Farmers are typically better informed about livestock issues including predation on their main farm compared to their other farms, which are often situated far away and hence visited less regularly. Consequently, when interrogating the potential predictors of the percentage of lambs lost (Table 6.1), I asked farmers to restrict their responses to their main farm only. For the other response variables (viz., predator tolerance and poison use), I used explanatory variables derived from the main and all the other farms as these data were less likely to be affected by lower visitation rates and hence the accuracy of reporting. Some farmers kept detailed written records concerning the management of their farms whereas others relied solely on their memory. The questionnaire included 85 groups of questions divided into five sections. In this chapter, I only used a subset of the sections, with the remaining questions forming part of a larger long-term study.

Causes of livestock losses and the ranking of predator species as threats to livestock

I first asked farmers whether they had livestock losses on their farms and if yes, what they considered were the main cause. Almost all farmers attributed some losses to predators and thus, I presented each of them with a list of six predators known to spatially overlap with livestock farms and asked them to rank them according to the level of livestock predation they were perceived to be responsible for on their farms from 1 (causing the most predation) to 6 (causing the least predation). Farmers could add species that were not in the list and rank them too. That allowed for the identification of the three main predators of livestock in the Central Karoo. Secondly, I asked them to explain how they inferred whether a particular species was responsible for a livestock attack and whether they reported their losses and to whom.

Spatio-temporal patterns of predator presence and perceived conflict with farmers

To determine where and when jackal, caracal and baboon first became a problem for the viability of small-livestock farming, I analysed farmer responses to the following three questions:

Q1: When was the first time you saw a jackal/caracal/baboon or their spoor on your farm (i.e year of onset of predator's presence on each farm)?

Q2: When – if ever – did jackal/caracal/baboon become a problem for lamb losses on your farm (i.e year of onset of perceived problem with predators on each farm)?

Q3: When – if ever – did lamb losses to jackal/caracal/baboon become a serious concern to the viability of your farm (i.e. year of onset of perceived severe problem with predators on each farm)?

I had separate question for each species and chose to focus on baboons rather than Cape fox due to the very negative attitudes farmers displayed towards them. The distinction between "problem" and "severe problem" was based on individual perception and may correspond to different levels of predation depending on the socio-economic situation of each farmer. I used the responses to these questions to produce cumulative histograms at three points in time (i.e. before 1994, before 2004, by 2014) for each predator specie across all farmers. I used 1994 as the lower cut-off date because this year coincides with the onset of democratic elections in South Africa, the restructuring of local government, as well as the termination of financial support for predator control. As the year of onset of the conflict may be biased by farmers who only started farming recently, I excluded the answers of farmers who started farming after 1994 (i.e. with less than 21 years of experience) and whose answer to any of the questions corresponded to the date when they started farming. I then performed Pearson's Chi-squared goodness of fit tests to determine whether the distribution of the farmers' responses corresponded to a uniform distribution (i.e. all time periods have equal probability to be cited by the respondents for each question Q1, Q2 and Q3). I tested the null hypothesis that all time periods have equal probability to be cited by the respondents (versus there is a trend).

I then overlaid the responses to question Q3 with the cadastral boundary of each respondent's farms to produce maps showing the cumulative spatial distribution of perceived severe problems with each predator at three points in time (i.e. before 1994, before 2004, by 2014). Cadastral boundaries were derived using a regional cadastral map (Farm Portions, Department of Rural Development and Land Reform, Chief Surveyor-General Office, Western Cape, 2013). The cadastral boundary was filled in with a different colour for jackal, caracal and baboon. All maps were created using the package ggplot2 (Wickham and Chang, 2016) in the Program R v.3.4.0 (R Development Core Team 2018).

Farmers' perceptions for changes in predator numbers in the Central Karoo

I asked farmers whether they thought jackal, caracal and baboon numbers had increased over the last decade in the Central Karoo. If they replied positively, I asked what reasons they thought caused the change. I grouped their answers into three broad categories after an initial qualitative, inductive content analysis using structural coding that allowed highlighting keywords or key locutions (e.g. predator control, lifestyle farming, nature reserve) and the recognition of three clear themes.

General modelling

All the models in this chapter were conducted in R 3.2.1 (R Development Core Team, 2017). I included predictor variables in GLMs based on the following selection process: I first selected variables of expected influence based on *a-priori* hypotheses. Then, to avoid collinearity among the variables in the model, I calculated Spearman's correlation coefficients for pairs of variables and only included variables with correlations where ($r \leq 0.7$). I included the remaining variables in multivariate global models that I used to generate and rank models with all combinations of predictor variables based on Akaike's Information Criterion, which was adjusted for small sample size (AIC_c) (Akaike, 1974; Burnham and Anderson, 2004), using the "MuMIN" package in R (Barton, 2013). I also computed the Bayesian Information Criterion (BIC) (Aho et al., 2014). I checked the top models for multicollinearity among variables by assessing Variance Inflation Factors (VIF) using the “car” package (Fox and Weisberg, 2011) and checked that the VIF < 2. Finally, I tested for model goodness of fit using a combination of overall goodness-of-fit ($p \leq 0.05$), Pseudo-R^2 (Hu et al., 2006) and log likelihood. For each predictor variable, I calculated the average marginal effect (AME) in the “margins” package (Leeper et al., 2018; Leeper, 2017) with robust standard errors (I followed Wooldridge, 2010 who recommends using robust standard errors in logistic regressions, otherwise the standard errors are too large) using “heteroscedasticity and autocorrelation consistent” estimators in package “sandwich” (Zeileis, 2006, 2004). The AME shows the change in probability when the predictor or independent variable increases by one unit. For continuous variables, this represents the instantaneous change given that the “unit” may be very small. For binary variables, the change is from 0 to 1. Finally, in each model, the variables that were not normally distributed were either log-transformed or square root-transformed when it improved the general model fit.

Model of reported lamb losses

I asked each respondent what percentage of lambs they had lost to predation compared to their pregnancy rate and in the previous year (2013). I also asked whether there was a time of year when livestock predation is highest. I then used a fractional regression analysis (i.e. regression model for percentages) to model the percentage of reported lambs lost as a function of seven possible variables related to the main farm of the respondents. The fractional response was bounded between [0;1] and was used as the dependent variable.

Table 6.1. Description of the variables that were hypothesized to influence the percentage of lambs killed by predators on the main farm of 77 respondents in 2013 in the Central Karoo, South Africa. Variables were included as predictors within the fractional regression analysis. Mean and range values for each variable are provided. Except if stated otherwise, all variables were extracted from the questionnaires.

Variables of predicted importance	Type	Unit *Mean* [range]	Description	Expected influence
Age	Continuous	Years *50.6* [25-76]	Farmer age as a proxy for farming experience.	–
Number of labourers	Discrete	*2*[a] [0-16]	Current number of labourers.	–
Main farm size	Continuous	Kilometres squared *59.73* [3.24-226.20]	The land area of the respondent's main farm, excluding land portions not encompassed by the perimeter fence. Farm size was extracted from the regional cadastral map (Farm Portions, Department of Rural Development and Land Reform, Chief Surveyor-General Office, Western Cape, 2013) in QGIS 2.18.2 (QGIS Development Team, 2017).	+
Relative mean main farm Terrain Ruggedness Index (TRI)	Continuous	Index *0.36* [0.14-1.00]	Relative mean of the absolute values of the differences between a central pixel and its neighbours (sensu Riley et al., 1999; Wilson et al., 2007). The most rugged farm has a value of 1. All the other farms are relative to the most rugged. TRI was calculated using the Digital Elevation Model (DEM) layer of the Western Cape (30 m precision) in QGIS 2.18.2 (QGIS Development Team, 2017).	+
Number of permanent artificial water sources	Discrete	*13*[a] [2-114]	Total number of permanent artificial water sources present on the respondent's main farm.	+
Rank 1 caracal	Boolean	Yes / No	Whether the caracal was ranked as the predator responsible for the most livestock losses.	+/-
Rank 1 baboons	Boolean	Yes / No	Whether the baboon was ranked as the predator responsible for the most livestock losses.	+

[a] *median*

Farmers' attitudes towards wildlife in general and predators in particular

a) Farmers' attitudes towards wildlife

Researchers have employed measures of "Wildlife Acceptance Capacity" (WAC) to understand the acceptability of wildlife populations within a given area. WAC was originally proposed by Decker and Purdy (1988) to reflect the "maximum wildlife population level in an area that is acceptable". When an animal population is perceived to have gone above a given person's internal threshold, that population becomes "unacceptable" and the person is supposedly motivated to take action to reduce the population. I followed Bruskotter et al. (2015) and used WAC concepts to explore the attitudes of farmers towards a set of 11 species of wildlife (including predators) that were classified as vermin after fencing expanded across the Karoo from the 1930s (Beinart, 2003). This includes species that damage fences (e.g. porcupines) or are perceived to prey on livestock (e.g. jackal) or on poultry (e.g. African wildcat) and crops (e.g. baboons) (Hey, 1967) .

I asked each farmer the question "To what extent should the population of each of the following species be managed in the Karoo?" Farmers had the choice to "exterminate the species completely", "reduce it greatly", "reduce it a little", "leave it at it is", "increase it a little" or "increase it greatly". They could also choose "unsure" as a response. I calculated percentages for each response and provided a visual description of the data by using a stacked bar plot built with the package Likert version 1.3.5 (Bryer et al., 2016) in R version 3.4.2. (R Development Core Team 2017). I used Chi-square tests of independence to test the null hypothesis that there was no relationship between the mesopredator species (amongst jackal, caracal, baboons) and the proportion of farmers who chose a management response that would reduce or exterminate the species from farmland.

To further understand farmers' attitudes towards predators and wildlife, I asked respondents to name their favourite wild animal (they were informed that they could choose species that were not living in the Karoo or even Africa). The extent to which a person is exposed to a species and the nature of the exposure are both considered to be important potential predictors of attitudes towards a species (Kansky and Knight, 2014). For instance, it has been shown that people with experience of wolves, either from living in areas where wolves are present or from having livestock losses to wolves, were less positive than the general public (Ericsson and Heberlein, 2003). I predicted that respondents would show a preference for emblematic carnivore species that do not occur in the Karoo and with which farmers have not had negative experiences relating to livestock. Furthermore, I predicted that they would select aesthetically appealing species, which have broad iconic status (e.g. tiger) (Small, 2012).

b) Farmers' attitudes towards jackal and caracal

I probed attitudes towards jackal and caracal in particular by doing two types of analyses. I first used word clouds to assess attitude salience towards both predators, i.e. how easily and quickly thoughts, expressed as words, come to mind when an attitude object – i.e., jackal or caracal – is introduced (Vaske and Manfredo, 2012). I asked farmers: "What is the first thing you think about when I say the word *jackal*?" I repeated the question for caracal. Newcomb (1950) suggested that "the more salient a person's attitude the more readily will it be expressed with a minimum of outer stimulation". Thus, I predicted a shorter time between asking the question and having an attitude expressed, through powerful words. I timed the latency to respond to the question using a stopwatch on my phone. I predicted both a shorter latency to reply and more negativity in the verbally-expressed attitudes towards the species that the respondents regards in general as the greatest threat to livestock on their farms amongst jackal and caracal (see Methods section and species ranking above). I analysed the data by categorizing farmers' answers into short word strings and generating a word cloud for the answers to each of the two questions. The size of the words is proportional to the frequency with which the words recurred (i.e. were used by respondents, Williams and Whiting, 2016). I then compared the proportions of positive and negative answers for each species with a Chi-square test of independence to test the null hypothesis that there is no relationship between the predator species and farmers' use of negative terms.

Considering the results that I obtained from the word clouds (i.e. whether farmers used the word "beautiful" as an answer for each species), I attempted to model farmers' tolerance towards jackal and caracal separately by using binary logistic regressions based on responses (yes/no) to the questions "Would you tolerate jackal/caracal on your farm if they caused 5% losses?" This level of loss is below the mean (29.4% of lambs lost to predators, see Results) for farmers in the sample area for 2013 but close to the aggregate predation (i.e. lambs and adults) rate reported for the years 2012-2014 for the Central Karoo (i.e. 4.7%, Conradie and Nattrass, 2017). Farmers could reply "yes", "no" or "I don't know". I used the positive answer to represent tolerance towards the predators in a hypothetical situation where they cause a low but realistic level of damage on farms. I pooled the "no" and "I don't know" answers together to represent intolerance as it is more robust to have a false negative than a false positive in the models. I modelled tolerance towards jackal and caracal separately as a function of seven possible variables, pre-selected to test particular hypotheses (Table 6.2).

Farmers' strategies to reduce livestock predation

a) Farmers' experience of various control methods and of their perceived efficacy

To explore farmers' strategies to reduce livestock predation on their farms, I first asked them whether they attempted to control predators and what methods they used. For the latter, I asked respondents if they had ever used any of the 12 different types of lethal and 19 different types of non-lethal methods that have or currently are being used on livestock farms in South Africa. If they had experience with the method, I asked them to rank it on a five-point Likert scale from 1 (does not work) to 5 (works very well). I then calculated a mean Likert scale score for the efficacy of each method. I transformed the five-point Likert scale into a three-point Likert scale (i.e. "works well", "works a little" and "does not work") because I had very low frequency for some of the categories. I graphed the results both for jackal and caracal separately. I assessed whether there was a difference in the perceived efficacy and cost of lethal versus non-lethal methods by comparing the mean score given by farmers to lethal versus non-lethal methods with a t-test. I used a Chi-square test – as recommended by Campbell (2007) – to test the null hypothesis that there is no relationship between the cost of the method used and the type of method used (i.e. lethal versus non-lethal).

Table 6.2. Description of the variables that were hypothesized to influence farmers' tolerance towards jackal/caracal presence that is resulting in a hypothetical 5% livestock loss rate on their farms. Variables were included as predictors within the logistic regressions. Except if stated otherwise, all variables were extracted from the questionnaires.

Variables of expected importance	Type	Unit *Mean* [range]	Description	Expected influence
Age	Continuous	Years *50.6* [24-76]	Farmer age.	- / +
Total farms size	Continuous	Kilometres squared *83.74* [5.70-260]	The cumulative area of all the farms of the respondent (i.e. main farm and additional portions). Farm size was extracted from the regional cadastral map (Farm Portions, Department of Rural Development and Land Reform, Chief Surveyor-General Office, Western Cape, 2013) in QGIS 2.18.2 (QGIS Development Team, 2017).	- / +
Rank 1 caracal	Boolean	Yes / No	Whether the caracal was ranked as the predator responsible for the most livestock losses (used only in the caracal model).	-
Rank 1 jackal	Boolean	Yes / No	Whether the jackal was ranked as the predator responsible for the most livestock losses (used only in the jackal model).	-
Percentage of lambs lost	Continuous	Probability units (range: 0 – 1) *0.294* [0.01-0.81]	Perceived percentage of lambs lost to predators on the respondent's farm(s).	-
Caracal perceived as beautiful	Boolean	Yes / No	Whether farmer replied *beautiful* or *cute* to the question "What is the first thing you think about when I say *caracal*"?	+

			(used only in the caracal model).	
Jackal perceived as beautiful	Boolean	Yes / No	Whether farmer replied *beautiful* to the question “What is the first thing you think about when I say *jackal*”? (used only in the jackal model).	+
Mesopredators in PA only	Boolean	Yes / No	Whether respondent thinks mesopredators should only occur in protected areas (PAs).	-
Mesopredators control each other	Boolean	Yes / No	Whether farmer thinks jackal and caracal can control each other’s populations.	+

To better understand why each farmer was using particular methods, I asked them two additional questions:

1) "Please rank the following methods from the most practical to the least practical if you wish to limit livestock losses to predators: selective killing of predators, eradication of predators, relocation of predators, avoidance of areas with higher predation risk, and use of husbandry techniques" (farmers could add suggestions if they wanted and the order of the answers presented to the farmers was randomised between interviews).

2) "How do you usually respond to fresh signs of jackal/caracal on your farm?" I gave eight possible answers: "you hunt or set up traps yourself", "you immediately deploy a trapper or professional hunter", "you observe and wait for damage before doing anything", "you immediately deploy a tracker", "you immediately deploy poison", "you remove livestock from areas with higher predation risk", "you do nothing and leave them alone", "you immediately deploy a herder". Farmers could also choose to give another answer. In the above questions, farmers could choose to respond that they did not know. I compared with a Chi-square test the proportion of farmers using lethal versus non-lethal methods in response to fresh signs for each predator separately. In each case, the null hypothesis was that the proportion of farmers using lethal methods was not significantly different from the proportion of farmers using non-lethal methods in response to fresh signs of jackal/caracal.

I used a t-test to determine whether the amount of effort farmers and their employees allocated to predator control was different for tolerant versus intolerant farmers. The chosen level of significance for all statistical tests was $\alpha = 0.05$.

b) Farmers' experience and use of illegal poison baiting

I asked farmers whether they believed poison was effective against predators and whether they had used poison on their farms recently. I tabled the experience of farmers with different types of poison according to their reported use throughout the questionnaire.

To explore potential determinants of poison use, I used a binary logistic regression where 1 denotes a farmer who uses poison on his farm(s) either regularly or as a last resort and 0 if the farmer never has or does not currently use poison. I selected a set of 10 *a-priori* variables (Table 6.3) as likely covariates of poison use and formulated predictions (see Introduction).

Table 6.3. Description of the variables hypothesized to influence poison use on farmland of 77 respondents in the Central Karoo. Variables were included as predictors within the binary logistic regression. Mean and range values for variables are provided when appropriate. Except if stated otherwise, all variables were extracted from the questionnaires.

Variables of expected importance	Type	*Mean* [range]	Description	Expected influence
Fall in employment	Discrete	[-9-8]	Difference between the number of farm workers on the farm at the time of the interview and when the farmer started farming.	+
Jackal, caracal and baboon in top 3	Boolean	Yes / No	Whether jackal, caracal and baboon were ranked as the three main predators causing livestock losses.	+
Cape fox in top 5	Boolean	Yes / No	Whether Cape fox was ranked as one of the five main predators causing livestock losses.	+
Poison efficacy	Boolean	Yes / No	Whether farmer believes poison is effective at killing predators.	+
Dominant jackal pair narrative	Boolean	Yes / No	Whether the respondent believes that killing a dominant jackal pair will result in an increase in jackal numbers and hence livestock losses.	-
Age	Continuous	*50.6* [25-76]	Farmer age.	+ / -
Years of education	Discrete	[10-15]	Number of completed years of formal education.	-
Percentage of lambs lost	Continuous	*Probability units* *0.294* [0.01-0.81]	Perceived percentage of lambs lost attributed to predators on the respondent's farm(s).	+
Relative Terrain Ruggedness Index (TRI)	Continuous	Index *0.36* [0.14-1.00]	Relative mean of the absolute values of the differences between a central pixel and its neighbours (sensu Riley et al., 1999; Wilson et al., 2007). The most rugged farm has a value of 1. All the other	+

			farms are relative to the most rugged. TRI was calculated using the Digital Elevation Model (DEM) layer of the Western Cape (30 m precision) in QGIS 2.18.2 (QGIS Development Team, 2017).	
Total farms size	Continuous	Kilometres squared *83.74* [5.70-260]	The cumulative area of all the farms of the respondent (i.e. main farm and additional portions). Farm size was extracted from the regional cadastral map (Farm Portions, Department of Rural Development and Land Reform, Chief Surveyor-General Office, Western Cape, 2013) in QGIS 2.18.2 (QGIS Development Team, 2017).	+ / -

Results

Farm and respondent attributes

Due to multiple farm ownership/lease-holdings, my sample of 77 farmers covered 382 farm portions or cadastres, of which 228 constitute main farms (see Methods section). Together, respondents' farms cover an area of 643 114 ha or 15% of the total surface area of the Central Karoo District Municipality that comprises the Laingsburg, Prince Albert and Beaufort West local municipalities. The survey achieved approximately 78% of the farming units in Laingsburg local municipality (based on 2013 farm census) or 43% of its total surface area. Collectively, these farms include approximately 50 000 ewes or 54% of the 92 604 sheep in the area (2013 Western Cape Agricultural Commodity and Infrastructure Census, http://www.elsenburg.com/gis/apps/agristats/, accessed May 8th 2018). As discussed earlier, my sample was non-random, however, due to the high percentage coverage of the Laingsburg local municipality, I am confident with the assumption that my sample is representative of the sheep farmers in that community and represent a meaningful subsample of the broader Central Karoo region.

All the respondents were men, though women were often present during the administration of the questionnaire and sometimes discussed answers with their husband or reminded them of a particular event. Patriarchy is a cultural norm in the study area with men typically assuming responsibility for farm operations in general and predator control in particular. The mean age of respondents at the time of the survey was 50.6 years (SD = 12.9, range = 24-76), with a mean of 25 years farming experience in the Karoo (SD = 13.2, range = 1-56). 85.7% of the respondents had attained a school leaving certificate and 58.4% had some level of tertiary education (18.2% had a university degree). Thirty nine percent held a National Diploma in Agriculture from the Grootfontein Agricultural Development Institute (one of the oldest agricultural colleges in South Africa, previously known as the Grootfontein College of Agriculture in Middleburg), Great Karoo, Eastern Cape. The number of full-time workers per farm had decreased from a median of three when the farmer had commenced farming to two in 2014. All the respondents were Christians even if not all of them were regular churchgoers. The mean size of all the respondents' farms was 8.37 km^2 (SD = 5.78, median = 7.0). Total size varied greatly and ranged from 0.57 to 26 km^2. When only including main farms, the size ranged from 0.32 to 22.62 km^2 (mean = 5.97, SD = 4.30, median = 4.64). Small-livestock farming was the main economic activity on most of the farms but cattle tenure was also reported, as well as crop or fruit farming and some tourism. Sheep dominated livestock production and the two main breeds were Dorpers and Merinos. The majority (58.7%) of the respondents for whom I had data regarding the number of ewes (n = 63) owned <1000 ewes but this number varied greatly in my sample (mean = 1205, SD = 1210.6, median = 800, range = 0-6000). The mean stocking rate (for the 63 respondents who had adequate records to reliably estimate it) was 144 ewes per thousand hectares of farmland. This is less than the estimated grazing capacity for the region of 167-333 small-stock unit (SSU; comprises sheep and goats for one unit each, and cattle for six units each) per 1000 ha (Hoffman et al., 1999; Saayman et al., 2016), i.e. between 167 and 333 small-stock units per thousand hectares, but my calculation does not take into account rams, lambs, replacement ewes and possible game species that farmers may have on their farms and that are included in the regional grazing capacity estimate.

Causes of livestock losses and the ranking of predator species as threats to livestock

Of the respondents, 98.7% claimed to have lost livestock to predators. Predators were perceived as the main cause (81.2%) of livestock losses, followed by theft (Figure 6.1). Most (72%, n = 75) farmers ranked jackal as the predator responsible for the most livestock losses followed by caracal (63%, n = 75) and Cape fox (30%, n = 57). Almost 39% of the respondents (n = 75) classified baboon as a threat and amongst them, 41% ranked baboon third in terms of livestock predator (Figure 6.2). The majority of farmers (55.8%) used a combination of spoor in the vicinity of a carcass, bite marks and feeding patterns to infer which predator was responsible for a livestock loss. Only 1.6% of farmers had eye witness accounts of an attack (themselves or their trapper or farm worker). Approximately two fifths of the respondents (42.6%) inferred culpability without direct evidence at all. Small-scale thefts or other causes of livestock disappearance might therefore have been attributed wrongly to predators in some cases.

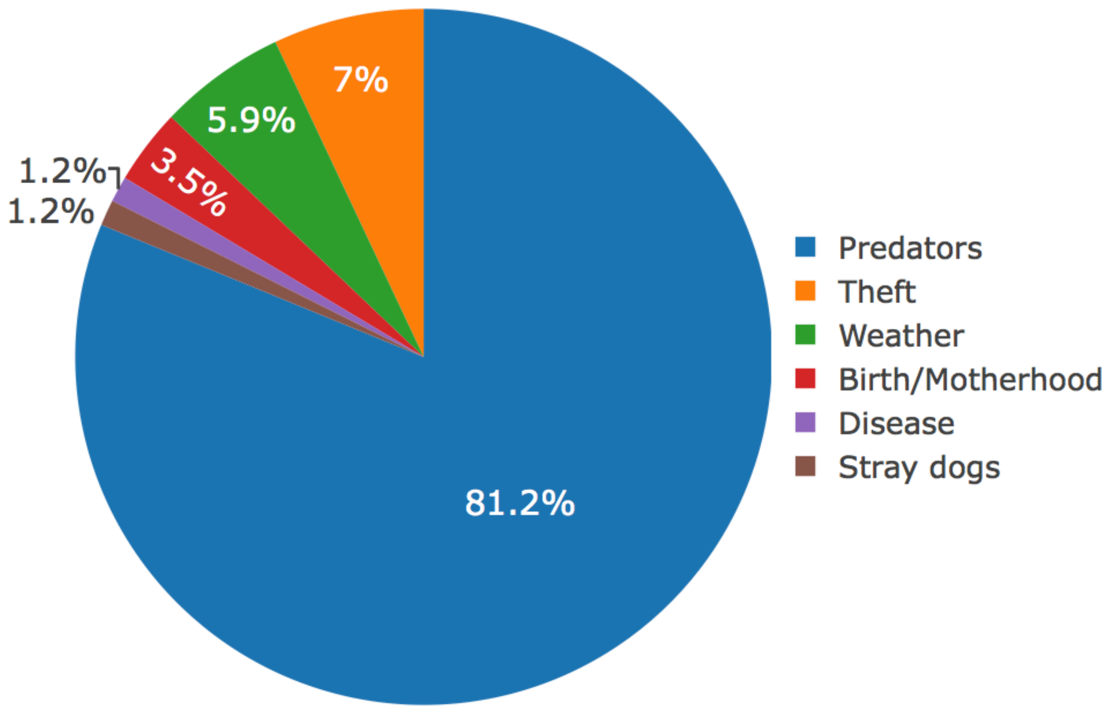


Figure 6.1. Reported causes of livestock losses by 77 small-livestock farmers interviewed in 2014-2015 in the Central Karoo District Municipality, South Africa.

Most farmers (75.3%) did not report the predation of their livestock to the relevant authority. Among those who did or sometimes did (24.7%), 31.6% reported the loss to farmers' associations ("Landbou vereniging"), just over a quarter reported the event to influential individuals in the community (such as a farmer expert in jackal hunting), 15.8% to the Karoo Predator Project and 10.5% to their immediate neighbours. Only one individual reported his losses to CapeNature (the provincial authority responsible for administering permits for the control of predators), and one to the group called "Mutilated by predators" (www.facebook.com/groups/mutilated/?ref=group_header), an online forum created by farmers that publishes pictures of sheep that have been attacked by predators but are still alive.

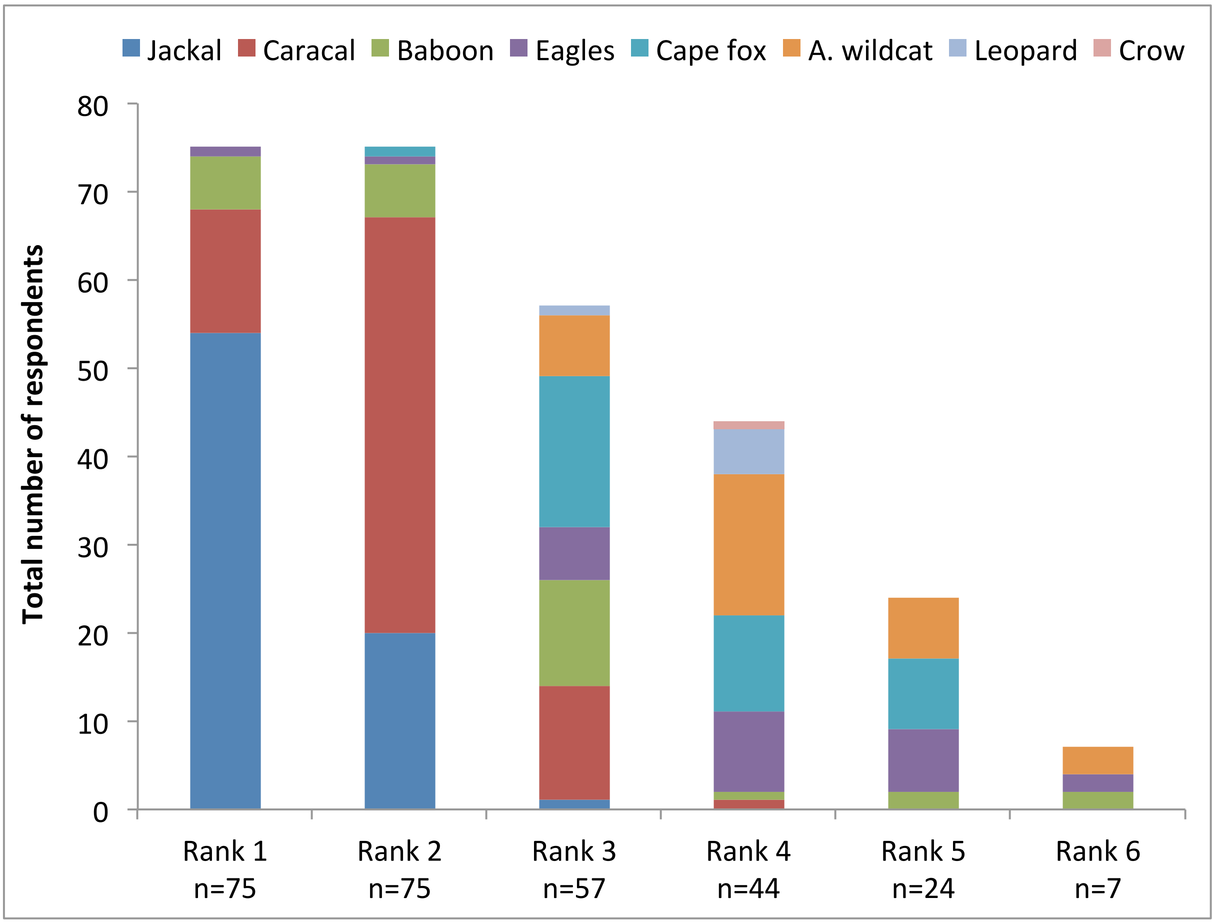


Figure 6.2. Histogram showing the number of farmers that ranked each of eight predators from the highest (Rank 1) to the lowest (Rank 6) cause of livestock losses on small-livestock farms in the Central Karoo District Municipality, South Africa. All respondents identified predators for ranks 1 and 2, but not always for the subsequent ranks.

Spatio-temporal patterns of predator presence and perceived conflict with farmers

All farmers had seen jackals on their land by 2014, and 95% of them thought that jackal predation was a problem, while 82% considered them a threat to the viability of their farm. The jackal problem had re-emerged relatively recently, with only 35% having seen a jackal on their land before 1994 and only 26% of the respondents thinking that jackal predation was a problem before 1994 (Figure 6.3a).

Prior to 1994, 84% of farmers had seen caracals on their land and 60% described them as being a problem in terms of sheep predation. However, only 9% of the farmers regarded caracals to be a serious threat to the viability of their farm(s) before 1994. By 2014, 90% described caracals as being a problem and 40% as a serious threat (Figure 6.3b).

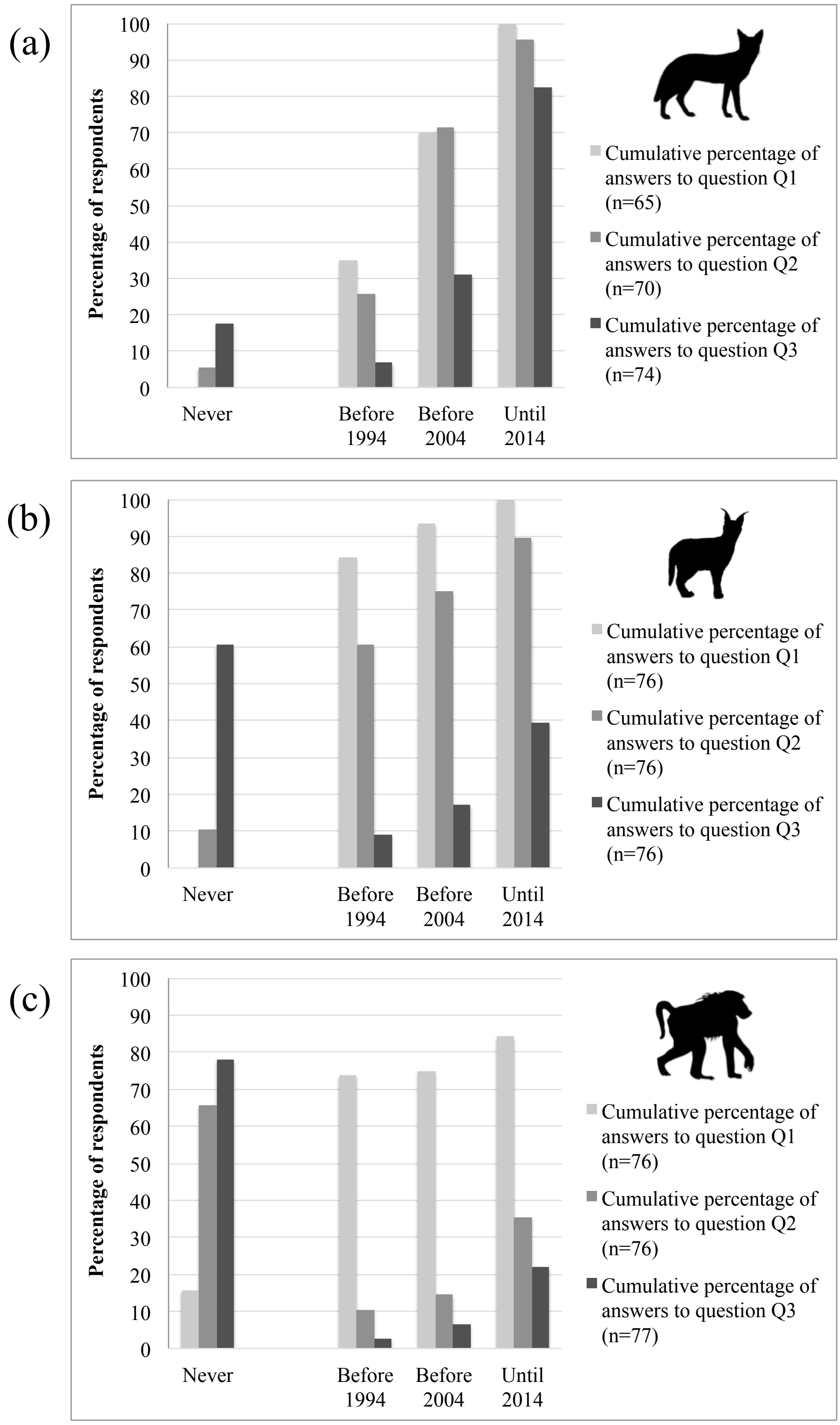


Figure 6.3. Cumulative percentage of answers from respondents to questions Q1: "When was the first time you saw a jackal/caracal/baboon or jackal/caracal/baboon spoor on your land?", Q2: "When – if ever – did jackal/caracal/baboon become a problem for lamb loss on your farm?" and Q3 "When – if ever – did lamb loss to jackal/caracal/baboon become a serious concern to the viability of your farm (i.e. a severe problem)?", for jackal (a), caracal (b) and baboon (c), at three points in time: before 1994 (i.e. 1994); before 2004 (i.e. 1994-2003); and by 2014 (i.e. 2004-2014). Respondents replying "never" to questions Q1, Q2 and Q3 are presented on the left of each graph.

Prior to 1994, 74% of the farmers had seen baboons on their land, but only 10% regarded them as a problem. By 2014, 22% regarded them as being a serious threat to the viability of their farm. The latter farmers experienced their most severe problems with baboons after 2004 (Figure 6.3c).

The reports of predator presence were significantly different between time periods, jackal and baboons being present mostly in the recent years, whereas caracal sightings were reported across all time periods (Figure 6.3): while the answers to question Q2 (i.e. first problem) for jackal were equally distributed between periods ($\chi^2 = 4.96$, df = 2, P = 0.08), the answers to question Q1 (i.e. first sighting; $\chi^2 = 18.41$, df = 2, P < 0.001) and to question Q3 (i.e. first severe problem; $\chi^2 = 24.78$, df = 2, P < 0.001) did not follow a uniform distribution. Respondents were more frequently situating the first severe problem with jackals in recent years, between 2004 and 2014 (61% of respondents, Figure 6.3a). For caracal, the responses to question Q1 (i.e. first sighting; $\chi^2 = 86.05$, df = 2, P < 0.001), question Q2 (i.e. first problem; $\chi^2 = 41.57$, df = 2, P < 0.001) and question Q3 (i.e. first severe problem; $\chi^2 = 6.45$ df = 2, P = 0.040) did not follow a uniform distribution. Respondents were more frequently situating caracal first sightings before 1994 (83%), while the first severe problems were mostly experienced in recent years, between 2004 and 2014 (55% of respondents, Figure 6.3b). For baboons, the responses to question Q1 (i.e. first sighting; $\chi^2 = 82.18$, df = 2, P < 0.001), question Q2 (i.e. first problem; $\chi^2 = 9.56$, df = 2, P = 0.008) and question Q3 (i.e. first severe problem; $\chi^2 = 10.71$, df = 2, P = 0.004) did not follow a uniform distribution either. Respondents were more frequently situating first sightings before 1994 (86%), while the first serious problems were mostly experienced in recent years, between 2004 and 2014 (71% of respondents, Figure 6.3c).

Cumulative sightings increased therefore significantly for all three species, by 65%, 16% and 11% for jackal, caracal and baboon respectively (Q1, Figure 6.3). Similarly, while conflict has been reported in this study since the 1990s, perceived severe predation problems (i.e. question Q3) significantly differ between periods and increased for all three species, in particular since 2004 (Q3, Figures 6.3 and 6.4). At the time of the interview, by 2014, 82% of farmers reported severe conflict with jackal, covering most farms within the study area (Figure 6.4), while farms reporting conflict with caracal and baboons were more scattered across the study site (Figure 6.4).

