

Ecology and diet of the caracal (*Caracal caracal*) on lethal and non-lethal control farms in the Karoo

Erin Cecilia Jooste

University of the Western Cape, Department of Biodiversity and Conservation Biology, Private Bag X17, Bellville, 7535, South Africa.



A thesis submitted in fulfilment of the requirements for the degree of *Magister Scientiae* in the Department of Biodiversity and Conservation Biology, Faculty of Science, University of the Western Cape

UNIVERSITY OF THE
WESTERN CAPE

Supervisor: Dr. Vanessa Couldridge
Co-supervisor: Dr. Jeannine McManus

December 2020

Ecology and diet of the caracal (*Caracal caracal*) on lethal and non-lethal control farms in the Karoo

Erin Cecilia Jooste

Keywords

Activity patterns; Caracal; Diet; Ecology; Generalized linear mixed models; Habitat selection; Human-carnivore conflict; Karoo; Lethal and non-lethal predator controls; Small-livestock farming.



Abstract

Human-wildlife conflict is an ongoing issue worldwide. Within South Africa, human-carnivore conflict (HCC) as a result of carnivore depredation on small-livestock causes large-scale losses, and promotes the use of predator management tools by farmers. Despite being one of the major offenders involved in HCC, caracals, and their ecology in particular, are understudied. This is mainly due to high levels of persecution, coupled with their elusive nature. Within the Karoo region of South Africa, pastoralists make use of large-scale lethal predator controls in an attempt to remove the offenders, or non-lethal predator controls to protect livestock and deter predators. However, the effects of these various predator control techniques on caracal ecology have not been widely tested. Therefore, the aims of this thesis were, firstly, to assess caracal diet on lethal and non-lethal treatment farms in the Karoo; secondly, to investigate the drivers of caracal habitat selection on a non-lethal farm in the Karoo; and finally, to evaluate caracal activity patterns on the non-lethal farm. To do this, I made use of two non-invasive techniques (i.e. scat analysis and camera trapping). Caracals appeared to favour natural prey across all sites, with livestock remains only found in scats collected at the lethal treatment farm. Caracals had the broadest dietary breadth on the non-lethal treatment site, and the narrowest on the lethal treatment site. The main components of caracal diet included small mammals, lagomorphs, rock hyraxes (*Procavia capensis*), wild ungulates and arthropods. Caracal habitat selection was explained by resource dispersion and environmental features. Interestingly, the presence of livestock was not a major consideration in caracal habitat selection. Caracals were mainly nocturnal but became increasingly crepuscular during winter. In addition, caracal activity overlapped significantly with black-backed jackals (*Canis mesomelas*), lagomorphs and common duikers (*Sylvicapra grimmia*). Caracals showed plasticity in their activity patterns based on seasonal temperature fluctuations, and partially human avoidance. This study contributes to understanding how caracal ecology differs on differently managed livestock farms. Throughout this study, the importance of both a natural prey base, as well as natural lands to caracal survival have been revealed. These findings can contribute to caracal conservation in HCC areas.

December 2020

Declaration

I declare that “**Ecology and diet of the caracal (*Caracal caracal*) on lethal and non-lethal control farms in the Karoo**” is my own work, that it has not been submitted for any degree or examination at any other university, and that all sources I have used or quoted have been indicated and acknowledged by complete references.

Full name: Erin Cecilia Jooste

Date: December 2020

Signature:

Erin Cecilia Jooste



UNIVERSITY *of the*
WESTERN CAPE

Acknowledgements

This project has been something that I have always been interested in so I would like to say thank you to everyone that made it possible:

- To my supervisors, Vanessa Couldridge and Jeannine McManus for their guidance, wisdom and assistance throughout this project.
- The Landmark Foundation for pioneering the “Shepherding Back Biodiversity” project and for allowing me to be a part of it. Thank you especially to Bool Smuts, Matthew Schurch and Stefan Goets for everything that you taught me. Thank you also to Matthew and Stefan for making sure that the cameras were checked regularly and for allowing me access to the data. Thank you also to the Landmark Foundation for providing logistical assistance during the duration of this project.
- Thank you to everyone who enabled me to build up my prey reference collection. A special thanks goes to Leigh Richards from the Durban Natural Science Museum for sending specimens, Jessica Comley for allowing access to the Rhodes University hair reference collection and to Gabriella Leighton and Ielhaam Fredericks for sharing their own referenced slides with me.
- Thank you to Gavin Maneveldt for access to the Histology lab and use of the microscope.
- I would like to thank the Karoo farmers who have allowed access to their property in order for this project to go ahead – especially Mr. Louw, Mr. Lubbe, Mr. Allison, and Mr. and Mrs. Loveridge.
- Thank you to Caitlin Smith and Jody Barends for proof-reading my work.
- Thank you to every volunteer that assisted me during this project especially Luther Adams, Wayne Jooste, Jodene Foster, Tim Ponton, Silindokhule Tokota, Kyle Jantjies, Laetitia Piers, Amy Schroeder, Adriaan Engelbrecht, Saloshnie Govender and Chris Hasselerharm.
- Thank you to the NRF (block grant reference number: 118696) for funding this work.
- Thank you to Cape Nature for allowing me to conduct this study on their lands (research permit number: CN44-59-5569).

- Thank you to the UWC ethics committee for providing ethical clearance for this study (ethics reference number: AR 19/2/3).
- Finally, thank you to my amazing family – my husband, Luther Adams for your love, encouragement and help; to my mom, brother, sister and brother-in-law, for emotional and logistical support during my masters. A special thank you to my brother for always being willing to take me to Beaufort West whenever I needed to do fieldwork and for fetching me again when I was done. Thank you to my dad for imparting your sense of adventure on me, this thesis is dedicated to you.



Table of Contents

Ecology and diet of the caracal (<i>Caracal caracal</i>) on lethal and non-lethal control farms in the Karoo.....	i
Keywords.....	ii
Abstract	iii
Declaration	iv
Acknowledgements	v
List of tables	ix
List of figures	x
List of appendices	xi
Chapter 1: General introduction.....	1
1.1 Human-wildlife conflict.....	1
1.1.1 Human-carnivore conflict.....	2
1.1.2 Human-carnivore conflict in South Africa	2
1.1.3 Predator management on livestock farms.....	3
1.1.4 Apex predators and humans as threats to mesopredators	5
1.2 Caracal ecology.....	6
1.2.1 Caracals on farmlands in southern Africa	7
1.3 Rationale for the study.....	8
1.4 Study sites	8
1.4.1 Geology and soils	9
1.4.2 Vegetation.....	9
1.5 Study aims and thesis structure.....	12
Chapter 2: Diet of caracals on lethal and non-lethal treatment farms in the Karoo, South Africa	13
2.1 Abstract.....	13
2.2 Introduction.....	14
2.3 Materials and methods	16
2.3.1 Study area	16
2.3.2 Scat collection	16
2.3.3 Scat analysis	17
2.3.4 Data analysis.....	18
2.4 Results.....	20

2.4.1	Pairwise comparisons	24
2.5	Discussion.....	25
2.6	Conclusions and management implications.....	28
Chapter 3: Caracal habitat selection and activity patterns on a predator-friendly farm in the Karoo, South Africa		30
3.1	Abstract.....	30
3.2	Introduction.....	31
3.3	Materials and methods	34
3.3.1	Camera-trapping surveys	34
3.3.2	Habitat selection	35
3.3.3	Activity patterns	41
3.4	Results.....	41
3.4.1	Caracal habitat selection.....	42
3.4.2	Caracal diel activity patterns	44
3.4.3	Predator-prey, competitor, human and livestock interactions	46
3.5	Discussion.....	49
3.5.1	Habitat selection	49
3.5.2	Diel activity patterns of caracals, prey, competitors, humans, and livestock 52	
3.5.3	Study limitations and future research	53
3.6	Conclusion	53
Chapter 4: Synthesis.....		55
4.1	Caracals in the Karoo.....	55
4.2	Limitations and knowledge gaps	57
4.3	Management implications.....	57
4.4	Conclusion	58
References.....		59
Appendices		79

List of tables

With abbreviated captions

Table 2.1 Diet of caracal expressed as the frequency of occurrence (FO), corrected frequency of occurrence (CFO), and mammalian biomass (MB), at three treatment sites, in the Karoo, South Africa.....	21
Table 3.1 The environmental variables considered in creating <i>a-priori</i> models for caracal habitat selection on a non-lethal treatment farm in the Karoo, South Africa.....	38
Table 3.2 The eight <i>a-priori</i> models developed to explain caracal habitat selection at camera trap locations on a non-lethal treatment farm in the Karoo, South Africa.....	40
Table 3.3 Summary of the <i>a-priori</i> models used to explain habitat selection of caracals on a non-lethal treatment farm in the Karoo, South Africa.	43
Table 3.4 Number of independent camera trap records (n), estimates of coefficients of overlap with caracal based on Dhat4 (Δ_4) and the 95% confidence intervals (CI), of wild prey, competitors, vehicles (human proxy), and livestock.	49



UNIVERSITY of the
WESTERN CAPE

List of figures

With abbreviated captions

Figure 1.1 Total monthly rainfall (mm), and average minimum and maximum temperatures (°C) for January 2018 to January 2020 for the Beaufort West region of South Africa.	9
Figure 1.2 The two main vegetation types in the Nama Karoo biome, namely Upper Karoo Hardeveld (a) and Eastern Upper Karoo (b).	10
Figure 1.3 Map displaying the locations of the three study sites.	11
Figure 2.1 Caracal scats collected at each of the three treatment sites.	17
Figure 2.2 Percentage of mammalian biomass consumed across the three treatments as based on seven mammal categories.	24
Figure 3.1 Locations of the camera trap stations installed between 2015 – 2020 on a farm in the Karoo, South Africa.	35
Figure 3.2 Summary of the diel activity patterns of caracals in the Karoo, South Africa.	45
Figure 3.3 Seasonal activity patterns of caracals on a non-lethal treatment farm in the Karoo, South Africa.	45
Figure 3.4 Density estimates of daily activity patterns of caracals and their main prey, competitors, humans, and livestock based on Dhat4 (Δ_4) estimators, on a predator-friendly farm in the Karoo, South Africa.	48

List of appendices

With abbreviated captions

Appendix 1 Prey items recorded in caracal scat collected at the control site, just outside of Beaufort West, Western Cape, South Africa.....	79
Appendix 2 Prey items recorded in caracal scat collected at the lethal treatment site, just outside of Beaufort West, Western Cape, South Africa.	82
Appendix 3 Prey items recorded in caracal scat collected at the non-lethal treatment site, just outside of Beaufort West, Western Cape, South Africa.	85
Appendix 4 The cumulative dietary Shannon diversity index against the increasing number of scats for the control (a), lethal (b) and non-lethal (c) treatment sites in the Karoo, South Africa.....	88
Appendix 5 Biomass consumed, as calculated from caracal scat (n = 58) collected at the control site, just outside of Beaufort West, Western Cape, South Africa.	89
Appendix 6 Biomass consumed, as calculated from caracal scat (n = 88) collected at the lethal treatment site, just outside of Beaufort West, Western Cape, South Africa.....	93
Appendix 7 Biomass consumed, as calculated from caracal scat (n = 96) collected at the non-lethal treatment site, just outside of Beaufort West, Western Cape, South Africa.	97
Appendix 8 Probability values associated with each adjusted residual calculated in the Chi-square diet analysis against the associated Bonferroni adjusted alpha values.	101
Appendix 9 Description and locations of camera trap stations on a non-lethal farm just outside of Beaufort West, Western Cape, South Africa.	102

Chapter 1: General introduction

1.1 Human-wildlife conflict

Human-wildlife conflict (HWC) can be defined as having the needs and behaviour of animals negatively impacting the goals of humans (Madden, 2004). This conflict may not always be between just the humans and the wildlife directly involved, but also between the humans affected by wildlife, and those attempting to speak on behalf of the wildlife, such as conservationists (Madden, 2004; Redpath et al., 2015). HWC is a worldwide phenomenon and affects societies from both developed and developing countries (Zarco-González & Monroy-Vilchis, 2014). The conflict arises as a result of a growing human population, and with that comes the need for more land for human settlements, along with increasing food production and plantations (Geist & Lambin, 2002). Areas that are more prone to conflict are those buffering protected areas, as animals often wander into these adjacent areas (Distefano, 2005). These conflicts have consequences for both the wildlife and humans involved. Ogada et al. (2003) noted that the species involved in the conflict are often those that are prone to extinction, as in the case of the critically endangered Bornean Orangutan (*Pongo pygmaeus*) (Swarna Nantha & Tisdell, 2009) and the endangered African wild dog (*Lycaon pictus*) (Gusset et al., 2009), but HWC can also commonly affect least concern species.

Human-wildlife conflict can take on many forms. It involves the collision of animals and vehicles (Storm et al., 2007); the raiding of village food stores by animals (Worthy & Foggin, 2008); the transmission of diseases from wildlife to domesticated livestock (Distefano, 2005); the raiding of crops by rodents, elephants, and primates (Saj et al., 2001; Fungo, 2011) and in extreme cases, the loss of human life (Woodroffe, 2000; Dunham et al., 2010). Although the various forms of HWC causes real problems, the effects can be exaggerated by those involved to receive more compensation, or in an attempt to eliminate the wildlife before they cause additional losses for them in the future; this is true particularly in poorer regions of the world (Kruuk, 1980; Mizutani, 1993; Oli et al., 1994; Rasmussen, 1999).

1.1.1 Human-carnivore conflict

Human-wildlife conflict often involves carnivores, and in that case, it is known as human-carnivore conflict (HCC) (Ogada et al., 2003; Thorn et al., 2012). This type of conflict is one of the most commonly reported forms of HWC worldwide. Carnivores maintain large home ranges, usually overlapping with agricultural lands; in addition, they require a protein-rich diet, which often places them right at the centre of conflict with humans (Treves & Karanth, 2003). On agricultural lands, all natural ecosystems are collapsed and thus the natural prey species of carnivores would often be in short supply (Graham et al., 2005; Gusset et al., 2009). Therefore, to supplement their diets, carnivores revert to domestic livestock, game and may even pose a threat to human lives (Treves & Karanth, 2003; Manoa & Mwaura, 2016). Human-carnivore conflict in the form of predators killing livestock on farmlands is a form of HCC that has been steadily increasing over the years, as a result of the expansion of agricultural lands into natural predator territories (Treves & Karanth, 2003; Manoa & Mwaura, 2016).