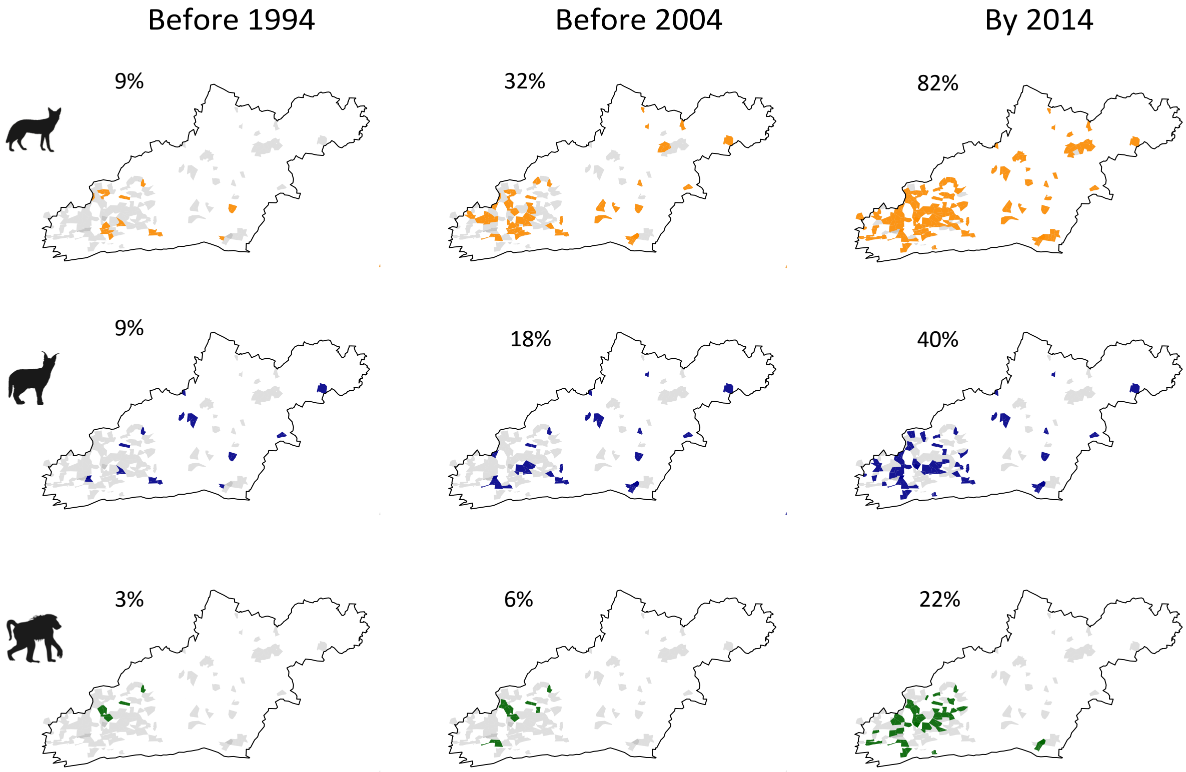


Figure 6.4. Panel of maps representing the spatio-temporal patterns of the severe conflict with the three main predators of small-livestock in the South African Central Karoo District Municipality. All farms surveyed in the region are represented in light grey polygons using the regional cadastral map. Farms reporting severe predation problems, at a level that is perceived to threaten the viability of the farm (Q3) are filled with a different colour for each of the three predator species (orange: jackal, blue: caracal and green: baboon). The year of onset of a serious predator problem for a given farm was used to build cumulative maps of conflict with time binned in three categories along the x-axis. The different percentages displayed on each map represent the percentage of farmers reporting having a severe conflict with the predator.

Farmers' perceptions for changes in predator numbers in the Central Karoo

Most of the respondents (97%) believed that predator numbers had increased since 2004, particularly jackals (96% of respondents) and baboons (69%), with 44% considering this true for caracal. No farmer thought that jackals were less numerous than in 2004 but three farmers thought that caracal numbers had declined and they attributed this decline to an increase in the jackal population. Only one farmer thought that baboons were less numerous than in 2004. Farmers attributed increased predator numbers to three primary reasons: changes in farming practices (43.6 %), ecological and environmental reasons (32.6 %) and economic reasons (23.8 %) (Table 6.4).

Table 6.4. Perceived reasons for the recent increase in jackal, caracal and baboon numbers in the Central Karoo District Municipality, South Africa. Reasons are classified into three main categories (in bold letters) according to key words given by farmers during interviews performed in 2014 and 2015. The total percentages of answers are given per predator species (in bold).

Cited reasons for the increase	Jackal (%)	Caracal (%)	Baboon (%)
Changes in farming practices	**41.0**	**44.7**	**45.1**
More lifestyle farms/farmers	9.3	16.1	4.9
No more predator control by farmers	10.6	8.9	25.6
Lack of knowledge/technique[1]	4.6	0.0	0.0
Farm, sheep, water and food management[2]	11.9	17.9	12.2
Change in predator hunting practice	4.6	1.8	2.4
Ecological and environmental	**28.5**	**26.8**	**42.7**
More natural areas for conservation	9.9	8.9	4.9
More game farms	6.0	7.1	2.4
No natural predators	1.3	3.6	12.2
Natural adaptability of the species	7.3	5.4	12.2
No more diseases such as rabies	2.0	0.0	0.0
Drought and prey change	2.0	1.8	11.0
Economic	**30.5**	**28.6**	**12.2**
Fencing in bad state	13.2	10.7	0.0
Less farmers and people on farms	12.6	14.3	4.9
No more government help	4.0	3.6	7.3
Decrease in wool price	0.7	0.0	0.0

[1] To track and trap predators.

[2] No more sheep corrals, corn distributed at waterholes, no more breeding season

Modelling of reported lamb losses

The percentage of lambs reportedly depredated in 2013 varied markedly among respondents (mean = 29.4%, 25th percentile = 14%, median = 25%, 75th percentile = 40%, range = 1-81%) with high losses (> 50% of lambs) reported by 10.4% of the respondents. Two individuals represented true outliers at opposite ends of the range with 1% and > 80% of lamb losses attributed to predators. None of the nine variables selected for multivariate modelling were collinear ($r \leq 0.7$ for all combinations). All predictor variables under the best model exhibited generalized VIF values < 2.0.

The fractional probit Model A (full model) shows that *age*, *relative farm terrain ruggedness index (TRI)*, *rank 1 caracal*, and the interaction between *rank 1 caracal* and *TRI* are all statistically significant variables explaining the percentage of lambs lost (Table 6.5). The variables *age*, *number of farm workers*, *farm size* and *TRI* all have statistically significant marginal effects (Table 6.6). After model selection, the best model (Model B) was comprised of five variables and one interaction (Table 6.5). Model selection was confirmed by comparing Model A to Model B (nested model) using an ANOVA to test whether reduction in the residual sum of squares is statistically significant. The Chi-square test yielded a p-value of 0.934, confirming that the two models were not statistically different from each other at the level $\alpha = 0.05$. It thus confirmed the selection of Model B because it was the most parsimonious. Model B shows that *age*, *number of farm workers*, *farm size*, *TRI*, *rank 1 caracal* and the interaction between *rank 1 caracal* and *TRI* are statistically significant variables explaining the percentage of lambs lost. The variables *age*, *number of farm workers*, *farm size*, *TRI* and *rank 1 caracal* all have statistically significant marginal effects (Table 6.6).

Table 6.5. Model explaining percentage of lambs lost [0; 1] on farmland in the Central Karoo for the year 2013, using fractional probits with robust standards errors. Please see Table 6.1 for variable description.

	Model A (full model)				Model B (best model)			
Independent variables	Estimates	Std. Error	z value	Pr(>|z|)	Estimates	Std. Error	z value	Pr(>|z|)
Intercept	-0.549	0.503	-1.091	0.275	-0.761	0.385	-1.973	0.048 *
Age	-0.011	0.004	-2.952	0.003 **	-0.011	0.004	-2.655	0.008 **
Number of farm workers	-0.090	0.049	-1.854	0.064	-0.055	0.018	-3.111	0.002 **
Main farm size (square kilometres – square root-transformed in model)	0.0640	0.041	1.570	0.116	0.099	0.023	4.254	0.000 ***
Relative mean main farm Terrain Ruggedness Index (TRI)	0.672	0.259	2.592	0.009 **	0.622	0.274	2.270	0.023 *
Number of permanent artificial water sources on farm (log-transformed in model)	0.074	0.071	1.046	0.295				
Rank 1 caracal	-1.617	0.474	-3.414	0.001 ***	-1.423	0.431	-3.300	0.001 ***
Rank 1 baboons	-0.171	0.228	-0.748	0.454				
Number of farm workers in interaction with main farm size (square kilometres – square root-transformed in model)	0.004	0.005	0.801	0.423				

Relative mean main farm Terrain Ruggedness Index (TRI) in interaction with rank 1 caracal	3.598	0.917	3.925	0.000 ***	3.489	0.951	3.671	0.000 ***
Number of observations	68				68			
Log likelihood	-28.32				-28.46			
AIC_c	80.50				72.79			
BIC	98.83				86.46			
Nagelkerke's R^2	0.40				0.38			

Significance code: * P < 0.050 ** P < 0.010 *** P < 0.001 for z values.

Table 6.6. Average marginal effects (df/dx) (calculated using robust standard errors – RSE and measured as percent gain) for the fractional regressions presented in Table 6.4, explaining the percentage of lambs lost on farmland in the Central Karoo in 2013.

	Model A (full model)				**Model B (best model)**			
Independent variables in their natural units	df/dx	RSE	z	P	df/dx	RSE	z	p
Age	-0.379	0.001	-2.964	0.003 **	-0.378	0.001	-2.661	0.008 **
Number of farm workers	-1.974	0.006	-3.113	0.002 **	-1.835	0.006	-3.123	0.002 **
Main farm size (square kilometres)	0.185	0.001	2.348	0.019 *	0.244	0.000	4.512	0.000 ***
Relative mean main farm Terrain Ruggedness Index (TRI)	39.61	0.081	4.914	0.000 ***	37.48	0.087	4.288	0.000 ***
Number of permanent artificial water sources on farms	0.255	0.002	1.062	0.288				
Rank 1 caracal	-6.703	0.076	-0.880	0.379	-2.516	0.046	-0.543	0.587
Rank 1 baboons	-5.784	0.079	-0.732	0.464				

Significance code: * $P < 0.050$ ** $P < 0.010$ *** $P < 0.001$ for z values.

For the following interpretations *percent lambs lost* is a measure between zero and 100 and the average marginal effects are interpreted as percentage points.

Conditional on the other variables in the model, percentage of lambs lost decreased by 0.38 percentage point for each additional year of age – a small, yet highly significant effect (Table 6.6). For each additional farm worker, the average marginal effect was to decrease percent lambs lost by approximately two percentage points. The average marginal effect was statistically significant (Table 6.6) and the number of farm workers was also significant in the fractional probit model (Table 6.5). Larger main farms had greater losses: with each additional square kilometre the average marginal effect on percent lambs lost was 0.24 percentage point. The effect was statistically significant in the average marginal effects (Table 6.6) and in the fractional probit model (Table 6.5). Farm size in Model B was no longer interacting significantly with the number of farm workers, as in Model A. The number of permanent artificial water sources on farms had a positive size effect on losses in Model A, but this effect was not statistically significant so the variable was not retained in the best model (Model B). Having a baboon as the number one ranked predator had a negative size effect in Model A (both in the average marginal effects and the fractional probit models) but this effect was not statistically significant in either case and the variable was not retained in the best model (Model B). Controlling for the other variables in Model B (best model), the average marginal effect of having caracal ranked first decreased lamb losses by 2.5 percentage points (Table 6.6) – however this effect was not statistically significant. In the fractional regression (Table 6.5), both *rank 1 caracal* and *TRI* in interaction with *rank 1 caracal* were highly significant. When the individual effects are teased out in the average marginal effects (Table 6.6), *rank 1 caracal* is no longer significant while relative mean main farm ruggedness remains significant. Conditional on the other variables in the model, the average marginal effect of a 10 percentage points increase in TRI was to increase lamb losses by 3.75 percentage points.

Among the respondents, 85.7% reported that livestock predation was worse during certain times of the year (Figure 6.6), in particular during the lambing season (55.7%) that on most farms is a biannual event, generally in April-May and in September. The latter corresponds to the jackals' breeding season in September-October during which 19.3% (i.e. the sum of whelping, weaning and pairing times in Figure 6.6) of respondents stated losses were higher.

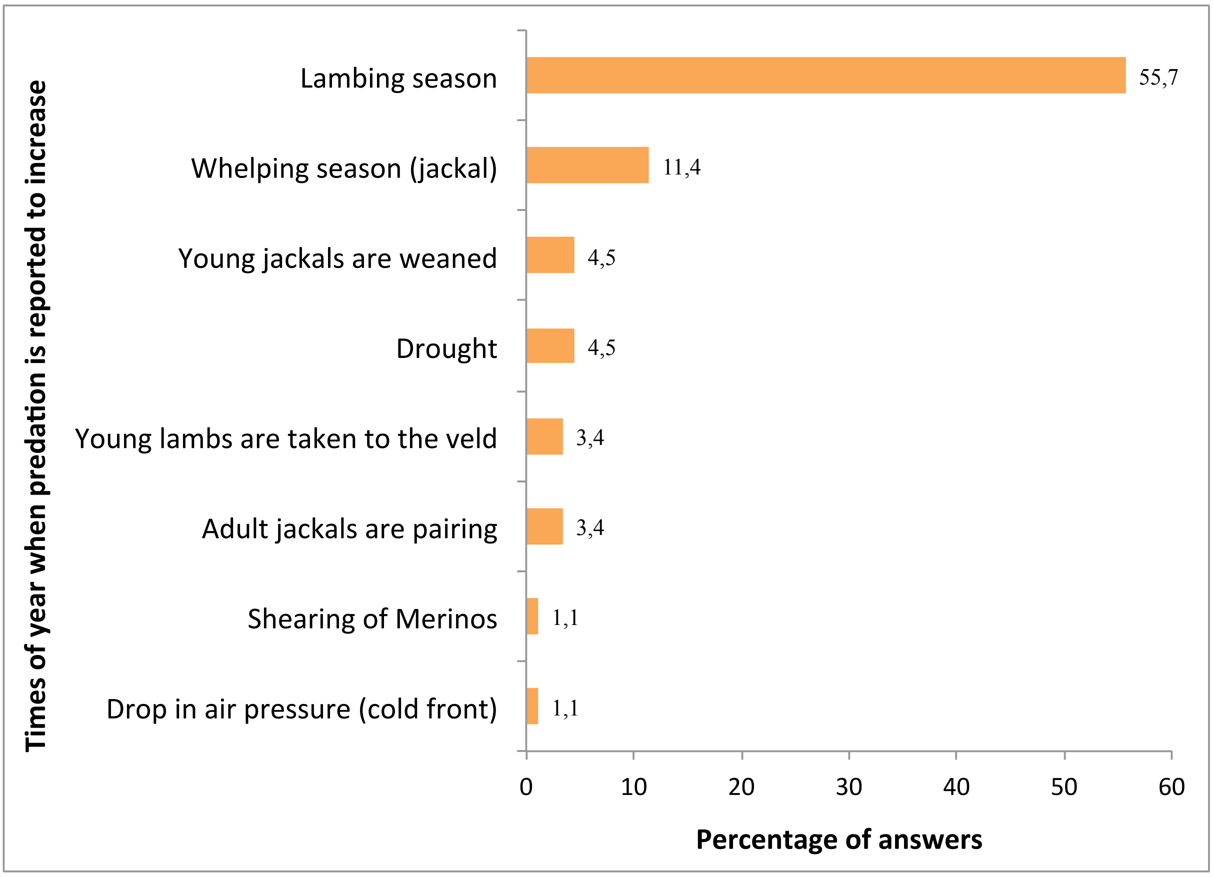


Figure 6.5. Times of year when livestock losses (adult sheep and lambs) are considered highest for the 77 small-livestock farmers interviewed in 2014 in the Central Karoo, South Africa.

Farmers' attitudes towards wildlife in general and predators in particular

a) Farmers' attitudes towards wildlife

I found extremely negative attitudes towards jackal, caracal and baboons by measuring "Wildlife Acceptance Capacity" (WAC) in my sample, with 57%, 42% and 29% of respondents respectively indicating that they wanted to exterminate those species from farmland. No farmer wanted these animals' populations to increase and only 3%, 4% and 16% wished that jackal, caracal and baboon populations respectively remained the same. The result from the Chi-square tests of independence rejected the null hypothesis and showed that the proportion of farmers with negative attitudes towards jackal or towards caracal was significantly higher (jackal: χ^2 = 7.298, df =1, P = 0.007; caracal: χ^2 = 5.920, df =1, P = 0.015) than towards baboons (and consequently towards the other wildlife species).

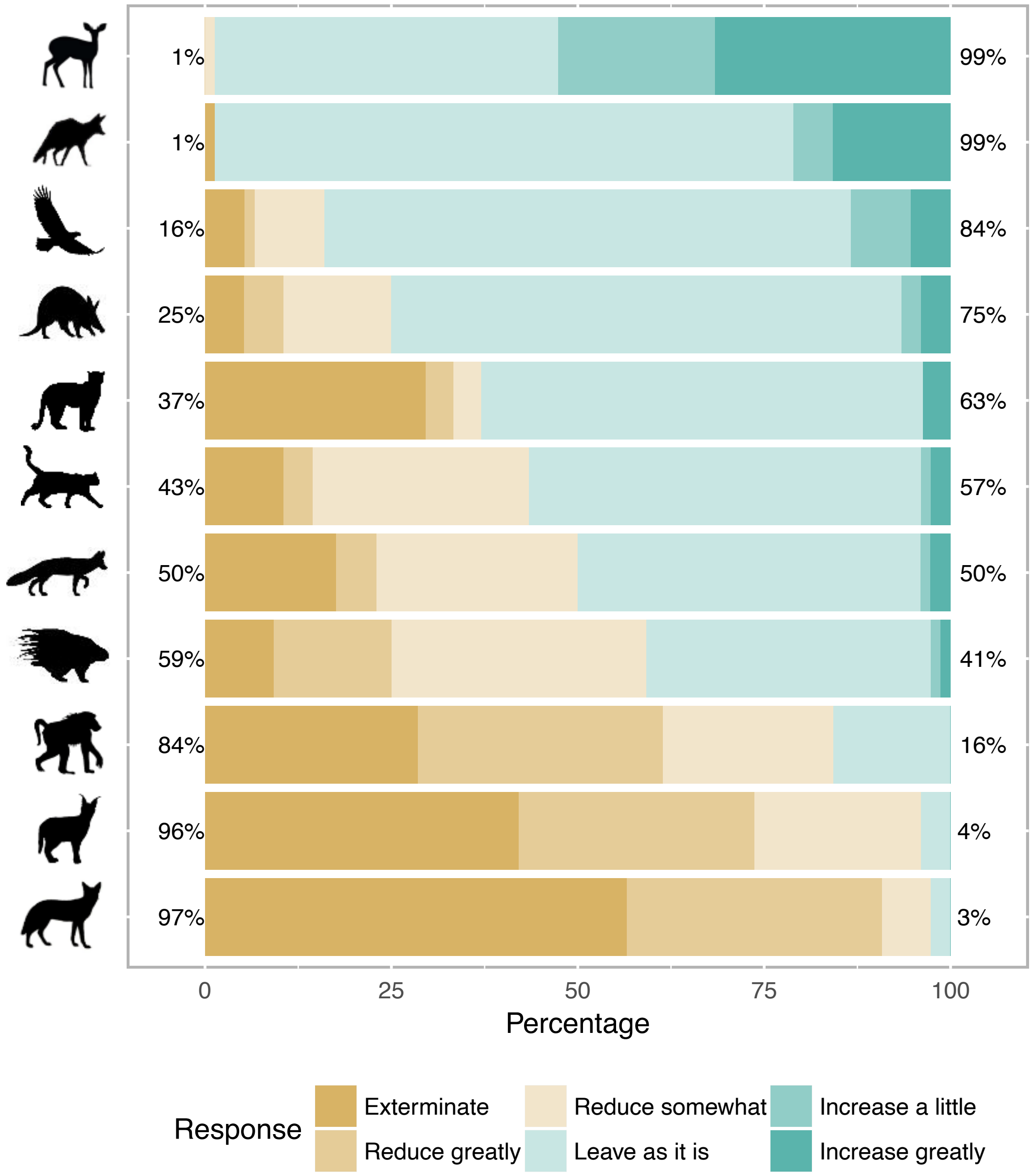


Figure 6.6. Percentage of farmers with positive (shades of turquoise, right of the graph) and negative (shades of brown, left of the graph) attitudes towards 11 species of wildlife. From top (most positive attitudes) to bottom (least positive attitudes): steenbok, n=76 respondents; bat-eared fox, n=76; eagles, n=75; aardvark, n=76; leopard, n=27; African wildcat, n=76; Cape fox, n=74; Cape porcupine, n=76; chacma baboon, n=70; caracal, n=76; black-backed jackal, n=76.

Regarding leopards, most respondents (63%) replied that they wanted their population to stay the same or to increase, but only a third of the farmers interviewed opted to answer that question, saying that they did not have enough experience with leopards (and indeed, we saw in Chapter 3 that leopards were absent of the Koup area where I conducted camera trapping surveys). The species that most farmers wanted to see increase were steenbok (53%) and bat-eared fox (21%) (Figure 6.6), though for the latter, one of the respondents wanted to exterminate them because: “They can attack lambs when they become too numerous. That’s what’s happening in the Free State. Groups of twenty *bakore* [i.e. the Afrikaans word for bat-eared foxes] are attacking and killing lambs. We must control them.”

Throughout the interviews, the intensity of farmers’ verbally-expressed attitudes was heavily dependent on the species being discussed. I noted words and expressions coming from the lexical fields of anger, desperation and frustration when the respondents talked about jackal: “There are too many jackals and now you can’t farm anymore, they must be killed, I hate them” and “Farmers should be in reserves too you see. I am crying for a divine intervention because I don’t see how I can survive with the jackal”. By contrast, it was more of a mocking hostility that was detectable when respondents talked about baboons: “He is a weird chap this one [laughter], but you can’t trust him because he will behave badly when you don’t look”. The mention of bat-eared fox mostly triggered words showing affection and a desire to protect the species: “Bat-eared foxes were poisoned when they were poisoning the crickets on the farms in the past, now you don’t see as many unfortunately. I like them, they don’t do any harm” and “They are funny, I like seeing them run when I drive my bakkie in the veld”. Farmers even showed some concern for the number of steenboks left in the wild: “Steenbokkie [i.e. affective Afrikaans term for steenbok] numbers are affected by jackals, I am very worried for them because I like them”.

During my time with the farmers, I very often heard them use the Afrikaans term “*ongedierte*” to refer to predators, which can be literally translated into “non-animal”, showing that predators do not even qualify to have the same (already low) rights as animals. A few respondents referred to caracals as “killing machines”, emphasizing the fact that they are not animals, but “machines” attacking their lambs. When the respondents gave human characteristics to predators, they were mostly negative traits (emphasized by the tone of the voice) such as “sly” (jackal), “cunning” (jackal), “mischievous” (jackal, baboon), “calculating” (jackal), “cheeky” (baboon, jackal), “naughty” (jackal, caracal), “fierce” (caracal), “cruel” (jackal, caracal, baboon), but note also the use of “clever” (jackal) with some admiration in the voice.

The question about farmers’ favourite animal was answered by 70 farmers. As expected, iconic species were the most frequently cited species (43 citations), even when they were well-known to be damage-causing species for farmers in other regions of the world: lion (n = 10), elephant (*Loxodonta Africana*) (n = 10), leopard (n = 8), wild dog (n = 1), tiger (n = 1) and snow leopard (n = 1), confirming my prediction that the lack of direct experience with these animals, and their glamorous appearance would encourage farmers to cite them rather than Karoo carnivores. Large felids (lion, tiger, cheetah and snow leopard) were cited 21 times whereas canids (wild dog and bat-eared fox) were only cited twice in total and ursids once (polar bear). Four farmers replied that they liked all animals, but one farmer clarified "except wild dogs" and another one "but no predator". Twenty-three respondents chose an herbivore species, including four citations for rhinoceros (no mention of which species though). Game species killed for meat and trophy such as the greater kudu (n=5) were cited nine times. Bird species were cited twice (black eagle (*Aquila verreauxii*) and korhaan) and interestingly, one respondent cited bats. Caracal got one citation and meerkat got two. No farmer cited jackal.

b) Farmers' attitudes towards jackal and caracal

I probed the attitudes towards jackal and caracal further by constructing word clouds based on farmers' answers to the questions: "What is the first thing you think about when I say *jackal/caracal*?"

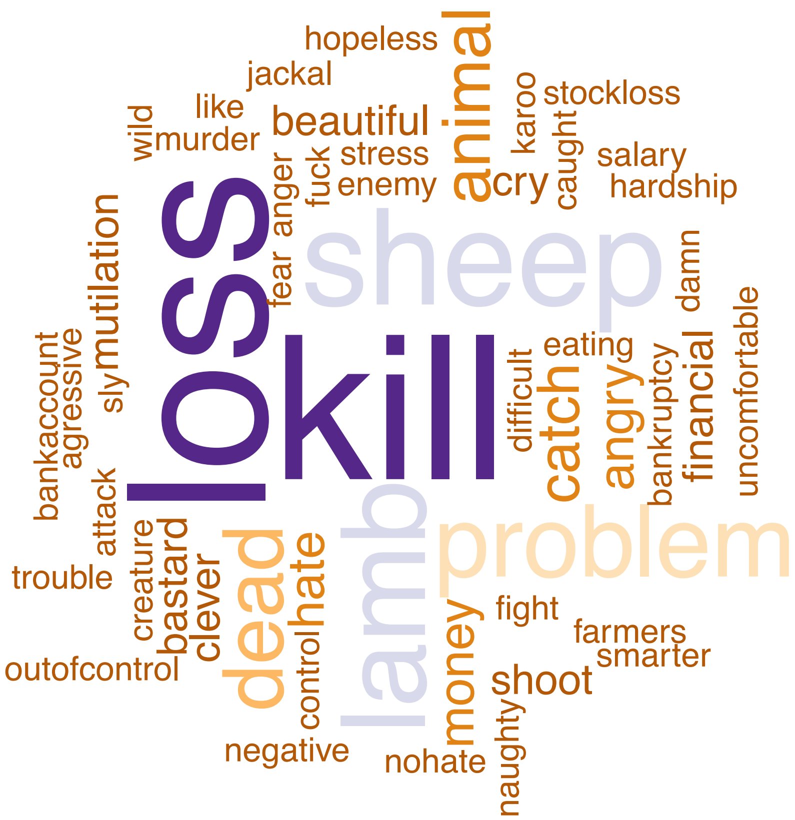


Figure 6.7. Word cloud of the respondent's answers to the question "What is the first thing you think about when I say *jackal*?" The size of the words is proportional to the number of times they were used in the answers. Maximum mentions are 21 for "kill". The word "nohate" was used to represent the sentence "I have no hate for the jackal".

As I expected, the mention of either predator names was very salient for farmers, with a mean response time of 4 seconds for *jackal* and 6 seconds for *caracal*. The discussion about jackal triggered a strong, mostly negative, emotional response from the farmers, with the most commonly used words being *kill* (n = 21), followed by *loss* (n = 20). In total, 73% of the thoughts had negative connotation and only 5% had positive connotation (Figure 6.7).

The word cloud for the term *caracal* showed that 61% of the thoughts triggered by caracal had negative connotations compared to 16% for positive connotations (Figure 6.8). The most commonly used word was *kill* (n = 18), followed by *loss* (n = 15). The most frequently used positive word was *beautiful* (n = 13), in third position. Farmers were significantly more negative towards jackal than caracal (χ^2 = 6.830, P = 0.009) in this word elicitation exercise. It is interesting to note that one farmer replied "Noodletjie" at the mention of the word *caracal*. Noodle is the name of his tame caracal. The suffix "-tjie" is an Afrikaans diminutive associated with affection. "Noodletjie" could therefore be translated by "little/young Noodle" in a positive, affectionate way.

Figure 6.8. Word cloud of the respondent's answers to the question "What is the first thing you think about when I say *caracal*?" The size of the words is proportional to the number of times they were used in the answers. Maximum mentions are 18 for "kill".

I then modelled farmers' tolerance towards jackal and caracal in separate models. The seven variables selected for multivariate GLMs did not show evidence of collinearity ($r \leq 0.7$ for all pairs). All predictor variables under the best model exhibited generalized VIF values < 2.0. For the following interpretations, the average marginal effects are interpreted as percentage points.

Perceiving jackal as beautiful and thinking that mesopredators should only be in PAs were significant in both the logistic regression model (Table 6.7) and the average marginal effects (Table 6.8). Retaining the variable *percentage of lamb losses* in the model, even if not statistically significant, improved the model, but controlling for farm size and farmer age weakened it (Table 6.7). The best model (Model B) showed that conditional on the other variables in the model, the average marginal effect of finding jackal beautiful increased the probability for a farmer of being tolerant towards jackal by almost 67 percentage points. The average marginal effects of believing that mesopredators should only occur in PAs decreased farmer tolerance towards jackal by more than 23 percentage points (Table 6.8). Conditional on the other variables, a 10% increase in lamb losses had an average marginal effect of decreasing farmer tolerance by more than 25 percentage points, but this effect was not significant (Table 6.8). The signs of the coefficients were similar to what I expected (Table 6.2) and age had a negative sign both in the binomial logistic model and the average marginal effects but its effect was not statistically significant in either case and it was not retained in the best model (Model B). Farmers with larger farms had, according to the average marginal effects, greater tolerance of jackal: with each additional square kilometre, the average marginal effect on tolerance was 0.1 percentage point. The effect was not statistically significant in the average marginal effects (Table 6.8) and in the fractional probit model (Table 6.7) and this variable was not retained in the best model (Model B). The Chi-square test with an associated p-value of 0.025 (likelihood ratio test) indicates that Model B as a whole, fits the data significantly better than an empty model.

Model A for caracal (Table 6.9) was specified to be comparable to Model A for jackal (Table 6.7). After model selection, the best binary logistic regression explaining farmers' tolerance towards caracal presents the same two statistically significant variables as in the jackal model. Conditional on the other variables, perceiving caracal as beautiful and thinking that mesopredators should only be in PAs were strongly and statistically significant determinants of farmers' attitudes in both the logistic regression (Table 6.9) and the average marginal effects (Table 6.10). Keeping the variables *percentage of lamb losses* and *rank 1 caracal* in the model, even if not statistically significant, improved the model, but controlling for farm size and farmer age rather weakened it (Table 6.9). The best model (Model B) showed that conditional on the other variables in the model, the average marginal effect of finding caracal beautiful increased the probability of a farmer being tolerant towards caracal by almost 43 percentage points (which is 1.5 times less than for the jackal model). The average marginal effects of believing that mesopredators should only occur in PAs decreased farmer's tolerance towards caracal by almost 30 percentage points (Table 6.10). This variable effect is larger than it is for jackal. Conditional on the other variables, a 10% increase in lamb losses had an average marginal effect of decreasing farmers' tolerance towards caracal by more than 27 percentage points, but this effect was not significant (Table 6.10). The best model (Model B) retained the variable *rank 1 caracal*, even if it was not significant at $\alpha = 0.05$. Its effect was to decrease farmers' tolerance by almost 24 percentage points when caracal is ranked first in terms of livestock losses on the farm. The signs of the coefficients were again the same as expected in Table 6.2 and age had once more a negative sign both in the binomial logistic model and the average marginal effects but its effect was not statistically significant in either case and it was not retained in the best model (Model B). Similar to the jackal model, farmers with larger farms had, according to the average marginal effects, greater tolerance towards caracal: with each additional square kilometre, the average marginal effect on tolerance was 0.1 percentage point. The effect was not statistically significant in the average marginal effects (Table 6.10) and in the fractional probit model (Table 6.9) and this variable was not retained in the best model (Model B). The Chi-square test with an associated p-value of 0.002 (likelihood ratio test) indicates that Model B as a whole, fits the data significantly better than an empty model.

Table 6.7. Results from binary logistic regressions using robust standard errors (RSE) explaining farmers' tolerance towards jackal assuming they cause only 5% of livestock losses on their farms. Significance code: * P < 0.050 ** P < 0.010 *** P < 0.001 for z values.

	Model A (full model)				Model B (best model)			
Independent variables	Estimates	Std. Error	z value	Pr(>|z|)	Estimates	Std. Error	z value	Pr(>|z|)
Intercept	0.552	1.610	0.343	0.731	0.289	0.558	0.517	0.605
Jackal perceived as beautiful	17.63	0.939	18.78	0.000 ***	17.85	0.821	21.73	0.000 ***
Total farm size (square kilometres – square root-transformed in model)	0.104	0.094	1.101	0.271				
Mesopredators should be in PA only	-1.095	0.575	-1.906	0.057	-1.091	0.532	-2.052	0.040 *
Mesopredators control each other	0.115	0.580	0.198	0.843				
Percent lambs loss	-2.576	1.675	-1.538	0.124	-1.269	1.493	-0.850	0.395
Age	-0.031	0.020	-1.548	0.122				
Rank 1 jackal	0.954	0.716	1.332	0.183				
Number of observations	70				71			
Log likelihood	-38.400				-41.376			
Prob > Chi^2	0.044				0.025			
AIC_c	95.16				91.36			
BIC	110.79				99.80			
Nagelkerke's R^2	0.26				0.17			

Table 6.8. Average marginal effects (df/dx) (calculated using robust standard errors – RSE and measured as percent gain) for the binary logistic regressions presented in Table 6.7, explaining farmers' tolerance towards jackal assuming they cause only 5% of losses on their farms.

	Model A (full model)				**Model B (best model)**			
Independent variables in their natural units	df/dx	RSE	z	p	df/dx	RSE	z	p
Jackal perceived as beautiful	66.402	0.053	12.50	0.000 ***	66.99	0.054	12.31	0.000 ***
Total farm size (square kilometres – square root-transformed in model)	0.122	0.001	1.155	0.248				
Mesopredators should be in PA only	-21.563	0.107	-2.011	0.044 *	-23.42	0.113	-2.073	0.038 *
Mesopredators control each other	2.154	0.109	0.197	0.844				
Percent lambs loss	-48.21	0.308	-1.564	0.118	-25.38	0.294	-0.864	0.387
Age	-0.587	0.004	-1.624	0.100				
Rank 1 jackal	16.61	0.111	1.494	0.135				

Significance code: * P < 0.050 ** P < 0.010 *** P < 0.001 for z values.

Table 6.9. Results from binary logistic regressions using robust standard errors (RSE) explaining farmers' tolerance towards caracal assuming they cause only 5% of losses on their farms. Significance code: * P < 0.050 ** P < 0.010 *** P < 0.001 for z values.

	Model A (full model)				Model B (best model)			
Independent variables	Estimates	Std. Error	z value	Pr(>|z|)	Estimates	Std. Error	z value	Pr(>|z|)
Intercept	1.041	1.382	0.753	0.451	0.784	0.628	1.248	0.212
Caracal perceived as beautiful	2.049	0.863	2.374	0.018 *	2.237	0.817	2.741	0.006 **
Total farm size (square kilometres – square root-transformed in model)	0.099	0.100	0.990	0.322				
Mesopredators should be in PA only	-1.492	0.633	-2.355	0.018 *	-1.473	0.588	-2.504	0.012 *
Mesopredators control each other	0.405	0.593	0.684	0.494				
Percent lambs loss	-2.294	1.678	-1.367	0.172	-1.482	1.573	-0.942	0.346
Age	-0.020	0.020	-0.994	0.320				
Rank 1 caracal	-1.661	1.153	-1.440	0.150	-1.415	1.088	-1.301	0.193
Number of observations	70				70			
Log likelihood	-37.651				-38.76			
Prob > Chi^2	0.006				0.002			
AIC_c	93.66				88.46			
BIC	109.29				98.77			
Nagelkerke's R^2	0.33				0.30			

Table 6.10. Average marginal effects (df/dx) (calculated using robust standard errors – RSE and measured as percent gain) for the binary logistic regressions presented in Table 6.9, explaining farmers' tolerance towards caracal assuming they cause only 5% of losses on their farms.

	Model A (full model)				**Model B (best model)**			
Independent variables in their natural units	df/dx	RSE	z	p	df/dx	RSE	z	p
Caracal perceived as beautiful	38.68	0.128	3.030	0.002 **	43.25	0.123	3.596	0.000 ***
Total farm size (square kilometres – square root-transformed in model)	0.114	0.001	1.051	0.293				
Mesopredators should be in PA only	-28.73	0.106	-2.705	0.007 **	-29.48	0.108	-2.722	0.006 **
Mesopredators control each other	7.457	0.109	0.687	0.492				
Percent lambs loss	-41.58	0.288	-1.443	0.149	-27.72	0.286	-0.970	0.332
Age	-0.359	0.003	-1.030	0.303				
Rank 1 caracal	-26.29	0.138	-1.910	0.056	-23.81	0.147	-1.621	0.105

Significance code: * P < 0.050 ** P < 0.010 *** P < 0.001 for z values.

Farmers' strategies to reduce livestock predation

a) Farmers' experience of various control methods and of their perceived efficacy

Almost all (97.4%) of the farmers used lethal control methods on mesopredators (Figures 6.9 and 6.10). To control jackal, farmers mostly used three methods: call and shoot at night ("roep-en-skiet") – which involves playbacks of conspecific challenge calls, or prey-in-distress calls using a sound device such as a FOXPRO (FOXPRO Inc., Lewiston, PA) to "call" the jackal closer to a hunter sitting at the back of a vehicle; gin traps, which are unpadded with offset jaws and are triggered when the animal steps on a trigger plate; and cage traps (each method is used by 94.7% of the farmers respectively). However only calling and shooting at night was reported as being very effective (efficacy score: 4.3/5) whereas gin trapping was reported as relatively effective (3.6/5) and cage trapping as ineffective (1.2/5), mostly because only the young inexperienced jackals could be trapped in cages (Table 6.11).

To control caracal, almost 95% of the farmers used trapping with cages, followed by gin-trapping (91%, score: 3.7/5). Cage trapping was considered to be the most effective method (efficacy score: 4.1/5, Table 6.11). Lethal methods such as conibear traps and coyote getters, popular in the USA, were rarely used by the respondents (Figures 6.9 and 6.10). Helicopter hunting was regarded as effective against jackal, but less so for caracal. Less than half of the respondents had experience with this method, which is currently not permitted in the Western Cape Province of South Africa (http://www.capenature.co.za/care-for-nature/conservation-in-action/biodiversity-compliance/wildlife-management/damage-causing-animals/, accessed June 15th 2018).

Approximately a quarter of the respondents reported that they had used an illegal (for use, possession and trade) agricultural pesticide, "two-step" (i.e. aldicarb, which is a carbamate insecticide and the active substance in the pesticide Temik®), to control predators, with a mean perceived efficacy of 3.2 for jackal and 2.7 for caracal. More than a third of farmers reported having used 1080 (Sodium Fluoroacetate) against both predators, with a perceived efficacy of 3.0 out of 5 for jackals and 2.4 for caracal. A slightly lower percentage of respondents reported using poison (1080) collars but efficacy scores were ≤2.5. About a quarter of farmers reported that they had also used 'other' poisons without mentioning which one(s), and that in the case of jackal, they were regarded as effective (mean score of 3.0/5).

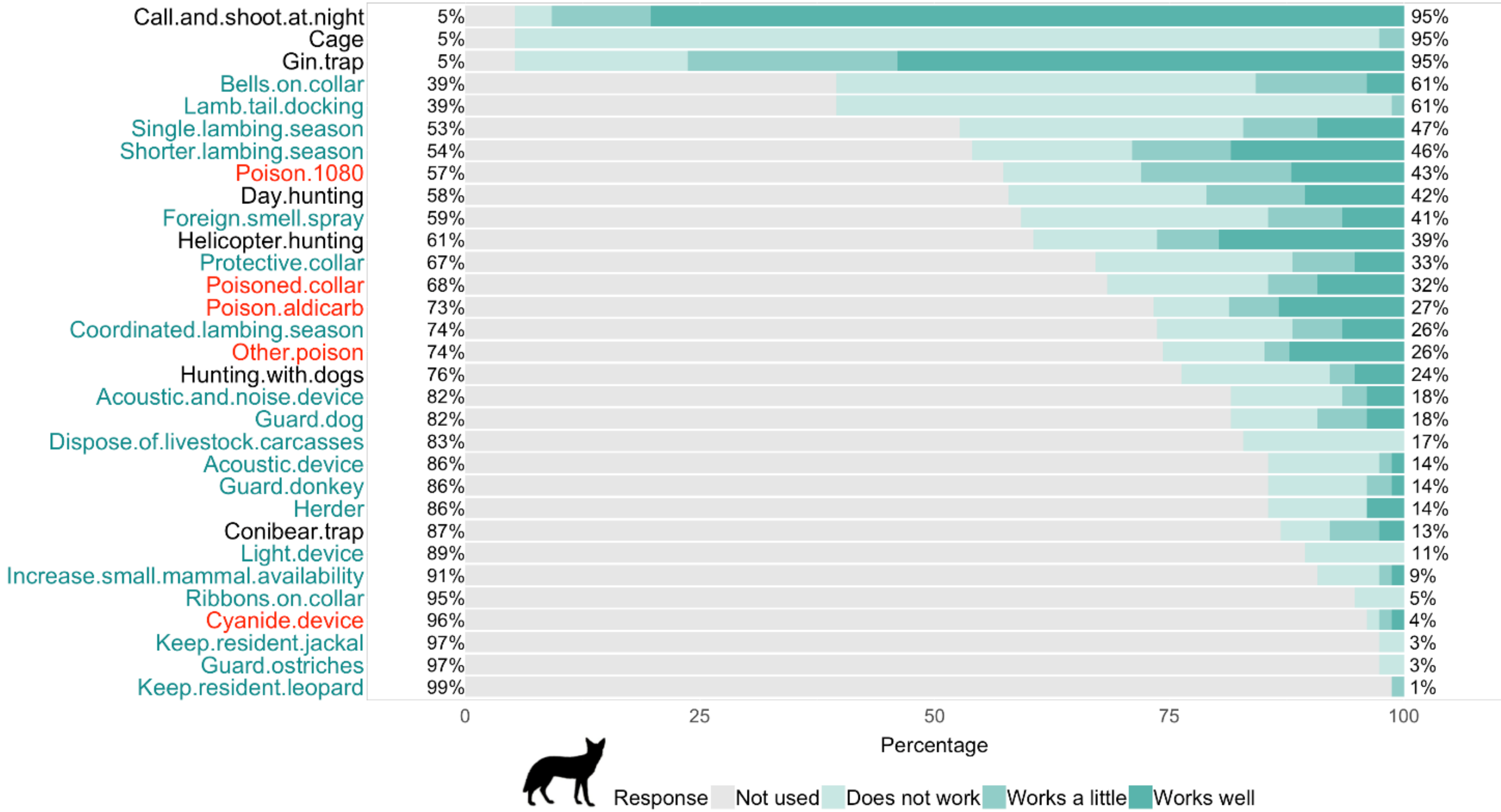


Figure 6.9. Percentage of farmers that have used (shades of green) or not (grey) a range of control methods against jackal predation on their farms. When the method has been used, its perceived efficacy was recorded at three levels: "does not work" (palest green shade), "works a little", "works well" (darkest green shade). On the y-axis, lethal methods are in black font, poisons in red and non-lethal methods in green. The percentages on the right y-axis represent the approximate percentage of farmers considering that a method was effective (two darkest shades of green).

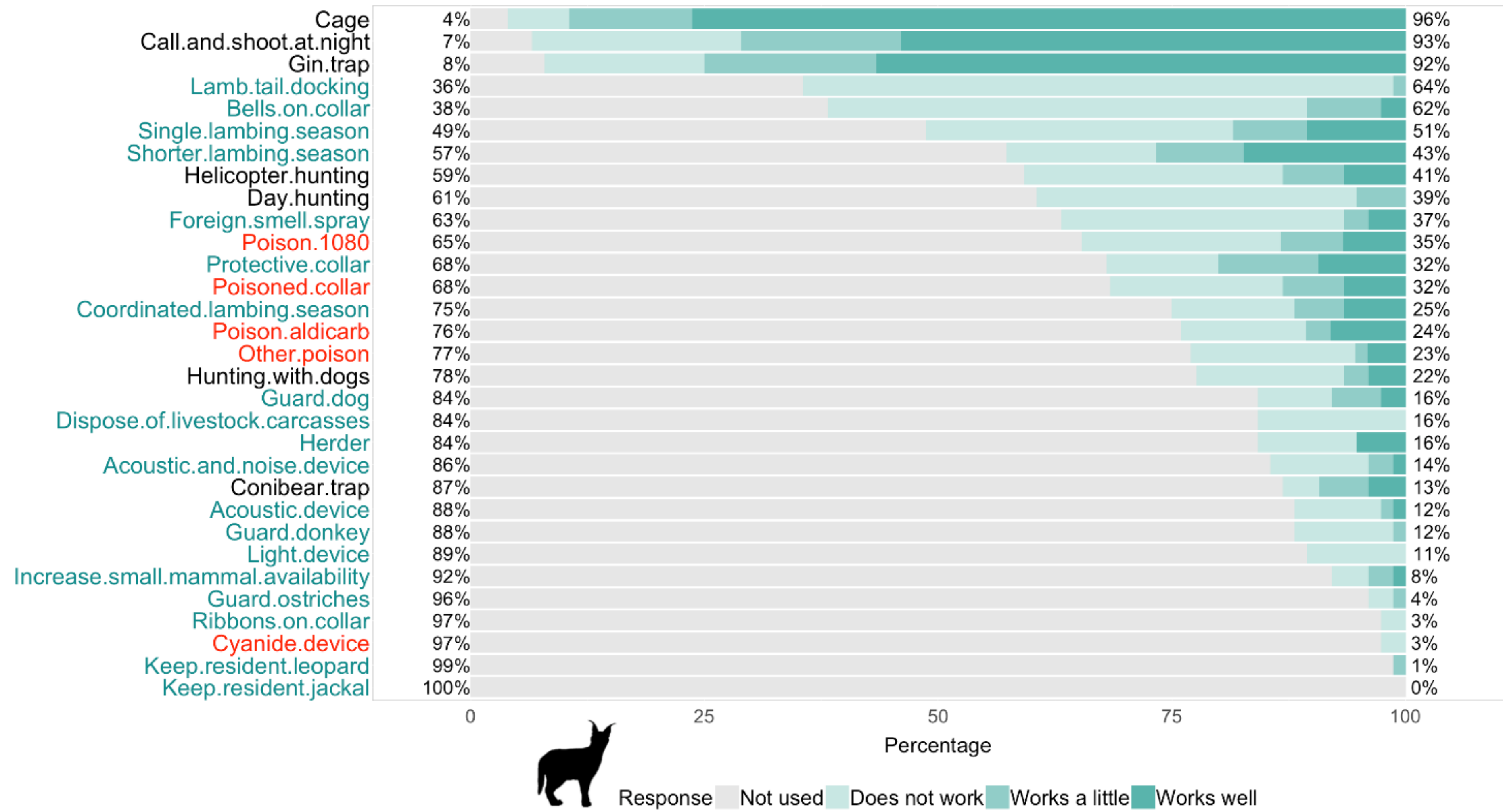


Figure 6.10. Percentage of farmers that have used (shades of green) or not (grey) a range of control methods against caracal predation on their farms. When the method has been used, its perceived efficacy was recorded at three levels: "does not work" (palest green shade), "works a little", "works well" (darkest green shade). On the y-axis, lethal methods are in black font, poisons in red and non-lethal methods in green. The percentages on the right y-axis represent the approximate percentage of farmers considering that a method was effective (two darkest shades of green).

Table 6.11. Mean Likert scale score of the perceived efficacy of various control methods used by farmers against black-backed jackal and caracal and percentage of farmers with experience of each method.

	Black-backed jackal		Caracal	
Methods used to control mesopredators	Mean Likert scale score for perceived efficacy[a]	Percentage of farmers with experience of the method (with the fraction of the sample in parenthesis)	Mean Likert scale score for perceived efficacy[a]	Percentage of farmers with experience of the method (with the fraction of the sample in parenthesis)
Gin trap	3.6 ± 1.2	94.7 (72/76)	3.7 ± 1.3	92.1 (70/76)
Cage	1.2 ± 0.5	94.7 (72/76)	4.1 ± 1.1	96.0 (73/76)
Conibear trap	2.7 ± 1.5	13.2 (10/76)	2.9 ± 1.3	13.2 (10/76)
Call and shoot at night	4.3 ± 0.9	94.7 (72/76)	3.4 ± 1.3	93.4 (71/76)
Day hunting	2.7 ± 1.4	42.1 (32/76)	1.4 ± 0.7	39.5 (30/76)
Helicopter hunting	3.3 ± 1.7	39.5 (30/76)	2.1 ± 1.3	40.8 (31/76)
Hunting with dogs	2.2 ± 1.6	23.7 (18/76)	2.1 ± 1.4	22.4 (17/76)
Poison 1080	3.0 ± 1.3	42.7 (32/75)	2.4 ± 1.3	34.7 (26/75)
Poisoned collar	2.5 ± 1.6	31.6 (24/76)	2.2 ± 1.4	31.6 (24/76)
Poison aldicarb (two-step)	3.2 ± 1.4	26.7 (20/75)	2.7 ± 1.6	24.0 (18/75)
Other poison	3.0 ± 1.5	25.7 (19/74)	1.9 ± 1.3	23.0 (17/74)
Cyanide device	2.7 ± 1.5	3.9 (3/76)	1.0 ± 0.0	2.6 (2/76)
Bells on collar	2.0 ± 1.0	60.5 (46/76)	1.7 ± 0.8	61.8 (47/76)
Ribbons on collar	1.2 ± 0.5	5.3 (4/76)	1.0 ± 0.0	2.6 (2/76)
Protective collar	2.2 ± 1.1	32.9 (25/76)	2.8 ± 1.2	32.0 (24/75)
Foreign smell spray	2.3 ± 1.1	40.8 (31/76)	1.9 ± 1.1	36.8 (28/76)
Herder	2.3 ± 1.4	14.5 (11/76)	2.3 ± 1.5	15.8 (12/76)
Guard dog	2.4 ± 1.4	18.4 (14/76)	2.2 ± 1.4	15.8 (12/76)
Guard donkey	1.9 ± 1.0	14.5 (11/76)	1.7 ± 0.7	11.8 (9/76)
Guard ostriches	1.0 ± 0.0	2.6 (2/76)	2.0 ± 1.0	3.9 (3/76)
Shorter lambing season	2.9 ± 1.3	46.0 (35/76)	2.8 ± 1.3	42.7 (32/75)
Single lambing season	2.1 ± 1.3	47.4 (36/76)	2.1 ± 1.3	51.3 (39/76)

Coordinated lambing season	2.5 ± 1.2	26.3 (20/76)	2.5 ± 1.1	25.0 (19/76)
Lamb tail docking	1.1 ± 0.3	60.5 (46/76)	1.1 ± 0.3	64.5 (49/76)
Dispose of livestock carcasses	1.0 ± 0.0	17.1 (13/76)	1.0 ± 0.0	15.8 (12/76)
Acoustic device	1.8 ± 1.0	14.5 (11/76)	1.7 ± 1.1	11.8 (9/76)
Light device	1.5 ± 0.5	10.5 (8/76)	1.2 ± 0.5	10.5 (8/76)
Acoustic and noise device	2.1 ± 1.2	18.4 (14/76)	1.8 ± 1.1	14.5 (11/76)
Increase small mammals' availability	2.0 ± 1.1	9.2 (7/76)	2.3 ± 1.2	7.9 (6/76)
Keep resident jackal(s)	2.0 ± 0.0	2.6 (2/76)	NA	0.0 (0/76)
Keep resident leopard	NA	1.3 (1/76)	3.0	1.3 (1/76)
Other method	NA	7.9[b] (6/76)	NA	1.3[c] (1/76)

[a]Likert scale scores range from 1 (not effective) to 5 (extremely effective).
[b]Having domestic dogs walking in the veld daily, barking and marking their territories; having guard alpacas; installing electric fences that are predator-proof; maintaining predator-proof fences; kraaling close to the house; spray ammonia on sheep wool.
[c]Having domestic dogs walking in the veld daily, barking and marking their territories.

b) The use of lethal versus non-lethal control methods

All farmers reported using so called jackal-proof fences in attempt to restrict the movement of predators onto their farms. Some farmers, in addition to using lethal management, also reported using some non-lethal tools such as protective collars or deterrents like spraying a foreign scent on lambs. Attempts were also made to adapt husbandry to reduce livestock losses to predators, including having a single and/or shorter lambing season (i.e. to synchronise pregnancies amongst ewes by not leaving the rams with them all the time) and coordinating their lambing season with their neighbours' (Figures 6.9 and 6.10). Protective collars and bells were reported as being inexpensive (around ZAR 10/bell and ZAR 100/collar) but as being labour intensive, as they require the adjustment of the straps of the collars as the lambs grow. Protective collars are also bulky and might therefore disturb the lambs when they are feeding. In addition, some farmers reported that bells quickly became "a signal for predators to come and eat" and that lambs with protective collars were now being attacked by predators on their rump rather than their neck (Figure 6.11).

At the time of the interviews, just above 40% of the farmers reported that a new strategy against jackal predation was to spray a foreign smell (i.e. deodorant, disinfectant, human urine) on lambs when they were having their tail docked (Table 6.11). Only about a sixth of the respondents had experience with a herder or with livestock guarding dogs. The perceived efficacy of these two non-lethal methods against caracal predation was similar to the perceived efficacy of using poisoned collars (method used by twice as many farmers) and was rather low. Farmers considered that these two non-lethal methods, when used against jackal, were similar in terms of efficacy to spraying foreign smells on lambs (which was used by twice to three times as many farmers and was considered rather ineffective, Table 6.11). Farmers explained that it was difficult to find reliable farm workers/herders who would in addition want to stay in the field for extended periods of time. The statutory minimum wage of ZAR 105/day (approximately US$ 7 at the time of writing) for a farm worker was also reported as being too expensive to spend on a herder. Almost a fifth of the farmers interviewed (n=15) reported having to now use family labour for controlling predators when this job had previously been done by farm workers before the 1990s. As for the livestock guarding dogs, farmers reported that the large areas covered by the camps, their rather rugged landscapes and the lack of flocking of the widely farmed Dorper sheep made it difficult for a single dog to provide protection. Most farmers thought that removing carcasses of dead animals and docked tails from the camps where the sheep were grazing were not effective strategies against predation by mesopredators (Table 6.11).

In general, for jackal, the mean reported efficiency score of lethal control methods was significantly higher than that of non-lethal methods ($t = 4.04$, $df = 28$, $p < 0.001$). Contrarily for caracal, the mean reported efficiency score of lethal control methods was not significantly higher than that of non-lethal methods ($t = 1.94$, $df = 28$, $P = 0.063$). When I asked the respondents whether they thought that using non-lethal methods to protect their sheep from predators was more expensive than using lethal methods, a significant ($\chi^2 = 15.00$, $df = 1$, $P < 0.001$) majority (59.7%) replied positively and 11.7% did not know.

Figure 6.11. Lambs of different ages each wearing a different type of protective collar against predation but nevertheless sustaining injuries from mesopredators, probably black-backed jackal. Pictures taken in 2013 in the Central Karoo District Municipality, South Africa. Photo courtesy of Mr. Gouws.

According to the respondents, the most practical solution to limit losses due to predators was their eradication (Figure 6.12), followed by selective killing. Avoidance of risky areas was not considered to be very practical (ranked third) but was used by some farmers, during the lambing season. Farmers perceive vegetation close to riverine habitat to provide cover for predators (see Chapter 3) to ambush sheep and hence attempted to keep them away from these areas when lambing. Using husbandry practices such as herding and kraaling (i.e. keeping livestock in a confined area overnight or during the lambing season) was ranked fourth in terms of practicality (Figure 6.12). Kraaling, even if generally recognised as effective at curbing nocturnal predation was seldom used because it is labour intensive and the cost of labour is high, and because of the impact it has on the fragile vegetation of the Karoo, with kraals creating bare patches that take a long time to recover if they ever do (Rowntree, 2013). The relocation of predators was viewed as the least practical method (ranked fifth).

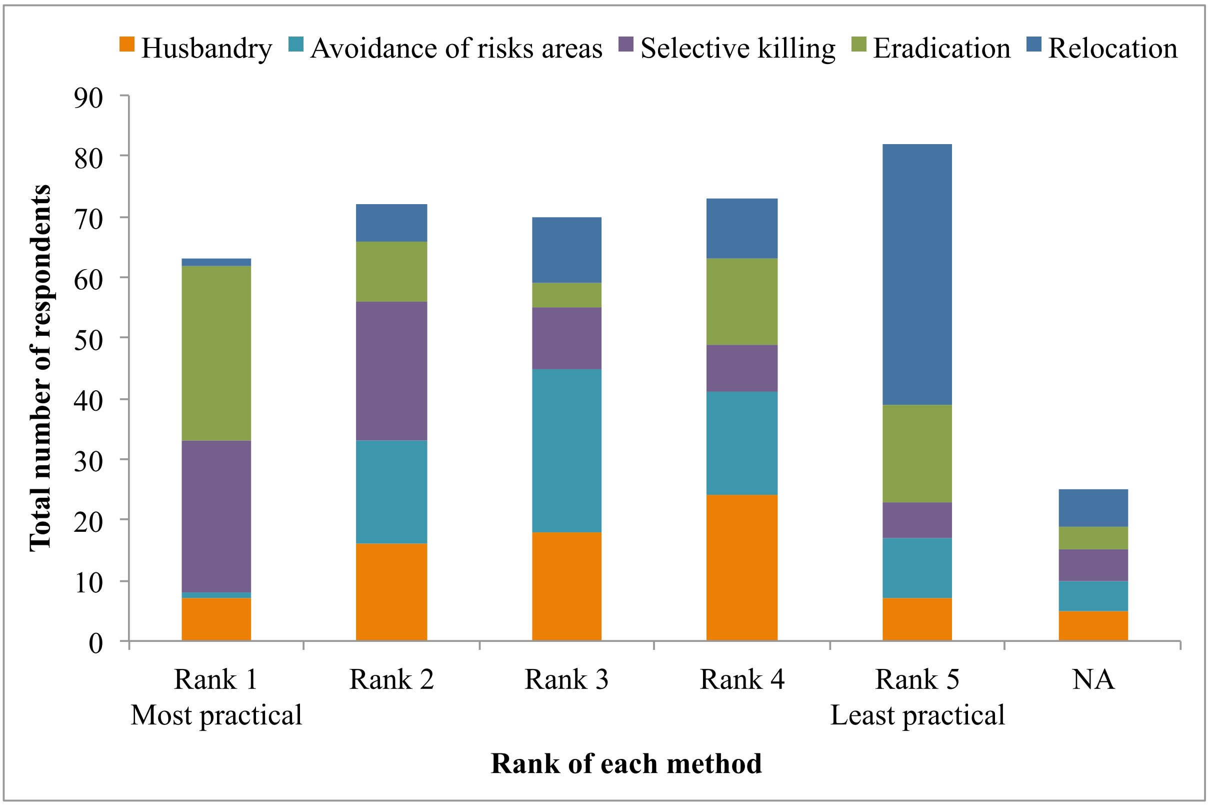


Figure 6.12. Histogram representing the rank farmers gave to five different proposed methods in terms of their practicality in reducing predation of livestock on their farms in the Central Karoo, South Africa.

Significantly more farmers responded to the question "How do you usually respond to fresh signs of jackal/caracal on your farm?" by quoting lethal actions, in particular trapping and hunting (Figure 6.13), rather than non-lethal action, both for jackal (χ^2 = 22.73, df = 1, p <

0.001) and caracal (χ^2 = 17.59, df = 1, p < 0.001). A minority replied that they would do nothing in line with my previous results (Figures 6.9 and 6.10, Table 6.10).

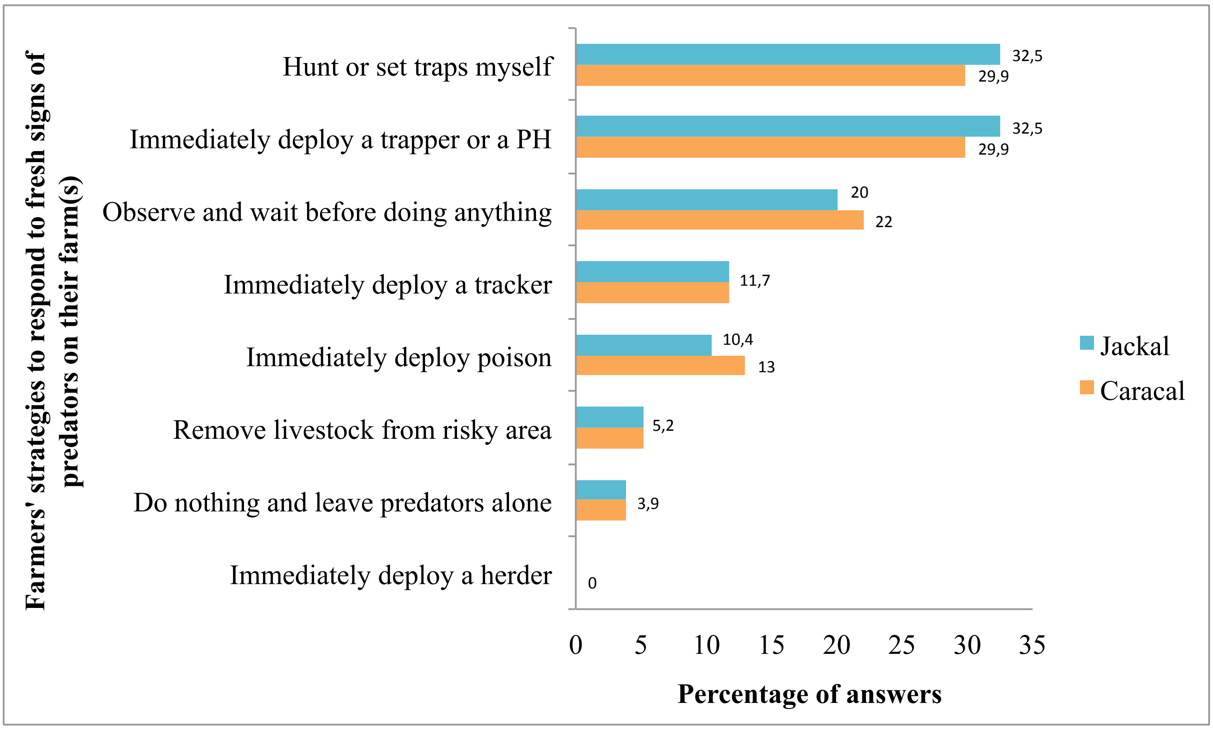


Figure 6.13. Histogram showing the percentage of answers respondents gave to the question "How do you usually respond to fresh signs of jackal/caracal on your farm?" Answers for jackal are represented in blue while answers for caracal are represented in orange. PH = professional hunter.

Predator control was mostly performed by trappers and professional hunters, but farmers also participated a lot (often with their sons). Most of the farmers (31.2%) hired a professional hunter on a part-time basis rather than relying on a permanently employed trapper. Almost a quarter of the respondents did not hire either a hunter or a trapper. Only one farmer reported having a full-time hunter on his farm (and by this he meant himself) and no respondents had both a full-time hunter and a full-time trapper.

Control effort represented a mean of 13.3 (± 33.2) hours/month/farming unit. The mean amount of time farmers spent controlling predators on their farms when they answered that they would tolerate both jackal and caracal if they caused a hypothetical 5% livestock loss was not significantly different from that of farmers who were intolerant, both towards jackal (t = -0.170, df = 75, P = 0.865) and caracal (t = -0.356, df = 75, P = 0.722).

c) Farmers' experience and illegal use of poison for baiting

Of the farmers who used poison ("gif") regularly, all believed that poison was effective against predators. The proportion of farmers using poison as a last resort and who believed it was effective against predators (84%) was significantly higher (χ^2 = 22.66, df = 1, p < 0.001) than the proportion who thought it was not effective or who did not know. Of those who reported not using poison, most (58%) thought that it was not effective or were unsure. Interestingly, 42% of the farmers who reported not using poison believed that poison was effective against predators (Table 6.12).

Table 6.12. Reported frequency of use of various types of poison by respondents, their experience with them and whether or not they think the poison is effective against mesopredators.

		Has experience with different types of poisons			Thinks poison is effective against mesopredators		
		1080	Two-step	Other	Yes	No	Unsure
Uses poison regularly	17% (13/76)	75% (9/12)	42% (5/12)	58% (7/12)	100% (13/13)	0% (0/13)	0% (0/13)
Uses poison as a last resort	33% (25/76)	56% (14/25)	44% (11/25)	32% (8/25)	84% (21/25)	12% (3/25)	4% 1/25)
Does not use poison	50% (38/76)	22% (8/37)	8% (3/37)	14% (5/37)	42% (16/38)	47% (18/38)	11% (4/38)
Total	100% (76/76)	43% (32/75)	27% (20/75)	27% (20/74)	66% (50/76)	28% (21/76)	6.6% (5/76)

When asked how they usually respond to fresh signs of predators on their farm(s) (section b) above), more than a tenth of the respondents declared that they would immediately deploy poison (Figure 6.13). This suggests that despite poison use being illegal to control predators in South Africa, its use was not always as a last resort and that it is readily available to most farmers. The poison 1080 can be legally obtained (e.g. legal supply) from a local licensed dealer in the Central Karoo, in the form of a "vetpil", which is a mixture of meat, animal fat and 1080 (Figure 6.14) but its use against predators is illegal except in poison collars against predation.

When I asked specifically about their use of poison as a method for controlling predators, more than 53% of the respondents declared that it was part of their overall anti-predation toolbox. When I asked whether they believed that poison was effective against predators, two thirds (66%) said yes, 28% said no and only about 6% said that they did not know. When asked whether they had used poison on their farm recently, only one farmer declined to answer. Of the remaining 76 farmers, 38 (50%) said that they had not and 50% said that they had, with 17% of them stating that they used poison regularly (Table 6.12). For 33% of the farmers, poison was a last resort method for dealing with the most elusive and difficult to catch predators (Table 6.12).

Figure 6.14. Photograph of the poison baits ("vetpil") containing a mixture of meat, fat and the compound 1080, made by a local dealer in the Central Karoo © Marine Drouilly – The Karoo Predator Project.

These farmers considered it important to try and minimize the risk of accidental poisoning of non-target species. To do so, some farmers reported hanging their poison baits up in trees or on wooden poles so that smaller carnivores such as mongoose and genet would not be able to reach them. Farmers who stated never using poison said that they were concerned with the harm it could do to non-target species and the ecosystem as a whole. In addition to being seen by some farmers as an effective strategy against predators, poison was also viewed as a cost-effective method.

The ten variables selected for multivariate GLMs did not show evidence of collinearity ($r \leq 0.7$ for all pairs). All predictor variables under the best model exhibited generalized VIF values < 2.0. After model selection, the best binary logistic regression explaining farmers' use of poison on their farms presented five statistically significant variables (Table 6.13). Fall in employment, having jackal, caracal and baboons in the top three predators on the farm, having Cape fox within the top five predators on the farm, considering poison as effective against predation and relative Terrain Ruggedness Index (TRI) were all significant covariates in both the logistic regression (Table 6.13) and the average marginal effects (Table 6.14). The best model (Model B) shows that conditional on the other variables in the model, having jackal, caracal and baboons ranked in the top three predators, and considering poison as effective against predation exhibited the strongest marginal effects (34.22 ± 0.10 % and 48.87 ± 0.10 %, respectively) among all categorical variables. Ranking Cape fox in the top five predators on the farm increased the average marginal effects of farmers using poison by more than 23 percentage points (Table 6.14). Conditional on the other variables in the model, a decrease of one farm worker on the farm was associated with a 5% (interquartile range: 0.03-0.08 %) increase in the probability of using poison. An increase of one unit in the relative Terrain Ruggedness Index (TRI) was associated with a 9% (interquartile range: 0.02-0.16 %) reduction in the probability of using poison (Table 6.14). Interestingly, the percentage of lamb losses was not retained in the best model (Table 6.13). In Model A, a 10% increase in lamb losses had an average marginal effect of increasing poison use by just over a percentage point, but this effect was not significant (Table 6.14). Number of years of education, age, believing in the dominant jackal pair narrative and farm size all had negative signs of their coefficients but their effects were not significant and the variables were not retained in the best model (Table 6.13).

The Chi-square test with an associated p-value < 0.001 (likelihood ratio test) indicates that Model B as a whole, fits the data significantly better than an empty model (Table 6.13).

Table 6.13. Binomial logistic regression analysis of poison use by farmers in the central Karoo in 2014. The left-hand column lists the independent variables and the other columns show the values of (in order): the partial logistic regression coefficients with the standard errors of the partial slope coefficients (SE) in parenthesis, the z-ratio and the significance level.

	Model A (full model)				**Model B (best model)**			
Independent variables	Estimates	Std. Error	z value	Pr(>|z|)	Estimates	Std. Error	z value	Pr(>|z|)
Intercept	2.279	2.631	0.866	0.386	-1.394	0.516	-2.700	0.007 **
Fall in employment	0.254	0.068	3.750	0.000 ***	0.246	0.070	3.532	0.000 ***
Total farm size	-0.001	0.003	-0.479	0.632				
Jackal, caracal and baboon are in the top 3 predators	1.658	0.511	3.246	0.001 **	1.485	0.499	2.975	0.003 **
Cape fox is in the top 5 predators	1.327	0.542	2.449	0.014 *	1.125	0.440	2.554	0.011 *
Poison is considered efficient against predation	1.943	0.59	3.260	0.001 **	1.920	0.486	3.951	0.000 ***
Farmer believes that killing the dominant pair of jackals will increase the number of jackals	-0.552	0.471	-1.173	0.241				
Age	-0.027	0.017	-1.540	0.124				
Years of education	-0.155	0.160	-0.971	0.331				
Percentage of lambs lost	0.064	1.034	0.062	0.950				
Relative Terrain Ruggedness Index (TRI)	-0.425	0.212	-2.001	0.045 *	-0.396	0.180	-2.203	0.028 *
Number of observations	66				69			

Log likelihood	-25.542				-27.95			
Prob > Chi^2	<0.001				<0.001			
AIC_c	77.97				69.26			
BIC	97.17				81.31			
Nagelkerke's R^2	0.61				0.58			

Significance Code: * P < 0.050 ** P < 0.010 *** P < 0.001 for z values.

Table 6.14. Average marginal effects (calculated using robust standard errors – RSE and measured as percent gain) for the binomial logistic regression of poison use by farmers in the Central Karoo in 2014.

	Model A (full model)				**Model B (best model)**			
Independent variables in their natural units	df/dx	RSE	z	p	df/dx	RSE	z	p
Fall in employment	5.463	0.013	4.264	0.000 ***	5.531	0.014	4.082	0.000 ***
Farm size	-0.032	0.001	-0.481	0.630				
Jackal, caracal and baboon are in the top 3 predators	36.51	0.089	4.108	0.000 ***	34.22	0.099	3.450	0.000 ***
Cape fox is in the top 5 predators	26.06	0.086	3.032	0.002 **	23.70	0.082	2.900	0.004 **
Poison is considered efficient against predation	46.67	0.105	4.454	0.000 ***	48.87	0.101	4.834	0.000 ***
Farmer believes that killing the dominant pair of jackals will increase the number of jackals	-12.23	0.103	-1.187	0.235				
Age	-0.571	0.003	-1.648	0.099				
Years of education	-3.344	0.034	-0.985	0.324				
Percentage of lambs lost	1.386	0.222	0.062	0.950				
Relative Terrain Ruggedness Index (TRI)	-9.145	0.040	-2.302	0.021 *	-8.908	0.036	-2.480	0.013 *

Significance Code: * P < 0.050 ** P < 0.010 *** P < 0.001 for z values.

Discussion

Causes of livestock losses and the ranking of predator species as threats to livestock

In my study, commercial small-livestock farmers considered predation to be the biggest threat to the survival of their business. This result is in accordance with previous studies conducted in the Central (Conradie and Piesse, 2016) and Little Karoo (Mann, 2014). In both of those studies, the second biggest threat was drought, whereas in this study it was theft and farmers often referred to thieves as *twee-been jakkalse* (two-legged jackals). Droughts are known to result in important reductions of livestock herds in semi-arid areas (e.g. Baringo, Kenya; Homewood and Lewis, 1987). My finding was surprising given the Central Karoo is a more arid region than the Little Karoo (see Chapter 2), and hence the impacts of drought were predicted to be greater. A similar result was found in Maasailand during the 2005-2006 drought where livestock mortality rates were significantly higher in an area experiencing above-average rainfall than in three other areas that had below-average rainfall (Nkedianye et al., 2011). The authors suggested that this result was a possible consequence of the immigration of livestock from drought-stricken areas and of the more market-oriented but less drought-resistant livestock breeds in the above-average rainfall area. In the Central Karoo, farmers owning more than one farm can move their sheep to the greener farm in case of drought (pers. obs.).

My results showed that jackal, caracal and then Cape fox and baboons were considered the main predators of livestock on small-livestock farms in the Central Karoo. Jackal, caracal and different species of baboons have been reported to kill livestock in other studies as well (Pirie et al., 2017), including outside of South Africa (Muriuki et al., 2017). In the main small-livestock areas of South Africa, jackal and caracal predation have been shown to respectively account for 65% and 30% of predation losses overall (van Niekerk, 2010). In the North West Province of South Africa, jackal (41%), caracal (20%) and leopard (15%) were believed to be responsible for most of predation incidents (n=149) occurring on private farmland (Thorn et al., 2012). In the Little Karoo, where Anysberg Nature Reserve is situated, Mann (2014) found that most respondents (56%, n = 53) ranked baboons as the most problematic wildlife species (responsible for livestock predation, crop damage and infrastructure damage). Baboons were followed by jackal (51%) and then caracal (21%). Worldwide, most of the conflicts with baboon species are due to crop raiding (Strum, 2010) but livestock predation has been reported in Zimbabwe (Butler, 2000; Sogbohossou et al., 2011). The report of Cape fox as the third ranked predator of livestock in my study is surprising because they had a low occupancy probability on farmland (see Chapter 3) and are rarely reported as being livestock predators in published studies (Kok and Nel, 2004). Feral dogs were also ranked highly as a threat to livestock in the Little Karoo (Mann, 2014), conforming to the global perception that they are a serious threat to livestock (Ciucci and Boitani, 1973; Van't Woudt, 1990; Young et al., 2011). My survey suggested that farmers who perceive feral dogs as a serious problem were mostly on farms that were close to towns.

Avian predation is generally less frequent than mammalian predation, but the killing of lambs and game species by large eagles is perceived to be a problem throughout the world. Species such as the black eagle in South Africa, the wedge-tailed eagle (*Aquila audax*) in Australia, the golden eagle (*Aquila chrysaetos*) in the USA and the white-tailed eagle (*Haliaeetus albicilla*) in Europe, have all been actively persecuted to protect small-livestock (Woodroffe et al., 2005). Losses to corvids are also widespread and may exceed those attributed to eagles (Davies, 1999). In my study, farmers sometimes reported large eagles as being a problem for predation on very young lamb, but there was only one mention of corvid as a problem and in this instance, it was ranked fourth.

Spatio-temporal patterns of predator presence, perceived conflict with farmers and perceptions for changes in predator numbers

More than 85% of the farmers surveyed consider at least one predator, in particular jackal, to pose a threat to their livelihood. Of concern to farmers and the local economy is that this threat is perceived to have increased for jackal, caracal and baboon, especially since 2000. This is in accordance with prediction (P1) and consistent with farmers' general perception that predator numbers are increasing (reported in Mann (2014) in the Little Karoo and for jackals in Humphries et al. (2015a) in KwaZulu Natal). Farmers largely ascribed this trend to changes in farming practices, including reduced lethal control, particularly of baboons. Other factors proposed by farmers to be driving increases in predator numbers include poor fencing (particularly for jackal) and reduced human presence (mostly relevant to jackal and caracal), particularly farm workers. Nattrass and Conradie (2018) showed that having less farm workers in total and in particular fewer living permanently on the farm resulted in a significant increase in livestock losses to predators. These changes mirror the decline in government support for commercial sheep farmers, including fencing and predator control operations (Nattrass et al., 2017). The expansion of PAs, the increase in lifestyle farms (Reed and Kleynhans, 2010) and the fall in farm worker employment (Western Cape Department of Agriculture, 2017) are also explanatory factors. Together these changes may have allowed wildlife species in general and predators in particular to recolonize places from which they were extirpated. It might also have allowed predator populations to increase firstly on lifestyle farms and PAs and subsequently on commercial farms. Similar recolonization by predators has been reported on other continents, e.g. cougars in North America (Davenport et al., 2010; Larue et al., 2012), grey wolves (Fabbri et al., 2014; Falcucci et al., 2013) and golden jackals in Europe (Arnold et al., 2012), and dingoes in Australia (Allen and West, 2013; Allen and West 2015). In addition, it seems that where carnivores have returned after prolonged absence, the conflict is particularly acute. This was the case in both Europe and the Americas (Blanco et al., 1992; Breitenmoser, 1998; Cozza et al., 1996; Kaczensky, 1999; Quigley and Crawshaw, 1992; Treves et al., 2002) and is attributed to the absence of appropriate livestock protection tools and to the need for farmers to re-adapt their job to the presence of carnivores. The latter often requires a radical change in the husbandry methods that they use, and is perceived as reducing the quality of rural life (Linnell et al., 2012, 1996).

Farmers' reported lamb losses

My results showed that the reported percentage of lamb losses was very high (mean of 29.4%). It was higher than the 10-14% of lamb losses reported for the Central Karoo between 2012 and 2014 in another study (Conradie and Nattrass, 2017), but lower than the 46% reported on monitoring farms across South Africa (reported in Turpie and Babatopie, 2018). Livestock losses in general were highest during the lambing season. A similar result was shown for jackal predating lambs in another study in the Free State of South Africa (Kamler et al., 2012a). In a global review on human-predator-prey conflict, Graham et al. (2005) found that predators killed between 0.02 and 2.6% of livestock annually. Higher reported levels of predation may actually be a consequence of other, more severe causes of mortality. These include theft, injury to livestock, diseases, accidents, poor nutrition, bad motherhood, venomous snake bites or adverse weather conditions (Graham et al., 2005; Hoogesteijn et al., 1993; A. J. Loveridge et al., 2010; Mazzolli et al., 2002; Oli et al., 1994; Quigley and Crawshaw, 1992), sometimes misidentified as predation (Pirie et al., 2017; Sillero-Zubiri et al., 2013). For example, in Zimbabwe, Rasmussen (1999) found that poor management of livestock accounted for 43% of stock losses, followed by disease (23%), with predators responsible for less than 2%. In southern Africa, more than 600 plant species are known to cause poisoning of livestock (Turpie and Babatopie, 2018), representing 264 851 small-livestock per year (Kellerman et al., 1996). In my study, more than 40% of the farmers inferred predator losses versus had actual evidence strengthening the assertion that in many other studies, other causes are likely to inflate the perceived severity of the predation problem (Wagner 1988, Rust et al. 2016). Deriving robust empirical evidence of the relative causes of livestock mortality remains a serious challenge for the small-livestock farming industry more generally, and research on the conflict between farmers and predators both locally and globally (Cozza et al., 1996; Turpie and Babatopie, 2018).