The combination of human-modified landscapes, the loss of a natural prey base, the specialization of carnivores for ungulate predation, and the inability of domestic livestock to adequately defend themselves against predators, creates conflict on farmlands (Mishra, 1997; Linnell et al., 1999). At times, carnivores have displayed “surplus killing”. This occurs when a predator gets into an enclosed area with unprotected livestock and kills more animals than it would eat (Nowell & Jackson, 1996; Linnell et al., 1999). This is due to the predatory instincts of the carnivore setting in when the prey behaves erratically in an attempt to escape (Nowell & Jackson, 1996). This often leads to the retaliatory killing of all carnivores on farms regardless of whether or not they are the problem-causing individuals (Gipson, 1975; Horstman & Gunson, 1982; Sacks et al., 1999). As a result, HCC is noted as one of the most prominent causes of the decline in carnivore numbers worldwide (Graham et al., 2005)

1.1.2 Human-carnivore conflict in South Africa

Human-carnivore conflict is particularly prevalent in South Africa. The total amount of land dedicated to grazing by livestock and game in South Africa amounts to 68.6% (Department of Agriculture Forestry and Fisheries, 2017). Therefore, along with this increased arena for conflict, livestock depredation by carnivores on farms is one of the

more common forms of conflict in South Africa (Butler, 2000; Schiess-Meier et al., 2007). In 2010, the reported monetary value of losses due to predation on farms totalled R1,390,453,062 in South Africa and R104,980,967 in the Western Cape alone (Van Niekerk, 2010). As a result, HCC on farms remains one of the main causes of the death of carnivores in South Africa (Kruuk, 2002).

Conflicts in the rural areas of southern Africa with larger predators such as lions (*Panthera leo*), leopards (*Panthera pardus*), spotted hyaenas (*Crocuta crocuta*) and cheetahs (*Acinonyx jubatus*) are well documented (Marker et al., 2003; Thorn et al., 2012). However, conflicts with smaller carnivores are not uncommon and have been highlighted since the mid-1970s (Gipson, 1975). Conflicts may readily arise with caracals (*Caracal caracal*) and black-backed jackals (*Canis mesomelas*). Caracals, along with black-backed jackals, are highly persecuted on farmlands in southern Africa due to their reputation as “livestock killers” (Lensing & Joubert, 1976; Marker & Dickman, 2005; Avenant & Du Plessis, 2008; Du Plessis et al., 2015). Caracals, black-backed jackals and leopards are considered to be the biggest contributors to livestock losses in South Africa (Avenant & Du Plessis, 2008). According to Avenant & Du Plessis (2008), livestock losses were reported at 2.8% in the 1980s, and have steadily been increasing along with the expansion of agricultural lands. In 2008, the amount of livestock losses due to predation by caracals and black-backed jackals had grown to 30-75% in areas of the Western Cape, Northern Cape, Eastern Cape, the Free State and Mpumalanga provinces of South Africa (Avenant & Du Plessis, 2008). These losses negatively affect food security and pose a threat to the livestock industry of South Africa (Thorn et al., 2012; Bergman et al., 2013; Nattrass et al., 2015; Kerley et al., 2017).

1.1.3 Predator management on livestock farms

The retaliatory killing of farm predators through lethal controls has been documented since 1652 when Jan van Riebeeck acquired sheep (*Ovis aries*) from the indigenous people of the Cape and had to defend them against the local predators (Nattrass et al., 2017). Today, lethal control continues throughout the world and is used on everything from spotted hyaenas in Kenya (Manoa & Mwaura, 2016), to wolves and coyotes (*Canis latrans*) in the United States of America (Kellert, 1985). Farmers in rural areas of southern Kenya have also admitted that they would kill a predator regardless of whether or not

there are laws against it (Rodriguez, 2007). In South Africa, the state condones lethal predator control measures as long as the pursuers possess the permits to do so (Molewa, 2010). These lethal controls may include the use of gin-traps, the fitting of poison collars on sheep and cattle to kill any animal that tries to bite it, shooting the predator, or using dog packs to track down the predator (Molewa, 2010).

Often, the effectiveness of lethal control depends on the social organization and resilience of the focal species (Frank & Woodroffe, 2001). While the numbers of apex predators such as lions and leopards have suffered as a result of intense lethal predator control methods, mesopredator numbers continue to rise (Minnie et al., 2016). Studies have shown that the lethal control of a predator does not necessarily provide a viable solution, particularly as these are mostly unselective (Treves & Karanth, 2003). This is due to the fact that up to 71% of the carnivores killed through lethal predator control methods on farms were not related to the attacks on livestock, meaning that the problem individuals were not successfully removed from the system (Gipson, 1975; Horstman & Gunson, 1982; Sacks et al., 1999). It has also been demonstrated that soon after the removal of carnivores, conflicts may resume in that very same area (Karanth & Madhusudan, 2002; Treves et al., 2004).

The state does promote non-lethal predator controls, which do not require a permit (Molewa, 2010). In a recent study comparing the effectiveness of lethal and non-lethal predator control methods, non-lethal controls were seen to be nearly 50% more effective than lethal controls (Treves et al., 2015), and have been shown to be significantly more cost-effective and effective at reducing depredation for longer periods of time (McManus et al., 2015). Thus, it is becoming more common for farmers to use non-lethal predator controls (Du Plessis et al., 2018). These non-lethal controls include bell collars, livestock-guarding dogs and the use of donkeys (Swanepoel, 2016). Other methods to serve against losses through predation, are through husbandry techniques such as herding and corralling (Turpie & Babatopie, 2018). These are old techniques of farming, which are proving to be increasingly effective. Herding refers to a technique whereby animals are brought together in a group and are moved around from one area to another under the supervision of a shepherd (Lesur et al., 2014). The animals are then placed in a corral at night, which is a protective enclosure (Swanepoel, 2016). By making use of this combination, veld resource limitation due to overgrazing is less of an issue, as the herd can simply be moved

into a new area for grazing when necessary (Lesur et al., 2014; McManus et al., 2018). Ogada et al. (2003) have also demonstrated that the presence of humans alone is enough to discourage depredation by carnivores such as lions, leopards and hyaenas.

1.1.4 Apex predators and humans as threats to mesopredators

Apex predators have a profound and mostly negative effect on the numbers of mesopredators in the wild (Bissett et al., 2015). These impacts on smaller predators are thought to be through one of two mechanisms, namely lethal and non-lethal effects (Gordon et al., 2015). In lethal effects, the apex predator may kill the mesopredator directly, and in non-lethal effects, the presence of an apex predator in a given environment may cause the mesopredator to change their behaviour and activity patterns (Durant, 2000), as well as how they use their environment, in order to avoid the apex predator (Ritchie & Johnson, 2009). The effects of apex predators on mesopredators are well documented in African wild dogs, spotted hyaenas, and lions (Gorman et al., 1998; Creel, 2001). In regions where African wild dogs and spotted hyaena distributions overlap, African wild dogs have had to increase their foraging times from 3.5 hours to 12 hours per day; this is to account for the losses experienced through kleptoparasitism by hyaenas (Gorman et al., 1998). Furthermore, the killing of African wild dogs by lions and spotted hyaenas have allowed for the fragmentation of their populations throughout their distribution (Creel & Creel, 1996).

Apex predators play an important role in structuring the ecosystem by removing old, sick, or weak individuals from a landscape (Lewis et al., 2017). In so doing, they also keep population numbers in check (Dorresteijn et al., 2015). In regions where humans are dominant, they may take on the role of apex predators (Dorresteijn et al., 2015; Kamler et al., 2020). The human impact on ecosystems can be seen in two ways, namely through bottom-up control or through the influence of top-down controls (Dorresteijn et al., 2015). In bottom-up control, humans change the landscape by using the land for agricultural processes which may, in turn, affect the abundances of herbivores on which predators depend, and also by causing fragmentation of predator populations (Foley et al., 2005; Muhly et al., 2013). In the top-down control mechanism, humans could directly kill the predator through lethal control measures (hunting, poisons, etc.) or through the harvesting of their prey items (Ordiz et al., 2013). Therefore, it is noted by Dorresteijn et al. (2015),

that by studying ecosystems in which humans and predators have coexisted in the past, it can provide a means for coexistence in present times.

1.2 Caracal ecology

The caracal, (*Caracal caracal*, Schreber, 1776) is a widespread species that occupies a wide range of habitats in Africa and Asia (Avgan et al., 2016). As a result of their high degree of adaptability, caracals are listed as least concern by the IUCN (Avgan et al., 2016). This is due to a large and stabilised population base in southern Africa, which houses the greatest concentration of caracals (Avgan et al., 2016). However, they are critically endangered in the northern regions of Africa and in some areas of Asia (Avgan et al., 2016).

Caracals are solitary, nocturnal, and elusive animals, and therefore many aspects of their ecology are not well known (Avenant & Nel, 1998; Du Plessis et al., 2015). As a result of their elusive nature, they are one of the least studied felids (Brodie, 2009). In particular, caracal activity is one of the most under-studied fields of caracal ecology (Du Plessis et al., 2015; Minnie et al., 2018). Although once thought to be strictly nocturnal, caracals have been shown to alter their patterns of activity depending on the ambient temperature, rather than the time of day, along the West Coast of South Africa (Avenant & Nel, 1998), and during winter months in Iran (Farhadinia et al., 2007). Another factor influencing their activity patterns is proximity to humans. When faced with persecution, caracals display increased nocturnal behaviour (Ramesh et al., 2017). In protected areas where human presence is minimal, caracals would be seen hunting during the day, as opposed to solely hunting at night (Meyer, n.d.). Minnie et al. (2018) have also suggested that caracal activity could be mirroring that of their main prey species in the area.

Caracals are generalist predators, consuming mammals, birds, arthropods, and reptiles (Avgan et al., 2016). As a result of their role in HCC on livestock farms, Du Plessis et al. (2015) noted that caracal diet is one of the best studied aspects of caracal ecology. Studies found that within the Karoo National Park, the preferred caracal diet consists of small mammals, such as rock hyrax (*Procavia capensis*), but this switches to smaller ungulates when the rock hyrax abundances decrease (Palmer & Fairall, 1988). In other semi-arid regions, caracals consume mostly smaller mammals, such as rodents, rock hyrax, and

hares, while on farmlands, larger prey items such as wild ungulates and livestock are favoured (Avenant & Nel, 2002). Therefore, they are known to take prey that is most abundant in their environment (Avenant & Nel, 2002; Melville et al., 2004). Caracals were found to consume livestock only when their natural prey abundances are low (Du Plessis et al., 2015; Drouilly et al., 2018a). In addition, they can also be beneficial on farms, as they control the rodent and small mammal populations that consume the groundcover on which livestock are dependent (Grobler, 1981; Stuart, 1982; Moolman, 1986; Palmer & Fairall, 1988; Stuart & Hickman, 1991).

Caracal home range size differs according to sex and habitat. In regions where the prey base is low, such as in arid regions, caracals defend larger territories, as opposed to regions in which prey species are abundant (Farhadinia et al., 2007). For females, this ranges from 7.39 km² in the West Coast National Park of South Africa (Avenant & Nel, 1998) to 57.3 km² in the Arava Valley in Israel (Weisbein & Mendelssohn, 1990). Many more studies have been done on the home range sizes of male caracals, and this varies between 15.2 km² in the Mountain Zebra National Park of South Africa (Moolman, 1986) and 1116 km² in the Harrat al-Harrah Reserve in Saudi Arabia (Van Heezik & Seddon, 1998).

Knowledge on caracal habitat selection in southern Africa is vastly lacking (Du Plessis et al., 2015). Caracal habitat selection is assumed to be based on the need for sufficient vegetation cover for ambush, as well as sufficient prey availability (Minnie et al., 2018). Within the KwaZulu-Natal midlands of South Africa, Ramesh et al. (2017) found that caracals favoured agricultural areas and exotic plantations over natural sites. This is due to the easily accessible prey on farmlands when natural prey abundances are low, and the cover that the exotic plantations provide from human persecution in the region (Melville & Bothma, 2006a; Ramesh et al., 2017).

1.2.1 Caracals on farmlands in southern Africa

Removing caracals using non-selective predator control methods encourages a certain ecological chain of events, which can exacerbate the problem. As a result of the intense conflict, compensatory life-history mechanisms appear to have come into play, with caracals on farmlands producing larger litters and reproducing at younger ages (Avenant & Du Plessis, 2008). By removing a territorial individual on a farm, it opens a new gap

for a young, dispersing, and inexperienced individual to fill (Avenant & Du Plessis, 2008). Furthermore, it may allow for increased immigration and compensatory reproduction, leading to a reduction in the natural prey base and thereby promoting the killing and consumption of livestock (Avenant & Du Plessis, 2008; Minnie et al., 2016). It is possible that through lethal control measures, those surviving individuals can pass on their learned aversion techniques to their offspring in order to promote the survival of their offspring (Jorgensen et al., 1978; Treves, 2002). Therefore, studies on the ecology of predators are useful in determining effective predator-control management techniques that can be used on farms (Ramesh et al., 2017).

1.3 Rationale for the study

Studies focussing on caracal diet and ecology, which are conducted in HCC prone areas, are important, as livestock depredation results in substantial losses for South Africa each year (Van Niekerk, 2010; Ramesh et al., 2017). Therefore, it is important to understand caracal ecology in order to devise effective predator management techniques (Kerley et al., 2017). Through the study of diet, the actual threat that caracals pose to South Africa's food security can be assessed. Similarly, through the study of caracal ecology, the hotspots of caracal habitat use can be brought to light, and we can better reduce HCC. No other studies have compared the effects of lethal and non-lethal husbandry techniques on the diet and behaviour of caracals in the Karoo, South Africa.

1.4 Study sites

The study took place in the Beaufort West district of the Western Cape province of South Africa in the Great Karoo. In this region, the dominant vegetation biome is Nama Karoo (Low & Rebelo, 1996). The area is characterised by low rainfall, averaging 220 mm per annum, with summer (October – March) being the rainy season (Figure 1.1) (Mucina et al., 2006). In summer, the daily temperatures can reach up to 43°C. As a result, prolonged droughts are common. During the winter months, temperatures can drop to -5°C, and snowfall and frost are common (Figure 1.1) (Booyesen & Rowsell, 1983; Mucina et al., 2006).