As predicted (P2c, P2d and P2g respectively), my results showed that larger, more rugged farms, and rugged farms where caracal is ranked as the main predator were more likely to suffer high percentages of lamb losses. Larger farms may be more difficult and time-consuming to patrol and hence detect and control predators. They may also hold larger predator populations (Kaartinen et al., 2009). Rugged terrain has been shown to be favoured by some predator species such as baboons that sleep on cliffs in the Karoo (Du Plessis et al., 2018) and caracals that rely on stealth and cover to ambush prey (Avenant et al., 2016; Drouilly et al., 2018c). They might also offer better hiding places from hunters and trappers. Having caracal ranked as the main predator on a farm that is not rugged had for effect to reduce the likelihood of lamb losses compared to having jackal ranked as the main predator. Caracal might be easier to control than jackal that would in addition likely cause more losses to livestock. The percentage of lamb losses on farmland was lower for older farmers, as expected (P2a). A similar result was obtained for farmers in the USA in conflict with grey wolves (Berger, 2006), and suggests that age may be a proxy for experience that may in turn be an important factor improving both livestock husbandry and predation management. In this regard, the mentorship program aiming to train livestock producers and farm workers on principles of ethical and best practices in predation management, run by the National Wool Grower's Association of South Africa (NWGA) through the Predation Management Forum[3] (PMF), may be a very important approach for reducing livestock losses and conflict with predators (https://www.pmfsa.co.za/home/goals/training/item/291-predation-management-training3, accessed September 28th 2018). Livestock losses also increased as the number of farm workers decreased as I predicted (P2b). Changes in both the labour laws and the minimum wages in South Africa (Department of Labour, 2002) are some of the major drivers of a reduced force of Karoo farms (Conradie and Piesse, 2016). A reduced labour force translates into poorer husbandry and less time spent on monitoring predators, which together may explain higher lamb losses (Nattrass and Conradie, 2018; Ogada et al., 2003). Contrary to my predictions (P2e and P2f), farms with more permanent artificial water sources, or where baboons were ranked as the main livestock predators did not have a higher percentage of lamb losses.

Farmers' attitudes towards wildlife in general and predators in particular

Even if non-predatory wildlife triggered rather positive attitudes in farmers (except Cape porcupines), attitudes towards predators were in general very negative (as expected, P3). That was particularly the case towards jackal and to a lesser extent caracal. The WAC was low for predators, with most farmers wanting to eradicate them or strongly reduce their numbers. To my knowledge, this is the first study to investigate attitudes and tolerance towards predators in the Karoo, making the comparison with published studies difficult. In some areas where large carnivores are still present, jackals trigger diverse responses from landowners. In Kenya for example, commercial ranchers want jackal on their property and displayed higher tolerance towards the species than communal farmers (Romañach et al., 2007). In South Africa and Zimbabwe, the attitudes of ranchers towards jackal were more polarized, with most ranchers being either very positive or very negative. Negative attitudes were reported to be linked to jackals killing game and livestock, while positive attitudes were attributed to their perceived ecological role and their low perceived threat (Lindsey et

[3] The Predation Management Forum (PMF) statement of intent is to provide a platform for liaison and coordination of activities of commodity organisations in the livestock and game ranching sectors, aimed at reducing losses incurred as a result of predation by means of ecologically and ethically acceptable methods which protect the biodiversity of South Africa.

al., 2005). Throughout the world, wild canids in particular seem to engender negative attitudes (Berg, 2001; Fanshawe et al., 1991; Kellert, 1985). Interestingly, attitudes were also very negative towards baboons, even if the primates did not cause as much damage as jackal or caracal. My results are in accordance with what Nattrass and Conradie (2018) found in the same area of the Central Karoo, with farmers culling entire baboon troops as a response to the threat they pose to livestock. Cape fox, African wildcat and leopard also triggered negative attitudes.

The topics of predation and predators were very salient to Karoo farmers. Salience helps explain attitudes (Vaske and Manfredo, 2012) and the word elicitation exercise I conducted revealed very negative words for jackal in particular. Farmers who described caracal and jackal as beautiful were more likely to be tolerant of them in a scenario where they caused low (5%) livestock losses, as I predicted (P4c). Similarly, farmers' favourite animals were iconic species with a glamorous physical appearance, even if they are known to cause damage to farmers in other parts of South Africa or the world. Kellert et al. (1996) defined aesthetic attitude as the physical appeal and beauty of wildlife. Previous studies have found that the public is more likely to support the protection of aesthetically pleasing species (Gunnthorsdottir, 2001; Kellert et al., 1996; Knight, 2008; Roque De Pinho et al., 2014). Herrmann et al. (2013) also found aesthetic values in local narratives regarding the cougar and the kodkod cat (*Leopardus guigna*) in Mapuche and Chilean stories. Caracals are not considered iconic animals outside of their distribution range but are nevertheless often imbued with high value by city dwellers who find predators alluring because of their power, beauty and link to wild nature (Macdonald, 2001). During the three years I have spent in the field collecting data for this PhD, no fewer than seven film makers from Europe contacted me to film caracals, attesting to their appeal. But the high value ascribed to caracal by an international audience is not always reflected at the local level, where farmers can suffer substantial costs from their presence. Rather, and similar to the cougar in North America (Mattson and Clark, 2010), caracals were simultaneously revered for their power and beauty and reviled for the threat they pose to livestock. In Brazil, ranchers often consider the jaguar to be the most beautiful animal in their environment but their response to the statement "jaguar deserve protection" was often "yes, but not on my ranch" (Zimmermann et al., 2005), similarly to what Karoo farmers told me regarding both jackal and caracal.

Finally, farmers' intolerance towards jackal and caracal was strongly influenced by their belief that these wild animals should only occur in PAs, as expected (P4d). Farmers clearly do not think it is a viable option to farm livestock with predators. This may explain the weak relationship between tolerance to predators and the perceived percentage of lambs lost to them, contrary to what I had predicted (P4b). This contrasts with other studies where the relationship between tolerance and losses was positive (e.g. Naughton-Treves et al., 2003). Contrary to my predictions, neither ranking jackal or caracal as the biggest predator of livestock (i.e. negative experience with the species, P4a) nor thinking that mesopredators can control each other's numbers (P4e) significantly impacted farmer tolerance.

Farmers' strategies to reduce livestock predation

As predicted (P5), almost all farmers I interviewed preferred to use lethal methods to control predators and opted for a lethal approach in response to fresh signs of jackal and caracal on their farm. This finding agrees with a recent review on management tools to reduce carnivore-livestock conflicts worldwide (Moreira-Arce et al., 2018), which revealed a clear preference for lethal options versus non-lethal tools. In the Karoo, like in many parts of the world, the principal method to resolve predator damage remains the "3-S treatment": shooting, shovelling, shutting-up (Marchini, 2014; Turpie and Babatopie, 2018), with almost no farmers reporting their lamb losses or applying for hunting permits to CapeNature, the provincial governmental authority responsible for wildlife outside of PAs. Lucherini and Merino (2008) noted that in the Andes, the local population mostly considered that the only good carnivore is a dead carnivore, similar to what I have heard repeatedly in the Karoo.

Due to the high cost of hiring a professional hunter on the farm and to the low trust many farmers had in their farm workers, some farmers conducted their own predator control, particularly night hunting (with call and shoot). However, this practice is discouraged by the Predation Management Forum due to the fact that using the wrong calls at the wrong time of the year may teach the jackals to avoid the hunters.

Effectiveness of lethal control has rarely been independently evaluated and thus mostly relies on farmers' perceptions (Treves et al., 2016). My results show that for jackal control, farmers gave significantly higher effectiveness scores to lethal versus non-lethal methods. Interestingly though, the mean reported efficacy score of lethal versus non-lethal methods for caracal was not significantly different. Despite the lack of scientific literature on the subject, both my results and a recent review (Moreira-Arce et al., 2018) suggest that lethal control does not curb livestock losses. This is especially the case if control efforts are not maintained, the target species is highly mobile (Novaro et al., 2004) or displays compensatory breeding (Knowlton et al., 1999), or if other factors (e.g. habitat, food availability) are not addressed. Lethal control might reduce livestock losses in the short term (Naughton-Treves and Treves, 2005) such as during the lambing season, but it has been shown that it is not an effective long-term solution (Blejwas et al., 2002). For example, in the Karoo, historical records show that humans succeeded in extirpating jackals from most Karoo sheep farms, although not in eradicating them completely, by the mid-twentieth century (Beinart 1998, 2003). Yet, within a few decades, the jackal had reclaimed its status as principal predator of sheep and most hunted and killed predator in the Karoo, showing that a constant large-scale culling effort is needed to keep populations low. Today, Karoo farmers report that both lethal and non-lethal methods to control predators are becoming less effective over time (Nattrass and Conradie, 2018). Killing predators in the Karoo has also been shown to be counter-productive as culling has been associated with greater livestock losses in the following year (Nattrass and Conradie, 2018). However, this study would benefit from being conducted over a larger time-frame. From the discussions I had with farmers during the interviews, it was clear that most farmers were controlling the target species (i.e., jackal, caracal) rather than specific individuals that may be responsible for most losses. Given that the jackal (and to a lesser extent the caracal) is a highly mobile compensatory breeder (Minnie et al., 2018a) and that livestock are constantly maintained in the environment, it is perhaps not surprising that episodic culling events are largely ineffective at reducing losses in the Karoo (Minnie et al., 2018b; Tensen et al., 2018). However, in the absence of appropriately scaled, before and after (with control) studies, the relative efficacy of different methods remains a largely subjective matter fomenting considerable conflict between different stakeholders in the Karoo and globally (Treves et al., 2016; van Eeden et al., 2018).

Non-lethal methods were seen by the respondents in this study as being more expensive, requiring additional farm labour, unpractical to put in place and less effective than lethal methods at controlling predation. Farmers thus had a lot less experience with non-lethal than with lethal control methods. The exception was jackal-proof fences that were used by all respondents. Fences mainly serve to limit the movement of predators and make individual farmers accountable for predators (Swanepoel, 2016). However, all the predators I equipped with GPS collars (see Chapter 5) were able to cross so called predator-proof fences and a young dispersing male jackal even crossed at least 67 of those fences over a period of four months between May and September (unpublished data).

Drivers of illegal poison baiting to control predators

My results showed that most farmers had experience with different types of illegal poisons. More than 53% declared using poison and 17% used it regularly, showing that its use is widespread despite being illegal. This supports the findings of two previous studies in the Karoo (Allan, 1989; Nattrass and Conradie, 2018). My results also showed that poison was not necessarily used as a last resort with a tenth of the respondents deploying poison immediately in response to fresh signs of jackal and caracal on their farms. Poison has also been used to exterminate golden jackal in Greece (Ntemiri et al., 2018) and to curb cattle losses due to golden jackals in Israel (Yom-Tov et al., 1995). The dramatic decrease of raptors in both countries was largely a result of secondary poisoning (Mendelssohn, 1962; Ntemiri et al., 2018). In another study in the northeast of South Africa, the proportion of farmers who used poison to kill carnivores was lower than in my study (about 20%, St John et al. (2012)).

Contrary to what Nattrass and Conradie (2018) found in the Central Karoo, the socio-economic variable linked to reduced farm workers had a statistically significant impact on poison use in my study, as predicted (P6a). Nattrass and Conradie (2018) also found that the widespread use of poison was a consequence of, as well as a response to, rising levels of predation. By contrast and contrary to my prediction (P6e), my results showed that there was no statistically significant relationship between the percentage of lamb losses and the use of poison. Rather, the use of poison increased when farmers listed jackal, caracal and baboon as a problem for livestock on their farms, and when they ranked Cape fox amongst the top five main predators, as predicted (P6b and P6c). Contrary to my prediction (P6f) though, the use of poison increased when farm ruggedness was lower, probably because those farms were easier to drive to set poison baits. Nattrass and Conradie (2018) also suggested that the use of poison might be a response to the harsher regulations surrounding the management of predators (PMF, 2016). I would argue against this suggestion, knowing that there is no oversight regarding what methods farmers use on private farmland and that enforcement is very rarely implemented. Rather, the use of poison is probably a response to the lack of farm workers on farms and to the fact that poison is considered to be particularly effective (as predicted, P6d), but also cheap, quick and silent against predators. On the opposite, believing in the dominant jackal pair narrative (P6g) and having more years of education (P6h) decreased the likelihood of using poison as I predicted, but these results were not statistically significant.

Conclusion

Jackal, caracal and baboons are clearly perceived as a serious and growing threat for the sustainability of small-livestock farming in the Central Karoo. In this chapter, I explored some of the characteristics, impacts, management and determinants of the resulting conflict between farmers and predators within the current socio-productive crisis that is impacting the Karoo. The general increase in both the extent and severity of perceived predator losses is a concern for farmers' livelihood and ultimately for the economy of the Central Karoo. These trends appear to be linked to the substantive changes experienced by the social (reduced labour and altered management practices), economic (reduced subsidies for fences and predator management) and ecological (more PAs, game and lifestyle farms) spheres that together may have facilitated the broad scale re-emergence of jackal as a severe problem, the persistence of caracal as a problem and the localised emergence of baboons as a threat to livestock and hence farmers' livelihood. In particular, the reduction in the number of farm workers and the relative threat posed by different predators and combinations of predators have emerged as significant predictors of both the reported amount of lamb losses and the likelihood of poison use on farmland.

People base their perceptions and attitudes on facts and personal experiences, but not only. Many other factors such as societal experiences, cultural norms and beliefs also play an important role (Dickman, 2010). I showed that the aesthetic aspect of predators could play a role in improving tolerance for predators, a field where very little research has been conducted. On the contrary, farmer intolerance towards mesopredators was not directly correlated to their perceived percentage of lambs lost, probably because farmers strongly believe that farming livestock with predators is not a viable option.

The widespread use of poison to control predators in my sample is a cause of concern due firstly to its illegality but mostly to its capacity for killing non-target wildlife (Ogada, 2014). Non-lethal techniques, when properly applied, have been shown to be cheaper and more effective than lethal control (McManus et al., 2014; Stone et al., 2017; Treves et al., 2016) but proven examples are scarce. A literature review on carnivore interventions in Europe and North America found that 80% of nonlethal methods effectively deter predation compared to just 29% of lethal control methods (Treves et al., 2016). These results are encouraging, but predator control strategies still remain largely understudied (Eklund et al., 2017; Thorn et al., 2012; Treves et al., 2016), and it will be crucial to objectively demonstrate the relative effectiveness of non-lethal methods to farmers if we are to discourage their increased reliance on lethal control (Moreira-Arce et al., 2018).

The complex synergy between cultural, social, economic, environmental and personal factors ultimately determines how costly predators are perceived to be, and therefore the level of antipathy felt towards them. Support for farmers to manage their livestock more efficiently through either consumer funded programmes or state subsidised interventions to increase tolerance towards jackal and caracal and limit lethal control methods and particularly poison use would best be realised by promoting the aesthetic appeal of predators, improving knowledge of their ecology and behaviour, and most of all, by improving the socio-economic and political environment to promote labour on farms. All of these factors are potentially more important than those that aim solely to reduce livestock losses.

Chapter 7

Synthesis

Typical Karoo landscape on a farm with windmills and a dam in the Central Karoo, South Africa © Nathalie Houdin & Denis Palanque – The Karoo Predator Project.

Livestock depredation by carnivores is increasing worldwide and the retaliatory response by farmers is one of the key conservation concerns in arid landscapes, in which wild prey abundance is naturally low (Zimmermann et al., 2009). Globally, farmer-predator conflict has resulted in both local extirpations and extinctions of predators, including non-target species (McManus et al., 2014). Such losses have polarised farmers and environmentalists over how to best manage livestock and predators on farmland (Howley et al., 2014; Te Velde et al., 2002). Despite the conflict, extensive small-livestock farming remains one of the few economically viable activities in these marginal and fragile landscapes (Nel and Hill, 2008).

South Africa is no exception to the global trend of rising conflict between livestock farming and predators (Kerley et al., 2018; McManus et al., 2014). The local conflict has impacted adversely on biodiversity, human livelihoods, food security and even local economies (Cloete and Olivier, 2010). Hardest hit have been large carnivores, which have been extirpated from most farmland in the country (van Sittert, 1998). Smaller predators have persisted but endure considerable welfare harms associated with both lethal and non-lethal management practices (Behrens et al., 2018). Since Hey (1964) described jackals as "public enemy number one of the sheep farmer" responsible for 500 000 lamb losses nationally, and van Niekerk (2010) estimated that more than 2 million sheep and goats were depredated annually by jackal and caracal (in the five major small-livestock provinces of South Africa), little progress has been made in resolving the conflict.

Despite the numerous harmful consequences of this farmer-livestock-wildlife conflict, very little research has been conducted on its drivers at the landscape level. Before my research, the mammalian and ground bird diversity within the Karoo was restricted to local, general or historical species lists that did not provide accurate data for species richness, distribution, abundance estimates and community structure and composition. Yet, such data are essential to understand how land use, especially private land, affects wildlife communities, and for the management of livestock, wildlife and predators in general (Roberts, 2011; Silveira et al., 2003; Tobler et al., 2008). In this chapter, I contextualise my findings within farmer-mesocarnivore-livestock conflict in Africa and the world, highlighting where I think my research has improved our understanding of the conflict. In addition, I discuss the feasibility of sheep farming industry in the Karoo and in drylands more generally. Finally, I offer recommendations for future research and propose possible changes in the type of interactions between the various stakeholders of the current conflict (Figure 7.3), that are improving the one initially presented in the introduction of this thesis (see Chapter 1, Figure 1.1).

Access to private farmland and the importance of a comparative study site

This study would not have been possible without the farmers themselves reaching out for assistance from University academics. In particular, the efforts of A/Prof Beatrice Conradie to both understand the economic challenges facing farmers in the region and to assist in the building of a collaborative interdisciplinary research team, were critical interventions that enabled this research. Equally important to realising this PhD were leaders in the farming community that convinced their neighbours to participate in the project, and so provide a large enough sample of contiguous farms (n = 22) to meet the requirement of a landscape-level assessment of the interactions between farmers, wildlife, predators and small-livestock.

Working on private farmland is challenging, particularly in the Karoo where there is limited information available on the personal contact details of farm owners, the extent and characteristics of their land. Consequently, arranging access to farms was both time-consuming and unpredictable and very reliant on farmers talking to each other to establish a network of contacts. With hindsight, I realise that the ethnographic approach I used with farmers was critical for building trust despite my often diametrically opposed personal beliefs on how to best manage predation challenges. This trust facilitated my understanding of their cultural and emotional values (Drury et al., 2011) as they pertain to livestock depredation, wildlife, and the changing socioeconomic and political landscapes. This relationship would not have been possible from the single visit interviews I also conducted (see Chapter 6). Norton (2000) states that “it is not just the way we focus our research that is important, it is also the way we as conservation biologists interact with landowners. On private lands it is not some remote government agency that controls the land but a landowner or manager who usually lives on the land and knows it intimately.” All those factors may explain why research on understanding ecological processes in modified ecosystems that dominate private land is still so limited (Norton, 2000), particularly in southern Africa, despite the importance of such land for biodiversity conservation (see Chapter 3). Drury et al. (2011) have stressed the importance of qualitative research for understanding the local context, highlighting new research topics and aiding accurate interpretation and analysis. In this thesis, I have incorporated interdisciplinary work (Table 7.1), using both quantitative and qualitative research methods. This allowed me to produce a cross-disciplinary – and more holistic analysis of the farmer-predator conflict issue – as recently advocated for in a special issue of the Journal of Range and Forage Science about the Karoo (Walker et al., 2018).

Having established the farmland study site and in the absence of any "before data" with which to compare the results, I became acutely aware of the need for a reference against which my "farm-findings" could be compared. This led to the selection of a nearby PA (Anysberg Nature Reserve), approximately the same size as the combined area of the 22 farms, and historically also used for small-livestock farming (see details in Chapter 2). The comparisons I drew between the farmland and the PA are of course limited because I cannot control for the many differences between the two sites that are not central to my main research questions (e.g. differences in biomes, grazing intensity). Simply stated, there is no control site for farmland that is not confounded by differences that may affect the variables of interest (Table 7.1). This begs the question of whether we should even attempt to use another site for comparison. I argued in Chapters 3 and 4 that there is value in comparing the farmland with Anysberg Nature Reserve, noting that its previous long-term use as small-livestock farms is actually an advantage for the purposes of considering how the removal of livestock and farm management practices from the landscape may influence wildlife. Furthermore, the proximity of the study sites (40 km at their nearest point) allows for movement of medium- and large-sized terrestrial vertebrates and complete overlap in the predicted distributions of most medium and large vertebrates in this region. A recent study by Woodgate et al. (2018) on the variation in medium and large mammal species richness and relative abundance across the entire Karoo (although not incorporating many sites in the succulent Karoo biome) revealed a cosmopolitan community of medium and large mammal taxa. In her study, she shows that mammal species richness is only affected by longitude and not by NDVI, annual precipitation or terrain roughness. These factors are important for the dietary and diversity comparisons between farmland and the PA in my study, for they suggest that differences are not solely a result of the obvious differences in biomes and other factors such as topography between my two sites. Probably, the differences in species diversity, relative abundance and space use between farmland and the PA are due to a complex mix of several factors, including biome, grazing pressure, and type and intensity of predator control on farmland. Disentangling these effects is a difficult task but I suggest future research questions to start addressing those needs (Table 7.2).

Farmland as an ecological trap for flexible mesopredators

While some species struggle to survive in our human-dominated world, others thrive, such as red foxes (Harris, 1981) and golden jackals (Ranc et al., 2015) in Europe, coyotes (Gehrt et al., 2011) and bobcats (Tigas et al., 2002) in the US and dingoes in Australia (Allen et al., 2015). These species share the trait of behavioral plasticity, which confers them resilience even in the face of extensive transformation of natural habitat and sustained lethal control (Fall and Jackson, 2002). Jackal and caracal have both adapted well to human modifications of the environment, thriving on Karoo farmland while other larger predators were extirpated (Hey, 1964). Historically there was however a time that farmers appeared to have realised their goal of excluding jackals from farmland, but this was only possible with substantial state support for both infrastructure and logistics (Beinart, 1998). Government support has since dried up (Nattrass and Conradie, 2015) and jackal and caracal appear to be expanding their range despite ongoing lethal management (see Chapter 6).

I interpret the relatively high occupancy of caracal and to a lesser extent jackal on farmland compared to the PA to be a consequence of four possible causes: 1) the availability of an abundant, easily catchable food source in the form of small-livestock (see Chapters 3, 4 and 5), 2) the establishment of permanent water across the entire farming landscape (Archer, 2000), 3) the low apparent human presence (see Chapter 3), and 4) the absence of large apex predators (see Chapters 3 and 4). Together, these factors create a discrepancy between habitat quality and functionality on farmland. Farmland represents a habitat suitable for survival and reproduction, resulting in an attractive sink or ecological trap, characterized by mortality risks that cannot be perceived by animals (Delibes et al., 2001). These sinks are common at the interface between wild areas and human-modified landscapes, such as park boundaries (A. Loveridge et al., 2010). Jackals have a higher occupancy in the PA than on farmland, which I assume is a consequence of sustained lethal management on the latter (see Chapter 6). I provide no estimate of survival and reproductive success on farmland, but I do show that farmers perceive jackals to have re-emerged as a major threat to livestock and livelihoods in the Karoo (see Chapter 6, Figures 6.3a and 6.4) and I have evidence of both jackal and caracal breeding on farmland (Figures 7.1 and 7.2).

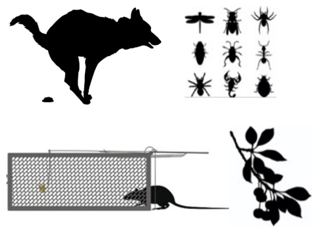
My suggestion that farmland may function as an ecological trap for jackal and caracal is in accordance with the findings of Minnie (2016), working approximately 200 km east of my study area. His research revealed that compensatory immigration of jackals from PAs to farmland was driven by what he defined as being "a maladaptive habitat selection" for seemingly attractive habitats situated on farmland. This maladaptive habitat selection has been highlighted in other species in the Carnivora order such as brown bears (*Ursus arctos)* in the Canadian Rocky Mountains (Lamb et al., 2017), leopards in the Phinda-Mkuze Complex in South Africa (Balme et al., 2010) and wild dogs around Hwange National Park in Zimbabwe (van der Meer et al., 2014). However, rather than talking about a "maladaptive habitat selection", I would argue that mesopredators display a "non-optimum habitat selection", as numerous mesopredators are still able to disperse, obtain a breeding territory, breed and even persist up to an old age on farmland, but the risk of being killed by a farmer is still probably higher than the risk of being killed by a wild apex predator in a PA.

Figure 7.1. Camera trap photograph placed in front of a potential jackal den on farmland in the Central Karoo. The pictures of the pups confirm that jackals breed on farmland in the Central Karoo, despite the high mortality risk.

Table 7.1. A summary of the main methods (i.e. camera trapping, scat analysis, GPS collaring of mesopredators, and interviews with farmers), findings and limitations of the research presented in this thesis.

Methods	Main findings	Limitations
	• Species richness was not significantly different between farmland and the PA. • Community structure, diversity and composition all differed with land use. • Carnivores, omnivores and medium-sized species occupancy probabilities were similar between the two areas. • Occupancy was higher for herbivores and large species in the PA and for insectivores and small species on farmland. • Human disturbance did not affect species richness or individual species occupancy in either area.	• Very low density and detection of wildlife on dryland → Hard to develop models fitting the sparse and heterogeneous data. • Need for a site to compare farmland to, but there is no PA with the same biotic and abiotic factors → biome, farm management methods and jackal abundance especially might have played a more significant role on species probability of use and RAI than what my study design was able to show.
	• Jackal and caracal diets differed markedly between farmland and the PA. • Small-livestock comprised the bulk of the prey in the scats of jackal and caracal on farmland. • No sheep remains were found on predator scats collected in the PA. • Jackal, caracal and leopard in the PA and caracal on farmland showed a preference for wild mammals. • Jackal on farmland showed a preference for small-livestock compared to similar-sized wild prey. • Jackal and caracal had large dietary breadth and high dietary overlap on farmland and in the PA to a lesser extent.	• Camera traps cannot be used to reliably quantify micromammals, invertebrates and fruit availability → I was therefore not able to determine predator preference for these potentially important dietary components. • Lambs are available throughout the year but I did not account for seasonal differences in other dietary components
	• GPS clusters and scats produced different estimates of diet composition. • Mesopredators actively killed livestock on farmland but not within the PA, even when jackals crossed to neighbouring farms. • GPS clusters revealed prey ranging from small to large for caracal, but only medium to large prey for jackal. • Most predation occurred between 18:00 and 06:00 hrs. • Adult male caracals depredated significantly more on livestock than other sex and age categories.	• Jackals on farmland were difficult to catch → Only a few were collared and I could not investigate the effect of sex and age on their diet. • Not enough manpower to visit all the GPS clusters → (Individual) predation rates could not be calculated.
	• Farmers perceive the severity of the conflict with jackal, caracal and baboon to be increasing, especially since the 2000s. • Reported percentage of lamb losses was linked to both environmental and socio-economic factors. • Farmers showed negative attitudes towards predators but positive attitudes towards other wildlife and non-local predators. • Tolerance to jackal and caracal was best explained by their perceived aesthetic appeal. • Farmers use lethal methods to control predators, considered cheaper, more practical and effective than non-lethal methods. • 53% of farmers reported using poison. Poison use did not correlate with reported livestock losses and was highest on farms with less labour.	• Farmers do not keep rigorous records on livestock losses and their causes → Impossible to compare the cost/benefit and real efficacy of different predation control methods. • No historical farm-level predator distribution exists for the Central Karoo → Impossible to determine whether farmers show a "shifting baseline syndrome".

Table 7.2. Most urgent research questions that need to be addressed following up this work to keep improving our understanding of the interactions between small-livestock farmers and biodiversity, including mesocarnivores in the Karoo.

Research questions	Recommendations for future research projects to address those questions	Potential research methods
• What are the effects of different farm management methods and jackal density on: 1) biodiversity levels? 2) Predators' and small carnivores' presence, relative abundance and space use?	Farms in the Karoo and more generally in South Africa present different management practices. Those management practices relate to both small-livestock (sheep density, grazing intensity (i.e. biomass of grazers if plant surveys cannot be conducted), presence of rotational system, presence of a lambing season, etc.) and predators (type of predator control, intensity and regularity of predator control, use of poison or not, type of poison used, etc.). Future research should investigate the impacts of those management practices on biodiversity levels and on the presence, relative abundance and space use of mesopredators and other small carnivores to identify what types of farmland management are beneficial/detrimental to which species. To do so, the full cooperation of the farming community is needed. Well-maintained fences between neighbouring farms is also a prerequisite to limit predators' and other small carnivores' movements between farms and to allow the effects of various management practices to be tested independently.	
• What are the effects of micromammal, invertebrate and fruit abundance on jackal diet on farmland across seasons?	Previous studies have shown strong seasonal differences in the consumption of wild ungulates and sheep by jackal on farmland, based on the birthing periods of both wild ungulates and sheep. In my study site, lambs were available year-round at the landscape level, so I did not investigate in details how jackal consumption of ungulates species varied with seasons. However, it would be valuable to look at the effects of micromammal, invertebrate and fruit abundance on jackal diet on farmland across seasons and on jackal/caracal prey preference (would jackal /caracal consume less sheep and show different prey preferences if all these other prey species were constantly available and abundant on farmland?).	
• What are jackal and caracal predation rates on small-livestock and on species considered as pest on farms with different management techniques?	Predation rates are important to investigate to quantify the impacts of jackal and caracal predation on small-livestock. Investigating them on farms with different management techniques would allow to find out which techniques lead to a decrease in livestock predation rates. In parallel, investigating the ecosystem services provided by mesocarnivores to farmers (i.e. limitation of prey species considered as pest) would probably improve farmers' perceptions of the species.	
• What are the cost/benefit and real efficacy of different control methods against jackal and caracal predation? Which methods allow to maximize biodiversity levels?	There is no robust cost-benefit analysis of the different control methods, lethal and non-lethal, used by farmers against jackal and caracal predation. Similarly, no before-after experiment has been conducted on the different types of predation control methods in terms of their efficiency and biodiversity impacts (including non-target species). Investigating those costs/benefits and biodiversity impacts would allow to draw recommendations for small-livestock farmers to follow if they want to control livestock predation on their farm while maximizing biodiversity levels.	

Part of the persistence of jackal and caracal on farmland could also be explained by their adaptability to a shifting prey base (see Chapter 4). I showed that mesopredators displayed a large niche breadth on farmland, which can make them more successful in adapting to changing land use because more prey is available to them and they are less vulnerable to dietary competition and fluctuation (Hayward and Kerley, 2008). Finally, their persistence could also be due to their adaptation to human presence, by reducing their probability of detection. This can be achieved by seldom resting in one place even when abundant food is available, by mostly killing their prey during twilight and night and by not consuming the prey entirely but rather moving on after reaching satiation (see Chapter 5).

Figure 7.2. Camera trap photograph placed at an artificial waterhole on a farm in the Central Karoo. The pictures of the caracal kittens confirm that the species breeds on farmland in the Central Karoo, despite the high mortality risk.

While mesopredators are clearly capable of surviving and breeding on farmland, they are nevertheless subject to heavy persecution. During the 3.5 years I spent in the field in the Central Karoo, I recorded the culling of 341 jackals and 202 caracals. These were mostly opportunistic recordings and are definitely an under-estimation of the total number of mesocarnivores killed on farmland in the Central Karoo. The conflict between farmers and predators is pervasive in the region and my results showed that it is growing both in intensity and coverage (see Chapter 6). The more negative attitudes of farmers towards jackal (see Chapter 6) is consistent with the results of Chapter 4, showing that jackals are the main predators of small-livestock and that they prefer small-livestock over similar-sized wild prey. This is a simple but important result in the context of understanding conflict in the Karoo, as farmers have long since claimed that jackals were targeting sheep over wild ungulates and were consistently recommended to simply increase the abundance of wildlife to offset livestock losses.

Conflict between farmers and predators is also the product of socio-economic and political landscapes

In addition to the ecological drivers presented above, I showed that the conflict between farmers and predators was also a consequence of socio-economic and political changes (see Chapter 6). The restructuring of the national government after the transition to democracy in 1994 resulted in a decrease of government support for predator control and in the modification of labour laws (which encouraged farmers to shed labour). I showed in Chapter 6 that both perceived livestock losses due to predators and actual poison use had increased with a reduction in farm labour. Labour losses from farms are reflected also in South Africa's rising unemployment rate, which is currently at 27.5% (third quarter of 2018; https://tradingeconomics.com/south-africa/unemployment-rate, accessed November 17th 2018). The current socio-productive crisis in the Karoo is now combined with the recent environmental threat of increasing droughts and the current exploitation of its physical resources (i.e. minerals, renewable energies, clear skies) by external stakeholders (Walker et al., 2018). Together, these threats exacerbate the conflict between farmers and predators as profit margins decrease.

Farmers in the Karoo claim that their quality of life has been reduced, that they are losing their right to manage their own land because decisions are made on their behalf by people who have got no knowledge of the reality "on the ground" and of their critical situation. Farmers are also frustrated by the fact that urban consumers, environmental NGOs and related activists do not pay sufficient (if any) attention to the welfare costs experienced by livestock when attacked and injured by predators. They instead focus their critical attention on the lethal management of predators (Nattrass and Conradie, 2015). Similar to the wolf in many countries worldwide (e.g. Ericsson and Heberlein, 2003), the jackal might end up becoming the symbol for the divide between primarily urban-based animal rightists and rural Karoo farmers. Yet, despite the high mortality risks predators and non-target wildlife are experiencing on farmland, the multispecies occupancy models presented in Chapter 3 revealed that wildlife species richness was not significantly different between farmland and the nearby PA, with all trophic guilds being present on farmland. This result is particularly important for it reveals that the environmental narrative that suggests wildlife has been decimated on farmland is largely incorrect and that small-livestock farmers are critical custodians of much of South Africa's extant biodiversity. Clearly, extensive small-livestock farmers can be classified as being good for biodiversity relative to crop farmers on whose land few animals persist (Newbold et al., 2015; Searchinger et al., 2015). The challenge for stock farmers therefore is to devise more humane and sustainable ways of reducing livestock losses while maintaining current levels of biodiversity on their land.

Poisoning, an effective solution to predation or a reaction to the mounting stressors on farmers?

The re-emergence of jackal as a major predator of livestock in the Central Karoo, the continued presence of caracal and the emergence of baboons as a threat to livestock (see Chapter 6), are all symptomatic of recent changes to the socio-political and economic landscape of South Africa. Together these factors have contributed to the current socio-economic crisis that farmers in the region are experiencing, and appear to have promoted the illegal use of methods including poisons to control predators on farmland (Nattrass and Conradie, 2018; see Chapter 6). Although the use of poisoned baits in South Africa has been banned since July 1991 (Notice Nr. R1716 of 26 July 1991) in terms of the Fertilizers, Farm Feeds, Agricultural Remedies and Stock Remedies Act (Act Nr. 36 of 1947) that prohibits in particular the use of any pesticides for purposes other than those indicated on labels, there are widely used because they are cheap, difficult to police and considered effective. Some poisons such as Temik® and other aldicarb formulations are even banned for trade, possession and use in South Africa. Poison use presents a particularly insidious threat to non-target wildlife (Ogada, 2014) and polarises stakeholders because of the ethical and welfare concerns linked to its use. There are however currently no data on the impacts of poison on predators in particular and wildlife in general on farmland in the Karoo. However, given the results presented in Chapter 6 and the recent findings of Nattrass and Conradie (2018), understanding the drivers of use and the impacts on target and non-target species remains a national challenge.

Alternative livelihoods, management methods and support structures to enable sustainable and humane small-livestock farming economy in the Karoo

One long term solution to the chronic conflict between farmers and livestock is for the farmers to consider an alternative land use to small-livestock farming. Game farming has been discussed as a possible alternative to small-livestock farming in my study area. However, at a recent farmers' meeting in Laingsburg (September 2018), N. Saayman, a researcher in plant sciences at the Western Cape Department of Agriculture in Elsenburg, cautioned against this suggestion. Saayman argued that natural vegetation in the Karoo cannot tolerate the sustained grazing pressure that is typical of extensive game farms and that when this land use is combined with the extremely low and unpredictable rainfall that typifies the Central Karoo, the land could become sub-economic.

I would suggest that before considering a change in land use, farmers should first attempt to simultaneously improve their management of livestock and predation. Achieving this will however require support from researcher (Table 7.2), government, consumers and NGOs who would benefit from improved food security, improved welfare for livestock and predators and reduced impact on the natural flora and fauna of the Karoo (Figure 7.3). One of the most important improvements that can be made to livestock management is for farmers to record livestock losses more systematically and accurately and for their data to be collated and monitored on a routine basis (Table 7.1). It was apparent to me during interviews that few farmers kept detailed written records of livestock losses or the number of predators killed in response to these losses. Most farmers relied predominantly on memory recall, which is known to be subject to "shifting baseline syndrome" (i.e. changing human perceptions of biological systems due to loss of experience about past conditions; Papworth et al., (2009)). The lack of robust data on livestock losses and their causes weakens the evidence that farmers present on the severity and extent of their losses, and the assistance they require to humanely manage predators that are targeting their livestock. In Chapter 4, I provide strong evidence in support of farmers' claims that jackal preferentially target livestock relative to similar-sized wild prey and further that both caracal and jackal consume large amounts of livestock on farmland. It is therefore in the farmers' best interest to start rigorously documenting the damage caused by predators versus the other causes of livestock losses, as is generally recommended for any human-wildlife conflict situation (Madden, 2004). That will also allow researchers to assist in identifying what types of farmland management are beneficial/detrimental to which wildlife species and to conduct rigorous cost-benefit analysis of different control methods, lethal and non-lethal, against jackal and caracal predation (Table 7.2). To do so, the full cooperation of the farming community is needed.