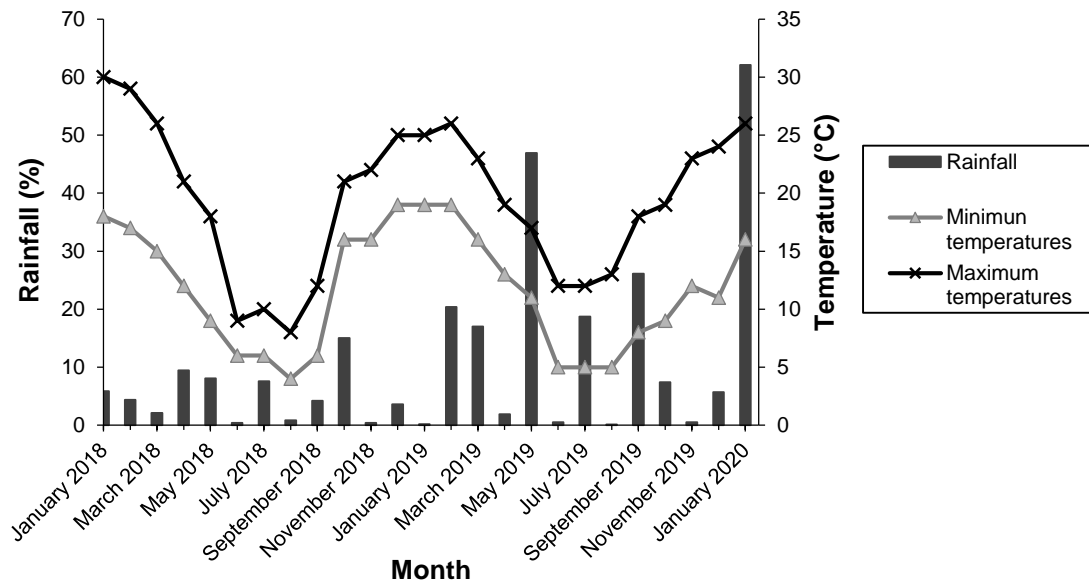


Figure 1.1 Total monthly rainfall (mm), and average minimum and maximum temperatures (°C) for January 2018 to January 2020 for the Beaufort West region of South Africa (data retrieved from: <https://www.worldweatheronline.com/>).

1.4.1 Geology and soils

The study sites for this thesis are located along the Nuweveld Mountain range. The altitude in this region varies from around 1150 m up to 1430 m (Mucina et al., 2006). The soils were created from the erosion of the underlying sedimentary and igneous rocks of the Cape Supergroup (Mucina et al., 2006). Soils are weakly structured, shallow, and predominantly basic due to the presence of lime deposits (Watkeys, 1999). On the outcrops, the soils are rich in calcium carbonate with medium sandy-clay loams (Watkeys, 1999; Mucina et al., 2006).

1.4.2 Vegetation

The Nama Karoo biome is characterized by low shrubs which are <1 m tall, interspersed with grasses, succulents, and geophytes (Mucina et al., 2006). Taller trees can also be found along the drainage lines and rocky outcrops (Mucina et al., 2006). The two main vegetation types found at these sites include the Upper Karoo Hardeveld and the Eastern Upper Karoo (Figure 1.2). The Upper Karoo Hardeveld can be found along steep hills, which are covered by large rocks and stones which support sparse dwarf Karoo scrub and drought-tolerant grasses (Mucina et al., 2006). Eastern Upper Karoo, on the other hand,

is found in flat areas and gently sloping plains and is dominated by dwarf shrubs and grasses (Mucina et al., 2006).

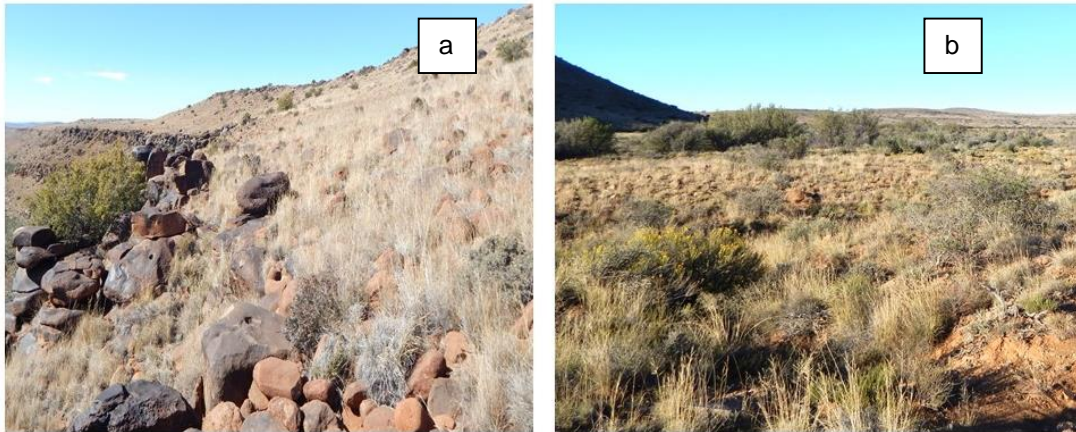


Figure 1.2 The two main vegetation types in the Nama Karoo biome, namely Upper Karoo Hardeveld (a) and Eastern Upper Karoo (b).

The study design included three treatment sites: a non-lethal treatment farm, a control site, and a lethal treatment farm (Figure 1.3). All sites were separated by “jackal-proof fencing” (wire mesh fencing secured by metal posts with rocks packed along the base).

UNIVERSITY of the
WESTERN CAPE

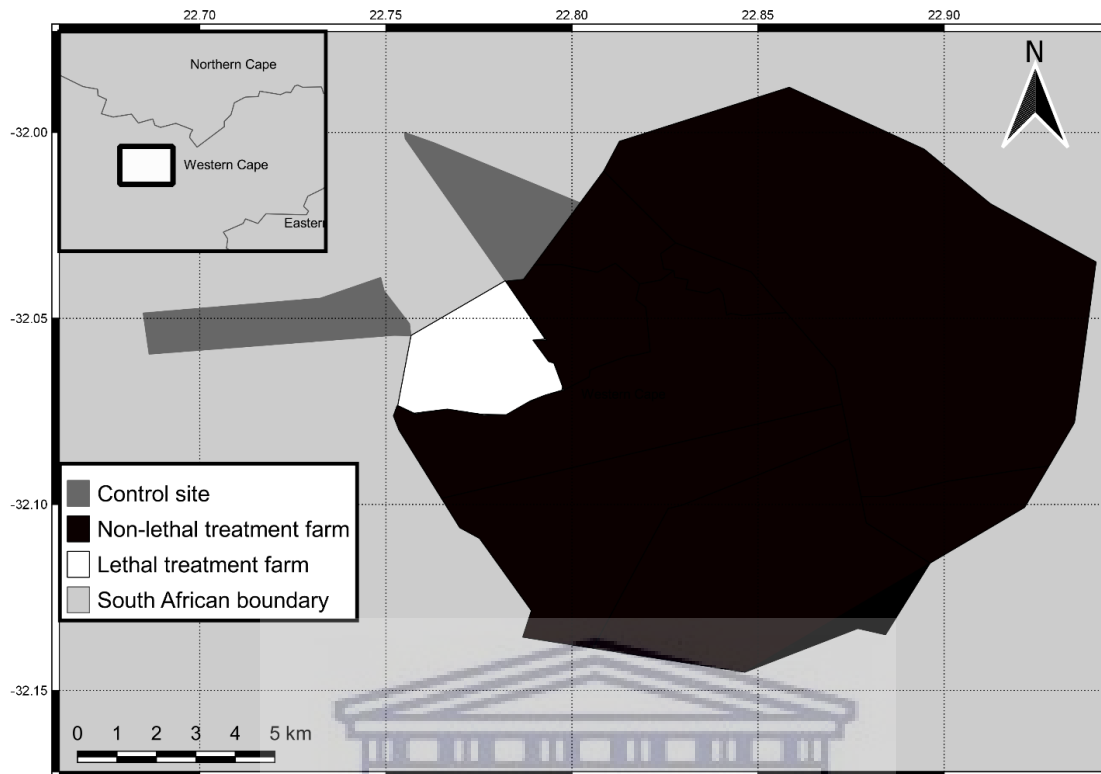


Figure 1.3 Map displaying the locations of the three study sites. The grey areas on the far left indicate the control site, the black area to the right of the map indicates the non-lethal treatment site and the white area between the control and non-lethal farm is the lethal treatment site. All sites are located just outside of the town of Beaufort West, in the Western Cape province of South Africa.

The non-lethal site, called Kromelboog (-32.018° ; 22.862°), at the time of the study encompassed 22 000 Ha and is managed for both livestock production and biodiversity conservation (McManus et al., 2018). Here, all lethal predator controls were removed in 2015, with ‘wildlife-friendly’ methods being used. These include 24-hour human herding and corralling at night, with specific seasons allocated for lambing (September to November). A separate 1 000 Ha area in which no grazing by livestock or livestock farming takes place, was used as a control site (-32.048° ; 22.754°). The lethal treatment site lies adjacent to the non-lethal site (Figure 1.3). The lethal treatment site (-32.054° ; 22.756°) encompasses 1 500 Ha on the western boundary of the non-lethal treatment farm (Figure 1.3). The lethal treatment farm continues lambing throughout the year. At the time of sampling, the lethal treatment site had 299 sheep (1 500 Ha; sheep density = 0.20), while the non-lethal treatment site had 1875 sheep (22 000 Ha; sheep density = 0.09).

Caracals and black-backed jackals are found at all three sites. The lethal treatment site had gin-traps set up along internal and external fences to catch predators, which the farmer then shot. In addition to the sheep, wild ungulates such as springbok (*Antidorcas marsupialis*), plains zebra (*Equus quagga*), kudu (*Tragelaphus strepsiceros*), steenbok (*Raphicerus campestris*), common duiker (*Sylvicapra grimmia*), gemsbok (*Oryx gazella*), Cape eland (*Tragelaphus oryx*), blesbok (*Damaliscus pygargus phillipsi*), and red hartebeest (*Alcelaphus buselaphus*) are also found on the farms (McManus et al., 2018).

1.5 Study aims and thesis structure

This study aims to assess the effects of lethal and non-lethal predator control on the diet and ecology of caracals in the Karoo, South Africa.

In this thesis, Chapter 2 investigates and compares the diet of caracals on lethal and non-lethal treatment livestock farms in the Karoo, as well as a control site (in which no farming takes place), through the use of scat analysis. The potential impacts of lethal and non-lethal predator controls on both caracals and the natural prey base are then discussed.

In Chapter 3, I investigate the habitat selection patterns of caracals on non-lethal treatment farms by testing eight *a-priori* models based on resource dispersion, human avoidance, livestock presence, interspecific competition, and environmental features, aided through the use of generalized linear mixed models (GLMMs). In addition, I examine the impact of temperature, human avoidance, prey availability, competitor avoidance, and livestock presence on the activity patterns of caracals on a non-lethal farm.

Chapter 4 provides an overview of my findings and discusses the major conclusions of this study. This chapter also provides management recommendations as well as suggestions for future research.

Chapter 2: Diet of caracals on lethal and non-lethal treatment farms in the Karoo, South Africa

2.1 Abstract

Caracals (*Caracal caracal*) are widespread, elusive predators in southern Africa. In the Karoo region of South Africa, caracals are considered a major contributor to small-livestock loss. As a result, pastoralists retaliate by using lethal controls, or in some cases non-lethal mechanisms, in an effort to reduce predation. Lethal controls are often indiscriminate, killing non-target species, thereby possibly limiting the amount of wild prey available to predators. The prolific use of lethal predator controls in this region raises the question of whether and how these techniques influence the diet of caracals. I assessed caracal diet from scat samples collected across three treatment sites on Karoo small-livestock farms to determine if the diet of caracals differs under these predator management techniques. The sites included a control site (no treatment), a lethal treatment site (a livestock farm that employed lethal predator controls), and a non-lethal treatment site (a livestock farm that employed non-lethal predator controls). Across all three treatment sites, caracals consumed small mammals, lagomorphs, rock hyraxes (*Procavia capensis*), invertebrates, and wild ungulates. On the non-lethal site, caracals showed a broader dietary niche breadth than on the lethal control site, possibly suggesting that more naturally occurring suitable prey is utilized on the non-lethal site. Domestic livestock were only consumed on the lethal treatment site and contributed less than 5% to the overall biomass consumed. This suggests that caracal diet differs under different husbandry management practices and highlights the importance of natural prey in caracal diet. In conclusion, where more natural prey is available, fewer livestock losses should occur due to caracal predation.

2.2 Introduction

Human-carnivore conflict (HCC) often arises as humans seek to inhibit predation on valued prey. Such conflict can lead to conservation issues if specific predators are completely removed from the system. For example, the exclusion of dingoes (*Canis dingo*) from farmlands through the use of wide-scale predator-proof fencing in South Australia has resulted in large-scale shrub encroachment (Gordon et al., 2017), where the absence of dingoes severely impacted upon trophic dynamics and ultimately caused a cascade in community structure.

As humans seek to manage wildlife, the predators involved would respond differently to challenges faced in areas that are managed for conservation, and those that are not. In particular, the diet of a predator is affected by habitat type, as this would have an influence on the type and availability of prey species (Avenant & Nel, 2002). For example, individuals residing in protected areas could have a different diet to individuals of the same species residing on nearby farmlands (Ott et al., 2007). This is due to a depleted natural prey base on farmlands in order to accommodate domestic livestock, which could in turn cause the carnivore to opt for livestock (Humphries et al., 2016).

Comparing carnivore diet in different land use zones, such as farmlands and more natural areas such as reserves, would therefore allow for a better understanding of why predation on livestock occurs (Bothma, 1966). It would also allow pastoralists to develop effective measures on how to reduce this threat based on the animal's ecology (Drouilly et al., 2018a). The optimal foraging theory predicts that as a particular food source becomes increasingly scarce, the predator makes greater use of alternative prey species, thereby increasing their dietary niche breadth (Pyke, 1984; González-Solís et al., 1997; Krebs & Davies, 2009).

Livestock farming dominates much of the landscape of South Africa, as is the case in the semi-arid region of the Karoo. Here, HCC is rife due to the threat of livestock predation. Understanding carnivore ecology in the region assists in understanding how severe the threat of predation is and how to effectively reduce it (Li et al., 2013; Du Plessis et al., 2015). In the Karoo, livestock farming is typically extensive, with livestock monitored sporadically (Nattrass & Conradie, 2018). Lethal carnivore control methods are employed

in an attempt to reduce predation (Drouilly et al., 2018a; Nattrass & Conradie, 2018). In some cases, non-lethal predator controls are employed, whereby carnivore deterrents are used and livestock are the focus of protection efforts, such as herding and corralling (McManus et al., 2015).

As a result of the extensive, and mainly lethal anti-predation measures used in South Africa in the past, many large carnivores have been extirpated from their historic ranges, leaving only the leopard (*Panthera pardus*) as the last free-roaming top carnivore, often restricted to mountainous regions (Norton, 1986; Sunquist & Sunquist, 2002). In the Karoo, caracals (*Caracal caracal*) and black-backed jackals (*Canis mesomelas*) are the dominant predators. This has facilitated their abundance in the area and has given them access to a wider range of prey items that would not be available to them if large predators were around (Prugh et al., 2009).

Caracals have generalist dietary behaviours, noted by their consumption of small (<1 g insects), to large (>30 kg ungulates) prey (Grobler, 1981; Palmer & Fairall, 1988; Avenant & Nel, 2002; Brackzkowski et al., 2012; Jansen, 2016; Drouilly et al., 2018a), and as a result, have been able to persist in a wide range of environments in southern Africa (Nowell & Jackson, 1996). Caracal diet in different regions often reflects which prey is most abundant in the environment (Avenant & Nel, 2002). Previous studies on caracal diet have mainly been conducted in reserves, where available prey occurs naturally (Grobler, 1981; Palmer & Fairall, 1988; Avenant & Nel, 1997; Melville et al., 2004). More recently, however, studies have been conducted on southern African farmlands (Pohl, 2015; Drouilly et al., 2018a; Neils, 2018; Jansen et al., 2019; Drouilly et al., 2020), but these have not determined whether caracal diet differs under lethal and non-lethal carnivore husbandry treatments.

In this study, I aimed to elucidate the diet of caracals on farms using different predator controls. My goals were firstly, to determine if caracal diet differed on lethal and non-lethal husbandry farms, and secondly, to assess the prevalence of domestic livestock in caracal diet under the different predator control methods. I predicted that more wild prey species will be consumed on non-lethal farms, as wild prey species would be less available on lethal treatment farms due to common lethal controls such as gin-traps (leg-hold traps) being indiscriminate, often killing non-target species which make up part of

the carnivore's natural diet (Rochlitz et al., 2010). Thus, I expected less dietary diversity on lethal treatment farms. I also expected livestock to be less accessible on the non-lethal treatment site due to a higher level of livestock protection. Therefore, I predicted that more livestock will be consumed on the lethal treatment site. This study may aid pastoralists in understanding caracal diet where livestock and natural prey are available, thus contributing to determining the best ways to reduce livestock depredation on their farms.

2.3 Materials and methods

2.3.1 Study area

The study was conducted at three sites. These included a control site where no livestock farming took place, one lethal treatment farm, and one non-lethal treatment farm. All treatment sites were separated by “jackal-proof fencing” (wire mesh fencing secured by metal posts with rocks packed along the base). All sites fall within the Beaufort West district of the Western Cape province of South Africa in the Great Karoo. See Chapter 1 for more information on the study sites.

2.3.2 Scat collection

Scats were randomly collected by walking along roads and game trails in each of the treatment sites (control, lethal, and non-lethal) between May 2018 and October 2018 (Figure 2.1). Caracal scats were differentiated from black-backed jackal scats based on shape (Stuart & Stuart, 1994), and origin was confirmed based on the presence of caracal fur, as they are self-groomers (Avenant & Nel, 2002). Any scats with uncertain origins were excluded from further analyses. As is the case with most felid species, caracals make use of scat deposits to mark their territory; therefore, a portion of the scat was left behind (Gorman & Trowbridge, 1989).

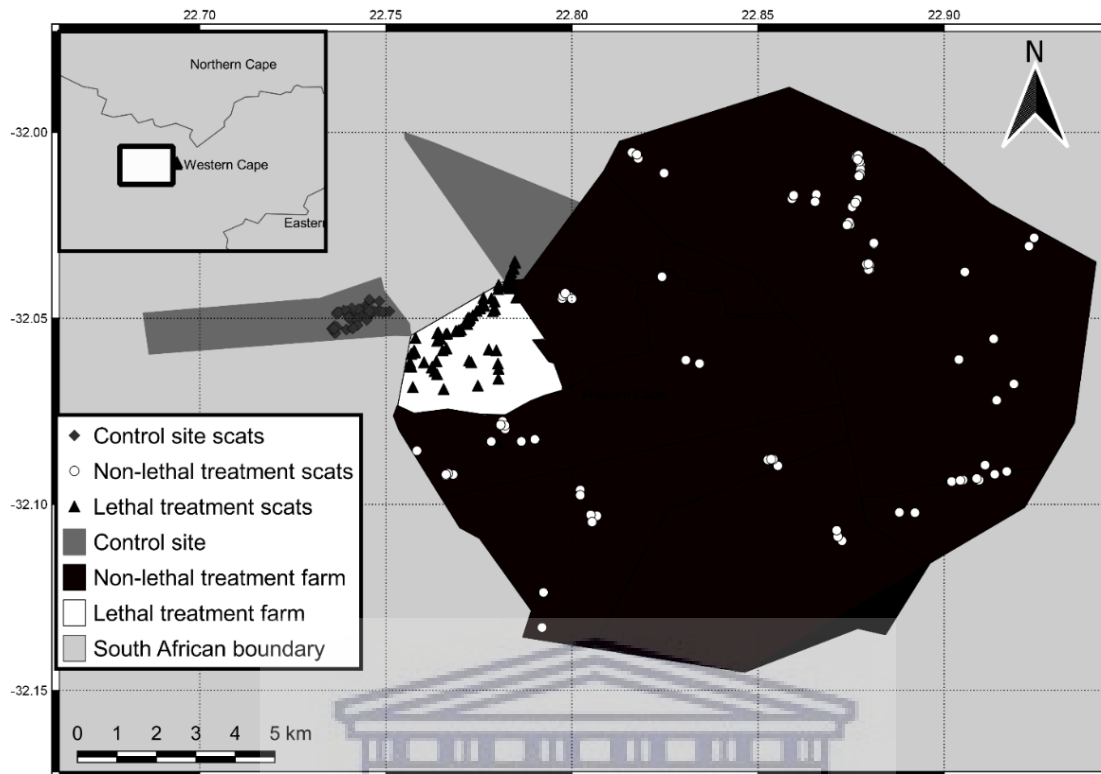


Figure 2.1 Caracal scats collected at each of the three treatment sites. Grey diamonds represent scats collected at the control site, black triangles represent scats collected at the lethal treatment site and white circles represent scats collected at the non-lethal treatment site.

2.3.3 Scat analysis

I processed the scats following procedures outlined in Melville et al. (2004). Individual scats were air-dried then weighed. Dried scats were placed in separate nylon stockings and soaked in boiling water to soften the scat (Klare et al., 2011). I washed the scats in their individual packages until only the insoluble matter remained (Melville et al., 2004). The scats were dried and the contents separated into the following groups: mammal hair, bone fragments, reptile (scales and claws), bird feathers, arthropod (wing and exoskeleton fragments), vegetation, gravel, and anthropogenic items (aluminium foil and fabric).

Mammalian hairs were placed in individual, labelled petri-dishes and left in 70% ethanol for at least 24 hours to clean them of any residual particles, rinsed in distilled water, and left to dry. Once dried, I randomly selected 15 hairs, and hair cuticular imprints were created on a clean microscope slide using clear nail polish (Ott et al., 2007). Photographs

were then taken of the hair cuticle imprints using a Leica DM500 microscope at 400x. The resulting imprints were compared to the Rhodes University hair reference collection, published keys (Dreyer, 1966; Keogh, 1979, 1983, 1985; Perrin & Campbell, 1980; Buys & Keogh, 1984; Schneider & Buramuge, 2006; Seiler, 2010; Taru & Backwell, 2014) and reference slides created from museum specimens. Rodent teeth were compared to published guides (De Graaf, 1981; Monadjem et al., 2015) for identification. Other macroscopic elements found in scats such as hooves, foot pads, and claws were used to confirm identifications.

2.3.4 Data analysis

I classified the prey items into 12 categories: invertebrates, reptiles, birds, wild ungulates, carnivores, domestic livestock (sheep, *Ovis aries*), small mammals (these included small rodents, shrews, and sengis), rock hyraxes (*Procavia capensis*), lagomorphs (these included Smith's red rock rabbit, *Pronolagus rupestris* and scrub hare, *Lepus saxatilis*), other mammals (these included Cape mole-rat, *Georychus capensis*; ground squirrel, *Xerus inauris* and unidentified mammals), anthropogenic items and vegetation.

To estimate caracal diet in each of the sites, I calculated the frequency of occurrence (FO), corrected frequency of occurrence (CFO) and mammalian biomass (MB) as outlined in Klare et al. (2011). These diet estimations have been used in previous caracal dietary studies (Brackzkowski et al., 2012; Jansen, 2016; Drouilly et al., 2018a), and were therefore selected for ease of comparison. The FO was expressed as n/N , where n is the number of prey items of a species and N is the total number of scat samples analysed. For the CFO, each scat had a weighting of one. If two prey items appeared in a scat, each item received a score of 0.5. Thus, this score decreased as the number of prey items per scat increased (Klare et al., 2011). These adjustments are necessary as the use of only FO overestimates the importance of small prey items such as invertebrates (Klare et al., 2011).

A biomass calculation is necessary to estimate how much of each prey item was consumed by the caracal. As in Jansen (2016), the percentage of mammalian biomass consumed was calculated according to the linear regression calculated for bobcats (*Lynx rufus*) developed by Baker et al. (1993):

$$y = 16.63 + 4.09 x$$

Where y is the weight of the prey consumed per scat collected (kg/scat) and x is the average body weight of the prey item (kg) (Bacon et al., 2011). This equation only applies to prey weighing ≤ 4.5 kg, as at this weight, the bobcat, and in this case the caracal, would ingest the entire animal, with the exception of some fur, rumen and viscera for prey such as rock hyraxes and lagomorphs (Jansen et al., 2019; Drouilly et al., 2020). For larger prey such as ungulates, the caracals will only feed on a portion of the prey item (Jansen et al., 2019; Drouilly et al., 2020). Therefore, Baker et al. (1993) proposed a correction factor of 27 for larger prey species. This biomass calculation was used as bobcats are closely related to caracals, have similar weight ranges, and would typically target similar sized prey (Baker et al., 1993; Skinner & Chimimba, 2005). Unidentified mammals were excluded from biomass calculations as prey weights are necessary for these analyses. Prey weights were taken from Stuart & Stuart (2015). Biomass was calculated as follows:

Biomass consumed (kg) = Prey weight (kg) x Number of occurrences

Relative biomass consumed (kg) = Correction factor x Frequency of occurrence.

A Chi-square analysis and Fisher's exact tests (when less than 5 prey items occurred in the category) were used to determine whether significant differences were present between the item categories consumed at each of the sites. Pairwise comparisons were also conducted to determine how similar the diets were to each other. Further, Bonferroni analyses were conducted to see where exactly these differences occurred. The results were assessed at $\alpha = 0.05$. In addition, I conducted a regression analysis to test whether the diversity of prey observed is linked to the number of scats collected. All statistical analyses were conducted in SPSS (version 23, IBM Corp, 2015).

Dietary niche breadth (B) developed by Levins (1968) was calculated to compare the degree of specialization at each of the three treatment sites. A specialist would have a relatively small niche breadth compared to a generalist (Donovan & Welden, 2001). The following equation was used:

$$B = \frac{1}{\sum p^2 i}$$

Where B is dietary niche breadth and p_i is the proportion of scats containing the resource i (Donovan & Welden, 2001).

Thereafter, the standardised niche breadth was calculated using the following equation:

$$B_A = \frac{B-1}{n-1}$$

Where B_A is the standardised niche breadth, which is a value between 0 and 1, B is the dietary niche breadth calculated using the equation above and n is the total number of food categories.

A Shannon index (H') was calculated using EstimateS software (Colwell, 2013) to test the sampling adequacy for diet diversity. H' is a measure of species diversity in a community. In this case, once the species diversity reaches an asymptote, it indicates that an adequate number of samples were collected at each site.

2.4 Results

A total of 242 caracal scats were analysed, with 58, 88, and 96 originating from the control, lethal and non-lethal treatment sites respectively. Excluding the number of unidentified mammals, a total of 38 prey taxa were recorded across the three sites (see Appendices 1-3). The control site had the fewest prey taxa recorded (20 prey taxa), followed by the lethal treatment site (27 prey taxa) and finally the non-lethal treatment site, which had the most prey taxa recorded (32). The regression analysis confirmed that the diversity of prey recorded among treatments was not as a result of biases in the sample sizes ($F_{1,2} = 18.81$, $p = 0.14$, $R^2 = 0.95$). The most commonly consumed prey items across the sites included small mammals, lagomorphs, rock hyraxes, invertebrates, and wild ungulates (Table 2.1). Reptiles were consumed in small amounts at all three sites, and birds were only consumed at the lethal and non-lethal treatment sites. Species diversity reached an asymptote at approximately 45 scats for the control site, and 70 and 75 scats for the lethal and non-lethal sites respectively (Appendix 4).

Table 2.1 Diet of caracal expressed as the frequency of occurrence (FO), corrected frequency of occurrence (CFO), and mammalian biomass (MB), at three treatment sites, in the Karoo, South Africa.