Future research should also attempt to assess micromammal, invertebrate and fruit availability on both farmland and PAs to understand how this influences mesopredator diet and livestock losses on farmland. I was unable to reliably quantify those biodiversity components using camera traps (Table 7.1). However, while acknowledging the detection limitations of this method, there were marked differences in the RAI of micromammals between the two sites, with significantly less on farmland. More recently, efforts to quantify micromammal abundance on farmland in the Karoo using appropriate methodology (i.e. Sherman trapping on grids) provide support for my findings with extremely low capture rates on farmland (M. Blackenberg and N. Hassan, pers. comm., December 2018). Given the importance of micromammals to the diet of both jackal and caracal within the PA in this study, the drivers of reduced micromammal presence on farmland remain an important challenge for future research (Table 7.2).

Improved livestock management could also be realised if farmers adopted the established guidelines of the South African Mohair Growers Association, which strives for sustainable good practice standards for economic, environmental, animal care and social accountability. Adoption of these guidelines demands a voluntary self-assessment model that allows producers to assess their farming practices (de Beer, 2010). This approach could serve as a foundation for certification systems such as those of the Wildlife Friendly Enterprises Network with their Certified Wildlife Friendly® and Certified Predator Friendly® production standards (http://wildlifefriendly.org/standards/, accessed November 18th 2018) (Figure 7.3). The results of Chapter 3 reveal that extensive small-livestock farming sustains medium- to large-sized faunal biodiversity. In addition, I showed that farmers display positive attitudes towards most wildlife species, including non-local predators (see Chapter 6). Wild animals are amongst the most marketable components of the environment (Treves and Jones, 2010) and farmers could use their presence on farmland as a marketing tool (for example, marketing their products as "wildlife friendly") to realize higher market prices to offset increased costs of improved husbandry (Figure 7.3). To encourage farmers to continue farming with wildlife, local and government support needs to be provided to farmers so that poor practices, including illegal poisoning are discouraged, while non-lethal alternatives and lethal methods that target specific damage-causing individuals are improved (Figure 7.3). In the European Union, between 2007 and 2013, over €20 billion was spent on agri-environmental schemes as part of the Common

Agriculture Policy (cited in Kross et al. 2018). Similarly, in the United States, financial support to producers through the Agricultural Act of 2014 – known as the Farm Bill – is provided to implement conservation practices on productive landscapes, through programs such as the United States Department of Agriculture's (USDA) Environmental Quality Incentives Program (EQIP) and the Conservation Stewardship Program (CSP). The USDA's Natural Resources Conservation Service (NRCS) also receives funds to educate farmers on the benefits of more environmentally-friendly farming practices (Kross et al., 2018). As shown in Chapter 3 of this thesis, small-livestock farmers in the Karoo could be stewards of wildlife outside of PAs, but to do so, the use of poison and other non-specific lethal methods with high welfare costs, will have to be curbed. Farmers are unlikely to adopt new methods unless provided with assistance to do so and the most likely route for such assistance is probably through the market place with consumers demanding sustainably produced free-range and wildlife-friendly meat and fibre at prices that make it worthwhile for farmers to continue farming (Figure 7.3). To generate achievable policy strategies and both sustainable development and conservation targets with regards to small-livestock farming in rangeland, the Government will need to be more involved in support of conservation on private lands (Kinnaird and O'Brien, 2012). The diagram in Figure 7.3 presents a summary of the improvements that could be brought to the system to meet those goals, in the light of what we learnt through this thesis.

Conclusion

This thesis offers an improved understanding of farmer-predator conflict in the drylands of the Karoo in South Africa. I have explored how small-livestock farming has influenced wildlife communities and predator diet and how predators are impacting livestock and livelihoods (Table 7.1). My results reveal multiple drivers of farmer-predator conflict, including ecological, environmental and socio-economic factors. Of concern to farmers is the re-emergence of jackals as major predators of livestock on farmland, the persistence of caracal and the emergence of baboons as a threat to livestock on farmland. These predators have persisted on farmland despite centuries of persecution. Their recent resurgence raises serious concerns for the sustainability of farming in the region and the welfare of predators, often subject to indiscriminate lethal control methods with poor welfare outcomes or with unknown consequences on non-target species (e.g. poisoning).

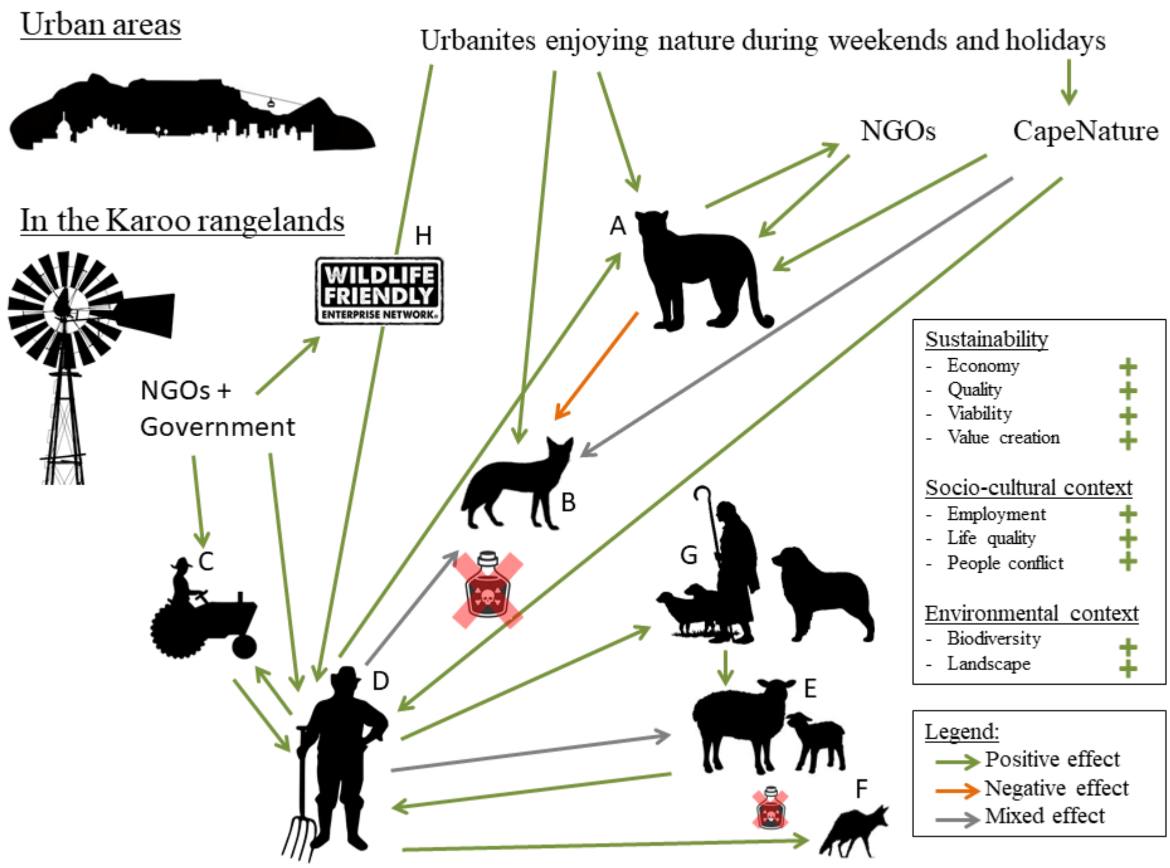


Figure 7.3. A diagram of the simplified improved interactions between the principal stakeholders involved in the small-livestock farmer – mesopredator conflict in the Central Karoo. A: large carnivores, B: mesopredators, C: farm workers, D: small-livestock farmers, E: small-livestock, F: medium to large size non-predatory wildlife species, G: non-lethal methods to limit predation such as herders and livestock guarding dogs, H: labelling organizations. The new sustainability, socio-cultural and environmental impacts of these interactions are presented in the bottom-right box. The arrows represent the effect a stakeholder has on another one, with their colour depicting whether the impact is positive (green), negative (orange) or mixed (grey). The major improvements are due to the involvement of the Government and NGOs in the system, through the supply of labour subsidies to boost employment on farmland, and certification systems supported by the general public (including urbanites) that would financially benefit the farmers. As a result, the farmers can now invest in non-lethal control methods such as livestock guarding dogs and employ herders, as well as stopping using poison, which will assist wildlife conservation on farmland.

Despite the repeated claims of select NGOs, indigenous wildlife (with the exception of large carnivores) has not been decimated on farmland and Karoo farmers are playing an important role as custodians of wildlife diversity on private land. However, farmers need support to farm with wildlife, support which is lacking from either national or provincial authorities, whose priorities have shifted since 1994. Therefore, new incentives for farmers to protect wildlife on their farms, will have to be devised if the currently worsening environmental (e.g. more frequent droughts), economic (e.g. higher labour costs) and socio-political (e.g. land redistribution, exploitation of physical resources by external stakeholders) conditions are combined with the already high predation losses. My results suggest that many of the poor management practices on farms, including illegal poison use, are linked to reduced labour on farms. Given that addressing the rising unemployment is national priority, the government needs to work with farmers to resolve the labour drain from small-livestock farms as it is wildlife that will pay the ultimate price. Finally, if we are to balance human and economic interests with biodiversity conservation in this changing ecological, socio-economic and political landscape, then we will need to find an equilibrium between the opposing demands of environmentalists wishing to protect wildlife from farmers and farmers wishing to be protected from wildlife (Naughton-Treves and Treves, 2005).

REFERENCES

Adams, V., Mundy, B., 1991. The valuation of high-amenity natural land. Appraisal J. 59, 48.

Aho, K., Derryberry, D., Peterson, T., 2014. Model selection for ecologists: The worldviews of AIC and BIC. Ecology.

Ahumada, J.A., Silva, C.E.F., Gajapersad, K., Hallam, C., Hurtado, J., Martin, E., McWilliam, A., Mugerwa, B., O'Brien, T., Rovero, F., Sheil, D., Spironello, W.R., Winarni, N., Andelman, S.J., 2011. Community structure and diversity of tropical forest mammals: data from a global camera trap network. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 366, 2703–2711.

Akaike, H., 1974. A new look at the statistical model identification. IEEE Trans. Automat. Contr. 19, 716–723.

Allan, D.G., 1989. Strychnine poison and the conservation of avian scavengers in the Karoo. South African J. Wildl. Res. 19, 102–106.

Allen, B.L., Allen, L.R., Andrén, H., Ballard, G., Boitani, L., Engeman, R.M., Fleming, P.J.S., Ford, A.T., Haswell, P.M., Kowalczyk, R., Linnell, J.D.C., Mech, L.D., Parker, D.M., 2017. Large carnivore science: non-experimental studies are useful, but experiments are better. Food Webs 13, 49–50.

Allen, B.L., Allen, L.R., Engeman, R.M., Leung, L.K.P., 2013a. Intraguild relationships between sympatric predators exposed to lethal control: Predator manipulation experiments. Front. Zool. 10, 39.

Allen, B.L., Engeman, R.M., Allen, L.R., 2011. Wild dogma: An examination of recent "evidence" for dingo regulation of invasive mesopredator release in Australia. Curr. Zool. 57, 568–583.

Allen, B.L., Fleming, P.J., Allen, L.R., Engeman, R.M., Ballard, G., Leung, L.K.P., 2013b. As clear as mud: A critical review of evidence for the ecological roles of Australian dingoes. Biol. Conserv. 159, 158–174.

Allen, B.L., Higginbottom, K., Bracks, J.H., Davies, N., Baxter, G.S., 2015. Balancing dingo conservation with human safety on Fraser Island: The numerical and demographic effects of humane destruction of dingoes. Australas. J. Environ. Manag. 22, 197–215.

Allen, B.L., West, P., 2013. Influence of dingoes on sheep distribution in Australia. Aust. Vet. J. 91, 261–267.

Allen, B.L., West, P., 2015. Dingoes are a major causal factor for the decline and distribution of sheep in Australia. Aust. Vet. J. 93, 90-92.

Allen, L.R., 2015. Demographic and functional responses of wild dogs to poison baiting. Ecol. Manag. Restor. 16, 58–66.

Allen, L.R., Sparkes, E.C., 2001. The effect of dingo control on sheep and beef cattle in Queensland. J. Appl. Ecol. 38, 76–87.

Andelt, W.F., Althoff, D.P., Case, R.M., Gipson, P.S., 1980. Surplus-killing by coyotes. J. Mammal. 61, 377–378.

Anderson, A.E., 1992. The puma on Uncompahgre Plateau, Colorado. Colorado Division of Wildlife Technical Publication, Fort Collins.

Anderson, C.R., Lindzey, F.G., 2003. Estimating Cougar Predation Rates from GPS Location Clusters. J. Wildl. Manage. 67, 307.

Andersone, Ž., Ozolinš, J., 2004. Public perception of large carnivores in Latvia. Ursus 15, 181–187.

Andheria, A.P., Karanth, K.U., Kumar, N.S., 2007. Diet and prey profiles of three sympatric large carnivores in Bandipur Tiger Reserve, India. J. Zool. 273, 169–175.

Apps, P., 2012. Smither's Mammals of Southern Africa: A Field Guide, Fourth. ed. Random House Struik, Cape Town, South Africa.

Archer, S., 2000. Technology and Ecology in the Karoo: A Century of Windmills, Wire and Changing Farming Practice. J. South. Afr. Stud. 26, 675–696.

Arnold, J., Humer, A., Heltai, M., Murariu, D., Spassov, N., Hackländer, K., 2012. Current status and distribution of golden jackals Canis aureus in Europe. Mamm. Rev. 42, 1–11.

Arsenault, R., Owen-Smith, N., 2002. Facilitation versus competition in herbivore assemblages. Oikos 97, 313–382.

Arthur, L., 1981. Coyote control: the public response. Rangel. Ecol. Manag. Range Manag. Arch. 34, 14–15.

Ashman, D.L., Christensen, G.C., Hess, M.L., Tsukamato, G.K., Wickersham, M.S., 1983. The mountain lion in Nevada.

Asquith, N.M., Wright, S.J., Clauss, M.J., 1997. Does mammal community composition control recruitment in neotropical forests? Evidence from Panama. Ecology 78, 941–946.

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.

Atickem, A., Stenseth, N.C., Drouilly, M., Bock, S., Roos, C., Zinner, D., 2018. Deep divergence among mitochondrial lineages in African jackals. Zool. Scr. 47, 1–8.

Atkinson, D., 2016. Is South Africa's Great Karoo region becoming a tourism destination? J.

Arid Environ. 127, 199–210.
Atwood, T.C., 2006. The influence of habitat patch attributes on coyote group size and interaction in a fragmented landscape. Can. J. Zool. 84, 80–87.
Aune, K.E., 1991. Increasing mountain lion populations and human-mountain lion interactions in Montana, in: Braun, C.E. (Ed.), Mountain Lion-Human Interaction, Symposium and Workshop. Colorado Division of Wildlife, Denver, pp. 86–94.
Avenant, N.L., 1993. The caracal, Felis caracal caracal SCHREBER 1776, as predator in the West Coast National Park. University of Stellenbosch.
Avenant, N.L., Drouilly, M., Power, J., Thorn, M., Martins, Q., Neils, A., Du Plessis, J., Do Linh San, E., 2016. A Conservation Assessment of Caracal caracal, in: Child, M.F., Raimondo, D., Do Lonh San, E., Roxburgh, L., Davies-Mostert, H. (Eds.), The Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.
Avenant, N.L., Du Plessis, J.J., 2008. Sustainable small stock farming and ecosystem conservation in southern Africa: A role for small mammals? Mammalia 72, 258–263.
Avenant, N.L., Nel, J. a J., 1997. Prey use by four syntopic carnivores in a strandveld ecosystem. South African J. Wildl. Res. 27, 86–93.
Avenant, N.L., Nel, J.A.J., 2002. Among habitat variation in prey availability and use by caracal Felis caracal. Mamm. Biol. 67, 18–33.
Avenant, N.L., Nel, J.A.J., 1998. Home-range use , activity , and density of caracal in relation. Afr. J. Ecol. 36, 347–359.
Avery, D.M., 1979. Upper Pleistocene and Holocene palaeoenvironments in the southern Cape: the micromammalian evidence from archaeological sites. University of Stellenbosch.
Avery, D.M., Avery, G., Palmer, N.G., 2005. Micromammalian distribution and abundance in the Western Cape Province, South Africa, as evidenced by Barn owls Tyto alba (Scopoli). J. Nat. Hist. 39, 2047–2071.
Avery, G., Avery, D.M., Braine, S., Loutit, R., 1987. Prey of coastal black-backed jackal Canis mesomelas (Mammalia: Canidae) in the Skeleton Coast Park, Namibia. J. Zool. 213, 81–94.
Azevedo, F.C.C., Lester, V., Gorsuch, W., Larivière, S., Wirsing, A.J., Murray, D.L., 2006. Dietary breadth and overlap among five sympatric prairie carnivores. J. Zool. 269, 127–135.
Azevedo, F.C.C., Murray, D.L., 2007. Evaluation of Potential Factors Predisposing Livestock

to Predation by Jaguars. J. Wildl. Manage. 71, 2379–2386.
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. Wildl. Soc. Bull. 35, 409–415.
Baeza, A., Estades, C.F., 2010. Effect of the landscape context on the density and persistence of a predator population in a protected area subject to environmental variability. Biol. Conserv. 143, 94–101.
Bailey, A., Conradie, B., 2013. The Effect of Predator Culling on Livestock Losses: Caracal Control in Cooper Hunting Club, 1976 – 1981 (No. 320). Cape Town, South Africa.
Baker, P.J., Boitani, L., Harris, S., Saunders, G., White, P.C.L., 2008. Terrestrial carnivores and human food production: Impact and management. Mamm. Rev. 38, 123–166.
Baker, S.E., Macdonald, D.W., 2000. Foxes and foxhunting on farms in Wiltshire: A case study. J. Rural Stud. 16, 185–201.
Baldi, R., Albon, S., Elston, D., 2001. Guanacos and sheep: Evidence for continuing competition in arid Patagonia. Oecologia 129, 561–570.
Balme, G.A., Slotow, R., Hunter, L.T.B., 2010. Edge effects and the impact of non-protected areas in carnivore conservation: Leopards in the Phinda-Mkhuze Complex, South Africa. Anim. Conserv. 13, 315–323.
Balmford, A., Green, R.E., Scharlemann, J.P.W., 2005. Sparing land for nature: Exploring the potential impact of changes in agricultural yield on the area needed for crop production. Glob. Chang. Biol. 11, 1594–1605.
Banerjee, K., Jhala, Y. V., Chauhan, K.S., Dave, C. V., 2013. Living with Lions: The Economics of Coexistence in the Gir Forests, India. PLoS One 8, e49457.
Barnard, P., Brown, C.J., Jarvis, A.M., Robertson, A., Van Rooyen, L., 1998. Extending the Namibian protected area network to safeguard hotspots of endemism and diversity. Biodivers. Conserv. 7, 531–547.
Barton, K., 2013. Package “MuMIn”: Multi-modal inference. Model selection and model averaging based on information criteria (AICc and alike). R package version 1.42.1. Reference manual.
Barua, M., Bhagwat, S.A., Jadhav, S., 2013. The hidden dimensions of human-wildlife conflict: Health impacts, opportunity and transaction costs. Biol. Conserv. 157, 309–316.
Bath, A.J., Buchanan, T., 1989. Attitudes of interest groups in Wyoming toward wolf restoration in Yellowstone National Park. Wildl. Soc. Bull. 17, 519–525.
Beckmann, J.P., Berger, J., 2003. Rapid ecological and behavioural changes in carnivores: the

responses of black bears (Ursus americanus) to altered food. J. Zool. 261, 207–212.
Behrens, K.G., Broadbent, N., Galgut, E., Gardner, J., Molefe, M., 2018. Ethical considerations in the management of livestock predation, in: Kerley, G.I.H., Wilson, S.L., Balfour, D. (Eds.), Livestock Predation and Its Management in South Africa: A Scientific Assessment. Centre for African Conservation Ecology, Nelson Mandela University, Port Elizabeth, pp. 82–105.
Beinart, W., 1998. The Night of the Jackal; Sheep, Pastures and Predators in the Cape. Past Present 158, 172–206.
Beinart, W., 2003. The Rise of Conservation in South Africa: Settlers, Livestock, and the Environment 1770–1950. Oxford University Press, New York, USA.
Bennett, N.J., Roth, R., Klain, S.C., Chan, K., Christie, P., Clark, D.A., Cullman, G., Curran, D., Durbin, T.J., Epstein, G., Greenberg, A., Nelson, M.P., Sandlos, J., Stedman, R., Teel, T.L., Thomas, R., Veríssimo, D., Wyborn, C., 2017. Conservation social science: Understanding and integrating human dimensions to improve conservation. Biol. Conserv. 205, 93–108.
Berg, K.A., 2001. Historical attitudes and images and the implications on carnivore survival. Endanger. Species Updat. 18, 186–189.
Berger, K.M., 2006. Carnivore-livestock conflicts: Effects of subsidized predator control and economic correlates on the sheep industry. Conserv. Biol. 20, 751–761.
Berger, W.H., Parker, F.L., 1970. Diversity of Planktonic Foraminifera in Deep-Sea Sediments. Science (80-.). 168, 1345–1347.
Bergman, D.L., De Waal, H.O., Avenant, N.L., Bodenchuk, M., Marlow, M.C., 2013. The Need to Address Black-backed Jackal and Caracal Predation in South Africa, in: Armstrong, J., Gallagher, G. (Eds.), 15th Wildlife Damage Management Conferences-Proceedings. DigitalCommons@University of Nebraska, Lincoln, Nebraska, pp. 86–94.
Berkes, F., Folke, C., Colding, J., 1998. Linking social and ecological systems : management practices and social mechanisms for building resilience. Cambridge University Press, Cambridge, UK.
Bernard, R.T.F., Stuart, C.T., 1987. Reproduction of the caracal Felis caracal from the Cape Province of South Africa. South African J. Zool. 22, 177–182.
Berny, P., 2007. Pesticides and the intoxication of wild animals. J. Vet. Pharmacol. Ther. 30, 93–100.
Bigalke, R., Rowe-Rowe, D., 1969. An analysis of the results of hunting black-backed jackals over a five year period in Natal. Lammergeyer 10, 70–80.

Bingham, J., Purchase, G. k, 2002. Reproduction in the jackals Canis adustus Sundevall, 1846, and Canis mesomelas Schreber, 1778 (Carnivora: Canidae), in Zimbabwe. African Zool. 37, 21–26.

Bjerke, T., Ødegårdstuen, T.S., Kaltenborn, B.P., 1998. Attitudes toward animals among Norwegian children and adolescents: Species preferences. Anthrozoos 11, 227–235.

Blanco, J.C., Reig, S., de la Cuesta, L., 1992. Distribution, status and conservation problems of the wolf Canis lupus in Spain. Biol. Conserv. 60, 73–80.

Blaum, N., Rossmanith, E., Popp, A., Jeltsch, F., 2007. Shrub encroachment affects mammalian carnivore abundance and species richness in semiarid rangelands. Acta Oecologica 31, 86–92.

Blejwas, K.M., Sacks, B.N., Jaeger, M.M., McCullough, D.R., 2002. The Effectiveness of Selective Removal of Breeding Coyotes in Reducing Sheep Predation. J. Wildl. Manage. 66, 451.

Blejwas, K.M., Williams, C.L., Shin, G.T., McCullough, D.R., Jaeger, M.M., 2006. Salivary DNA evidence convicts breeding male coyotes of killing sheep. Wildl. Manag. 70, 1087–1093.

Blom, A., Van Zalinge, R., Mbea, E., Heitkönig, I.M.A., Prins, H.H.T., 2004. Human impact on wildlife populations within a protected Central African forest. Afr. J. Ecol. 42, 23–31.

Boast, L., Houser, A.M., Horgan, J., Reeves, H., Phale, P., Klein, R., 2016. Prey preferences of free-ranging cheetahs on farmland: scat analysis versus farmers' perceptions. Afr. J. Ecol. 54, 424–433.

Bond, I., Child, B., de la Harpe, D., Jones, B., Barnes, J., Anderson, H., 2004. Private land contribution to conservation in South Africa, in: Child, B. (Ed.), Parks in Transition: "Biodiversity, Rural Development and the Bottom Line." Earthscan Publications, London, pp. 29–62.

Bongaarts, J., 1996. Population Pressure and the Food Supply System in the Developing World. Popul. Dev. Rev. 22, 483.

Bonkoungou, E.G., 2001. Biodiversity in Drylands : Challenges and Opportunities for Conservation and Sustainable Use, The Global Drylands Initiative. Nairobi, Kenya.

Boshoff, A., Landman, M., Kerley, G., 2016. Filling the gaps on the maps: Historical distribution patterns of some larger mammals in part of southern Africa. Trans. R. Soc. South Africa 71, 23–87.

Bothma, J. d. P., 2012. Literature review of the ecology and control of the black-backed jackal and caracal in South Africa. An independent review commissioned by

CapeNature.

Bothma, J. d. P., 1966. Notes on the stomach contents of certain Carnivora (Mammalia) from the Gemsbok National Park. Koedoe 9, 37–39.

Bothma, J. du P., Walker, C., 1999. The caracal, in: Larger Carnivores of the African Savannas. Springer, Berlin, Heidelberg, pp. 117–129.

Bothma, J.D.P., 1971a. Control and ecology of the black-backed jackal Canis mesomelas in the Transvaal. Zool. Africana 6, 187–193.

Bothma, J.D.P., 1971b. Food of Canis mesomelas in South Africa. Zool. africana 6, 195–203.

Bothma, J.D.P., Nel, J.A.J., Macdonald, A., 1984. Food niche separation between four sympatric Namib Desert carnivores. J. Zool. 202, 327–340.

Bothma, J.P., le Riche, E., 1994. Range use by an adult male caracal in the southern Kalahari. Koedoe 37, 105–108.

Boutin, S., 1992. Predation and Moose Population Dynamics: A Critique. J. Wildl. Manage. 56, 116.

Bowland, J.M., Bowland, A.E., 1991. Differential passage rates of prey components through the gut of serval Felis serval and black-backed jackal Canis mesomelas. Koedoe 34, 37–39.

Braczkowski, A., Watson, L., Coulson, D., Lucas, J., Peiser, B., Rossi, M., 2012a. The diet of caracal, Caracal caracal , in two areas of the southern Cape, South Africa as determined by scat analysis. South African J. Wildl. Res. 42, 111–116.

Braczkowski, A., Watson, L., Coulson, D., Randall, R., 2012b. Diet of leopards in the southern Cape, South Africa. Afr. J. Ecol. 50, 377–380.

Brand, M., Schutte-Vlok, A., Huisamen, J., 2018. Anysberg Nature Reserve and World Heritage Site. Protected Area Management Plan 2018-2028. Cape Town.

Brandon, K., Redford, K.H., Sanderson, S.E., 2001. Parks in Peril: People, Politics, and Protected Areas. The Nature Conservancy, Washington DC.

Brashares, J.S., 2003. Ecological, behavioral, and life-history correlates of mammal extinctions in West Africa. Conserv. Biol. 17, 733–743.

Brassine, M.C., Parker, D.M., 2012. Does the presence of large predators affect the diet of a mesopredator? Afr. J. Ecol. 50, 243–246.

Breitenmoser-Wursten, C., Henschel, P., Sogbohossou, E., 2008. Caracal caracal [WWW Document]. IUCN Red List Threat. Species. URL http://www.iucnredlist.org/details/3847/0 (accessed 2.26.16).

Breitenmoser, U., 1998. Large predators in the Alps: the fall and rise of man's competitors.

Biol. Conserv. 83, 279–289.
Breuer, T., 2005. Diet choice of large carnivores in northern Cameroon. Afr. J. Ecol. 43, 97–106.
Broman, D.J.A., Litvaitis, J.A., Ellingwood, M., Tate, P., Reed, G.C., 2014. Modeling Bobcat Lynx rufus Habitat Associations Using Telemetry Locations and Citizen-Scientist Observations: Are the Results Comparable? Wildlife Biol. 20, 229–237.
Broom, D.M., 2010. Animal Welfare: An Aspect of Care, Sustainability, and Food Quality Required by the Public. J. Vet. Med. Educ. 37, 83–88.
Bruskotter, J.T., Singh, A., Fulton, D.C., Slagle, K., 2015. Assessing Tolerance for Wildlife: Clarifying Relations Between Concepts and Measures. Hum. Dimens. Wildl. 20, 255–270.
Bruskotter, J.T., Wilson, R.S., 2014. Determining where the wild things will be: Using psychological theory to find tolerance for large carnivores. Conserv. Lett. 7, 158–165.
Brussaard, L., Caron, P., Campbell, B., Lipper, L., Mainka, S., Rabbinge, R., Babin, D., Pulleman, M., 2010. Reconciling biodiversity conservation and food security: Scientific challenges for a new agriculture. Curr. Opin. Environ. Sustain. 2, 34–42.
Bryer, J., Speerschneider, K., Bryer, M., 2016. Package “likert”. R package version 1.3.5. Reference manual. (No. 1.3.5). CRAN.
Burnham, K.P., Anderson, D.R., 2004. Multimodel inference: Understanding AIC and BIC in model selection. Sociol. Methods Res. 33, 261–304.
Burnham, K.P., Overton, W.S., 1979. Robust Estimation of Population Size When Capture Probabilities Vary Among Animals. Ecology 60, 927–936.
Butchart, S.H.M., Scharlemann, J.P.W., Evans, M.I., Quader, S., Aricò, S., Arinaitwe, J., Balman, M., Bennun, L.A., Bertzky, B., Besançon, C., Boucher, T.M., Brooks, T.M., Burfield, I.J., Burgess, N.D., Chan, S., Clay, R.P., Crosby, M.J., Davidson, N.C., de Silva, N., Devenish, C., Dutson, G.C.L., Fernández, D.F.D., Fishpool, L.D.C., Fitzgerald, C., Foster, M., Heath, M.F., Hockings, M., Hoffmann, M., Knox, D., Larsen, F.W., Lamoreux, J.F., Loucks, C., May, I., Millett, J., Molloy, D., Morling, P., Parr, M., Ricketts, T.H., Seddon, N., Skolnik, B., Stuart, S.N., Upgren, A., Woodley, S., 2012. Protecting important sites for biodiversity contributes to meeting global conservation targets. PLoS One 7, e32529.
Butler, J.R.A., 2000. The economic costs of wildlife predation on livestock in Gokwe communal land, Zimbabwe. Afr. J. Ecol. 38, 23–30.
Campbell, I., 2007. Chi-squared and Fisher-Irwin tests of two-by-two tables with small

sample recommendations. Stat. Med. 26, 3661–3675.
CapeNature, 2016. CapeNature's Biodiversity Stewardship programme [WWW Document]. URL http://www.capenature.co.za/care-for-nature/stewardship/ (accessed 1.24.18).
Capitani, C., Bertelli, I., Varuzza, P., Scandura, M., Apollonio, M., 2004. A comparative analysis of wolf (Canis lupus) diet in three different Italian ecosystems. Mamm. Biol. 69, 1–10.
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., Macdounal, D.W., Martyr, D., McDougal, C., Nath, L., O'Brien, T., Seidensticker, J., Smith, D.J.L., Sunquist, M., Tilson, R., Wan Shahruddin, W.N., 2001. The use of photographic rates to estimate densities of tigers and other cryptic mammals. Anim. Conserv. 4, 75–79.
Carbone, C., Gittleman, J.L., 2002. A common rule for the scaling of carnivore density. Science (80-.). 295, 2273–2276.
Carbone, C., Teacher, A., Rowcliffe, J.M., 2007. The costs of carnivory. PLoS Biol. 5, e22.
Cardillo, M., 2003. Biological determinants of extinction risk: Why are smaller species less vulnerable? Anim. Conserv. 6, 63–69.
Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Bininda-Emonds, O.R.P., Sechrest, W., Orme, C.D.L., Purvis, A., 2005. Evolution: Multiple causes of high extinction risk in large mammal species. Science (80-.). 309, 1239–1241.
Carey, C., Dudley, N., Stolton, S., 2000. Squandering paradise? The importance and vulnerability of the world's protected areas. WWF - World Wide Fund For Nature, Gland, Switzerland.
Carl, G.R., Robbins, C.T., 1988. The energetic cost of predator avoidance in neonatal ungulates: hiding versus following. Can. J. Zool. 66, 239–246.
Caro, T.M., 1999. Densities of mammals in partially protected areas: The Katavi ecosystem of western Tanzania. J. Appl. Ecol. 36, 205–217.
Caro, T.M., 1994. Cheetahs of the Serengeti Plains: group living in an asocial species. University of Chicago Press, Chicago.
Caro, T.M., Stoner, C.J., 2003. The potential for interspecific competition among African carnivores. Biol. Conserv. 110, 67–75.
Carrillo, E., Wong, G., Cuarón, A.D., 2008. Monitoring Mammal Populations in Costa Rican Protected Areas under Different Hunting Restrictions. Conserv. Biol. 14, 1580–1591.
Carroll, C., Noss, R.F., Paquet, P.C., 2001. Carnivores as focal species for conservation planning in the rocky mountain region. Ecol. Appl. 11, 961–980.

Carvalho, J.C., Gomes, P., 2004. Feeding resource partitioning among four sympatric carnivores in the Peneda-Gerês National Park (Portugal). J. Zool. 263, 275–283.
Carvalho, J.C., Gomes, P., 2001. Food habits and trophic niche overlap of the red fox, European wild cat and common genet in the Peneda-Gerês National Park. Galemys 13, 39–48.
Casey, A.L., Krausman, P.R., Shaw, W.W., Shaw, H.G., 2005. Knowledge of and attitudes toward mountain lions: A public survey of residents adjacent to saguaro national park, arizona. Hum. Dimens. Wildl. 10, 29–38.
Cavalcanti, S.M.C., Gese, E.M., 2010. Kill rates and predation patterns of jaguars (Panthera onca) in the southern Pantanal, Brazil. J. Mammal. 91, 722–736.
Cavallini, P., Volpi, T., 1996. Variation in the diet of the red fox in a Mediterranean area. Rev. d'écologie 51.
Ceríaco, L.M.P., 2012. Human attitudes towards herpetofauna: The influence of folklore and negative values on the conservation of amphibians and reptiles in Portugal. J. Ethnobiol. Ethnomed. 8, 8.
Chakrabarti, S., Jhala, Y. V, Dutta, S., Qureshi, Q., Kadivar, R.F., Rana, V.J., 2016. Adding constraints to predation through allometric relation of scats to consumption. J. Anim. Ecol. 85, 660–670.
Chame, M., 2003. Terrestrial Mammal Feces: A Morphometric Summary and Description. Mem. Inst. Oswaldo Cruz 98, 71–94.
Chao, A., Chazdon, R.L., Colwell, R.K., Shen, T.-J., 2004. A new statistical approach for assessing similarity of species composition with incidence and abundance data. Ecol. Lett. 8, 148–159.
Chape, S., Harrison, J., Spalding, M., Lysenko, I., 2005. Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets, in: Philosophical Transactions of the Royal Society B: Biological Sciences. pp. 443–455.
Chen, Y., Gillieson, D., 2009. Evaluation of landsat TM vegetation indices for estimating vegetation cover on semi-arid rangelands: A case study from Australia. Can. J. Remote Sens. 35, 435–446.
Child, M., Roxburgh, L., Do Linh San, E., Raimondo, D., Davies - Mostert, H., 2016. The Red List of Mammals of South Africa, Swaziland and Lesotho.
Chowdhury, N., Jadhav, S., 2012. Eco-psychiatry: Culture, Mental Health and Ecology with Special Reference to India, in: Chavan, B., Gupta, N., Arun, P., Sidana, A., Jadhav, S. (Eds.), Community Health in India. Jaypee Brothers India, pp. 521–542.

Ćirović, D., Penezić, A., Krofel, M., 2016. Jackals as cleaners: Ecosystem services provided by a mesocarnivore in human-dominated landscapes. Biol. Conserv. 199, 51–55.

Ciucci, P., Boitani, L., 1973. Wolf and Dog Depredation on Livestock in Central Italy. Source Wildl. Soc. Bull. 26, 504–514.

Claeskens, G., Hjort, N.L., 2008. Model Selection and Model Averaging. Cambridge University Press, Cambridge.

Clinchy, M., Sheriff, M.J., Zanette, L.Y., 2013. Predator-induced stress and the ecology of fear. Funct. Ecol. 27, 56–65.

Cloete, S.W.P., Olivier, J.J., 2010. South African industry, in: Cottle, D. (Ed.), The International Sheep and Wool Handbook. Nottingham University Press, Nottingham, pp. 95–110.

Coates Palgrave, M., Coates Palgrave, K., 2002. Trees of southern Africa, edn 3. ed. Random House Struik (Pty) Ltd, Cape Town.

Colman, N.J., Gordon, C.E., Crowther, M.S., Letnic, M., 2014. Lethal control of an apex predator has unintended cascading effects on forest mammal assemblages. Proceedings. Biol. Sci. 281, 20133094. https://doi.org/10.1098/rspb.2013.3094

Colwell, R.K., Mao, C.X., Chang, J., 2004. Interpolating, Extrapolating, and Comparing Incidence-Based Species Accumulation Curves. Ecology 85, 2717–2727.

Colyn, R.B., Radloff, F.G.T., O'Riain, M.J., 2018. Camera trapping mammals in the scrubland's of the Cape Floristic Kingdom—the importance of effort, spacing and trap placement. Biodivers. Conserv. 27, 503–520.

Connell, J.H., 1978. Diversity in Tropical Rain Forests and Coral Reefs. Science (80-.). 199, 1302–1310.

Connolly, G.E., Timm, R.M., Howard, W.E., Longhurst, W.M., 1976. Sheep Killing Behavior in Captive Coyotes. J. Wildl. Manage. 40, 400–407.

Conradie, B., 2012. Are hunting clubs the solution to small stock depredation ? The case of Ceres , 1979 and 1980. Agrekon 37–41.

Conradie, B., Landman, A., 2015. Wool versus mutton in extensive grazing areas. South African J. Agric. Extention 43, 22–31.

Conradie, B., Nattrass, N., 2017. The robustness of self-report data on predation: A comparison of two Karoo surveys. African J. Agric. Resour. Econ. 12, 217–229.

Conradie, B., Piesse, J., 2016. Ranking perceived risk to farmers: How important is the environment ? African J. Agric. Resour. Econ. 11, 263–276.