Prey categories	Control			Lethal			Non-lethal		
	% FO ¹	% CFO	% MB	% FO ²	% CFO	% MB	% FO ³	% CFO	% MB
Invertebrates	12.90	10.90		5.52	2.79		14.63	11.03	
Reptiles	2.42	1.36		1.66	1.33		2.93	2.04	
Birds	0.00	0.00		0.55	0.57		0.98	0.62	
Mammals	54.84	61.24	100.00	61.33	66.52	100.00	56.59	63.50	100.00
Wild ungulates	12.10	11.85	25.97	12.15	13.78	21.76	8.78	9.89	17.24
Carnivores	4.03	2.80	9.09	2.21	2.28	2.97	3.41	3.55	5.86
Domestic sheep (<i>Ovis aries</i>)	0.00	0.00	0.00	2.76	2.85	4.95	0.00	0.00	0.00
Small mammals	16.13	22.02	21.79	17.13	17.93	19.23	14.15	16.82	17.36
Rock hyraxes (<i>Procavia capensis</i>)	8.06	7.80	20.49	14.36	13.29	30.45	14.63	15.44	34.03
Lagomorpha	9.68	13.01	20.19	11.05	11.83	19.23	12.68	16.20	24.21
Other mammals	4.84	3.76	2.47	1.66	4.56	1.41	2.93	1.60	1.30
Anthropogenic items	0.00	0.00		1.66	2.00		0.00	0.00	

Vegetation	29.84	26.50	29.28	26.79	24.88	22.81
------------	-------	-------	-------	-------	-------	-------

¹ based on 124 prey occurrences and 58 scats collected July – September 2018

² based on 181 occurrences and 88 scats collected May – September 2018

³ based on 205 occurrences and 96 scats collected May – September 2018



UNIVERSITY *of the*
WESTERN CAPE

Overall, there was a significant difference in caracal diet between sites: Chi-square ($\chi^2 = 25.42$; d.f. = 12,1; $p = 0.01$) and Fisher's exact tests ($\chi^2 = 10.49$; d.f. = 6,1; $p = 0.04$). The Chi-square compared the prevalence of invertebrates, wild mammals, and vegetation in caracal diet amongst the three treatment sites, while the Fisher's exact tests compared the prevalence of reptiles, birds, domestic sheep and anthropogenic items in caracal diet amongst the three treatment sites. The CFO indicated that mammals made up the largest proportion of caracal diet across all sites. However, this proportion was slightly higher for the lethal treatment site (66.52%) compared to the non-lethal (63.50%) and control (61.24%) sites. Small mammals were the most commonly consumed prey items for both the control (22.02%) and the lethal treatment (17.93%) sites. At the non-lethal site, rock hyraxes were the most commonly consumed mammalian prey item (14.63%).

Mammalian biomass consumed at all three treatment sites amounted to approximately 25.59 kg. The mammals contributing the most were rock hyraxes (most frequent), lagomorphs, springbok, steenbok, and common duiker (less frequent). Together, these prey species contributed 65.91% to the total mammalian biomass consumed. The mammalian biomass consumed was highest for rock hyraxes at both the lethal (30.45%) and non-lethal (34.03%) sites. However, at the control site, wild ungulates dominated the mammalian biomass consumed, amounting for 25.97% (Figure 2.2). Sheep remains were only found in the scats collected at the lethal treatment site and contributed less than 5% of the total mammalian biomass consumed at that site. Overall, although higher numbers of small mammals such as Karoo bush rats (*Myotomys unisulcatus*) and hairy-footed gerbils (*Gerbillurus paebe*) were consumed, when the correction factors were applied, larger mammals such as steenbok and common duiker were seen to be of greater importance to caracal diet. The broadest dietary niche breadth was found at the non-lethal site (0.56), and with the narrowest at the lethal control site (0.48), while the control site had a standardised dietary niche breadth of 0.50.

Total mammalian biomass consumed at the control site was 24.37 kg (Appendix 5), of which rock hyraxes, lagomorphs, springbok, Karoo bush rats, and African wildcats (*Felis silvestris lybica*) contributed 66.40% of the overall biomass consumed (Figure 2.2). The total mammalian biomass consumed at the lethal treatment site was 24.81 kg (Appendix 6), which was slightly more than at the control site. Rock hyraxes, lagomorphs, common duiker, springbok, bush pig (*Potamochoerus larvatus*), and sheep contributed 70.47% to

the total amount consumed (Figure 2.2). Domestic livestock contributed less than 5% of the total biomass consumed (Table 2.1). The total mammalian biomass consumed on the non-lethal treatment site was 25.17 kg (Appendix 7), which was more than the other treatment sites. At this site, rock hyraxes, lagomorphs, steenbok, hairy-footed gerbil, and springbok contributed over 70% to the overall biomass (Figure 2.2).

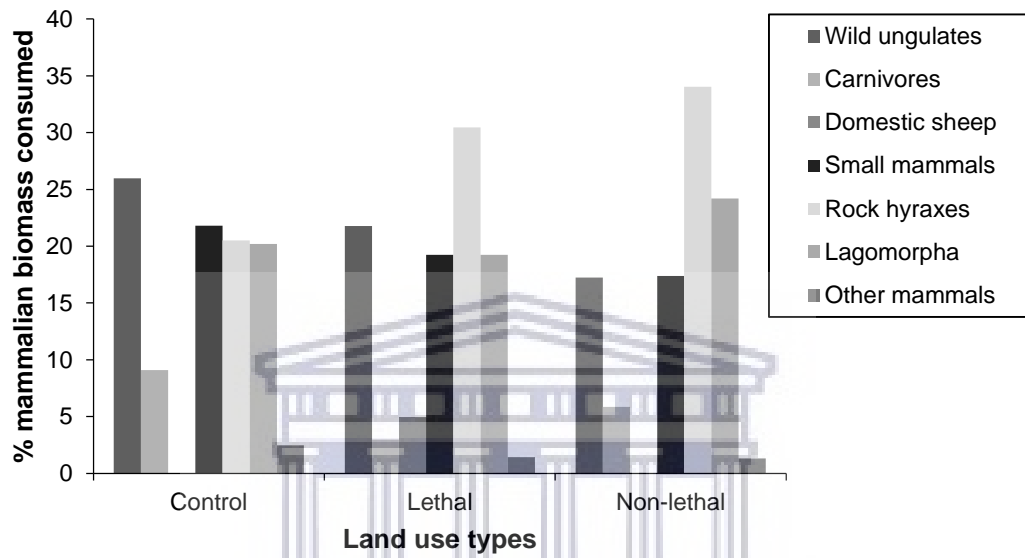


Figure 2.2 Percentage of mammalian biomass consumed across the three treatments as based on seven mammal categories. Small mammals included small rodents and shrews; other mammals included cape mole-rats and ground squirrels.

2.4.1 Pairwise comparisons

The control site was similar to both the lethal and non-lethal treatment sites, as no significant differences were recorded from the Chi-square ($\chi^2 = 11.27$; d.f. = 6,1 [lethal]; $\chi^2 = 2.20$; d.f. = 4,1 [non-lethal]; $p > 0.05$) and Fisher's exact tests (d.f. = 6,1 [lethal]; d.f. = 4,1 [non-lethal]; $p > 0.05$). However, significant differences were found between the lethal and non-lethal treatment sites in both the Chi-square ($\chi^2 = 18.40$; d.f. = 6,1; $p = 0.05$) and Fisher's exact tests (d.f. = 6,1; $p = 0.002$). These differences were accounted for in the invertebrate and domestic livestock categories on the lethal and non-lethal treatment sites as revealed by the Bonferroni analyses (Appendix 8).

2.5 Discussion

The diet of ‘damage-causing’ animals is of great concern to pastoralists in South Africa. However, many dietary studies have focused outside the areas of conflict (Du Plessis et al., 2015; Minnie et al., 2018). From the farms studied, caracal diet differed significantly across the three land use types, although with no differences found when comparing the control and lethal sites, and control and non-lethal sites. However, significant differences were found between the two treatment sites. At each site, small mammals, lagomorphs, rock hyraxes, invertebrates, and wild ungulates were the most commonly consumed items. These results concur with other studies on caracal diet in the area (Palmer & Fairall, 1988; Drouilly et al., 2018a). Vegetation was consumed in large quantities at all sites, but was considered as ingested and not prey (Speelman, 1939; Bothma, 1965). Invertebrates were more prominent in caracal diet on the non-lethal treatment site, and accounted for the significant difference between caracal diet on the lethal and non-lethal sites (Table 2.1). Similar to findings on caracal diet in reserves and other arid regions, arthropods are likely consumed to supplement their diet when preferred foods such as rock hyraxes and lagomorphs are sparse (Palmer & Fairall, 1988; Kok & Nel, 2004; Melville et al., 2004; Drouilly et al., 2018a). Invertebrates, and coleopterans in particular, are common in arid areas and can reach large enough sizes to be effectively captured by felids (Palmer & Fairall, 1988).

The presence of domestic livestock (sheep) was only found in scats collected on the lethal treatment site. However, this low prevalence of livestock in caracal scats is not common in other studies conducted on South African farmlands (Pringle & Pringle, 1979; Moolman, 1984; Jansen, 2016; Drouilly et al., 2018a). The non-lethal treatment site had the broadest niche breadth, while the lethal treatment site had the narrowest. This could suggest that the type of husbandry technique used (i.e. lethal vs non-lethal predator control) could affect the type of prey available to predators (although this could not be quantified) and that caracal diet differs accordingly.

Caracals have a varied diet across their range. They have had to adjust to different prey bases and seasonal fluctuations in available resources in different habitats, therefore they are considered generalists and opportunistic feeders (Avenant & Nel, 2002). It was found that small mammals represent a large proportion of caracal diet in the Karoo, but this is

somewhat surprising as livestock grazing and trampling on farmlands is known to have a negative impact on rodent populations (Hoffmann & Zeller, 2005). On the other hand, this could explain why the proportion of small mammals was slightly higher in caracal diets on the lethal treatment site, as the livestock remain in one corral, whereas on the non-lethal treatment site, the livestock are moved into different areas of the farm on a fortnightly basis (pers. comm.).

Rock hyraxes and lagomorphs also featured significantly in caracal diet, as was the case in other studies conducted throughout South Africa (Grobler, 1981; Moolman, 1984; Palmer & Fairall, 1988; Drouilly et al., 2018a). During the summer months, rock hyraxes forage far from their crevices during only the darker parts of the day to evade predators. However, since food quality and quantity is lower during the winter months, they have to forage far from their crevices at all times and spend more time basking, which makes them especially vulnerable to predators (Brown & Downs, 2005). This could explain why rock hyraxes featured so significantly in caracal diet at the sites sampled.

Wild ungulates were another group of highly consumed mammals at all sites. It was expected that neonates of wild ungulates would be preferentially consumed over adults as a result of energy requirements and reducing the risk of injury (Avenant & Nel, 2002). As found elsewhere, caracals only consumed wild ungulates that employ the hider maternal strategy (steenbok, springbok and common duiker) and not the follower maternal strategy (black wildebeest, *Connochaetes gnou* and blesbok, *Damaliscus pygargus phillipsi*), making them easier prey (Klare et al., 2010; Drouilly et al., 2018a).

Although caracals are elusive, and primarily nocturnal, strictly diurnal prey was also recorded in caracal diet (such as ground squirrels) at all sampled sites. Avenant & Nel (1998) suggested that caracals in the West Coast National Park of South Africa displayed more diurnal activity during the cooler months. This was surprising to observe on farmlands in the Karoo, however, as caracals are highly persecuted, making diurnal activity risky. However, as scat sampling occurred during the winter months when small mammal numbers were possibly low (Melville & Bothma, 2006b), it may have been necessary for caracals to adjust their activity patterns in order to increase their encounter rates with diurnal prey (Avenant & Nel, 2002).

With livestock production comes competition between farmers and wildlife for available resources, often reducing natural prey and forcing predators to target domestic livestock (Sillero-Zubiri & Laurenson, 2001). Farmlands in the Karoo are typically vast and host large herds of unguarded livestock, as well as boreholes and reduced competitors, which allow livestock to persist at high densities (Turpie & Babatopie, 2018). Therefore, adopting the optimal foraging theory, it was expected that carnivores would select this easily accessible prey with a more clumped distribution (Pyke, 1984; González-Solís et al., 1997; Krebs & Davies, 2009). However, caracals appeared to preferentially select natural prey species. In arid regions, caracals have larger home ranges (Bothma & Le Riche, 1994; Marker & Dickman, 2005), and would therefore display broader niche breadths in order to maintain metabolic processes (Kok & Nel, 2004). Therefore, if there are low levels of natural prey available, livestock depredation could become an increased problem (Kaunda & Skinner, 2003).

Domestic livestock was only consumed at the lethal treatment site and contributed less than 5% to the overall mammalian biomass consumed there. This could be attributed to the different management styles of the husbandry sites which allowed for a higher density of sheep on the lethal treatment site (0.20 per Ha) in comparison to the non-lethal site (0.09 per Ha). Domestic livestock have been bred to have little to no physical defensive mechanisms against predators (Diamond, 2002), apart from behavioural adaptations that livestock may make use of to evade predation (Shrader et al., 2008). Nonetheless, the observed low abundance of sheep remains in caracal scat is indicative of their opportunistic nature, mirroring results by Drouilly et al. (2018a), who stated that caracals consume livestock in accordance with their accessibility. These results are similar to other studies focusing on Eurasian lynx (*Lynx lynx*) in the boreal forests of Norway (Odden et al., 2006). Although presented with large quantities of free-ranging sheep in the forests, lynx still preferred wild roe deer (*Capreolus capreolus*) which occurred in low densities during summer (Odden et al., 2006). Even when lynx were lactating and energy requirements were higher, sheep were ignored and females travelled more than 10 km in search of either roe deer or hare (Odden et al., 2006). This could be as a result of an innate aversion to sheep and owing to the creation of a specific search image engrained in them while learning to hunt as kittens (Odden et al., 2006). Similar findings were published for caracals in Namaqualand (Jansen, 2016), the Kgalagadi Transfrontier Park (Melville et

al., 2004), and in the Laingsburg region of the Karoo (Drouilly et al., 2018a), where caracals were found to select wild prey over livestock.

Conversely to the lethal treatment site, which had the lowest dietary niche breadth recorded, the non-lethal treatment site had a wider range of prey consumed, and caracals were found to have a significantly different diet between these sites. A broader niche breadth indicates more generalist behaviour, as opposed to a narrower niche breadth which alludes to a more specialised diet. This could suggest that less natural prey was available to caracals on the lethal treatment sites as a result of the indiscriminate nature of lethal controls employed by farmers in the area (Allan, 1989; Du Plessis, 2013; Ogada, 2014). Hayward & Kerley (2008) suggested that animals with larger dietary niche breadths are less susceptible to prey fluctuations and competition in their environment, ultimately leading to higher survival rates.

2.6 Conclusions and management implications

This is the first study to compare caracal diet on husbandry sites that employ lethal and non-lethal carnivore management practices. The generalist nature of caracals, along with high levels of both dietary and behavioural plasticity, allows them to persist on farmlands despite being highly persecuted. Caracals at the non-lethal treatment site had a broader niche breadth in comparison to those on the lethal treatment site, possibly suggesting that a greater variety of suitable prey occurred there. Domestic livestock was only consumed at the lethal treatment site and was found to contribute very little to the overall biomass consumed there. Domestic livestock herds were not guarded on the lethal treatment site, which could result in easier access to them than on the non-lethal treatment site where they were guarded 24/7 by herders. It is therefore suggested that livestock should be guarded in the evening, particularly during the lambing season and when small mammal numbers are low. Across all three treatments, caracals consumed small mammals, lagomorphs, rock hyraxes, invertebrates, and wild ungulates. Furthermore, this study has shown the importance of natural prey in caracal diet. Therefore, it can be inferred that if pastoralists allow a natural prey base to develop on their farms, it could reduce livestock depredation by caracals.

This study could be improved through the inclusion of more lethal and non-lethal husbandry sites, which was not possible during the scope of this thesis. There also cannot be absolute certainty that caracals captured and consumed prey and then defecated at the same site. However, a relationship was found between scat deposition and kill sites by Jansen et al. (2019), when looking at caracal GPS cluster visitations in combination with scat analysis. Further, no livestock losses were reported on the non-lethal treatment site at the time of sampling and no sheep remains were found in scats on the control and non-lethal treatment sites, ruling out the consumption of domestic livestock at one site and defecation at another. Based on the aforementioned, it is likely that this study captured accurate scat sites. Finally, future studies should take prey availability be taken into account at each of the sites in order to test caracal prey preference in relation to availability, as well as whether lethal controls do actually decrease the amount of available natural prey.



Chapter 3: Caracal habitat selection and activity patterns on a predator-friendly farm in the Karoo, South Africa

3.1 Abstract

There is a great need to understand the ecology of animals involved in human-wildlife conflict in order to develop effective management plans. Caracals (*Caracal caracal*), are highly persecuted on South African livestock farms as a result of this conflict, but due to their elusive nature, baseline information regarding their ecology is lacking. Therefore, I aimed to evaluate the effects of non-lethal predator management on caracal habitat selection and activity patterns. I used data from camera trap stations set up on a non-lethal predator control livestock farm in the Karoo, South Africa to evaluate the drivers of caracal habitat selection. Additionally, these camera trap data were used to assess the activity patterns of caracals, their main prey, competitors, humans, and livestock. Resource dispersion explained caracal habitat selection most strongly, while livestock had the weakest relationship to caracal presence. Scrub hare (*Lepus saxatilis*) presence, adequate vegetation cover, and rugged terrain provided optimal habitats for caracals on the farm. While caracals were historically persecuted on the farm and are still heavily persecuted on neighbouring farms, caracals did not display spatial human avoidance, but could instead be displaying temporal avoidance. The activity pattern analysis revealed that caracals were predominantly nocturnal throughout the year, shifting to crepuscular behaviour during winter months. Caracal activity patterns overlapped significantly with black-backed jackals (*Canis mesomelas*), lagomorphs, and common duikers (*Sylvicapra grimmia*). Surprisingly, caracal activity overlapped with rock hyraxes (*Procavia capensis*) the least, despite rock hyraxes making up a large component of caracal diet in the Karoo. Caracal activity patterns could therefore be attributed to human avoidance and temperature fluctuations. In conclusion, the presence of sufficient wild prey and natural environments on farms could aid in human-caracal coexistence.

3.2 Introduction

Mesopredators are well-adapted to life in altered environments, particularly livestock farms. However, living in these altered landscapes places them at greater risk of human-induced mortality as a result of human-carnivore conflict (Ramesh et al., 2017). Understanding which conditions or combinations of conditions strongly influence animal habitat selection and activity patterns on farmlands is essential to reduce human-carnivore conflict (Selvan et al., 2019).

Animal habitat selection is one of the most important aspects of animal ecology because it relates to how animals balance resources and threats in changing environments (Fernández et al., 2007). According to Hutto (1985), habitat selection is the choice, involving both innate and learned behaviours, made by an animal according to its requirements at both spatial and temporal scales of the environment. On one hand, it can be thought of as a function of the availability, arrangement and quantity of resources within a given environment (Dolman, 2012). Conversely, factors such as vegetation (namely the height and density thereof), and other physical landscape parameters such as terrain ruggedness and elevation, may affect resource selection functions (Apolloni et al., 2018). Available literature indicates that the distribution of predators is driven by the availability of prey, shelter, territoriality, absence of human disturbance, as well as connectivity to other occupied locations to find mates (Harper, 2007; Selvan et al., 2019). Therefore, through the study of these habitat selection patterns, we can understand the stability and survival ability of wild populations, as well as gain insight into the interactions of wildlife species and the communities surrounding them (Guo et al., 2017), thereby shedding light on the ability of species to survive under variable environmental conditions.

Human-altered landscapes are prevalent throughout the world. This affects the spatial arrangement of wildlife (Rich et al., 2016). Wildlife has had to adapt to patches of land harbouring suitable habitats; however, even these more suitable patches are affected by surrounding activities, which in turn affects the arrangement and availability of resources (Dellinger et al., 2013; Apolloni et al., 2018). One of the most common forms of land alteration is the conversion to agricultural lands (Rich et al., 2016). Mesopredators are able to thrive in land designated for the production of livestock, as they benefit from the

available livestock and the lack of larger predators (Ramesh et al., 2017). However, with a changing landscape comes a change in the type and amount of available prey. This leads to changes in behaviour and prey selection (Moreira-Arce et al., 2015a). In the natural forests of southern Chile, the culpeo fox (*Lycalopex culpaeus*) preferentially selected olivaceous field mice (*Abrotrix olivaceus*) over more abundant long-tailed colilargo (*Oligoryzomys longicaudatus*) and Chilean climbing mice (*Irenomys tarsalis*) but switched to these alternative prey in areas that have been transformed to exotic plantations (Moreira-Arce et al., 2015a). This demonstrates that the change in land use would ultimately affect prey availability and the way in which predators use their environment (Endler, 1986). It is therefore important to study mesopredator behaviours in natural systems as well as altered systems in order to see how they are affected by human-altered landscapes.

An important aspect of predator habitat selection is the availability of prey (known as the resource dispersion hypothesis; MacDonald, 1983). Likewise, avoiding human activity is equally important (Martín-Díaz et al., 2018). However, it is not always possible to find a habitat that satisfies both of these requirements simultaneously and predators may adapt their activity patterns to address these constraints (Martín-Díaz et al., 2018).

Alterations to diel activity patterns allow an animal to gain all the necessary resources while minimizing risks (Kitchen et al., 2000). These risks include, but are not limited to, human-induced mortality (Dorresteijn et al., 2015), predation (Ritchie & Johnson, 2009) and interspecific competition (Garvey et al., 2015). For this reason, the study of diel activity patterns should provide insight into how animals balance resources and threats under different conditions.

Threats and resource constraints change an individual's behaviour, thus changing population dynamics and altering evolutionary processes (Monterroso et al., 2013). For example, Kitchen et al. (2000) demonstrated that coyote (*Canis latrans*) populations that were exposed to intensive human persecution for more than 50 years (studied during 1983 – 1988) were nocturnal compared to the now diurnally active coyote populations in the same region that were exposed to human activity but with no persecution for eight years (studied in 1996 – 1997). Animals change their behaviour based on resources and threats, thus these factors affect species ecology (Monterroso et al., 2013; Tang et al., 2019).

Animal activity cycles could also depend on the activity of other animals. Different species occupying similar areas could adjust their activity patterns in order to coexist (Gerber et al., 2012). Prey species may re-adjust their activity periods to evade predation (Brown et al., 1988; Eccard et al., 2008; Gliwicz & Dąbrowski, 2008). Similarly, a predator may adjust their activity patterns to match that of their prey. Heurich et al. (2014), found that Eurasian lynx (*Lynx lynx*) activity patterns across Europe varied and seemed to mirror the most important ungulate prey in each region. Therefore, through the study of animal activity patterns, we can gain insight into a species' energetics, foraging effort and exposure to risk (Rowcliffe et al., 2014).

Caracals have previously been studied in southern Africa through the use of radio and GPS collars (Stuart, 1982; Norton & Lawson, 1985; Bothma & Le Riche, 1994; Avenant & Nel, 1998; Marker & Dickman, 2005; Ramesh et al., 2017; Jansen et al., 2019; Drouilly et al., 2020), with few of these studies concentrating on agricultural areas (Stuart, 1982; Marker & Dickman, 2005; Ramesh et al., 2017; Jansen et al., 2019; Drouilly et al., 2020). In conflict areas of southern Africa, male caracals occupy very large home range sizes in comparison to those in protected areas (Marker & Dickman, 2005). It is assumed that caracals would select habitats with sufficient vegetation cover and sufficient prey availability (Minnie et al., 2018), as well as steep terrain that would be difficult for humans to traverse (Guo et al., 2017). Caracals also exhibit more nocturnal activity in human-carnivore conflict zones, possibly to avoid human confrontation (Gaynor et al., 2018). However, in areas of little to no persecution, caracals display increased diurnal activity (Avenant & Nel, 1998). That being said, very little is known about caracal activity patterns and the factors influencing them under different environmental conditions, with most of the information available being concentrated on lethal treatment farms or within reserves (Du Plessis et al., 2015; Minnie et al. 2018).

In this study, I aim to identify the drivers of caracal habitat selection and diel activity patterns on a non-lethal livestock farm in the Karoo region of South Africa. I test whether the resource dispersion hypothesis, human avoidance, livestock presence, interspecific competition or environmental features are primary driving forces for caracal habitat selection. In addition, I examine the effect of prey, competitor, human and livestock presence, as well as the effects of seasonality on caracal activity patterns and discuss how this relates to human-carnivore conflict. I hypothesize that caracals would select habitats

that are rich in prey and would display increased diurnal behaviour in the non-lethal environment.

3.3 Materials and methods

The study took place on a livestock farm in the Karoo, where non-lethal controls are employed to prevent livestock predation. Between October 2015 and January 2017, livestock were free-roaming with no lethal predator controls in place. From January 2017 onwards, livestock were actively managed through the use of shepherds and corralling at night. The farm culminated a total area of 22 000 Ha (see Chapter 1 for more information).

3.3.1 Camera-trapping surveys

I used data from 31 camera trap stations (Cuddeback Attack IRTM) for this study (Figure 3.1). The cameras were set up across the farm at approximately 2 km intervals, in varying habitats within the farm borders (Appendix 9). Data was collected between October 2015 and January 2020. The cameras were programmed to take one photo followed by a 10 second video at each trigger, with three minute intervals before taking another photo. The cameras were positioned on posts approximately 40 cm above the ground and placed where caracals and other mammals were considered more likely to be captured in order to document all possible mammals on the farm. No baits or lures were used at the camera trap stations. As caracals generally lack identifying features, individuals and sexes could not be distinguished using camera trap images.

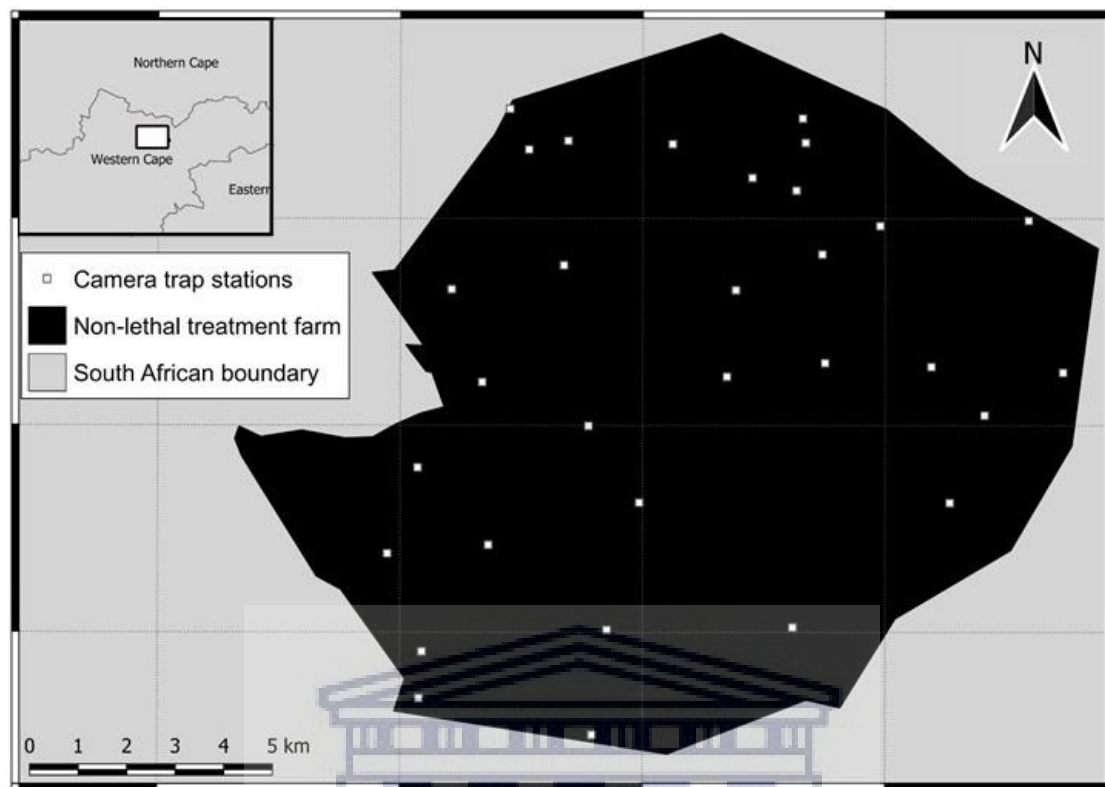


Figure 3.1 Locations of the camera trap stations installed between 2015 – 2020 on a farm in the Karoo, South Africa.

Images were tagged using digiKam (version 6.4.0, digiKam Team, 2020), EXIFTool (version 10.05, Harvey, 2015) and the R package CamTrapR (Niedballa et al., 2020). Consecutive images of the same species were filtered by one hour to eliminate duplicated records of the same individual. Therefore, data were considered independent events (Romero-Muñoz et al., 2010). The number of camera trap nights for each station was calculated as the sum of the days the camera trap was operational at a station (Soyumert et al., 2019).