Conradie, B., Piesse, J., 2013. The Effect of Predator Culling on Livestock Losses: Ceres,

South Africa, 1979-1987. African J. Agric. Resour. Econ. 8, 19.
Conradie, B., Piesse, J., Piesse, J., 2015. Productivity benchmarking of free-range sheep operations for Laingsburg, South Africa. Agrekon 54, 1–17.
Conradie, B., Piesse, J., Thirtle, C., 2009. District-level total factor productivity in agriculture: Western Cape Province, South Africa, 1952-2002. Agric. Econ. 40, 265–280.
Conradie, B., Piesse, J., Vink, N., Winter, K., 2002. Explaining declining agricultural total factor productivity in the Karoo districts of the Western Cape, 1952 to 2002. Agrekon 1–23.
Constant, N.L., Bell, S., Hill, R.A., 2015. The impacts, characterisation and management of human–leopard conflict in a multi-use land system in South Africa. Biodivers. Conserv. 24, 2967–2989.
Convention on Biological Diversity-Republic of South Africa, 2014. South Africa's fifth annual report, Convention on Biological Diversity.
Courchamp, F., Langlais, M., Sugihara, G., 1999. Cats protecting birds: Modelling the mesopredator release effect. J. Anim. Ecol. 68, 282–292.
Cowling, R.M., 1986. Description of the Karoo Biome project. National Scientific Programmes Unit: CSIR, SANSP Report 122.
Cowling, R.M., Pressey, R.L., Lombard, A.T., Desmet, P.G., Ellis, A.G., 1999. From representation to persistence: Requirements for a sustainable system of conservation areas in the species-rich mediterranean-climate desert of southern Africa. Divers. Distrib. 5, 51–71.
Cowling, R.M., Richardson, D.M., 1995. Fynbos: South Africa's unique floral kingdom. Fernwood Press, Cape Town.
Cozza, K., Fico, R., Battistini, M.L., Rogers, E., 1996. The damage-conservation interface illustrated by predation on domestic livestock in central Italy. Biol. Conserv. 78, 329–336.
Creel, S., Christianson, D., 2008. Relationships between direct predation and risk effects. Trends Ecol. Evol. 23, 194–201.
Cromsigt, J.P.G.M., Prins, H.H.T., Olff, H., 2009. Habitat heterogeneity as a driver of ungulate diversity and distribution patterns : Interaction of body mass and digestive strategy. Divers. Distrib. 15, 513–522.
Crooks, K.R., 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. Conserv. Biol. 16, 488–502.
Crooks, K.R., Soulé, M.E., 1999. Mesopredator release and avifaunal extinctions in a

fragmented system. Nature 400, 563–566.
Cupples, J.B., Crowther, M.S., Story, G., Letnic, M., 2011. Dietary overlap and prey selectivity among sympatric carnivores: could dingoes suppress foxes through competition for prey? J. Mammal. 92, 590–600.
Cusack, J.J., Dickman, A.J., Rowcliffe, J.M., Carbone, C., Macdonald, D.W., Coulson, T., 2015. Random versus game trail-based camera trap placement strategy for monitoring terrestrial mammal communities. PLoS One 10, e0126373.
Dale, B.W., Adams, L.G., Bowyer, R.T., 1994. Functional Response of Wolves Preying on Barren-Ground Caribou in a Multiple-Prey Ecosystem. J. Anim. Ecol. 63, 644.
Dar, N.I., Minhas, R.A., Zaman, Q., Linkie, M., 2009. Predicting the patterns, perceptions and causes of human-carnivore conflict in and around Machiara National Park, Pakistan. Biol. Conserv. 142, 2076–2082.
Darkoh, M.B.K., 2003. Regional perspectives on agriculture and biodiversity in the drylands of Africa. J. Arid Environ. 54, 261–279.
Davenport, M.A., Nielsen, C.K., Mangun, J.C., 2010. Attitudes toward mountain lion management in the Midwest: Implications for a potentially recolonizing large predator. Hum. Dimens. Wildl. 15, 373–388.
Davies, J., 2017. The land in drylands: Thriving in uncertainty through diversity, Global Land Outlook Working Paper.
Davies, J., Poulsen, L., Schulte-Herbrüggen, B., Mackinnon, K., Crawhall, N., Henwood, W.D., Dudley, N., Smith, J., Gudka, M., 2012. Conserving dryland biodiversity. International Union for Conservation of Nature and Natural Resources, United Nations Environment Programme- World Conservation Monitoring Programme (UNEP-WCMC), and United Nations Convention to Combat Desertification (UNCCD), Nairobi, Kenya.
Davies, R., 1997. Caracal, in: Mills, M.G.L., Hes, L. (Eds.), The Complete Book of Southern African Mammals. Struik, Cape Town, South Africa, pp. 186–187.
Davies, R.A.G., 1999. The extent, cost and control of livestock predation by eagles with a case study on black eagles (Aquila verreauxii) in the Karoo. J. Raptor Res. 33, 67–72.
de Beer, E.., 2010. Sustainable Mohair Industry Production Guidelines: Pre-Farm Gate.
De Jongh, M., 2002. No fixed abode: The poorest of the poor and elusive identities in rural South Africa. J. South. Afr. Stud. 28, 441–460.
de Waal, H.O., 2017. Demography and morphometry of black-backed jackals Canis mesomelas in South Africa and Namibia. Bloemfontein.

Dean, R.J., Milton, S.J., 1999. The Karoo: Ecological Patterns and Processes. Cambridge University Press, Cambridge.

Dean, W.R.J., Hoffinan, M.T., Meadows, M.. E., Milton, S.J., 1995. Desertification in the semi-arid Karoo, South Africa: Review and reassessment. J. Arid Environ. 30, 247–264.

Decker, D., Lipscomb, J., 1991. Toward an organizational philosophy about integrating biological and human dimensions in management (No. 1), Human Dimensions Perspective Series, 1. Denver, Colorado.

Decker, D., Purdy, K., 1988. Toward a concept of wildlife acceptance. Wildl. Soc. Bull. 16, 53–57.

Decker, D.J., Chase, L.C., 1997. Human Dimensions of Living with Wildlife: A Management Challenge for the 21st Century. Source Wildl. Soc. Bull. 25, 788–795.

Delahay, R.J., Cheeseman, C.L., Clifton-Hadley, R.S., 2001. Wildlife disease reservoirs: The epidemiology of Mycobacterium bovis infection in the Eeuropean badger (Meles meles) and other British mammals, in: Tuberculosis. pp. 43–49.

Delibes, M., Gaona, P., Ferreras, P., 2001. Effects of an Attractive Sink Leading into Maladaptive Habitat Selection. Am. Nat. 158, 277–285.

Demma, D.J., Barber-Meyer, S.M., Mech, L.D., 2007. Testing Global Positioning System Telemetry to Study Wolf Predation on Deer Fawns. J. Wildl. Manage. 71, 2767–2775.

Department of Agriculture Forestry and Fisheries, 2012. A profile of the South African mutton market value chain. Pretoria, South Africa.

Department of Labour, 2002. Basic Conditions of Employment Act, no 75 of 1997. Department of Labour, Pretoria, South Africa.

Desmet, P.G., Cowling, R.M., 1999. The climate of the Karoo – a functional approach, in: Dean, W.R.J., Milton, S.J. (Eds.), The Karoo – Ecological Processes and Patterns. Cambridge University Press, Cambridge, pp. 3–16.

DeVault, T.L., Rhodes, O.E., Shivik, J.A., 2003. Scavenging by vertebrates: Behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. Oikos.

Dickman, A.J., 2010. Complexities of conflict: The importance of considering social factors for effectively resolving human-wildlife conflict. Anim. Conserv. 13, 458–466.

Didan, K., 2015. MOD13Q1 MODIS/Terra Vegetation Indices 16-Day L3 Global 250m SIN Grid V006 [Data set].

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.

Do Linh San, E., Malongwe, N.B., Fike, B., Somers, M.J., Walters, M., 2009. Autumn diet of black-backed jackals (Canis Mesomelas) in the thicket biome of South Africa. Wildl. Biol. Pract. 5, 96–103.

Doherty, T.S., Ritchie, E.G., 2017. Stop Jumping the Gun: A Call for Evidence-Based Invasive Predator Management. Conserv. Lett. 10, 15–22.

Donadio, E., Buskirk, S.W., 2006. Diet, Morphology, and Interspecific Killing in Carnivora. Am. Nat. 167, 524–536.

Dorazio, R.M., Royle, J.A., Söderström, B., Glimskär, A., 2006. Estimating species richness and accumulation by modeling species occurrence and detectability. Ecology 87, 842–54.

Douglas, R.M., 1989. A new method of cross-sectioning hair of larger mammals. S. Afr. J. Wildl. Res./S.-Afr. Tydskr. Natuurnavors 19, 73–76.

Drouilly, M., Clark, A., O'Riain, M.J., 2018a. Multi-species occupancy modelling of mammal and ground bird communities in rangeland in the Karoo: A case for dryland systems globally. Biol. Conserv. 224, 16–25.

Drouilly, M., Clark, A., O'Riain, M.J., 2018b. Dietary niche relationships among predators on farmland and a protected area. J. Wildl. Manage. 82, 507–518.

Drouilly, M., Tafani, M., Nattrass, N., O'Riain, J., 2018c. Spatial, temporal and attitudinal dimensions of conflict between predators and small-livestock farmers in the Central Karoo. African J. Range Forage Sci. Karoo Spec. Issue Trajectories Chang. Anthr. 35, 245–255.

Drury, R., Homewood, K., Randall, S., 2011. Less is more: The potential of qualitative approaches in conservation research. Anim. Conserv. 14, 18–24.

Du Plessis, J.J., Avenant, N.L., Botha, A., Mkhize, N.R., Müller, L., Mzileni, N., O'Riain, M.J., Parker, D.M., Potgieter, G., Richardson, P.R.K., Rode, S., Viljoen, N., Hawkins, H.-J., Tafani, M., 2018. Past and current management of predation on livestock, in: Kerley, G.I.H., Wilson, S.L., Balfour, D. (Eds.), Livestock Predation and Its Management in South Africa: A Scientific Assessment. Centre for African Conservation Ecology, Nelson Mandela University, Port Elizabeth, pp. 125–177.

Du Plessis, J.J., Avenant, N.L., De Waal, H.O., 2015. Quality and quantity of the scientific information available on black-backed jackals and caracals : contributing to human – predator conflict management ? South African J. Wildl. Res. 45, 138–157.

Du Toit, A., 1926. Geology of South Africa. Olivier and Boyd Limited, Edinburgh, Scotland.

Du Toit, J.T., Cumming, D.H.M., 1999. Functional significance of ungulate diversity in

African savannas and the ecological implications of the spread of pastoralism. Biodivers. Conserv. 8, 1643–1661.
Dudley, N., 2008. Guidelines for Applying Protected Area Management Categories. Gland, Switzerland.
Duncan, C., Nilsen, E.B., Linnell, J.D.C., Pettorelli, N., 2015. Life-history attributes and resource dynamics determine intraspecific home-range sizes in Carnivora. Remote Sens. Ecol. Conserv. 1, 39–50.
Eason, C.T., Spurr, E.B., 1995. Review of the toxicity and impacts of brodifacoum on non-target wildlife in new zealand. New Zeal. J. Zool. 22, 371–379.
Eberhardt, A.L.L., Garrott, R.A., Smith, D.W., White, P.J., Peterson, R.O., 2009. Assessing the Impact of Wolves on Ungulate Prey Published by : Ecological Society of America. Ecol. Appl. 13, 776–783.
Eklund, A., López-Bao, J.V., Tourani, M., Chapron, G., Frank, J., 2017. Limited evidence on the effectiveness of interventions to reduce livestock predation by large carnivores. Sci. Rep. 7, 1–9.
Ericsson, G., Heberlein, T.A., 2003. Attitudes of hunters, locals, and the general public in Sweden now that the wolves are back. Biol. Conserv. 111, 149–159.
Esterhuizen, W.C.N., Norton, P.M., 1985. The leopard as a problem animal in the Cape Province, as determined by the permit system. Bontebok 4, 9–16.
Estes, R., 1991. The behavior guide to African mammals : including hoofed mammals, carnivores, primates, A Wake Forest studium book. University of California Press.
Fabbri, E., Caniglia, R., Kusak, J., Galov, A., Gomerčić, T., Arbanasić, H., Huber, D., Randi, E., 2014. Genetic structure of expanding wolf (Canis lupus) populations in Italy and Croatia, and the early steps of the recolonization of the Eastern Alps. Mamm. Biol. 79, 138–148.
Fabricius, C., Burger, M., Hockey, P.A.R., 2003. Comparing biodiversity between protected areas and adjacent rangeland in xeric succulent thicket, South Africa: Arthropods and reptiles. J. Appl. Ecol. 40, 392–403.
Falcucci, A., Maiorano, L., Tempio, G., Boitani, L., Ciucci, P., 2013. Modeling the potential distribution for a range-expanding species: Wolf recolonization of the Alpine range. Biol. Conserv. 158, 63–72.
Fall, M.W., Jackson, W.B., 2002. The tools and techniques of wildlife damage management - Changing needs: An introduction. Int. Biodeterior. Biodegrad. 49, 87–91.
Fanshawe, J.H., Frame, L.H., Ginsberg, J.R., 1991. The wild dog—Africa's vanishing

carnivore. Oryx 25, 137–146.

Farhadinia, M.S., Akbari, H., Beheshti, M., Sadeghi, A., 2007. Ecology and status of the Caracal, Caracal caracal, (Carnivora: Felidae), in the Abbasabad Naein Reserve, Iran. Zool. Middle East 41, 5–10.

Farhadinia, M.S., Nezami, B., Hosseini-Zavarei, F., Valizadeh, M., 2009. Persistence of Persian leopard in a buffer habitat in north- eastern Iran. Cat News 51, 34–36.

Farias, A.A., Kittlein, M.J., 2008. Small-scale spatial variability in the diet of pampas foxes (Pseudalopex gymnocercus) and human-induced changes in prey base. Ecol. Res. 23, 543–550.

Fedriani, J.M., Fuller, T.K., Sauvajot, R.M., York, E.C., 2000. Competition and intraguild predation among three sympatric carnivores. Oecologia 125, 258–270.

Fedriani, J.M., Palomares, F., Delibes, M., 1999. Niche relations among three sympatric Mediterranean carnivores. Oecologia 121, 138–148.

Ferguson, J.W.H., Galpin, J.., de Wet, M.J., 1988. Factors affecting the activity patterns of black-backed jackals Canis mesomelas. J. Zool. 214, 55–69.

Ferguson, J.W.H., Nel, J.A.J., De Wet, M.J., 1983. Social organization and movement patterns of Black-backed jackals Canis mesomelas in South Africa. J. Zool. 199, 487–502.

Fishbein, M., Ajzen, I., 2010. Predicting and changing behavior: The reasoned action approach. Psychology Press, New York.

Fleishman, E., McDonal, N., Mac Nally, R., Murphy, D.D., Walters, J., Floyd, T., 2003. Effects of floristics, physiognomy and non-native vegetation on riparian bird communities in a Mojave Desert watershed. J. Anim. Ecol. 72, 484–490.

Floyd, T.J., Mech, L.D., Jordan, P.A., 1978. Relating Wolf Scat Content to Prey Consumed. J. Wildl. Manage. 42, 528.

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., Holling, C.S., 2004. Regime Shifts, Resilience, and Biodiversity in Ecosystem Management. Annu. Rev. Ecol. Evol. Syst. 35, 557–581.

Forbes, R., 2012. 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. Rhodes University.

Forman, D.W., 2005. An assessment of the local impact of native predators on an established population of British water voles (Arvicola terrestris). J. Zool. 266, 221–226.

Fox, J., Weisberg, S., 2011. Multivariate linear models in R. An R Companion to Applied

Regression. SAGE publications, Inc., Los Angeles.
Fox, J.L., Chundawat, R.S., 1988. Observations of snow leopard stalking, killing, and feeding behavior. Mammalia 52, 137–140.
Fox, J.W., 2013. The intermediate disturbance hypothesis should be abandoned. Trends Ecol. Evol. 28, 86–92.
Franke, A., Caelli, T., Kuzyk, G., Hudson, R.J., 2006. Prediction of wolf (Canis lupus) kill-sites using hidden Markov models. Ecol. Modell. 197, 237–246.
Fritts, S.H., Paul, W.J., Mech, L.D., Scott, D.P., 1992. Trends and management of wolf-livestock conflicts in Minnesota. Washington, D.C.
Fuller, T., Sievert, P., 2001. Carnivore demography and the consequences of changes in prey availability. Carniv. Conserv. 163–179.
Fuller, T.K., Biknevicius, a R., Kat, P.W., Van Valkenburgh, B., Wayne, R.K., 1989. The ecology of three sympatric jackal species in the Rift Valley of Kenya. Afr. J. Ecol. 27, 313–323.
Gallo, J. a., Pasquini, L., Reyers, B., Cowling, R.M., 2009. The role of private conservation areas in biodiversity representation and target achievement within the Little Karoo region, South Africa. Biol. Conserv. 142, 446–454.
Gáspero, P.G., Easdale, M.H., Pereira, J.A., Fernández-Arhex, V., Von Thüngen, J., 2018. Human-carnivore interaction in a context of socio-productive crisis: Assessing smallholder strategies for reducing predation in North-west Patagonia, Argentina. J. Arid Environ. 150, 92–98.
Gastón, A., Blázquez-Cabrera, S., Garrote, G., Mateo-Sánchez, M.C., Beier, P., Simón, M.A., Saura, S., 2016. Response to agriculture by a woodland species depends on cover type and behavioural state: insights from resident and dispersing Iberian lynx. J. Appl. Ecol. 53, 814–824.
Gehrt, S.D., Brown, J.L., Anchor, C., 2011. Is the urban coyote a misantrhopic synanthrope? The case from Chicago. Cities Environ. 4, 3.
Geldmann, J., Barnes, M., Coad, L., Craigie, I.D., Hockings, M., Burgess, N.D., 2013. Effectiveness of terrestrial protected areas in reducing habitat loss and population declines. Biol. Conserv. 161, 230–238.
Gelman, A., Carlin, J.B., Stern, H.S., Dunson, D., Vehtari, A., Rubin, D.B., 2004. Bayesian Data Analysis, third edit. ed. CRC Press, Boca Raton, FL.
Giorgi, M., Mengozzi, G., 2011. Malicious animal intoxications: Poisoned baits. Vet. Med. (Praha). 56, 173–179.

Glen, A.S., Dickman, C.R., 2014. Carnivores of Australia : past, present and future. CSIRO Publishing, Collinwood, Australia.

Glen, A.S., Gentle, M.N., Dickman, C.R., 2007. Non-target impacts of poison baiting for predator control in Australia. Mamm. Rev. 37, 191–205.

Glennon, M.J., Didier, K.A., 2010. A general model for site-based conservation in human-dominated landscapes: The landscape species approach, in: Landscape-Scale Conservation Planning. Springer, Dordrecht, Netherlands, pp. 369–392.

Głowaciński, Z., Profus, P., 1997. Potential impact of wolves Canis lupus on prey populations in eastern Poland. Biol. Conserv. 80, 99–106.

Goldenberg, M., Goldenberg, F., Funk, S.M., Henschel, J., Millesi, E., 2010. Diet composition of black-backed jackals, canis mesomelas in the Namib Desert. Folia Zool. 59, 93–101.

Gordon, I.J., Hester, A.J., Festa-Bianchet, M., 2004. The management of wild large herbivores to meet economic, conservation and environmental objectives. J. Appl. Ecol. 41, 1021–1031.

Gore, M.L., Kahler, J.S., 2012. Gendered risk perceptions associated with human-wildlife conflict: Implications for participatory conservation. PLoS One 7, e32901.

Goszczyński, J., 1974. Studies on the food of foxes. Acta Theriol. (Warsz). 19, 1–18.

Gotelli, N., Colwell, R., 2011. Estimating species richness. Biol. Divers. Front. Meas. Assess. 12, 39–54.

Grafton, R.N., 1965. Food of the black-backed jackal: a preliminary report. Zool. Africana 1, 41–53.

Graham, K., Beckerman, A.P., Thirgood, S., 2005. Human–predator–prey conflicts: ecological correlates, prey losses and patterns of management. Biol. Conserv. 122, 159–171.

Green, R.E., 2005. Farming and the Fate of Wild Nature. Science (80-.). 307, 550–555.

Green, R.E., Newton, I., Shultz, S., Cunningham, A.A., Gilbert, M., Pain, D.J., Prakash, V., 2004. Diclofenac poisoning as a cause of vulture population declines across the Indian subcontinent. J. Appl. Ecol. 41, 793–800.

Grobler, J.H., 1981. Feeding behaviour of the caracal Felis caracal Schreber 1776 in the Mountain Zebra National Park. South African J. Zool. 16, 259–262.

Groves, C., Kutner, R.L.S., Stoms, D.M., Murray, M.P., Scott, J.M., Schafale, M., Weakley, A.S., Pressey., R.L., 2000. Owning up to our responsibilities: who owns lands important for biodiversity, in: Stein, B., Kutner, L.S., Adams, J.S. (Eds.), Precious Heritage: The

Status of Biodiversity of the United States. Oxford University Press, New York, USA, pp. 275–300.
Gunnthorsdottir, A., 2001. Physical attractiveness of an animal species as a decision factor for its preservation. Anthrozoos 14, 204–214.
Gusset, M., Swarner, M.J., Mponwane, L., Keletile, K., McNutt, J.W., 2009. Human-wildlife conflict in northern Botswana: Livestock predation by endangered African wild dog lycaon pictus and other carnivores. Oryx 43, 67–72.
Hails, R.S., 2002. Assessing the risks associated with new agricultural practices. Nature 418, 685–688.
Haines, A.M., Janecka, J.E., Tewes, M.E., Grassman, L.I., Morton, P., 2006. The importance of private lands for ocelot Leopardus pardalis conservation in the United States. Oryx 40, 90–94.
Hall-Martin, A.., Botha, B.P., 1980. A note on feeding habits, ectoparasites and measurements of the Black-Backed Jackal Canis mesomelas from Addo Elephant National Park. Koedoe 23, 157–162.
Hall, C., McVittie, A., Moran, D., 2004. What does the public want from agriculture and the countryside? A review of evidence and methods. J. Rural Stud. 20, 211–225.
Harmsen, B.J., Foster, R.J., Silver, S., Ostro, L., Doncaster, C.P., 2010. Differential use of trails by forest mammals and the implications for camera-trap studies: A case study from Belize. Biotropica 42, 126–133.
Harris, S., 1981. An estimation of the number of foxes (Vulpes vulpes) in the city of Bristol, and some possible factors affecting their distribution. J. Appl. Ecol. 18, 455–465.
Harvey, C.A., Komar, O., Chazdon, R., Ferguson, B.G., Finegan, B., Griffith, D.M., Martínez-Ramos, M., Morales, H., Nigh, R., Soto-Pinto, L., Van Breugel, M., Wishnie, M., 2008. Integrating agricultural landscapes with biodiversity conservation in the Mesoamerican hotspot. Conserv. Biol. 22, 8–15.
Hayward, M.W., Hayward, G.J., 2010. Potential amplification of territorial advertisement markings by black-backed jackals (Canis mesomelas). Behaviour 147, 979–992.
Hayward, M.W., Henschel, P., O'Brien, J., Hofmeyr, M., Balme, G., Kerley, G.I.H., 2006. Prey preferences of the leopard (Panthera pardus). J. Zool. 270, 298–313.
Hayward, M.W., Jedrzejewski, W., Jedrzewska, B., 2012. Prey preferences of the tiger Panthera tigris. J. Zool. 286, 221–231.
Hayward, M.W., Kerley, G.I.H., 2008. Prey preferences and dietary overlap amongst Africa's large predators. South African J. Wildl. Res. 38, 93–108.

Hayward, M.W., Kerley, G.I.H., 2005. Prey preferences of the lion (Panthera leo). J. Zool. 267, 309–322.

Hayward, M.W., Marlow, N., 2014. Will dingoes really conserve wildlife and can our methods tell? J. Appl. Ecol. 51, 835–838.

Hayward, M.W., Porter, L., Lanszki, J., Kamler, J.F., Beck, J.M., Kerley, G.I.H., Macdonald, D.W., Montgomery, R.A., Parker, D.M., Scott, D.M., O'Brien, J., Yarnell, R.W., 2017. Factors affecting the prey preferences of jackals (Canidae). Mamm. Biol. 85, 70–82.

Hazzah, L., Borgerhoff Mulder, M., Frank, L., 2009. Lions and Warriors: Social factors underlying declining African lion populations and the effect of incentive-based management in Kenya. Biol. Conserv. 142, 2428–2437.

Hebblewhite, M., Merrill, E.H., McDonald, T.L., 2005. Spatial decomposition of predation risk using resource selection functions: an example in a wolf-elk predator-prey system. Oikos 111, 101–111.

Hebblewhite, M., Percy, M., Merrill, E.H., 2007. Are All Global Positioning System Collars Created Equal? Correcting Habitat-Induced Bias Using Three Brands in the Central Canadian Rockies. J. Wildl. Manage. 71, 2026–2033.

Heberlein, T.A., 2013. Navigating Environmental Attitudes. Navig. Environ. Attitudes 26, 1–240.

Henne, D.R., 1975. Domestic sheep mortality on a western Montana ranch. University of Montana.

Herbst, M., Mills, M.G.L., 2010. The feeding habits of the southern african wildcat, a facultative trophic specialist, in the Southern Kalahari (Kgalagadi Transfrontier Park, South Africa/Botswana). J. Zool. 280, 403–413.

Herrmann, T.M., Schüttler, E., Benavides, P., Gálvez, N., Söhn, L., Palomo, N., 2013. Values, animal symbolism, and human-animal relationships associated to two threatened felids in Mapuche and Chilean local narratives. J. Ethnobiol. Ethnomed. 9, 41.

Hey, D., 1967. Recent developments in the control of vertebrate problem animals in the province of the Cape of Good Hope, Republic of South Africa. Paper 30., in: Proceedings of the 3rd Vertebrate Pest Conference. DigitalCommons@University of Nebraska, Lincoln, Nebraska, pp. 158–164.

Hey, D., 1964. The control of vertebrate problem animals in the Cape of Good Hope Republic of South Africa. Paper 11., in: Proceedings of the 2nd Vertebrate Pest Conference. at DigitalCommon s@University of Nebraska - Lincoln, Lincoln, Nebraska, pp. 57–70.

Heydon, M.J., Reynolds, J.C., 2000. Fox (Vulpes vulpes) management in three contrasting

regions of Britain, in relation to agricultural and sporting interests. J. Zool. 251, 237–252.
Hilton-Taylor, C., 1996. Patterns and characteristics of the flora of the Succulent Karoo Biome, southern Africa, in: van der Maesen, L., van der Burgt, X., van Medenbach de Rooy, J. (Eds.), Proceedings of the XIVth Congress of the “Association Pour l’Etude Taxonomique de La Flore d’Afrique Tropicale” (AETFAT) - The Biodiversity of African Plants. Kluwer Academic Publishers, Dordrecht, Netherlands, pp. 58–72.
Hilty, J.A., Brooks, C., Heaton, E., Merenlender, A.M., 2006. Forecasting the effect of land-use change on native and non-native mammalian predator distributions. Biodivers. Conserv. 15, 2853–2871.
Hiscocks, K., Perrin, M.R., 1988. Home range and movements of black-backed jackals at Cape Cross Seal Reserve, Namibia. South African J. Wildl. Res. 18, 97–100.
Hiscocks, K., Perrin, M.R., 1987. Feeding observations and diet of black-backed jackals in an arid coastal environment. South African J. Wildl. Res. 17, 55–58.
Hoffman, M.T., Cousins, B., Meyer, T., Petersen, A., Hendricks, H., 1999. Historical and contemporary land use and the desertification of the Karoo, in: Dean, D.J., Milton, S.J. (Eds.), The Karoo: Ecological Patterns and Processes. Cambridge University Press, Cambridge, UK, pp. 257–273.
Hoffmann, A., Zeller, U., 2005. Influence of variations in land use intensity on species diversity and abundance of small mammals in the Nama Karoo, Namibia. Belgian J. Zool. 135, 91–96.
Holekamp, K.E., Smale, L., Berg, R., Cooper, S.M., 1997. Hunting rates and hunting success in the spotted hyena (Crocuta crocuta). J. Zool. 242, 1–15.
Holling, C.S., Allen, C.R., 2002. Adaptive inference for distinguishing credible from incredible petterns in nature. Ecosystems 5, 319-328.
Holmern, T., Nyahongo, J., Røskaft, E., 2007. Livestock loss caused by predators outside the Serengeti National Park, Tanzania. Biol. Conserv. 135, 518–526.
Holmes, J., 2006. Impulses towards a multifunctional transition in rural Australia: Gaps in the research agenda. J. Rural Stud. 22, 142–160.
Homewood, K., Lewis, J., 1987. Impact of Drought on Pastoral Livestock in Baringo, Kenya 1983-85. J. Appl. Ecol. 24, 615.
Hone, J., 2007. Wildlife damage control. CSIRO Publishing: Collingwood, Victoria.
Hoogesteijn, R., Hoogesteijn, A., Mondolfi, E., 1993. Jaguar predation and conservation: cattle mortality caused by felines on three ranches in the Venezuelan Llanos. Symp.

Zool. Soc. London 65, 391–407.
Hoogland, J.L., 2006. Conservation of the black-tailed prairie dog. Island Press, Washington, DC.
Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecol. Monogr. 75, 3–35.
Horstman, L., Gunson, J., 1982. Black bear predation on livestock in Alberta. Wildl. Soc. Bull. 10, 34–39.
Hosseini-Zavarei, F., Farhadinia, M.S., Beheshti-Zavareh, M., Abdoli, A., 2013. Predation by grey wolf on wild ungulates and livestock in central Iran. J. Zool. 290, 127–134.
Howley, P., Yadav, L., Hynes, S., Donoghue, C.O., Neill, S.O., 2014. Contrasting the attitudes of farmers and the general public regarding the “multifunctional” role of the agricultural sector. Land use policy 38, 248–256.
Hsieh, T.C., Ma, K.H., Chao, A., 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods Ecol. Evol. 7, 1451–1456.
Hu, B., Shao, J., Palta, M., 2006. Pseudo-R^2 In Logisitc Regression Model. Stat. Sin. 16, 847–860.
Huete, A.R., Jackson, R.D., 1988. Soil and atmosphere influences on the spectra of partial canopies. Remote Sens. Environ. 25, 89–105.
Humphries, B.D., Hill, T.R., Downs, C.T., 2015a. Landowners’ perspectives of black-backed jackals (Canis mesomelas) on farmlands in KwaZulu-Natal, South Africa. Afr. J. Ecol. 53, 540–549.
Humphries, B.D., Ramesh, T., Downs, C.T., 2015b. Diet of black-backed jackals (Canis mesomelas) on farmlands in the KwaZulu-Natal Midlands, South Africa. Mammalia 80, 405–412.
Humphries, B.D., Ramesh, T., Hill, T.R., Downs, C.T., 2016. Habitat use and home range of black-backed jackals (Canis mesomelas) on farmlands in the Midlands of KwaZulu-Natal, South Africa. African Zool. 51, 1–9.
Hunter, M.L., Yonzon, P., 2013. Altitudinal Distributions of Birds, Mammals, People, Forests and Parks in Nepal. Conserv. Biol. 7, 420–423.
Husseman, J.S., Murray, D.L., Power, G., Mack, C., Wenger, C.R., Quigley, H., 2003. Assessing Differential Prey Selection Patterns between Two Sympatric Large Carnivores Assessing differential prey selection between two patterns sympatric large carnivores.

Oikos 101, 591–601.
Huston, M., 1979. A General Hypothesis of Species Diversity. Am. Nat. 113, 81–101.
Ilvkhulhv, I., 2016. Trends in the Agricultural Sector 2015. Pretoria.
Ingle, M., 2010. Making the most of “nothing”: astro-tourism, the Sublime, and the Karoo as a “space” destination’. Transform. Crit. Perspect. South. Africa 74, 87–111.
Inskip, C., Carter, N., Riley, S., Roberts, T., MacMillan, D., 2016. Toward human-carnivore coexistence: Understanding tolerance for tigers in Bangladesh. PLoS One 11, e0145913.
Inskip, C., Zimmermann, A., 2009. Human-felid conflict: a review of patterns and priorities worldwide. Oryx 43, 18.
Jaccard, P., 1912. The distribution of the flore of the alpine zone. New Phytol. 11, 37–50.
Jacobs, J., 1974. Quantitative measurement of food selection - A modification of the forage ratio and Ivlev’s electivity index. Oecologia 14, 413–417.
Jacoby, P.W., 1989. A Glossary of terms used in range management : a definition of terms commonly used in range management.
Jadhav, S., Barua, M., 2012. The Elephant Vanishes: Impact of human–elephant conflict on people’s wellbeing. Health Place 18, 1356–1365.
Jędrzejewska, B., Jędrzejewski, W., 1998. Diets and hunting habits of predators, in: Predation in Vertebrate Communities: The Bialowieza Primeval Forest as a Case Study. Springer-Verlag, Berlin Heidelberg, pp. 180–208.
Jenks, K., Chanteap, P., Damrongchainarong, K., Cutter, P., Cutter, P., Redford, T., Lynam, A., Howard, J., Leimgruber, P., 2011. Using relative abundance indices from camera-trapping to test wildlife conservation hypotheses-an example from Khao Yai National Park, Thailand. Trop. Conserv. Sci. 4, 113–131.
Jennelle, C.S., Runge, M.C., MacKenzie, D.I., 2002. The use of photographic rates to estimate densities of tigers and other cryptic mammals: a comment on misleading conclusions. Anim. Conserv. 5, 119–120.
Jenner, N., Groombridge, J., Funk, S.M., 2011. Commuting, territoriality and variation in group and territory size in a black-backed jackal population reliant on a clumped, abundant food resource in Namibia. J. Zool. 284, 231–238.
Jethva, B.D., Jhala, Y. V., 2004. Foraging ecology, economics and conservation of Indian wolves in the Bhal region of Gujarat, Western India. Biol. Conserv. 116, 351–357.
Jetz, W., Carbone, C., Fulford, J., Brown, J.H., 2004. The scaling of animal space use. Science (80-.). 306, 266–268.
Jones, M.E., Barmuta, L.A., 2000. Niche differentiation among sympatric Australian dasyurid

carnivores. J. Mammal. 81, 434–447.
Joppa, L.N., Pfaff, A., 2009. High and far: Biases in the location of protected areas. PLoS One 4, e8273.
Jordaan, J.W., Grobler, H.J.F., 2011. Farmer support and extension to land reform farms in the Central Karoo - part 2: a baseline assessment of farm-level economic viability. South African J. Agric. Ext. 39, 45–54.
Jost, L., 2006. Entropy and diversity. Oikos 113, 363–375.
Joubert, D.F., Ryan, P.G., 1999. Differences in mammal and bird assemblages between commercial and communal rangelands in the Succulent Karoo, South Africa. J. Arid Environ. 43, 287–299.
Kaartinen, S., Luoto, M., Kojola, I., 2009. Carnivore-livestock conflicts: Determinants of wolf (Canis lupus) depredation on sheep farms in Finland. Biodivers. Conserv. 18, 3503–3517.
Kabir, M., Ghoddousi, A., Awan, M.S., Awan, M.N., 2014. Assessment of human-leopard conflict in Machiara National Park, Azad Jammu and Kashmir, Pakistan. Eur. J. Wildl. Res. 60, 291–296.
Kaczensky, P., 1999. Large Carnivore Depredation on Livestock in Europe. Ursus 11, 59–71.
Kaltenborn, B.P., Bjerke, T., Nyahongo, J.W., Williams, D.R., 2006. Animal preferences and acceptability of wildlife management actions around Serengeti National Park, Tanzania. Biodivers. Conserv. 15, 4633–4649.
Kaltenborn, B.P., Bjerke, T., Vitterso, J., 1999. Attitudes toward large carnivores among sheep farmers, wildlife managers, and research biologists in Norway. Hum. Dimens. Wildl. 4, 57–73.
Kamler, J.F., Foght, J.L., Collins, K., 2010. Single black-backed jackal (Canis mesomelas) kills adult impala (Aepyceros melampus). Afr. J. Ecol. 48, 847–848.
Kamler, J.F., Jacobsen, N., Macdonald, D., 2008. Efficiency and safety of Soft Catch traps for capturing black-backed jackals and excluding non-target species. South African J. Wildl. Res. 38, 113–116.
Kamler, J.F., Klare, U., Macdonald, D.W., 2012a. Seasonal diet and prey selection of black-backed jackals on a small-livestock farm in South Africa. Afr. J. Ecol. 50, 299–307.
Kamler, J.F., Stenkewitz, U., Klare, U., Jacobsen, N.F., MacDonald, D.W., 2012b. Resource partitioning among cape foxes, bat-eared foxes, and black-backed jackals in South Africa. J. Wildl. Manage. 76, 1241–1253.
Kansky, R., Kidd, M., Knight, A.T., 2014. Meta-analysis of attitudes toward damage-causing

mammalian wildlife. Conserv. Biol. 28, 924–938.
Kansky, R., Knight, A.T., 2014. Key factors driving attitudes towards large mammals in conflict with humans. Biol. Conserv.
Karanth, K.K., Nichols, J.D., Hines, J.E., Karanth, K.U., Christensen, N.L., 2009. Patterns and determinants of mammal species occurrence in India. J. Appl. Ecol. 46, 1189–1200.
Kauffman, M.J., Sanjayan, M., Lowenstein, J., Nelson, A., Jeo, R.M., Crooks, K.R., 2007a. Remote camera-trap methods and analyses reveal impacts of rangeland management on Namibian carnivore communities. Oryx 41, 70–78.
Kauffman, M.J., Varley, N., Smith, D.W., Stahler, D.R., MacNulty, D.R., Boyce, M.S., 2007b. Landscape heterogeneity shapes predation in a newly restored predator-prey system. Ecol. Lett. 10, 690–700.
Kaunda, S.K.K., 1998. Black backed jackal (Canis mesomelas) predation of impala (Aepyceros melampus) at Mokolodi Nature Reserve, Botswana. University of Pretoria.
Kaunda, S.K.K., Skinner, J.D., 2003. Black-backed jackal diet at Mokolodi Nature Reserve, Botswana. Afr. J. Ecol. 41, 39–46.
Kellerman, T.S., Naudé, T.W., Fourie, N., 1996. The distribution, diagnoses and estimated economic impact of plant poisonings and mycotoxicoses in South Africa. Onderstepoort J. Vet. Res. 63, 65–90.
Kellert, S.R., 1993. Values and Perceptions of Invertebrates. Conserv. Biol. 7, 845–855.
Kellert, S.R., 1985. Public perceptions of predators, particularly the wolf and coyote. Biol. Conserv. 31, 167–189.
Kellert, S.R., Black, M., Rush, C.R., Bath, A.J., 1996. Human Culture and Large Carnivore Conservation in North America. Conserv. Biol. 10, 977–990.
Kellner, K., 2017. jagsUI: A Wrapper Around rjags to Streamline JAGS Analyses. R package version 1.4.9. Reference manual. (No. 1.4.9). CRAN.
Keogh, H.J., 1985. A photographic reference system based on the cuticular scale patterns and groove of the hair of 44 species of southern African Cricetidae and Muridae. South African J. Wildl. Res. 15, 109–159.
Keogh, H.J., 1983. A photographic reference system of the microstructure of the hair of southern African bovids. South African J. Wildl. Res. 13, 89–131.
Kerley, G.I.H., Wilson, S.L., Balfour, D., 2018. Livestock predation and its management in South Africa: a scientific assessment. Centre for African Conservation Ecology, Nelson Mandela University, Port Elizabeth.
Kerley, L.L., Goodrich, J.M., Miquelle, D.G., Smirnov, E.N., Quigley, H.B., Hornocker,

M.G., 2002. Effects of roads and human disturbance on Amur tigers. Conserv. Biol. 16, 97–108.