3.3.2 Habitat selection

The small sample size available did not allow for the use of occupancy analyses (Allen et al., 2018), therefore I used a generalized linear mixed model (GLMM) to assess caracal habitat selection. GLMMs were selected as they provide value where data are not normally distributed and where random effects are at play (Bolker et al., 2009). The variables used in the models are explained below.

3.3.2.1 Biotic variables

Caracal presence or absence was inferred from camera trap data, indicating areas used by caracals and those areas not used but available to them. According to Jennelle et al. (2002), this is the best use of camera trap data when individuals cannot be individually identified, for studies such as density estimates. As in other studies, I used camera traps with caracal activity as presence locations and cameras without as absence locations in the models (Bowkett et al., 2008; Jenks et al., 2011; Rovero et al., 2013; Martin et al., 2015; Rovero et al., 2017; Allen et al., 2018; Soyumert et al., 2019).

As the camera traps were set up to target medium to large mammals (> 1 kg), small mammals such as rodents and shrews could not be represented in this analysis despite playing a large role in caracal diet on the non-lethal treatment farm (see Chapter 2). Therefore, prey species used in this analysis were springbok (*Antidorcas marsupialis*), common duiker (*Sylvicapra grimmia*), steenbok (*Raphicerus campestris*), rock hyrax (*Procavia capensis*), scrub hare (*Lepus saxatilis*) and Smith's red rock rabbit (*Pronolagus rupestris*), as these were found to be important prey in the area in previous dietary studies in the Karoo (Palmer & Fairall, 1988; Drouilly et al., 2018a; Chapter 2 of this thesis). Competitors such as black-backed jackals (*Canis mesomelas*) and vehicle activity (used as a proxy for human presence), were also included in the models. In addition, I also included livestock (sheep, *Ovis aries*) presence, as these could also influence caracal habitat selection. For models involving caracal competitors, main prey and livestock, I used relative abundance indices (RAI) per 100 camera trap nights (O'Brien & Kinnaird, 2011; Allen et al., 2018; Soyumert et al., 2019). These data were derived from the camera trap images taken between October 2015 and January 2020, while livestock data could only be used from October 2015 to January 2017, as the sheep were free-roaming on the farm without a shepherd during this time. The following equation was used to calculate RAI:

$$RAI = \left(\frac{E}{TN} \right) * 100$$

Where E is the number of independent events per camera trap station and TN is the number of trap nights per camera trap station. Although the use of RAIs have been debated as they do not account for imperfect detection (O'Connell et al., 2011), this index

is useful when attempting to understand the environmental drivers influencing abundance (Carbone et al., 2001; O'Brien et al., 2003; Rovero & Marshall, 2009; Martin et al., 2015; Rovero et al., 2017).

3.3.2.2 Environmental variables

Variables were selected based on those that were suspected to affect caracal behaviour as based on available literature (Avenant & Nel, 1998; Adibi et al., 2014; Singh et al., 2014; Ramesh et al., 2017). Aspect (orientation of the slope), elevation (distance above sea level), terrain ruggedness (a measure of the brokenness, rockiness, and steepness of the surface) and slope (degree of incline of the surface) were derived from a digital elevation model (DEM; STRM, 2018) in QGIS (version 3.4, QGIS Development Team, 2018). Veld types (National Vegetation Map 2018, SANBI 2018) were clipped to camera trap locations. Within QGIS, the camera trap's Euclidean distance to homesteads and water points in kilometres were also calculated. A description of the variables, as well as their sources can be found in Table 3.1.

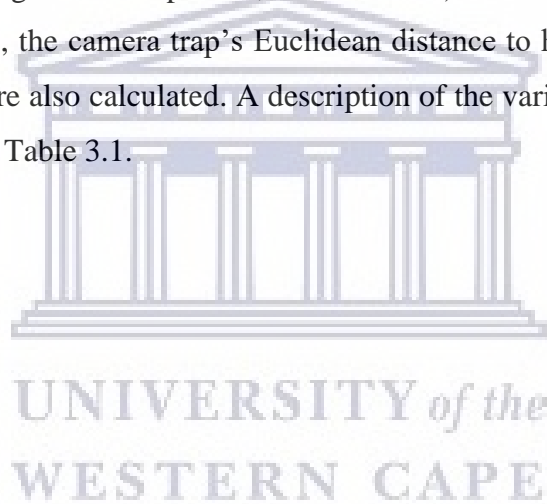


Table 3.1 The environmental variables considered in creating *a-priori* models for caracal habitat selection on a non-lethal treatment farm in the Karoo, South Africa. Habitat variables were based on habitat layers in GIS, and GPS locations.

Variable	Description	Resolution (m)	Units	Source
Veld types	Upper Karoo Hardeveld or Eastern	-	km ²	NVM, 2018 ¹
Homesteads	Upper Karoo Euclidean distance to homesteads	90	km	GPS locations
Water points	Euclidean distance to water points	90	km	GPS locations
Aspect	Digital elevation model	90	°	SRTM ²
Elevation	Digital elevation model	90	m	SRTM ²
Terrain ruggedness	Digital elevation model	90	m	SRTM ²
Slope	Digital elevation model	90	°	SRTM ²

¹South African National Biodiversity Institute (2006-2018). The Vegetation Map of South Africa, Lesotho and Swaziland, Mucina, L., Rutherford, M.C. and Powrie, L.W. (Eds), Online, <http://bgis.sanbi.org/Projects/Detail/186>, Version 2018

²Shuttle Radar Topography Mission “SRTM” (<http://srtm.csi.cgiar.org/>)

3.3.2.3 Analysis

To ensure parsimonious models, I used two criteria to select variables into models, namely receiver operating characteristic (ROC) using the R package “pROC” (Robin et al., 2011), as well as the Akaike’s Information Criterion (AIC; Burnham et al., 2011). Before performing the GLMMs, the data set was split in half for training and testing the models. The ROC curve is based on pairs of sensitivity and specificity values (Metz, 1979). The sensitivity value is defined as the probability that a model yields a positive prediction where an animal actually occurs, whereas the specificity value would provide

a low number where the animal does not occur (Boyce et al., 2002). From the resulting area under the curve (AUC), the predictive power of the model could then be assessed, with an AUC value of 0.5, it could be assumed that the model has poor predictive power, whereas an AUC value of 1 would have absolute predictive power (Cumming, 2000). I also calculated the Akaike's Information Criterion difference adjusted for small sample sizes (AICc; Guo et al., 2017) using the R package "AICcmodavg" (Mazerolle, 2019) and ranked the variables in terms of highest ROC and lowest AICc. All variables were added to the models in a forward stepwise method, and any variable that did not improve the model (both improved ROC, and reduced AICc by > 1), was excluded from the analysis. GLMMs were performed in R (version 3.6.3; R Core Team, 2016) using the "lme4" package (Bates et al., 2020).

Following methods set out in Soyumert et al. (2019), I used the presence/absence data of caracals as the dependent variable, as collected from the camera traps, the RAI values of prey and competitors as the fixed effect and the camera trap locations as the random factor. Prior to analyses, all prey, competitor, human and livestock RAI values were log-transformed for a better approximation to normality (Soyumert et al., 2019). Biases may arise from using presence/absence camera trap data, such as imperfect detection of target species, however, this was overcome by conducting multiple surveys (RAIs per 100 trap nights; Mackenzie & Royle, 2005). Finally, the pseudo-replication issue that could emerge from using camera trap stations as sampling units was reduced through the use of long-term data (Soyumert et al., 2019). For the models themselves, I tested eight *a-priori* models (Table 3.2), based on human avoidance, resource selection, livestock presence, interspecific competition and environmental features.

Table 3.2 The eight *a-priori* models developed to explain caracal habitat selection at camera trap locations on a non-lethal treatment farm in the Karoo, South Africa. Provided is the name of the model, the hypothesis behind it, as well as the references used to develop it.

Model Name	Hypothesis	Reference
Human Avoidance	The distribution of caracals will be dictated by avoiding areas frequented by humans.	Ramesh et al., 2017
Resource Dispersion: Prey Availability	The distribution of caracals will be dictated by the distribution of prey species.	Moolman, 1984; Avenant & Nel, 1998; Van Heezik & Seddon, 1998; Melville et al., 2004
Livestock Presence	The distribution of caracals will be dictated by the distribution of livestock.	Avenant & Du Plessis, 2008; Du Plessis et al., 2015
Interspecific Competition	The distribution of caracals will be dictated by trying to avoid areas frequented by black-backed jackals.	Pringle & Pringle, 1979; Bothma, 2012
Environmental Features: Water	The distribution of caracals will be dictated by areas close to water points.	Bothma & Le Riche, 1994; Adibi et al., 2014
Environmental Features: Vegetation Cover	The availability of cover will dictate the distribution of caracals.	Norton & Lawson, 1985; Avenant & Nel, 1998
Environmental Features: Abiotic Features	Habitat heterogeneity will dictate the distribution of caracals.	Avenant & Nel, 1998; Singh et al., 2014
Global Model	The distribution of caracals will be dictated by a combination of human avoidance, resource dispersion, competition, and environmental features.	

3.3.3 Activity patterns

Caracal activity on the non-lethal treatment farm was separated into three categories, namely nocturnal (19:01 – 04:00), diurnal (07:01 – 16:00), and crepuscular (04:01 – 07:00 and 16:01 – 19:00) (adapted from Singh et al., 2014). The data were further classified into the four seasons: Summer (December - February), which is also the rainy season; Autumn (March – May); Winter (June – August), which is also the dry season; and Spring (September – November). This was to test if a significant difference in caracal activity existed between seasons. I used the Shapiro-Wilks test for normality, thereafter a two-way analysis of variance (ANOVA) was performed on the data in SPSS (version 23, IBM Corp, 2015) to test for significant differences between the activity categories over the 24-hour period, seasonal differences, as well as the effect of season on caracal activity.

3.3.3.1 Predator-prey, competitor, human and livestock interactions

I used a kernel density estimate to assess the relationship of diel activity patterns of caracals and their main prey, competitors, humans, and livestock (species mentioned above), based on the camera trap images (Ridout & Linkie, 2009). An optimal overlap estimator of Dhat4 (Δ_4) was used as all species records had more than 75 detections, as recommended by Meredith & Ridout (2018). These analyses were based on 10 000 permutations at a 95% confidence interval (Meredith & Ridout, 2016). Estimates of overlap ranged from 0 (no overlap) to 1 (complete overlap). All overlapping analyses were conducted using the overlap package (Ridout & Linkie, 2009) in R. To test whether caracal activity patterns differed from that of their main prey, competitors, humans and livestock, the “overlapEst” function was used. Prior to analyses, time records were converted to radians to allow for a better fit of the density curves to trigonometric functions (Meredith & Ridout, 2018)

3.4 Results

Caracals were photographed a total of 383 times over a total of 44 887 trap nights. Their presence was documented at 25 of the 31 camera trap stations.

3.4.1 Caracal habitat selection

As expected, the best model explaining caracal habitat selection was the global model, followed by the resource dispersion model, abiotic factors, interspecific competition, vegetation, water availability, the human avoidance model, and finally the livestock model (Table 3.3). The global model ranked the best according to the AICc weight ($AICc_w = 0.38$) and ROC value (0.88; Table 3.3). This is likely due to the AIC generally indicating a lower AIC value when more variables are used in a model (Boyce et al., 2002). This model included a range of variables including black-backed jackal relative abundance ($p = 0.04$), scrub hare relative abundance ($p = 0.07$) and vegetation cover ($p = 0.07$). The resource dispersion model also ranked highly ($AICc_w = 0.16$) with an ROC value of 0.80 (Table 3.3), and showed the importance of scrub hare abundance ($\beta = 1.90$; $SE = 0.47$; $p = 0.06$; Table 3.3) on caracal habitat selection. Only terrain ruggedness and aspect were retained for the models when testing the physical environmental features. Caracals avoided less rugged terrain ($\beta = -1.32$; $SE = 0.41$), and favoured northern slopes on the farm ($\beta = 1.56$; $SE = 0.003$; Table 3.3). The interspecific competition model also ranked among the top four models dictating caracal habitat selection. In this case, with an increase in black-backed jackal abundance came an increase in caracal activity ($\beta = 1.49$; $SE = 0.51$; Table 3.3). Within the remaining environmental models, vegetation cover had a positive effect on caracal presence ($\beta = 1.39$; $SE = 0.60$), and so did an increasing distance to water points ($\beta = 0.93$; $SE = 0.36$; Table 3.3).

The human avoidance and livestock models had a poor fit to the data overall. The human avoidance model included distance to homesteads ($p = 0.88$) and produced an $AICc_w$ of only 0.02 and an ROC value of 0.53 (Table 3.3). For the human avoidance model, vehicle activity did not contribute meaningfully to the model, while increased caracal activity was discovered with an increasing distance from homesteads ($\beta = -0.15$; $SE = 0.13$; Table 3.3). The livestock model, which contained sheep presence data ($p = 0.78$), had a high ROC value of 0.72 and low $AICc_w$ of 0.02 (Table 3.3), with caracals displaying a negative association to the presence of sheep in the livestock model ($\beta = -0.29$; $SE = 0.04$; Table 3.3).

Table 3.3 Summary of the *a-priori* models used to explain habitat selection of caracals on a non-lethal treatment farm in the Karoo, South Africa. Included are the Akaike's Information Criterion difference adjusted for small sample sizes (AICc), receiver operator characteristic (ROC), standard error (SE), the Wald statistic (Z-value), the associated *p*-value (with significant *p*-values indicated in bold), and degrees of freedom (d.f.). Data are based on camera trap surveys from 2015 – 2020. Livestock models were based on data from 2015 – 2017.