Kiffner, C., Stoner, C., Caro, T., 2013. Edge effects and large mammal distributions in a national park. Anim. Conserv. 16, 97–107.

Kiffner, C., Wenner, C., Laviolet, A., Yeh, K., Kioko, J., 2015. From savannah to farmland: Effects of land-use on mammal communities in the Tarangire-Manyara ecosystem, Tanzania. Afr. J. Ecol. 53, 156–166.

Kingdon, J., 2015. The Kingdon field guide to African mammals, 2nd editio. ed. Princeton University Press, London.

Kinnaird, M., O'Brien, T.G., 2012. Effects of private-land use, livestock management, and human tolerance on diversity, distribution, and abundance of large african mammals. Conserv. Biol. 26, 1026–1039.

Kissui, B.M., 2008. Livestock predation by lions, leopards, spotted hyenas, and their vulnerability to retaliatory killing in the Maasai steppe, Tanzania. Anim. Conserv. 11, 422–432.

Kitchen, A.M., Gese, E.M., Schauster, E.R., 2000. Changes in coyote activity patterns due to reduced exposure to human persecution. Can. J. Zool. 78, 853–857.

Klare, U., Kamler, J.F., MacDonald, D.W., 2011. A comparison and critique of different scat-analysis methods for determining carnivore diet. Mamm. Rev. 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. J. Wildl. Manage. 74, 1030–1042.

Kluever, B.M., Gese, E.M., 2016. Spatial response of coyotes to removal of water availability at anthropogenic water sites. J. Arid Environ. 130, 68–75.

Knight, A.J., 2008. "Bats, snakes and spiders, Oh my!" How aesthetic and negativistic attitudes, and other concepts predict support for species protection. J. Environ. Psychol. 28, 94–103.

Knight, R.L., 1999. Private lands: The neglected geography. Conserv. Biol. 13, 223–224.

Knopff, K.H., Knopff, A.A., Warren, M.B., Boyce, M.S., 2009. Evaluating Global Positioning System Telemetry Techniques for Estimating Cougar Predation Parameters. J. Wildl. Manage. 73, 586–597.

Knowlton, F.F., Gese, E.M., Jaeger, M.M., 1999. Coyote Depredation Control: An Interface between Biology and Management. J. Range Manag. 52, 398–412.

Kok, O.B., Nel, J.A.J., 2004. Convergence and divergence in prey of sympatric canids and

felids: Opportunism or phylogenetic constraint? Biol. J. Linn. Soc. 83, 527–538.
KPMG Services (Pty) Ltd, 2012. Small Enterprise Development Agency: Research on the performance of the agricultural sector.
Krebs, C.J., 1999. Ecological Methodology, 2nd ed. ed. Addison-Wesley Educational Publishers, Inc., Menlo Park, California.
Krofel, M., 2008. Opportunistic hunting behaviour of black-backed jackals in Namibia. Afr. J. Ecol. 46, 220–222.
Kross, S.M., Ingram, K.P., Long, R.F., Niles, M.T., 2018. Farmer Perceptions and Behaviors Related to Wildlife and On-Farm Conservation Actions. Conserv. Lett. 11, e12364.
Kruuk, H., 1986. Interactions between Felidae and their prey species: a review, in: Douglas, M.S. (Ed.), Cats of the World: Biology Conservation and Management. National Wildlife Federation, Washington, D.C., pp. 353–374.
Kruuk, H., 1972. Surplus killing by carnivores. J. Zool. 166, 233–244.
Kuiper, T.R., Parker, D.M., 2013. Grass height is the determinant of sheep grazing effects on small mammals in a savanna ecosystem. Rangel. J. 35, 403–408.
Kurberg, L., 2005. The effect of grazing on Bat-eared foxes, and how farmers in Namibia perceive the Bat-eared fox. University of Uppsala.
Kurek, P., Holeksa, J., 2015. Grains in the diets of medium-sized carnivores -a case of diplochory? Polish J. Ecol. 63, 286–290.
Laliberté, A.S., Ripple, W.J., 2004. Range Contractions of North American Carnivores and Ungulates. Bioscience 54, 123.
Laliberté, E., Legendre, P., Bill Shipley, 2015. Package “FD”: Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology. R package version 1.0-12. Reference manual.
Lamb, C.T., Mowat, G., McLellan, B.N., Nielsen, S.E., Boutin, S., 2017. Forbidden fruit: human settlement and abundant fruit create an ecological trap for an apex omnivore. J. Anim. Ecol. 86, 55–65.
Lamprecht, J., 1978. Diet, foraging behavior and interspecific food competition of jackals in Serengeti-National-Park, East-Africa. Zeitschrift für Säugetierkd. 43, 210–223.
Lanszki, J., Heltai, M., Szabó, L., 2006. Feeding habits and trophic niche overlap between sympatric golden jackal (Canis aureus) and red fox (Vulpes vulpes) in the Pannonian ecoregion (Hungary). Can. J. Zool. 84, 1647–1656.
Larkin, P.A., 1955. Interspecific Cormpetition and Population Control in Freshwater Fish. J. Fish. Res. Board Canada 13, 327–342.

Larrucea, E.S., Brussard, P.F., Jaeger, M.M., Barrett, R.H., 2007. Cameras, Coyotes, and the Assumption of Equal Detectability. J. Wildl. Manage. 71, 1682–1689.

Larsen, T.H., Williams, N.M., Kremen, C., 2005. Extinction order and altered community structure rapidly disrupt ecosystem functioning. Ecol. Lett. 8, 538–547.

Larue, M.A., Nielsen, C.K., Dowling, M., Miller, K., Wilson, B., Shaw, H., Anderson, C.R., 2012. Cougars are recolonizing the midwest: Analysis of cougar confirmations during 1990-2008. J. Wildl. Manage. 76, 1364–1369.

Lawes, M.J., Kruger, S.C., Maddock, a H., 1999. Diet choice and capture success of wild dog (Lycaon pictus) in Hluhluwe-Umfolozi Park, South Africa. J. Zool. 248, 543–551.

Leeper, T., Arnold, J., Arel-Bundock, V., 2018. Package “margins”: Marginal Effects for Model Objects. R package version 0.3.23. Reference manual.

Leeper, T.J., 2017. Interpreting regression results using average marginal effects with R’s margins. Reference manual.

Legendre, Laliberté, 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91, 299–305.

Lenth, B.E., Knight, R.L., Brennan, M.E., 2008. The Effects of Dogs on Wildlife Communities. Nat. Areas J. 28, 218–227.

Levi, T., Kilpatrick, A.M., Mangel, M., Wilmers, C.C., 2012. Deer, predators, and the emergence of Lyme disease. Proc. Natl. Acad. Sci. 109, 10942–10947.

Levins, R., 1968. Evolution in changing environments: some theoretical explorations. Princeton University Press., Princeton.

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. Biol. Conserv. 125, 113–121.

Lindsey, P.A., Havemann, C.P., Lines, R., Palazy, L., Price, A.E., Retief, T.A., Rhebergen, T., van der Waal, C., 2013. Determinants of Persistence and Tolerance of Carnivores on Namibian Ranches: Implications for Conservation on Southern African Private Lands. PLoS One 8, 1–14.

Lindstedt, S.L., Miller, B.J., Buskirk, S.W., 1986. Home range, time, and body size in mammals. Ecology 67, 413–418.

Link, W.A., Eaton, M.J., 2012. On thinning of chains in MCMC. Methods Ecol. Evol. 3, 112–115.

Linnell, J.D.C., Odden, J., Mertens, A., 2012. Mitigation methods for conflicts associated with carnivore depredation on livestock, in: Boitani, L., Powell, R. (Eds.), Carnivore

Ecology and Conservation. Oxford University Press, Oxford, pp. 314–332.
Linnell, J.D.C., Odden, J., Smith, M.E., Aanes, R., Swenson, J.E., 1999. Large carnivores that kill livestock: do problem animals really exist? Wildl. Soc. Bull. 27, 698–705.
Linnell, J.D.C., Smith, M.E., Odden, J., Kaczensky, P., Swenson, J.E., 1996. Strategies for the reduction of carnivore-livestock conflicts: a review. Nina Oppdragsmeld. 443, 188.
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. Anim. Conserv. 4, 345–349.
Liordos, V., Kontsiotis, V.J., Anastasiadou, M., Karavasias, E., 2017. Effects of attitudes and demography on public support for endangered species conservation. Sci. Total Environ. 595, 25–34.
Liu, A., Wang, J., Liu, Z., Wang, J., 2005. Monitoring desertification in arid and semi-arid areas of China with NOAA-AVHRR and MODIS data, in: International Geoscience and Remote Sensing Symposium (IGARSS). IEEE, Seoul, South Korea, pp. 2362–2364.
Lodé, T., 1993. Diet composition and habitat use of sympatric polecat and American mink in western France. Acta Theriol. (Warsz). 2, 161–166.
Lombaard, L.J., 1971. Age determination and growth curves in the black-backed jackal, Canis mesomelas, Schreber, 1775 (Carnivora: Canidae). Ann. Transvaal Museum 27, 135–181.
Long, R., MacKay, P., Zielinski, W., Ray, J., 2008. Noninvasive Survey Methods for Carnivores. Island Press, Washington DC.
Lovegrove, B., 1993. The living deserts of southern Africa. Fernwood Press, Cape Town.
Loveridge, A., Hemson, G., Davidson, Z., Macdonald, D., 2010. African lions on the edge: reserve boundaries as ‘attractive sinks,’ in: Loveridge, A.J., Macdonald, D.W. (Eds.), Biology and Conservation of Wild Felids. Oxford University Press, Oxford, pp. 283–304.
Loveridge, A.J., Macdonald, D.W., 2003. Niche separation in sympatric jackals (Canis mesomelas and Canis adustus). J. Zool. 259, 143–153.
Loveridge, A.J., Macdonald, D.W., 2002. Habitat ecology of two sympatric species of jackals in Zimbabwe. J. Mammal. 83, 599–607.
Loveridge, A.J., Nel, J.A.J., 2004. Black-backed jackal (Canis mesomelas), in: Sillero-Zubiri, C., Hoffmann, M., Macdonald, D.W. (Eds.), Canids: Foxes, Wolves, Jackals and Dogs Status Survey and Conservation Action Plan. IUCN/SSC Canid Specialist Group, Gland, Switzerland, pp. 161–166.
Loveridge, A.J., Wang, S.W., Frank, L.G., Seidensticker, J., 2010. People and wild felids:

conservation of cats and management of conflicts, in: Macdonald, D.W., Loveridge, A.J. (Eds.), Biology and Conservation of Wild Felids. Oxford University Press, New York, pp. 161–195.

Lucherini, M., Merino, M.J., 2008. Perceptions of Human–Carnivore Conflicts in the High Andes of Argentina. Mt. Res. Dev. 28, 81–85.

Lyngdoh, S., Gopi, G.V., Selvan, K.M., Habib, B., 2014. Effect of interactions among ethnic communities, livestock and wild dogs (Cuon alpinus) in Arunachal Pradesh, India. Eur. J. Wildl. Res. 60, 771–780.

Macdonald, D., 2001. Postscript - carnivore conservation: science, compromise and tough choices, in: Gittleman, J., Funk, S., Macdonald, D., Wayne, R. (Eds.), Carnivore Conservation. Cambridge Univ Press, Cambridge, UK, pp. 524–538.

Macdonald, D., Loveridge, A., 2010. Biology and conservation of wild felids. Oxford University Press, New York, USA.

Macdonald, D., Sillero-Zubiri, C., 2004. Biology and Conservation of Wild Canids. Oxford University Press, New York, USA.

Macdonald, D.W., 1976. Food Caching by Red Foxes and Some Other Carnivores. Z. Tierpsychol. 42, 170–185.

MacKenzie, D.I., Bailey, L.L., 2004. Assessing the fit of site-occupancy models. J. Agric. Biol. Environ. Stat. 9, 300–318.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, A.A., Langtimm, C.A., 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83, 2248–2255.

Mackenzie, D.I., Royle, J.A., 2005. Designing occupancy studies: general advice and allocating survey effort. J. Appl. Ecol. 42, 1105–1114.

Madden, F., 2004. Creating Coexistence between Humans and Wildlife: Global Perspectives on Local Efforts to Address Human–Wildlife Conflict. Hum. Dimens. Wildl. 9, 247–257.

Maestas, J.D., Knight, R.L., Gilgert, W.C., 2003. Biodiversity across a Rural Land-Use Gradient. Conserv. Biol. 17, 1425–1434.

Maestre, F.T., Quero, J.L., Gotelli, N.J., Escudero, A., Ochoa, V., Delgado-Baquerizo, M., García-Gómez, M., Bowker, M.A., Soliveres, S., Escolar, C., García-Palacios, P., Berdugo, M., Valencia, E., Gozalo, B., Gallardo, A., Aguilera, L., Arredondo, T., Blones, J., Boeken, B., Bran, D., Conceição, A.A., Cabrera, O., Chaieb, M., Derak, M., Eldridge, D.J., Espinosa, C.I., Florentino, A., Gaitán, J., Gabriel Gatica, M., Ghiloufi, W., Gómez-González, S., Gutiérrez, J.R., Hernández, R.M., Huang, X., Huber-Sannwald, E., Jankju, M., Miriti, M., Monerris, J., Mau, R.L., Morici, E., Naseri, K., Ospina, A., Polo, V., Prina, A., Pucheta, E., Ramírez-Collantes, D.A., Romão, R., Tighe, M., Torres-Díaz, C., Val, J., Veiga, J.P., Wang, D., Zaady, E., 2012. Plant species richness and ecosystem multifunctionality in global drylands. Science (80-.). 335, 214–218.

Maitima, J.M., Mugatha, S.M., Reid, R.S., Gachimbi, L.N., Majule, A., Lyaruu, H., Pomery, D., Mathai, S., Mugisha, S., 2009. The linkages between land use change, land degradation and biodiversity across East Africa. African J. Environ. Sci. Technol. 3, 310–325.

Majić, A., Bath, A.J., 2010. Changes in attitudes toward wolves in Croatia. Biol. Conserv. 143, 255–260.

Manfredo, M., Vaske, J., Sikorowski, L., 1996. Human dimensions of wildlife management, in: Ewert, A. (Ed.), Natural Resource Management: The Human Dimension. Westview Press, Inc, Boulder, Colorado, pp. 53–72.

Manfredo, M.J., 2015. Essays on Human–Wildlife Conflict 10 Years After the Durban World Parks Congress: An Introduction. Hum. Dimens. Wildl. 20, 285–288.

Manfredo, M.J., Zinn, H.C., 1996. Population change and its implications for wildlife management in the New West: A case study of Colorado. Hum. Dimens. Wildl. 1, 62–74.

Mann, G., 2014. The ecology of leopards (Panthera pardus) in the Little Karoo, South Africa. Rhodes University.

Mann, G.K.H., O'Riain, M.J., Parker, D.M., 2015. The road less travelled: assessing variation in mammal detection probabilities with camera traps in a semi-arid biodiversity hotspot. Biodivers. Conserv. 24, 531–545.

Marchini, S., 2014. Who's in conflict with whom? Human dimensions of the conflicts involving wildlife, in: Applied Ecology and Human Dimensions in Biological Conservation. Springer, Berlin, Heidelberg, pp. 189–209.

Marchini, S., Macdonald, D.W., 2012. Predicting ranchers' intention to kill jaguars: Case studies in Amazonia and Pantanal. Biol. Conserv. 147, 213–221.

Marker, L., Dickman, A., 2005. Notes on the spatial ecology of caracals (Felis caracal), with particular reference to Namibian farmlands. Afr. J. Ecol. 43, 73–76.

Marker, L.L., Mills, M.G.L., Macdonald, D.W., 2003. Factors Influencing Perceptions of Conflict and Tolerance toward Cheetahs on Namibian Farmlands. Conserv. Biol. 17,

1290–1298.
Márquez, C., Vargas, J.M., Villafuerte, R., Fa, J.E., 2013. Understanding the propensity of wild predators to illegal poison baiting. Anim. Conserv. 16, 118–129.
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. J. Zool. 283, 81–87.
Mateo-Tomás, P., Olea, P.P., Sánchez-Barbudo, I.S., Mateo, R., 2012. Alleviating human-wildlife conflicts: Identifying the causes and mapping the risk of illegal poisoning of wild fauna. J. Appl. Ecol. 49, 376–385.
Mattson, D.J., Clark, S.G., 2010. People, Politics, and Cougar Management, in: Hornocker, M.G., Negri, S. (Eds.), Cougar : Ecology and Conservation. University of Chicago Press, Chicago, p. 306.
Mazzolli, M., Graipel, M.E., Dunstone, N., 2002. Mountain lion depredation in southern Brazil. Biol. Conserv. 105, 43–51.
McCann, K., Theron, L.J., Morrison, K., 2007. Conservation priorities for the Blue Crane (Anthropoides paradiseus) in South Africa - The effects of habitat changes on distribution and numbers. Ostrich 78, 205–211.
McDonald, J.E.J., Fuller, T.K., 2005. Effects of spring acorn availability on black bear diet, milk composition, and cub survival. J. Mammology 86, 1022–1028.
McGranahan, C., 2015. What is Ethnography? Teaching ethnographic sensibilities without fieldwork. Journal 4, 23–36.
McLeod, L.J., Saunders, G.R., McLeod, S.R., Dawson, M., Van De Ven, R., 2010. The potential for participatory landscape management to reduce the impact of the red fox (Vulpes vulpes) on lamb production. Wildl. Res. 37, 695–701.
McManus, J.S., Dickman, A.J., Gaynor, D., Smuts, B.H., Macdonald, D.W., 2014. Dead or alive? Comparing costs and benefits of lethal and non-lethal human–wildlife conflict mitigation on livestock farms. Oryx 49, 1–9.
Mcnaughton, S.J., Georgiadis, N.J., 1986. Ecology of African Grazing and Browsing Mammals. Annu. Rev. Ecol. Syst. 17, 39–65.
Meek, P.D., Ballard, G., Claridge, A., Kays, R., Moseby, K., O'Brien, T., O'Connell, A., Sanderson, J., Swann, D.E., Tobler, M., Townsend, S., 2014. Recommended guiding principles for reporting on camera trapping research. Biodivers. Conserv. 23, 2321–2343.
Melville, H., Bothma, J., Mills, M., 2004. Prey selection by caracal in the Kgalagadi

Transfrontier Park. South African J. Wildl. Res. 34, 67–75.
Mendelssohn, H., 1962. Mass destruction of bird-life owing to secondary poisoning from insecticides and rodenticides. Atl. Nat. 17, 247–248.
Meriggi, A., Brangi, A., Matteucci, C., Sacchi, O., 1996. The feeding habits of wolves in relation to large prey availability in northern Italy. Ecography (Cop.). 19, 287–295.
Messier, F., Crête, M., 1985. Moose-wolf dynamics and the natural regulation of moose populations. Oecologia 65, 503–512.
Meyer, N.F.V., Esser, H.J., Moreno, R., van Langevelde, F., Liefting, Y., Ros Oller, D., Vogels, C.B.F., Carver, A.D., Nielsen, C.K., Jansen, P.A., 2015. An assessment of the terrestrial mammal communities in forests of Central Panama, using camera-trap surveys. J. Nat. Conserv. 26, 28–35.
Middleton, N., Stringer, L., Goudie, A., Thomas, D.S.G., 2011. The Forgotten Billion: MDG achievement in the drylands. New York, USA.
Miller, J.R.B., Jhala, Y. V., Jena, J., 2016. Livestock losses and hotspots of attack from tigers and leopards in Kanha Tiger Reserve, Central India. Reg. Environ. Chang. 16, 17–29.
Mills, G., Hex, L., 1997. The complete book of southern African mammals. Struik Publishers, Cape Town, South Africa.
Mills, M., Shenk, T.M., 1992. Predator-Prey Relationships: The Impact of Lion Predation on Wildebeest and Zebra Populations. J. Anim. Ecol. 61, 693.
Minnie, L., 2016. Effects of lethal management on black-backed jackal population structure and source-sink dynamics. Nelson Mandela Metropolitan University.
Minnie, L., Avenant, N., Kamler, J., Butler, H., Parker, D., Drouilly, M., du Plessis, J., Do Linh San, E., 2016a. A conservation assessment of Canis mesomelas, in: Child, M., Roxburgh, L., Do Linh San, E., Raimondo, D., Davies - Mostert, H. (Eds.), The Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.
Minnie, L., Avenant, N.L., Drouilly, M., Samuels, I., 2018a. Biology and ecology of the black-backed jackal and caracal, in: Kerley, G.I.H., Wilson, S.L., Balfour, D. (Eds.), Livestock Predation and Its Management in South Africa: A Scientific Assessment. Centre for African Conservation Ecology, Nelson Mandela University, Port Elizabeth, pp. 178–204.
Minnie, L., Gaylard, A., Kerley, G.I.H., 2016b. Compensatory life-history responses of a mesopredator may undermine carnivore management efforts. J. Appl. Ecol. 53, 379–387.
Minnie, L., Zalewski, A., Zalewska, H., Kerley, G.I.H., 2018b. Spatial variation in

anthropogenic mortality induces a source–sink system in a hunted mesopredator. Oecologia 186, 939–951.

Mishra, C., 1997. Livestock depredation by large carnivores in the Indian trans-Himalaya: Conflict perceptions and conservation prospects. Environ. Conserv. 24, 338–343.

Mishra, C., Allen, P., McCarthy, T., Madhusudan, M.D., Bayarjargal, A., Prins, H.H.T., 2003. The Role of Incentive Programs in Conserving the Snow Leopard. Conserv. Biol. 17, 1512–1520.

Mitchley, J., Price, M.F., Tzanopoulos, J., 2006. Integrated futures for Europe's mountain regions: Reconciling biodiversity conservation and human livelihoods. J. Mt. Sci. 3, 276–286.

Mittermeier, R.A., Robles, P., Hoffmann, M., Pilgrim, J., Brooks, T., Goettsch, C., Lamoreux, J., Seligmann, P.P.A., 2005. Hotspots Revisited : Earth ' s Biologically Richest and Most Endangered Terrestrial Ecoregions, 2nd editio. ed. Cemex, Sierra Madre.

Moehlman, P.D., 1987. Social organization in jackals. Am. Sci. 75, 366–375.

Moehlman, P.D., 1983. Socioecology of silverbacked and golden jackals (Canis mesomelas and Canis aureus). Adv. study Mamm. Behav. 7, 423–453.

Moehlman, P.D., 1979. Jackal helpers and pup survival. Nature 277, 382–383.

Montag, J., 2003. Compensation and predator conservation: limitations of compensation. Carniv. Damage Prev. News 2–6.

Moore, J.H., Sittimongkol, S., Campos-Arceiz, A., Sumpah, T., Eichhorn, M.P., 2016. Fruit gardens enhance mammal diversity and biomass in a Southeast Asian rainforest. Biol. Conserv. 194, 132–138.

Morehouse, A.T., Boyce, M.S., 2011. From venison to beef: Seasonal changes in wolf diet composition in a livestock grazing landscape. Front. Ecol. Environ. 9, 440–445.

Moreira-Arce, D., Ugarte, C.S., Zorondo-Rodríguez, F., Simonetti, J.A., 2018. Management Tools to Reduce Carnivore-Livestock Conflicts: Current Gap and Future Challenges, in: Rangeland Ecology & Management. Elsevier, pp. 389–394.

Msuha, M.J., Carbone, C., Pettorelli, N., Durant, S.M., 2012. Conserving biodiversity in a changing world: land use change and species richness in northern Tanzania. Biodivers. Conserv. 21, 2747–2759.

Mueller, T., Olson, K.A., Fuller, T.K., Schaller, G.B., Murray, M.G., Leimgruber, P., 2008. In search of forage: Predicting dynamic habitats of Mongolian gazelles using satellite-based estimates of vegetation productivity. J. Appl. Ecol. 45, 649–658.

Mukherjee, S., Goyal, S.P., Johnsingh, A.J.T., Pitman, M.R.P.L., 2004. The importance of rodents in the diet of jungle cat (Felis chaus), caracal (Caracal caracal) and golden jackal (Canis aureus) in Sariska Tiger Reserve, Rajasthan, India. J. Zool. 262, 405–411.

Müller, D.K., 2002. Reinventing the Countryside: German Second-home Owners in Southern Sweden. Curr. Issues Tour. 5, 426–446.

Muriuki, M.W., Ipara, H., Kiringe, J.W., 2017. The cost of livestock lost to lions and other wildlife species in the Amboseli ecosystem, Kenya. Eur. J. Wildl. Res. 63, 60.

Murray, M.H., St. Clair, C.C., 2015. Individual flexibility in nocturnal activity reduces risk of road mortality for an urban carnivore. Behav. Ecol. 26, 1520–1527.

Myers, N., Kent, J., 2003. New consumers: The influence of affluence on the environment. Proc. Natl. Acad. Sci. U. S. A. 100, 4963–8.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–8.

Nagendra, H., 2008. Do Parks Work? Impact of Protected Areas on Land Cover Clearing. AMBIO A J. Hum. Environ. 37, 330–337.

Nattrass, N., Conradie, B., 2018. Predators, livestock losses and poison in the South African Karoo. J. Clean. Prod. 194, 777–785.

Nattrass, N., Conradie, B., 2015. Jackal Narratives and Predator Control in the Karoo, South Africa. J. South. Afr. Stud. 41, 753–771.

Nattrass, N., Conradie, B., Conradie, I., 2015. The Koup Fencing Project: Community-led job creation in the Karoo. African J. Agric. Resour. Econ. Vol. 10, 131–145.

Nattrass, N., Conradie, B., Drouilly, M., O 'Riain, M.J., 2017. A brief history of predators, sheep farmers and government in the Western Cape, South Africa, CSSR Working paper No 398. Cape Town, South Africa.

Naughton-Treves, L., Grossberg, R., Treves, A., 2003. Paying for tolerance: The impact of livestock depredation and compensation payments on rural citizens' attitudes toward wolves. Conserv. Biol. 17, 1500–1511.

Naughton-Treves, L., Treves, A., 2005. Evaluating lethal control in the management of human-wildlife conflict, in: Woodroffe, R., Thirgood, S., Rabinowitz, A. (Eds.), People and Wildlife: Conflict or Coexistence? Cambridge University Press, New York, USA, pp. 86–106.

Nel, E., Hill, T., 2008. Marginalisation and demographic change in the semi-arid Karoo, South Africa. J. Arid Environ. 72, 2264–2274.

Nel, J.A.J., Loutit, R., Bothma, J.P., 1997. Prey used by black-backed jackals along a desert coast. South African J. Wildl. Res. 27, 100–104.

Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennett, D.J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L.K., Alhusseini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D.L.P., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R.P., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M., Mace, G.M., Scharlemann, J.P.W., Purvis, A., 2015. Global effects of land use on local terrestrial biodiversity. Nature 520, 45–50.

Newcomb, T.M., 1950. Social Psychology. Holt, Rinehart, and Winston Inc., New York.

Newing, H., 2010. Conducting research in conservation: Social science methods and practice. Routledge, Oxon, UK.

Newsome, A., 1990. The control of vertebrate pests by vertebrate predators. Trends Ecol. Evol. 5, 187–191.

Nie, M.A., 2002. Wolf Recovery and Management as Value-based Political Conflict. Ethics, Place Environ. 5, 65–71.

Niemeijer, D., Puigdefabregas, J., White, R., Lal, R., Winslow, M., Ziedler, J., Prince, S., Archer, E., King, C., Shapiro, B., Wessels, K., Nielsen, T., Portnov, B., Reshef, I., Thonell, J., Lachman, E., Mcnab, D., 2005. Dryland Systems, in: Hassan, R., Scholes, R., Neville, A. (Eds.), Ecosystems and Human Well-Being: Current State and Trends. Island Press, Washington DC, pp. 623–662.

Niemiec, R.M., Pech, R.P., Norbury, G.L., Byrom, A.E., 2017. Landowners' Perspectives on Coordinated, Landscape-Level Invasive Species Control: The Role of Social and Ecological Context. Environ. Manage. 59, 477–489.

Nkedianye, D., de Leeuw, J., Ogutu, J.O., Said, M.Y., Saidimu, T.L., Kifugo, S.C., Kaelo, D.S., Reid, R.S., 2011. Mobility and livestock mortality in communally used pastoral areas: the impact of the 2005-2006 drought on livestock mortality in Maasailand. Pastoralism 1, 17.

Norton, D.A., 2000. Conservation Biology and Private Land: Shifting the Focus. Conserv. Biol. 14, 1221–1223.

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 J. Wildl. Res. 16, 47–52.

Novaro, A.J., 1995. Sustainability of Harvest of Culpeo Foxes in Patagonia. Oryx 29, 18–22.

Novaro, A.J., Funes, M.C., Jiménez, J.E., 2004. Patagonian foxes: Selection for introduced prey and conservation of culpeo and chilla foxes in Patagonia, in: Biology and Conservation of Wild Canids. Oxford University Press, New York, USA, pp. 243–254.

Noy-Meir, I., 1973. Desert ecosystems: environment and producers. Annu. Rev. Ecol. Syst. 4, 25–51.

Ntemiri, K., Saravia, V., Angelidis, C., Baxevani, K., Probonas, M., Kret, E., Mertzanis, Y., Iliopoulos, Y., Georgiadis, L., Skartsi, D., Vavylis, D., Manolopoulos, A., Michalopoulou, P., Xirouchakis, S.M., 2018. Animal mortality and illegal poison bait use in Greece. Environ. Monit. Assess. 190, 488.

O'Brien, T.G., Baillie, J.E.M., Krueger, L., Cuke, M., 2010. The wildlife picture index: Monitoring top trophic levels. Anim. Conserv. 13, 335–343.

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. Anim. Conserv. 6, 131–139.

O'Connell, A., Nichols, J., Ullas Karanth, K., 2011. Camera Traps in Animal Ecology: Methods and Analyses. Springer, Tokyo, Japan.

Oates, J.F., 1999. Myth and Reality in the Rain Forest: How Conservation Strategies are Failing in West Africa. University of California Press, Berkeley.

Odden, J., Linnell, J.D.C., Andersen, R., 2006. Diet of Eurasian lynx, Lynx lynx, in the boreal forest of southeastern Norway: The relative importance of livestock and hares at low roe deer density. Eur. J. Wildl. Res. 52, 237–244.

Odden, J., Linnell, J.D.C., Moa, P.F., Herfindal, I., Kvam, T., Andersen, R., 2002. Lynx Depredation on Domestic Sheep in Norway. J. Wildl. Manage. 66, 98.

Odling-Smee, L., 2005. Dollars and sense. Nature 437, 614–616.

Ogada, D., Botha, A., Shaw, P., 2016. Ivory poachers and poison: Drivers of Africa's declining vulture populations. Oryx 50, 593–596.

Ogada, D.L., 2014. The power of poison: Pesticide poisoning of Africa's wildlife. Ann. N. Y. Acad. Sci. 1322, 1–20.

Ogada, M.O., Woodroffe, R., Oguge, N.O., Frank, L.G., 2003. Limiting Depredation by African Carnivores: the Role of Livestock Husbandry; Limitando la Depredación de Carnívoros Africanos: el Papel de la Crianza de Ganado. Conserv. Biol. 17, 1521–1530.

Ogutu, J.O., Bhola, N., Reid, R., 2005. The effects of pastoralism and protection on the density and distribution of carnivores and their prey in the Mara ecosystem of Kenya. J. Zool. 265, 281–293.

Ogutu, J.O., Kuloba, B., Piepho, H.P., Kanga, E., 2017. Wildlife population dynamics in

human-dominated landscapes under community-based conservation: The example of Nakuru Wildlife Conservancy, Kenya. PLoS One 12, e0169730.
Oindo, B.O., 2002. Predicting mammal species richness and abundance using multi-temporal NDVI. Photogramm. Eng. Remote Sensing 68, 623–629.
Oindo, B.O., Skidmore, a. K., 2002. Interannual variability of NDVI and species richness in Kenya. Int. J. Remote Sens. 23, 285–298.
Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., Mcglinn, D., Minchin, P.R., O' hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H., Szoecs, E., Wagner, H., 2017. Package "vegan": Community Ecology Package. R package version 2.4-4. Reference manual.
Oli, M.K., Taylor, I.R., Rogers, M.E., 1994. Snow leopard Panthera uncia predation of livestock: An assessment of local perceptions in the Annapurna Conservation Area, Nepal. Biol. Conserv. 68, 63–68.
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. Mamm. Biol. 75, 375–378.
Oosthuizen, W.H., Meÿer, M.A., David, J.H.M., Summers, N.M., Kotze, P.G.H., Swanson, S.W., Shaughnessy, P.D., Meyer, M.A., David, J.H.M., Summers, N.M., Kotze, P.G.H., Swanson, S.W., Shaughnessy, P.D., 1997. Variation in jackal numbers at the Van Reenen Bay seal colony with comments on likely importance of jackals as predators. South African J. Wildl. Res. 27, 26–29.
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 Zool. 42, 31–37.
Owen-Smith, N., Cromsigt, J.P.G.M., Le Roux, E., 2017. Smaller ungulates are first to incur imminent extirpation from an African protected area. Biol. Conserv. 216, 108–114.
Page-Nicholson, S.K., Marnewick, K.A., Beverley, G., Davies-Mostert, H.T., Watermeyer, J.P., Parker, D.M., 2017. Socio-Economic Factors Influencing Attitudes of Landowners Towards Free-Roaming Cheetahs. African J. Wildl. Res. 47, 114–127.
Palmer, A.R., Hoffman, M.T., 1997. Nama Karoo, in: Cowling, R.M., Richardson, D.M., Pierce, S.M. (Eds.), Vegetation of Southern Africa. Cambridge University Press, Cambridge, pp. 167–186.
Palmer, R., Fairall, N., 1988. Caracal and African wild cat diet in the Karoo National Park and the implications thereof for hyrax. South African J. Wildl. Res. 18, 30–34.

Palomares, F., Caro, T.M., 1999. Interspecific Killing among Mammalian Carnivores. Am. Nat. 153, 492–508.

Papworth, S.K., Rist, J., Coad, L., Milner-Gulland, E.J., 2009. Evidence for shifting baseline syndrome in conservation. Conserv. Lett. 2, 93–100.

Parker, D., Watermeyer, J., Davies-Mostert, H., Beverley, G., Marnewick, K., 2018. Attitudes and tolerance of private landowners shape the African wild dog conservation landscape in the greater Kruger National Park. Endanger. Species Res. 36, 173–181.

Parker, D.M., Whittington-Jones, B.M., Bernard, R.T.F., Davies-Mostert, H.T., 2014. Attitudes of Rural Communities Toward Dispersing African Wild Dogs in South Africa. Hum. Dimens. Wildl. 19, 512–522.

Pauly, D., 1995. Anecdotes and the shifting baseline syndrome of fisheries. Trends Ecol. Evol. 10, 430.

Pech, R.P., Jiebu, Arthur, A.D., Yanming, Z., Hui, L., 2007. Population dynamics and responses to management of plateau pikas Ochotona curzoniae. J. Appl. Ecol. 44, 615–624.

Peet, R.K., 1974. The Measurement of Species Diversity. Annu. Rev. Ecol. Syst. 5, 285–307.

Pépin, D., Angibault, J.M., 2007. Selection of resting sites by the European hare as related to habitat characteristics during agricultural changes. Eur. J. Wildl. Res. 53, 183–189.

Perrin, M.R., Campbell, B.S., 1979. Key to the mammals of the Andries Vosloo Kudu Reserve (eastern Cape), based on their hair morphology, for use in predator scat analysis. South African J. Wildl. Res. 10, 1–14.

Petchey, O.L., Gaston, K.J., 2002. Functional diversity (FD), species richness and community composition. Ecol. Lett. 5, 402–411.

Pettorelli, N., 2013. The Normalized Difference Vegetation Index. Oxford University Press, Oxford.

Pettorelli, N., Lobora, A.L., Msuha, M.J., Foley, C., Durant, S.M., 2010. Carnivore biodiversity in Tanzania: revealing the distribution patterns of secretive mammals using camera traps. Anim. Conserv. 13, 131–139.

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. Clim. Res. 46, 15–27.

Pianka, E.R., 1973. The structure of lizard communities. Annu. Rev. Ecol. Syst. 4, 53–74.

Pianka, E.R., 1969. Sympatry of Desert Lizards (Ctenotus) in Western Australia. Ecology 50, 1012–1030.

Pirie, T.J., Thomas, R.L., Fellowes, M.D.E., 2017. Increasing game prices may alter farmers' behaviours towards leopards (Panthera pardus) and other carnivores in South Africa. PeerJ 5, e3369.

Pitman, R.T., Mulvaney, J., Ramsay, P.M., Jooste, E., Swanepoel, L.H., 2014. Global Positioning System-located kills and faecal samples: A comparison of leopard dietary estimates. J. Zool. 292, 18–24.

Pitman, R.T., Swanepoel, L.H., Ramsay, P.M., 2012. Predictive modelling of leopard predation using contextual Global Positioning System cluster analysis. J. Zool. 288, 222–230.

Plummer, M., 2017. JAGS Version 4.3.0 user manual.

PMF, 2016. Predation Management Forum manual. Pretoria, South Africa.

Podgórski, T., Schmidt, K., Kowalczyk, R., Gulczyńska, A., 2008. Microhabitat selection by Eurasian lynx and its implications for species conservation. Acta Theriol. (Warsz). 53, 97–110.

Pohl, C.F., 2015. The diet of caracal (Caracal caracal) in the southern Free State. University of the Free State.

Polis, G., Myers, C., Holt, R.D., 1989. The Ecology and Evolution of Intraguild Predation: Potential Competitors That Eat Each Other. Annu. Rev. Ecol. Syst. 20, 297–330.

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. Biol. Conserv. 109, 297–310.

Pressey, R.L., 1994. Ad Hoc Reservations: Forward or Backward Steps in Developing Representative Reserve Systems? Conserv. Biol. 8, 662–668.

Pringle, J.A., Pringle, V.L., 1979. Observations on the Lynx Felis Caracal in the Bedford District. South African J. Zool. 14, 1–4.

Prins, H.H.T., 2000. Competition Between Wildlife and Livestock in Africa, in: Wildlife Conservation by Sustainable Use. Springer, Dordrecht, Netherlands, pp. 51–80.

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.

Puri, R., 2010. Participant observation, in: Newing, H. (Ed.), Conducting Research in Conservation. Routledge, Oxon, UK, pp. 107–119.

QGIS Development Team, 2017. Open Source Geospatial Foundation Project.

Qi, J., Chehbouni, A., Huete, A.R., Kerr, Y.H., Sorooshian, S., 1994. A modified soil adjusted vegetation index. Remote Sens. Environ. 48, 119–126.

Quigley, H.B., Crawshaw, P.G., 1992. A conservation plan for the jaguar Panthera onca in the Pantanal region of Brazil. Biol. Conserv. 61, 149–157.

R Development Core Team, 2017. R: A language and environment for statistical computing.

Rabinowitz, A.R., 1986. Jaguar predation on domestic livestock in Belize. Wildl. Soc. Bull. 14, 170–174.

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. J. Anim. Ecol. 73, 410–423.

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. Biol. Conserv. 89, 113–120.

Ramesh, T., Kalle, R., Downs, C.T., 2017. Space use in a South African agriculture landscape by the caracal (Caracal caracal). Eur. J. Wildl. Res. 63, 11.

Ramesh, T., Kalle, R., Downs, C.T., 2015. Sex-specific indicators of landscape use by servals: Consequences of living in fragmented landscapes. Ecol. Indic. 52, 8–15.

Ranc, N.G., Cagnacci, F., Banea, O.C., Berce, T., Ćirović, D., Csànyi, S., Giannatos, G., Heltai, M., Lanszki, J., Lapini, L., 2015. Where to go next? Predicting habitat suitability of an expanding mesocarnivore: the golden jackal (Canis aureus) in Europe, in: ICCB : 27th International Congress for Conservation Biology, 4th European Congress for Conservation Biology. Montpellier, France.

Rannestad, O.T., Danielsen, T., Moe, S.R., Stokke, S., 2006. Adjacent pastoral areas support higher densities of wild ungulates during the wet season than the Lake Mburo National Park in Uganda. J. Trop. Ecol. 22, 675–683.

Rasmussen, G.S.A., 1999. Livestock predation by the painted hunting dog Lycaon pictus in a cattle ranching region of Zimbabwe: A case study. Biol. Conserv. 88, 133–139.

Rautenbach, I.L., 1982. Mammals of the Transvaal (ECOPLAN monograph). Ecoplan, Pretoria, South Africa.

Rautenbach, T., 2010. Assessing the diet of the Cape Leopard (Panthera pardus) in the Cederberg and Gamka Mountains, South Africa. Nelson Mandela Metropolitan University.

Rebelo, A.G., Siegfried, W.R., 1992. Where should nature reserves be located in the Cape Floristic Region, South Africa? Models for the spatial configuration of a reserve network aimed at maximizing the protection of floral diversity. Conserv. Biol. 6, 243–252.

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 Ecol. Evol. 28, 100–109.

Reed, L., Kleynhans, T., 2010. Agricultural Land Purchases for Alternative Uses - Evidence from Two Farming Areas in the Western Cape Province, South Africa. Agrekon 48, 332–351.

Reiter, D.K., Brunson, M.W., Schmidt, R.H., 1999. Public attitudes toward wildlife damage management and policy. Wildl. Soc. Bull. 27, 746–758.

Reynolds, J.C., Tapper, S.C., 1996. Control of mammalian predators in game management and conservation. Mamm. Rev. 26, 127–155.

Rich, L.N., Miller, D.A.W., Robinson, H.S., McNutt, J.W., Kelly, M.J., 2016. Using camera trapping and hierarchical occupancy modelling to evaluate the spatial ecology of an African mammal community. J. Appl. Ecol. 53, 1225–1235.

Richardson, J. a., 1998. Wildlife utilization and biodiversity conservation in Namibia: Conflicting or complementary objectives? Biodivers. Conserv. 7, 549–559.

Riley, R., DeGloria, S., Elliot, R., 1999. A terrain ruggedness index that quantifies topographic heterogeneity. Intermt. J. Sci. 5, 23–27.

Riley, S.J., Aune, K., Mace, R.D., Madel, M., 1994. Translocation of nuisance grizzly bears in northwestern Montana. Int. Conf. Bear Res. Manag. 9, 567–573.

Riley, S.J., Decker, D.J., 2000. Risk perception as a factor in wildlife stakeholder acceptance capacity for cougars in montana. Hum. Dimens. Wildl. 5, 50–62.

Riley, S.P.D., Sauvajot, R.M., Fuller, T.K., York, E.C., Kamradt, D.A., Bromley, C., Wayne, R.K., 2003. Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. Conserv. Biol. 17, 566–576.

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 (80-.). 343, 1241484.

Ripple, W.J., Newsome, T.M., Wolf, C., Dirzo, R., Everatt, K.T., Galetti, M., Hayward, M.W., Kerley, G.I.H., Levi, T., Lindsey, P.A., Macdonald, D.W., Malhi, Y., Painter, L.E., Sandom, C.J., Terborgh, J., Van Valkenburgh, B., 2015. Collapse of the world's largest herbivores. Sci. Adv.

Ritchie, E.G., Johnson, C.N., 2009. Predator interactions, mesopredator release and biodiversity conservation. Ecol. Lett. 12, 982–998.

Roberts, N.J., 2011. Investigation into survey techniques of large mammals: surveyor competence and camera-trapping vs. transect-sampling. Biosci. Horizons 4, 40–49.

Rochlitz, I., Pearce, G., Broom, D., 2010. The impact of snares on animal welfare. Cambridge, UK.

Roemer, G.W., Gompper, M.E., Van Valkenburgh, B., 2009. The Ecological Role of the Mammalian Mesocarnivore. Bioscience 59, 165–173.

Romañach, S.S., Lindsey, P.A., Woodroffe, R., 2007. Determinants of attitudes towards predators in central Kenya and suggestions for increasing tolerance in livestock dominated landscapes. Oryx 41, 185–195.

Rondeaux, G., Steven, M., Baret, F., 1996. Optimization of soil-adjusted vegetation indices. Remote Sens. Environ. 55, 95–107.

Roque De Pinho, J., Grilo, C., Boone, R.B., Galvin, K.A., Snodgrass, J.G., 2014. Influence of aesthetic appreciation of wildlife species on attitudes towards their conservation in Kenyan agropastoralist communities. PLoS One 9, e88842.

Rosas-Rosas, O.C., Bender, L.C., Valdez, R., 2008. Jaguar and puma predation on cattle calves in northeastern Sonora, Mexico. Rangel. Ecol. Manag. 61, 554–560.

Røskaft, E., Händel, B., Bjerke, T., Kaltenborn, B.P., 2007. Human attitudes towards large carnivores in Norway. Wildlife Biol. 13, 172–185.

Rouget, M., Richardson, D.M., Cowling, R.M., 2003. The current configuration of protected areas in the Cape Floristic Region, South Africa—reservation bias and representation of biodiversity patterns and processes. Biol. Conserv. 112, 129–145.

Roux, P.W., Theron, G.K., 1986. Vegetation change in the Karoo biome, in: Cowling, R.M., Roux, P.W., Pieterse, A.J.H. (Eds.), The Karoo Biome: A Preliminary Synthesis. Part 2 - Vegetation and History. Council for Scientific and Industrial Research, Pretoria, pp. 50–69.

Rovero, F., Marshall, A.R., 2009. Camera trapping photographic rate as an index of density in forest ungulates. J. Appl. Ecol. 46, 1011–1017.

Rovero, F., Martin, E., Rosa, M., Ahumada, J.A., Spitale, D., 2014. Estimating species richness and modelling habitat preferences of tropical forest mammals from camera trap data. PLoS One 9, e103300.

Rowcliffe, J.M., Kays, R., Carbone, C., Jansen, P.A., 2013. Clarifying assumptions behind the estimation of animal density from camera trap rates. J. Wildl. Manage. 77, 876–876.

Rowe-Rowe, D., 1978. The small carnivores of Natal. Lammergeyer 1–48.

Rowe-Rowe, D.T., 1983. Black-backed jackal diet in relation to food availability in the Natal Drakensberg. South African J. Wildl. Res. 13, 17–23.

Rowe-Rowe, D.T., 1976. Food of the black-backed jackal in nature conservation and farming areas in Natal. Afr. J. Ecol.

Rowntree, K.M., 2013. The evil of sluits: A re-assessment of soil erosion in the Karoo of South Africa as portrayed in century-old sources. J. Environ. Manage. 130, 98–105.

Royle, J.A., Nichols, J.D., 2003. Estimating abundance from repeated presence-absence data or point counts. Ecology 84, 777–790.

Rühe, F., Ksinsik, M., Kiffner, C., 2008. Conversion factors in carnivore scat analysis: sources of bias. Wildlife Biol. 14, 500–506.

Rust, N.A., Taylor, N., 2016. Carnivores, Colonization, and Conflict: A Qualitative Case Study on the Intersectional Persecution of Predators and People in Namibia. Anthrozoos 29, 653–667.

Rust, N.A., Tzanopoulos, J., Humle, T., MacMillan, D.C., 2016. Why Has Human–Carnivore Conflict Not Been Resolved in Namibia? Soc. Nat. Resour. 29, 1079–1094.

Ruth, T.K., Buotte, P.C., Quigley, H.B., 2010. Comparing Ground Telemetry and Global Positioning System Methods to Determine Cougar Kill Rates. J. Wildl. Manage. 74, 1122–1133.

Saayman, N., Morris, C.D., Cupido, C.F., Botha, J.C., Swart, R., 2016. Does grazing management matter in the Arid Koup region of the Karoo, South Africa, in: The Future Management of Grazing and Wild Lands in a High-Tech World: Proceedings 10th International Rangeland Congress. Saskatoon, Canada, pp. 186–187.

Saberwal, V.K., 1996. Pastoral Politics: Gaddi Grazing, Degradation, and Biodiversity Conservation in Himachal Pradesh, India. Conserv. Biol. 10, 741–749.

Sacks, B.N., Neale, J.C.C., McCullough, D.R., Jaeger, M.M., 1999. Territoriality and breeding status of coyotes relative to sheep predation. J. Wildl. Manage. 63, 593–605.

Sand, H., Wabakken, P., Zimmermann, B., Johansson, Ö., Pedersen, H.C., Liberg, O., 2008. Summer kill rates and predation pattern in a wolf-moose system: Can we rely on winter estimates? Oecologia 156, 53–64.

Santangeli, A., Arkumarev, V., Rust, N., Girardello, M., 2016. Understanding, quantifying and mapping the use of poison by commercial farmers in Namibia – Implications for scavengers' conservation and ecosystem health. Biol. Conserv. 204, 205–211.

Saunders, G., Coman, B., Kinnear, J., Braysher, M., 1995. Managing vertebrate pests: foxes. Australian Government Publ. Service - Bureau of Rural Sciences, Camberra, Australia.

Sax, B., 2017. Animals in Folklore. Oxford Handb. Anim. Stud. 456–472.

Schmidt, K., Jędrzejewski, W., Okarma, H., Kowalczyk, R., 2009. Spatial interactions between grey wolves and Eurasian lynx in Białowieża Primeval Forest, Poland. Ecol.

Res. 24, 207–214.
Schumann, M., Watson, L.H., Schumann, B.D., 2008. Attitudes of Namibian commercial farmers toward large carnivores: The influence of conservancy membership. South African J. Wildl. Res. 38, 123–132.
Scott, J.M., Davis, F.W., Mcghie, R.G., Wright, R.G., Estes, J., Scott, J.M., Davis, I.F.W., Mcghie, R.G., Wright, R.G., Groves, C., 2001. Nature Reserves : Do they capture the full range of America ' s biological diversity ? Ecol. Appl. 11, 999–1007.
Searchinger, T.D., Estes, L., Thornton, P.K., Beringer, T., Notenbaert, A., Rubenstein, D., Heimlich, R., Licker, R., Herrero, M., 2015. High carbon and biodiversity costs from converting Africa's wet savannahs to cropland. Nat. Clim. Chang. 5, 481–486.
Séquin, E.S., Jaeger, M.M., Brussard, P.F., Barrett, R.H., 2003. Wariness of coyotes to camera traps relative to social status and territory boundaries. Can. J. Zool. 81, 2015–2025.
Shannon, C.E., 1948. A mathematical theory of communication. Bell Syst. Tech. J. 27, 379–423.
Sharp, T., Saunders, G., 2010. Assessing the humaneness of commonly used invasive animal control methods. Canberra, Australia.
Shaw, J.M., Reid, T.A., Schutgens, M., Jenkins, A.R., Ryan, P.G., 2018. High power line collision mortality of threatened bustards at a regional scale in the Karoo, South Africa. Ibis (Lond. 1859). 160, 431–446.
Sheldon, J.W., 1992. Wild dogs: the natural history of the non-domestic Canidae. Academic Press, San Diego, California.
Sikes, R.S., Gannon, W.L., 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. J. Mammal. 92, 235–253.
Sillero-Zubiri, C., Burruss, D., Matchano, A., Robinson, O., 2013. Predation on livestock and pastoralist's attutudes towards wild carnivores in Termit and Tin-Toumma, East Niger.
Sillero-Zubiri, C., Laurenson, K., 2001. Interactions between carnivores and local communities: conflic or co-existence?, in: Gittleman, J., S.Funk, S., Macdonald, D.W., Wayne, R.K. (Eds.), Proceedings of a Carnivore Conservation Symposia. Zoological Society of London, UK, pp. 282–312.
Silveira, L., Jácomo, A.T. a., Diniz-Filho, J.A.F., 2003. Camera trap, line transect census and track surveys: a comparative evaluation. Biol. Conserv. 114, 351–355.
Simbi, T., Aliber, M., 2000. Agricultural employment crisis in South Africa (No. 13).
Sinclair, A.R.E., Krebs, C.J., 2002. Complex numerical responses to top-down and bottom-up

processes in vertebrate populations. Philos. Trans. R. Soc. B Biol. Sci. 357, 1221–1231.
Singh, R., Qureshi, Q., Sankar, K., Krausman, P.R., Goyal, S.P., 2014. Population and habitat characteristics of caracal in semi-arid landscape, western India, Journal of Arid Environments.
Skead, C.J., 1987. Historical mammal incidence in the Cape Province: Vol. 2–The eastern half of the Cape Province, including the Ciskei, Transkei and East Griqualand, in: Boshoff, A., Kerley, G., Lloyd, P. (Eds.), Nature and Environmental Conservation. Centre for African Conservation Ecology, Nelson Mandela Metropolitan University., Port Elizabeth, pp. 267–311.
Skinner, J.D., 1979. Feeding behaviour in Caracal Felis caracal. J. Zool. 189, 523–525.
Skinner, J.D., Chimimba, C.T., 2005. The Mammals of the Southern African Sub-region. Cambridge University Press, Cape Town, South Africa. https://doi.org/10.1017/CBO9781107340992
Skogen, K., Mauz, I., Krange, O., 2008. Cry Wolf! Narratives of Wolf Recovery in France and Norway. Rural Sociol. 73, 105–133.
Slagle, K., Bruskotter, J.T., Singh, A.S., Schmidt, R.H., 2017. Attitudes toward predator control in the United States: 1995 and 2014. J. Mammal. 98, 7–16.
Smailes, P.J., 2002. From rural dilution to multifunctional countryside: Some pointers to the future from South Australia. Aust. Geogr. 33, 79–95.
Small, E., 2012. The new Noah’s Ark: Beautiful and useful species only. Part 2. The chosen species. Biodiversity 13, 37–53.
Smith, B.P., Appleby, R.G., 2018. Promoting human-dingo co-existence in Australia: Moving towards more innovative methods of protecting livestock rather than killing dingoes (Canis dingo). Wildl. Res. 45, 1–15.
Smith, J.A., Wang, Y., Wilmers, C.C., 2015. Top carnivores increase their kill rates on prey as a response to human-induced fear. Proc. R. Soc. B Biol. Sci. 282, 20142711.
Smithers, R., 1971. The Mammals of Botswana. National Museums of Rhodesia, Salisbury, Rhodesia.
Sogbohossou, E.A., De Iongh, H.H., Sinsin, B., De Snoo, G.R., Funston, P.J., 2011. Human-carnivore conflict around pendjari biosphere reserve, northern benin. Oryx 45, 569–578.
Somers, M.J., Nel, J.A.J., 2004. Habitat selection by the Cape clawless otter (Aonyx capensis) in rivers in the Western Cape Province, South Africa. Afr. J. Ecol. 42, 298–305.
Soulé, M.E., Bolger, D.T., Alberts, A.C., Wrights, J., Sorice, M., Hill, S., 1988. Reconstructed Dynamics of Rapid Extinctions of Chaparral-Requiring Birds in Urban

Habitat Islands. Conserv. Biol. 2, 75–92.
Spaulding, R., Krausman, P.R., Ballard, W.B., 1973. Observer Bias and Analysis of Gray Wolf Diets from Scats. Wildl. Soc. Bull. 28, 947–950.
St John, F.A. V., Keane, A.M., Edwards-Jones, G., Jones, L., Yarnell, R.W., Jones, J.P.G., 2012. Identifying indicators of illegal behaviour: carnivore killing in human-managed landscapes. Proc. R. Soc. B 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. J. Appl. Ecol. 39, 204–216.
Stander, P.E., 1990. A suggested management strategy for stock-raiding lions in Namibia. South African J. Wildl. Res. 20, 37–43.
Stanley, T.R., Royle, J.A., 2005. Estimating site occupancy and abundance using indirect detection indices. J. Wildl. Manage. 69, 874–883.
Statistics South Africa, 2011. Census 2011 - Census in brief. Pretoria, South Africa.
Steenweg, R., Hebblewhite, M., Kays, R., Ahumada, J., Fisher, J.T., Burton, C., Townsend, S.E., Carbone, C., Rowcliffe, J.M., Whittington, J., Brodie, J., Royle, J.A., Switalski, A., Clevenger, A.P., Heim, N., Rich, L.N., 2017. Scaling-up camera traps: monitoring the planet's biodiversity with networks of remote sensors. Front. Ecol. Environ. 15, 26–34.
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. Biodivers. Conserv. 17, 3579–3587.
Stephens, P.A., D'Sa, C.A., Sillero-Zubiri, C., Leader-Williams, N., 2001. Impact of livestock and settlement on the large mammalian wildlife of Bale Mountains National Park, southern Ethiopia. Biol. Conserv. 100, 307–322.
Stirling, I., Latour, P.B., 1978. Comparative hunting abilities of polar bear cubs of different ages. Can. J. Zool. 56, 1768–1772.
Stone, S.A., Breck, S.W., Timberlake, J., Haswell, P.M., Najera, F., Bean, B.S., Thornhill, D.J., 2017. Adaptive use of nonlethal strategies for minimizing wolf–sheep conflict in Idaho. J. Mammal. 98, 33–44.
Strum, S.C., 2010. The Development of Primate Raiding: Implications for Management and Conservation. Int. J. Primatol. 31, 133–156.
Stuart, C., 1982. Aspects of the biology of the caracal (Felis caracal Schreber, 1776) in the Cape Province, South Africa. University of Natal.
Stuart, C., 1981. Notes on the mammalian carnivores of the Cape Province, South Africa. Bontebok 1, 1–58.

Stuart, C., 1976. Diet of the black-backed jackal Canis mesomelas in the central Namib Desert, South West Africa. African Zool. 11, 193–205.
Stuart, C., Stuart, T., 2013. Caracal, in: Kingdon, J., Hoffmann, M. (Eds.), The Mammals of Africa. Volume V: Carnivores, Pangolins, Equids and Rhinoceroses. Academic Press, Amsterdam, The Netherlands, pp. 174–179.
Stuart, C., Wilson, V., 1988. The Cats of Southern Africa. Chipingali Wildlife Trust, Bulawayo, Zimbabwe.
Stuart, C.T., Hickman, G.C., 1991. Prey of caracal Felis caracal in two areas of Cape Province, South Africa. Rev. Zool. africaine 105, 373–381.
Svoboda, N.J., Belant, J.L., Beyer, D.E., Duquette, J.F., Martin, J.A., 2013. Identifying bobcat Lynx rufus kill sites using a global positioning system. Wildlife Biol. 19, 78–86.
Swan, G.J.F., Redpath, S.M., Bearhop, S., McDonald, R.A., 2017. Ecology of Problem Individuals and the Efficacy of Selective Wildlife Management. Trends Ecol. Evol. 32, 518–530.
Swanepoel, J., 2016. Habits of the hunters: the biopolitics of combatting predation amongst small stock farmers in southern Namibia. J. Contemp. African Stud. 34, 129–146.
Swanepoel, L.H., 2008. Ecology and conservation of leopards, Panthera pardus, on selected game ranches in the Waterberg region, Limpopo, South Africa. University of Pretoria.
Swanson, A., Kosmala, M., Lintott, C., Simpson, R., Smith, A., Packer, C., 2015. Snapshot Serengeti, high-frequency annotated camera trap images of 40 mammalian species in an African savanna. Sci. Data 2, 150026.
Tambling, C.., Avenant, N.L., Drouilly, M., Melville, H., 2018. The Role Of Mesopredators In Ecosystems: Potential Effects Of Managing Their Populations On Ecosystem Processes And Biodiversity, in: Kerley, G.I.H., Wilson, S.L., Balfour, D. (Eds.), Livestock Predation and Its Management in South Africa: A Scientific Assessment. Centre for African Conservation Ecology, Nelson Mandela University, Port Elizabeth, pp. 205–227.
Tambling, C.J., Cameron, E.Z., Du Toit, J.T., Getz, W.M., 2010. Methods for Locating African Lion Kills Using Global Positioning System Movement Data. J. Wildl. Manage. 74, 549–556.
Tambling, C.J., Laurence, S.D., Bellan, S.E., Cameron, E.Z., Du Toit, J.T., Getz, W.M., 2012. Estimating carnivoran diets using a combination of carcass observations and scats from GPS clusters. J. Zool. 286, 102–109.
Te Velde, H., Aarts, N., Van Woerkum, C., 2002. Dealing with ambivalence: Farmers' and

consumers' perceptions of animal welfare in livestock breeding. J. Agric. Environ. Ethics 15, 203–219.

Tensen, L., Drouilly, M., van Vuuren, B.J., 2018. Genetic structure and diversity within lethally managed populations of two mesopredators in South Africa. J. Mammal. 99, 1411–1421.

Thamm, A.G., Johnson, M.R., 2006. The Cape Supergroup, in: Johnson, M.R., Annhaeusser, C.R., Thomas, R.J. (Eds.), The Geology of South Africa. Geological Society of South Africa and Council for Geoscience, Johannesburg; Council for Geoscience, Pretoria, pp. 443–461.

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? Biol. Conserv. 150, 23–32.

Thorn, M., Green, M., Scott, D., Marnewick, K., 2013. Characteristics and determinants of human-carnivore conflict in South African farmland. Biodivers. Conserv. 22, 1715–1730.

Thornton, C., Quinn, M., 2009. Coexisting with cougars: public perceptions, attitudes, and awareness of cougars on the urban-rural fringe of Calgary, Alberta, Canada. Human-Wildlife Conflicts 3, 282–295.

Thornton, D.H., Sunquist, M.E., Main, M.B., 2004. Ecological separation within newly sympatric populations of coyotes and bobcats in south-central Florida. J. Mammal. 85, 973–982.

Thrupp, L.A., 2000. Linking Agricultural Biodiversity and Food Security: the Valuable Role of Agrobiodiversity for Sustainable Agriculture. Int. Aff. 76, 265–281.

Tigas, L.A., Van Vuren, D.H., Sauvajot, R.M., 2002. Behavioral responses of bobcats and coyotes to habitat fragmentation and corridors in an urban environment. Biol. Conserv. 108, 299–306.

Tobler, M.W., Carrillo-Percastegui, S.E., Leite Pitman, R., Mares, R., Powell, G., 2008. An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals. Anim. Conserv. 11, 169–178.

Tobler, M.W., Hartley, A.Z., Carrillo-Percastegui, S.E., Powell, G.V.N., 2015. Spatiotemporal hierarchical modelling of species richness and occupancy using camera trap data. J. Appl. Ecol. 52, 413–421.

Todd, S.W., 2006. Gradients in vegetation cover, structure and species richness of Nama-Karoo shrublands in relation to distance from livestock watering points. J. Appl. Ecol.

43, 293–304.
Todd, S.W., Hoffman, M.T., 1999. A fence-line contrast reveals effects of heavy grazing on plant diversity and community composition in Namaqualand, South Africa. Plant Ecol. 142, 169–178.
Torres, D.F., Oliveira, E.S., Alves, R.R.N., 2018. Conflicts Between Humans and Terrestrial Vertebrates: A Global Review. Trop. Conserv. Sci. 11, 1–15.
Treves, A., Jones, S.M., 2010. Strategic tradeoffs for wildlife-friendly eco-labels. Front. Ecol. Environ. 8, 491–498.
Treves, A., Jurewicz, R.R., Naughton-Treves, L., Harper, E., Mladenoff, D., Rose, R., Sickley, T., Wydeven, A., 2002. Wolf depredation on domestic animals in Wisconsin, 1976-2000. Wildl. Soc. Bull. 30, 231–241.
Treves, A., Karanth, K.U., 2003. Human-Carnivore Conflict and Perspectives on Carnivore Management Worldwide. Conserv. Biol. 17, 1491–1499.
Treves, A., Krofel, M., McManus, J., 2016. Predator control should not be a shot in the dark. Front. Ecol. Environ.
Turkkan, N., Pham-gia, N., 1993. Computation of the highest posterior density interval in bayesian analysis. J. Stat. Comput. Simul. 44, 243–250.
Turpie, J., Babatopie, A., 2018. The socio-economic impacts of livestock predation and its prevention in South Africa, in: Kerley, G., Wilson, S., Balfour, D. (Eds.), Livestock Predation and Its Management in South Africa: A Scientific Assessment. Centre for African Conservation Ecology, Nelson Mandela University, Port Elizabeth, Port Elizabeth, pp. 53–81.
UNCCD, 2014. The Land in numbers-Livelihoods at a tipping point. Bonn, Germany.
UNCCD, 2012. Biodiversity - The Big Unknown [WWW Document]. URL http://www.unccd.int/fr/programmes/Thematic-Priorities/Biodiv/Pages/the-big-unknown.aspx (accessed 10.10.17).
UNEP, 2016. Healthy Environment, Healthy People. Nairobi, Kenya.
United Nations - Department of Economic and Social Affairs - Population Division, 2015. World Population Prospects: The 2015 Revision, Key Findings and Advance Tables. New York, USA.
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. J. Appl. Ecol. 49, 73–81.
Van't Woudt, B.D., 1990. Roaming, stray, and feral domestic cats and dogs as wildlife

problems, in: Proceedings of the Fourteenth Vertebrate Pest Conference. DigitalCommons@University of Nebraska, Lincoln, Nebraska, pp. 291–295.

van Bommel, L., Johnson, C., 2017. Predation control, in: Ferguson, D., Lee, C., Fisher, A. (Eds.), Advances in Sheep Welfare. Woodhead Publishing, Duxford, UK, pp. 177–196.

Van de Ven, T.M.F.N., Tambling, C.J., Kerley, G.I.H., 2013. Seasonal diet of black-backed jackal in the Eastern Karoo, South Africa. J. Arid Environ. 99, 23–27.

van der Meer, E., Fritz, H., Blinston, P., Rasmussen, G.S.A., 2014. Ecological trap in the buffer zone of a protected area: Effects of indirect anthropogenic mortality on the African wild dog Lycaon pictus. Oryx 48, 285–293.

Van der Merwe, N.J., 1953. The coyote and the black-backed jackal. A comparison of certain similar characteristics. Fauna and Flora 3, 44–51.

van der Merwe, I. Van Der, Tambling, C.J., Thorn, M., Scott, D.M., Yarnell, R.W., Green, M., Cameron, E.Z., Bateman, P.W., 2009. An Assessment of Diet Overlap of Two Mesocarnivores in the North West Province, South Africa. African Zool. 44, 288–291.

Van der Weyde, L.K., Mbisana, C., Klein, R., 2018. Multi-species occupancy modelling of a carnivore guild in wildlife management areas in the Kalahari. Biol. Conserv. 220, 21–28.

van Eeden, L.M., Crowther, M.S., Dickman, C.R., Macdonald, D.W., Ripple, W.J., Ritchie, E.G., Newsome, T.M., 2018. Managing conflict between large carnivores and livestock. Conserv. Biol. 32, 26–34.

van Heezik, Y.M., Seddon, P.J., 1998. Range size and habitat use of an adult male caracal in northern Saudi Arabia. J. Arid Environ. 40, 109–112.

van Niekerk, H.N., 2010. The cost of predation on small livestock in South Africa by medium-sized predators. University of the Free State.

van Sittert, L., 2016. Routinising genocide: the politics and practice of vermin extermination in the Cape Province c.1889–1994. J. Contemp. African Stud. 34, 111–128.

van Sittert, L., 1998. Keeping the enemy at bay: The extermination of wild carnivora in the Cape Colony, 1889-1910. Environ. Hist. Durh. N. C. 3, 333–356.

van Teijlingen, E.R., Hundley, V., 2001. The importance of pilot studies. Soc. Res. Updat. 1–4.

Vashon, J.H., Meehan, A.L., Jakubas, W.J., Organ, J.F., Vashon, A.D., McLaughlin, C.R., Matula, G.J., Crowley, S.M., 2008. Spatial Ecology of a Canada Lynx Population in Northern Maine. J. Wildl. Manage. 72, 1479.

Vaske, J., Manfredo, M., 2012. Social psychological considerations in wildlife management., in: Decker, D., Riley, S., Siemer, W. (Eds.), Human Dimensions of Wildlife

Management. Johns Hopkins University Press., Baltimore, MD, pp. 43–57.
Venter, J.M., Mocke, C., De Jager, J.M., 1986. Climate, in: Cowling, R.M., Roux, P.W., Pieterse, A.J.H. (Eds.), The Karoo Biome: A Preliminary Synthesis. Part I - Physical Environment. Council for Scientific and Industrial Research, Pretoria, pp. 39–52.
Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89, 2290–2301.
Visser, J.N.J., 1986. Geology, in: Cowling, R.M., Roux, P.W., Pieterse, A.J.H. (Eds.), The Karoo Biome: A Preliminary Synthesis. Part 1 - Physical Environment. Council for Scientific and Industrial Research, Pretoria, pp. 1–17.
Vlok, J., Schutte-Vlok, A.., 2010. Plants of the klein karoo, 1st ed, Hatfield: Umdaus Press. Umdaus Press, Hatfield, UK.
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. Cape Town, South Africa.
Volmer, R., Hertler, C., 2016. The effect of competition on shared food resources in carnivore guilds. Quat. Int. 413, 32–43.
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. Mamm. Biol. 77, 196–203.
Wagner, F.H., 1988. Predator control and the sheep industry: the role of science in policy formation. Regina Books, Claremont, California.
Waits, L.P., Paetkau, D., 2005. Non-invasive genetic sampling tools for wildlife biologists: A review of applications and recommendations for accurate data collection. J. Wildl. Manage. 69, 1419–1433.
Walker, C., 1996. Signs of the wild: A field guide to the spoor and signs of the mammals of southern Africa. Struik Nature, Cape Town.
Walker, C., Milton, S.J., O'Connor, T.G., Maguire, J.M., Dean, W.R.J., 2018. Drivers and trajectories of social and ecological change in the Karoo, South Africa. African J. Range Forage Sci. 35, 157–177.
Walton, L.R., Joly, D.O., 2003. Canis mesomelas. Mamm. Species 715, 1–9.
Wang, E., 2002. Diets of ocelots (Leopardus pardalis), margays (L. wiedii), and oncillas (L. tigrinus) in the Atlantic Rainforest in southeast Brazil. Stud. Neotrop. Fauna Environ. 37, 207–212.
Wang, S.W., Macdonald, D.W., 2006. Livestock predation by carnivores in Jigme Singye Wangchuck National Park, Bhutan. Biol. Conserv. 129, 558–565.

Ward, M.A., Summers, A.F., Rosasco, S.L., Beard, J.K., Soto-Navarro, S.A., Hallford, D.M., 2017. Effects of Stress from Predation in Gestating Ewes—A Case Study, Guide B-411. New Mexico State University, Las Cruces, USA.

Watkeys, M., 1999. Soils of the arid south-western zone of Africa, in: Milton, S.J., Dean, W.R.J. (Eds.), The Karoo: Ecological Patterns and Processes. Cambridge University Press, Cambridge, UK, pp. 18–19.

Watson, J.E.M., Dudley, N., Segan, D.B., Hockings, M., 2014. The performance and potential of protected areas. Nature 515, 67–73.

Weaver, J.L., 1993. Refining the Equation for Interpreting Prey Occurrence in Gray Wolf Scats. J. Wildl. Manage. 57, 534.

Webb, N.F., Hebblewhite, M., Merrill, E.H., 2008. Statistical Methods for Identifying Wolf Kill Sites Using Global Positioning System Locations. J. Wildl. Manage. 72, 798–807.

Wegge, P., Pokheral, C.P., Jnawali, S.R., 2004. Effects of trapping effort and trap shyness on estimates of tiger abundance from camera trap studies. Anim. Conserv. 7, 251–256.

Weissnar, T., du Rand, G., 2012. Consumer perception of Karoo lamb as a product of origin and their consequent willingness to purchase. Food Res. Int. 47, 272–278.

Wessels, J.S.F., Willemse, B.J., 2013. The impact of changed land use on farmland values and farmland valuations: An example from the south-eastern Nama Karoo. Agrekon 52, 133–151.

Western Cape Department of Agriculture, 2017. AgriWorker Household Census, 31 March 2017.

Western Cape Department of Agriculture, 2013. Western Cape AgriStats [WWW Document]. URL http://www.elsenburg.com/gis/apps/agristats/ (accessed 3.10.18).

Western Cape Government Provincial Treasury, 2013. Regional Development Profile Central Karoo District. Cape Town, South Africa.

Western, D., Russell, S., Cuthill, I., Somers, M., 2009. The Status of Wildlife in Protected Areas Compared to Non-Protected Areas of Kenya. PLoS One 4, e6140.

Wickham, H., Chang, W., 2016. Package “ggplot2”: Create Elegant Data Visualisations Using the Grammar of Graphics. R package version 2.2.1. Reference manual., CRAN Repository.

Wiegand, T., Naves, J., Garbulsky, M.F., Fernandez, N., 2008. Animal habitat quality and ecosystem functioning: Exploring seasonal patterns using NDVI. Ecol. Monogr. 78, 87–103.

Williams, R.E., Allred, B.W., Denio, R.M., Paulsen, H.A., 1968. Conservation, Development,

and Use of the World's Rangelands. J. Range Manag. 21, 355–360.
Williams, S.T., Maree, N., Taylor, P., Belmain, S.R., Keith, M., Swanepoel, L.H., 2018. Predation by small mammalian carnivores in rural agro-ecosystems: An undervalued ecosystem service? Ecosyst. Serv. 30, 362–371.
Williams, V., Whiting, M., 2016. A picture of health? Animal use and the Faraday traditional medicine market, South Africa. J. Ethnopharmacol. 179, 265–273.
Wilmers, C.C., Crabtree, R.L., Smith, D.W., Murphy, K.M., Getz, W.M., 2003. Trophic facilitation by introduced top predators: Grey wolf subsidies to scavengers in Yellowstone National Park. J. Anim. Ecol. 72, 909–916.
Wilson, C., Tisdell, C., 2005. Knowledge of birds and willingness to support their conservation: An Australian case study. Bird Conserv. Int. 15, 225–235.
Wilson, J.B., 1991. Methods for fitting dominance/diversity curves. J. Veg. Sci. 2, 35–46.
Wilson, M.F.J., O 'connell, B., Brown, C., Guinan, J.C., Grehan, A.J., 2007. Multiscale Terrain Analysis of Multibeam Bathymetry Data for Habitat Mapping on the Continental Slope. Mar. Geod. 30, 3–35.
Wobeser, G., Bollinger, T., Leighton, F.A., Blakley, B., Mineau, P., 2004. Secondary poisoning of eagles following intentional poisoning of coyotes with anticholinesterase pesticides in western Canada. J. Wildl. Dis. 40, 163–172.
Woodgate, Z., Distiller, G., O'Riain, J., 2018. Variation in mammal species richness and relative abundance in the Karoo. African J. Range Forage Sci. 35, 325–334.
Woodroffe, Ginsberg, 1998. Edge effects and the extinction of populations inside protected areas. Science (80-.). 280, 2126–8.
Woodroffe, R., Frank, L.G., 2005. Lethal control of African lions (Panthera leo): local and regional population impacts. Anim. Conserv. 8, 91–98.
Woodroffe, R., Ginsberg, J.R., 1999. Conserving the African wild dog Lycaon pictus. I. Diagnosing and treating causes of decline. Oryx 33, 132–142.
Woodroffe, R., Thirgood, S., Rabinowitz, A., 2005. People and Wildlife Conflict or Coexistence. Cambridge University Press, Cambridge, UK.
Wooldridge, J., 2010. Econometric Analysis of Cross Section and Panel Data, 2nd editio. ed. MIT Press, Cambridge, USA.
Woolman, S., Bishop, M., 2007. Down on the farm and barefoot in the kitchen: Farm labour and domestic labour as forms of servitude. Dev. South. Afr. 24, 595–606.
Wretenberg, J., Pärt, T., Berg, Å., 2010. Changes in local species richness of farmland birds in relation to land-use changes and landscape structure. Biol. Conserv. 143, 375–381.

Yarnell, R.W., Phipps, W.L., Burgess, L.P., Ellis, J.A., Harrison, S.W.R., Dell, S., MacTavish, D., MacTavish, L.M., Scott, D.M., 2013. The Influence of Large Predators on the Feeding Ecology of Two African Mesocarnivores: The Black-Backed Jackal and the Brown Hyaena. South African J. Wildl. Res. 43, 155–166.

Yom-Tov, Y., Ashkenazi, S., Viner, O., 1995. Cattle predation by the golden jackal Canis aureus in the Golan Heights, Israel. Biol. Conserv. 73, 19–22.

Young, J.K., Olson, K.A., Reading, R.P., Amgalanbaatar, S., Berger, J., 2011. Is Wildlife Going to the Dogs? Impacts of Feral and Free-roaming Dogs on Wildlife Populations. Bioscience 61, 125–132.

Zabala, J., Zuberogoitia, I., 2003. Badger, Meles meles (Mustelidae, Carnivora), diet assessed through scat-analysis: A comparison and critique of different methods. Folia Zool. 52, 23–30.

Zar, J., 1999. Biological Statistics. Prentice Hall, New Jersey, USA.

Zavaleta, E.S., Hulvey, K.B., 2004. Realistic Species Losses Disproportionately Reduce Grassland Resistance to Biological Invaders. Science (80-.). 306, 1175–1177.

Zeileis, A., 2006. Object-Oriented Computation of Sandwich Estimators. J. Stat. Softw. 16, 16.

Zeileis, A., 2004. Econometric Computing with HC and HAC Covariance Matrix Estimators. J. Stat. Softw. 11.

Zimmermann, A., Baker, N., Inskip, C., Linnell, J.D.C., Marchini, S., Odden, J., Rasmussen, G., Treves, A., 2009. Contemporary Views of Human-Carnivore Conflicts on Wild Rangelands, in: du Toit, J.T., Kock, R., Deutsch, J.C. (Eds.), Wild Rangelands: Conserving Wildlife While Maintaining Livestock in Semi-Arid Ecosystems. Blackwell Publishing, Oxford, UK, pp. 129–151.

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, 406–412.

Zipkin, E.F., Dewan, A., Andrew Royle, J., 2009. Impacts of forest fragmentation on species richness: A hierarchical approach to community modelling. J. Appl. Ecol. 46, 815–822.

LIST OF TABLES

LIST OF FIGURES