Model	Model Structure	AICc	ROC	SE	Z-value	<i>p</i> -value	d.f.
Global Model	Jackal+Scrub+Cover	29.18	0.88	1.392	-1.72	0.09	30, 27
	Black-backed jackal abundance			0.702	2.08	0.04	
	Scrub hare abundance			0.548	1.83	0.07	
	Vegetation cover			0.874	1.80	0.07	
Resource Dispersion: Prey Availability	Scrub	30.87	0.80	0.340	1.29	0.20	30, 29
	Scrub hare abundance			0.472	1.90	0.06	
Environmental Features: Abiotic Factors	Terrain+Aspect	32.39	0.70	0.618	-0.23	0.82	30, 28
	Terrain ruggedness			0.410	-1.32	0.19	
	Aspect			0.003	1.56	0.12	
Interspecific Competition	Jackal	32.57	0.73	0.362	1.34	0.18	30, 29
	Black-backed jackal abundance			0.510	1.49	0.14	
Environmental Features: Vegetation Cover	Cover	32.75	0.66	0.812	-0.31	0.76	30, 29
	Vegetation cover			0.601	1.39	0.16	

Environmental Features: Water Availability	Water	34.03	0.59	0.435	1.21	0.23	30, 29
	Distance to water points			0.359	0.93	0.35	
Human Avoidance	Homesteads	34.87	0.53	0.563	1.67	0.10	30, 29
	Distance to homesteads			0.129	-0.15	0.88	
Livestock Presence	Sheep	44.67	0.72	0.527	0.96	0.34	30, 28
	Livestock presence			0.043	-0.29	0.78	

3.4.2 Caracal diel activity patterns

Caracal activity peaked during nocturnal hours (from 19:01 to 04:00; Figure 3.2), with 62% of the records falling within this time period. Moreover, caracals in this area were crepuscular 31% of the time and diurnal 7% of the time. There was a significant difference between caracal activity amongst the three activity time categories ($F_{2,49} = 22.50$; $p < 0.001$), as well as between seasons ($F_{3,49} = 3.30$; $p < 0.05$). There was no significant difference between the distribution of activity within the various activity time categories and season ($F_{6,49} = 1.30$; $p = 0.28$). According to the post-hoc tests, caracals displayed predominantly nocturnal behaviour in all seasons but were increasingly crepuscular in winter and autumn (Figure 3.3). Similarly, diurnal activity was highest during winter, and the least diurnal activity occurred during the summer months (Figure 3.3).

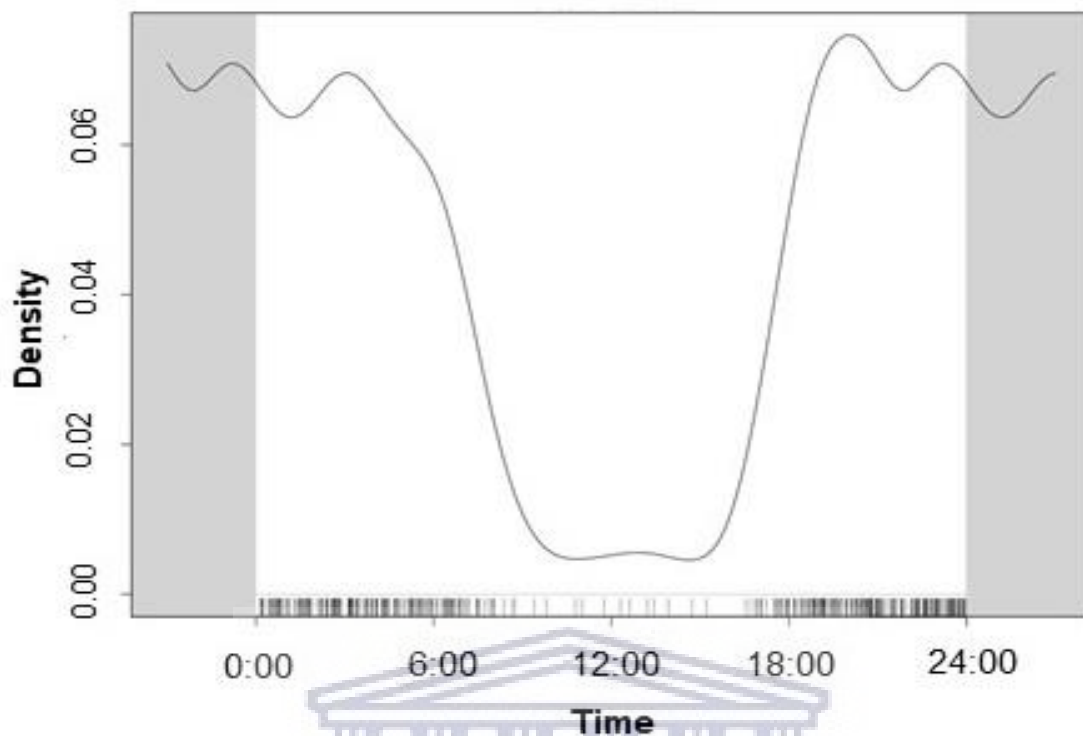


Figure 3.2 Summary of the diel activity patterns of caracals in the Karoo, South Africa. Black “rug” marks along the x-axis represents the independent photographic events (n = 383). Data are based on camera trap surveys from 2015 – 2020.

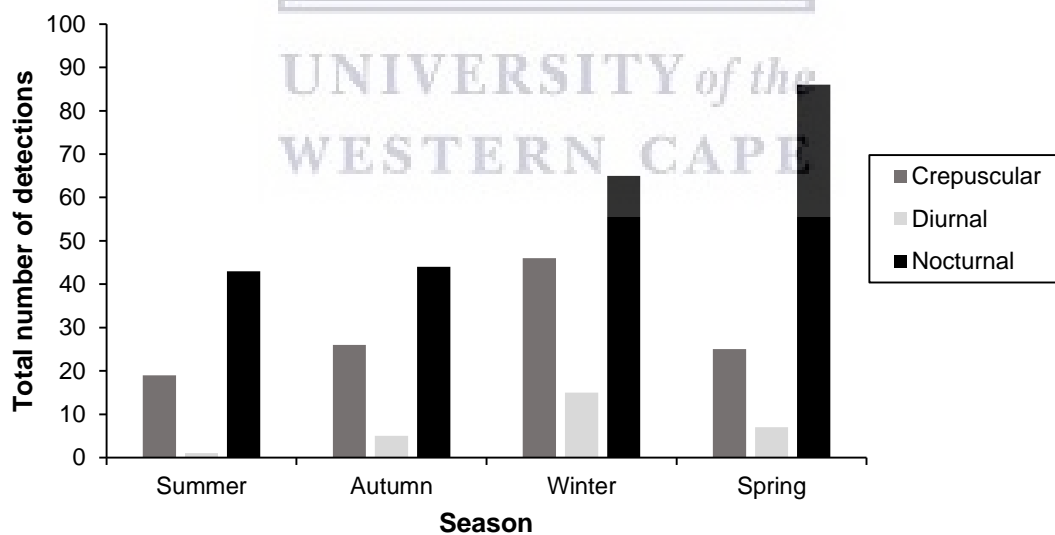
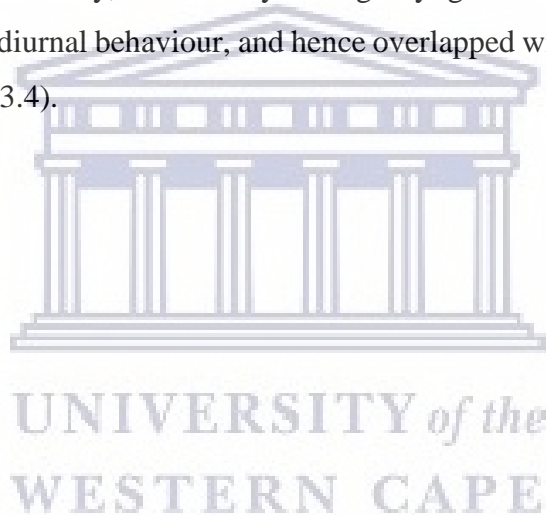
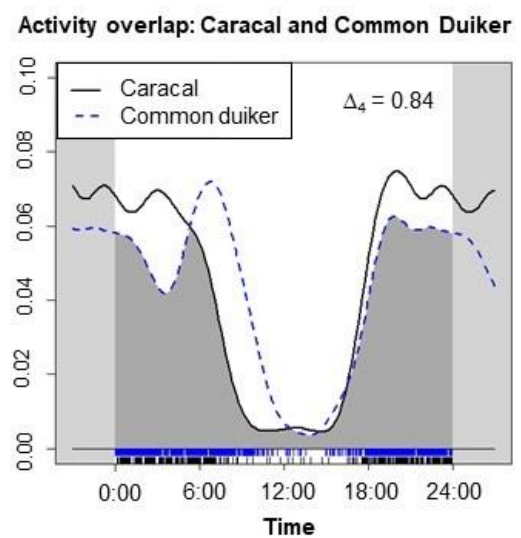
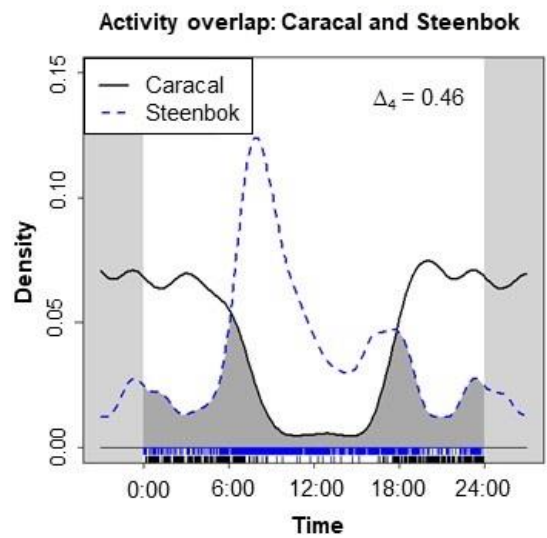
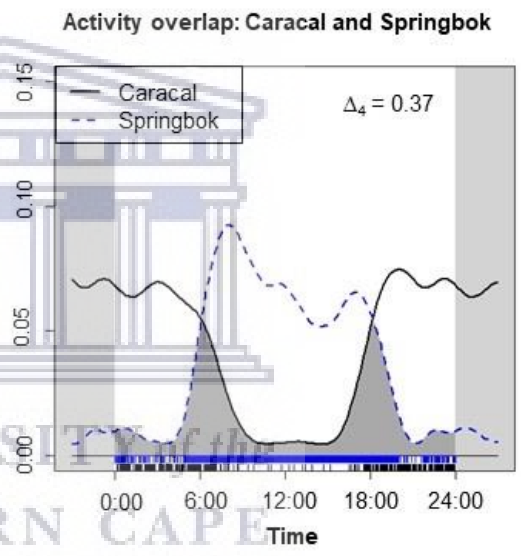
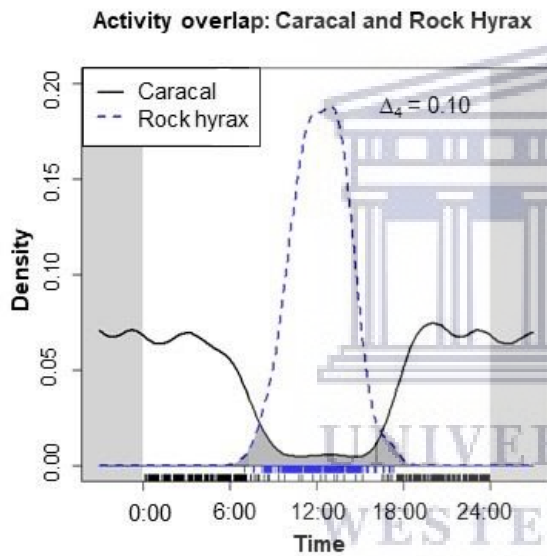
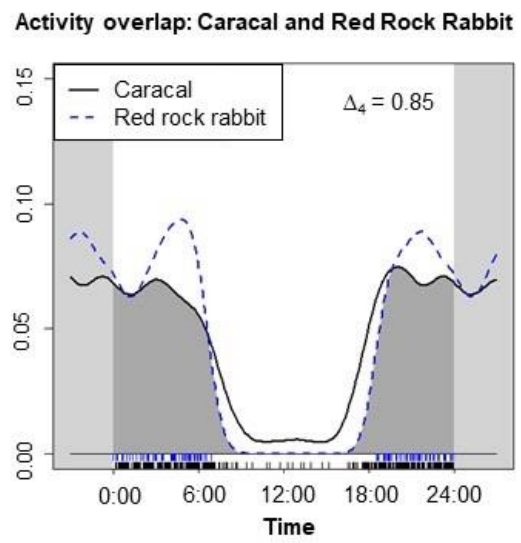
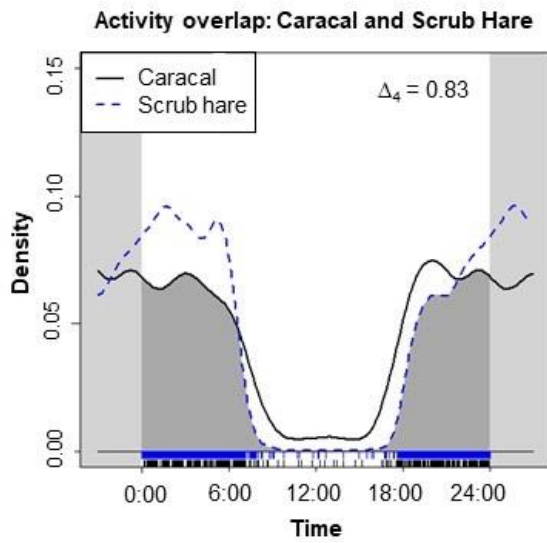


Figure 3.3 Seasonal activity patterns of caracals on a non-lethal treatment farm in the Karoo, South Africa. Data are based on 383 caracal detections from camera trap surveys between 2015 – 2020.

3.4.3 Predator-prey, competitor, human and livestock interactions

Caracal activity overlapped considerably with their competitor, the black-backed jackal, which displayed more diurnal activity than caracals. Caracal activity also synchronized strongly with the following potential prey species: Smith's red rock rabbit, common duiker and scrub hare (Figure 3.4; Table 3.4). Other prey, such as steenbok, were slightly more crepuscular, with an activity peak at 7 am, while springbok displayed more diurnal behaviour and were active roughly from dawn to dusk, with decreased activity during the hottest parts of the day, which is around 13:00 to 15:00 (Figure 3.4), and therefore had low overlap with caracal activity. Livestock were highly crepuscular, with activity peaks at 6 am and 6 pm, and had low overlap with caracal activity (Figure 3.4). Human activity, as measured by vehicle activity, was mostly during daylight hours (Figure 3.4). Rock hyraxes displayed fully diurnal behaviour, and hence overlapped with caracal activity the least (Figure 3.4; Table 3.4).





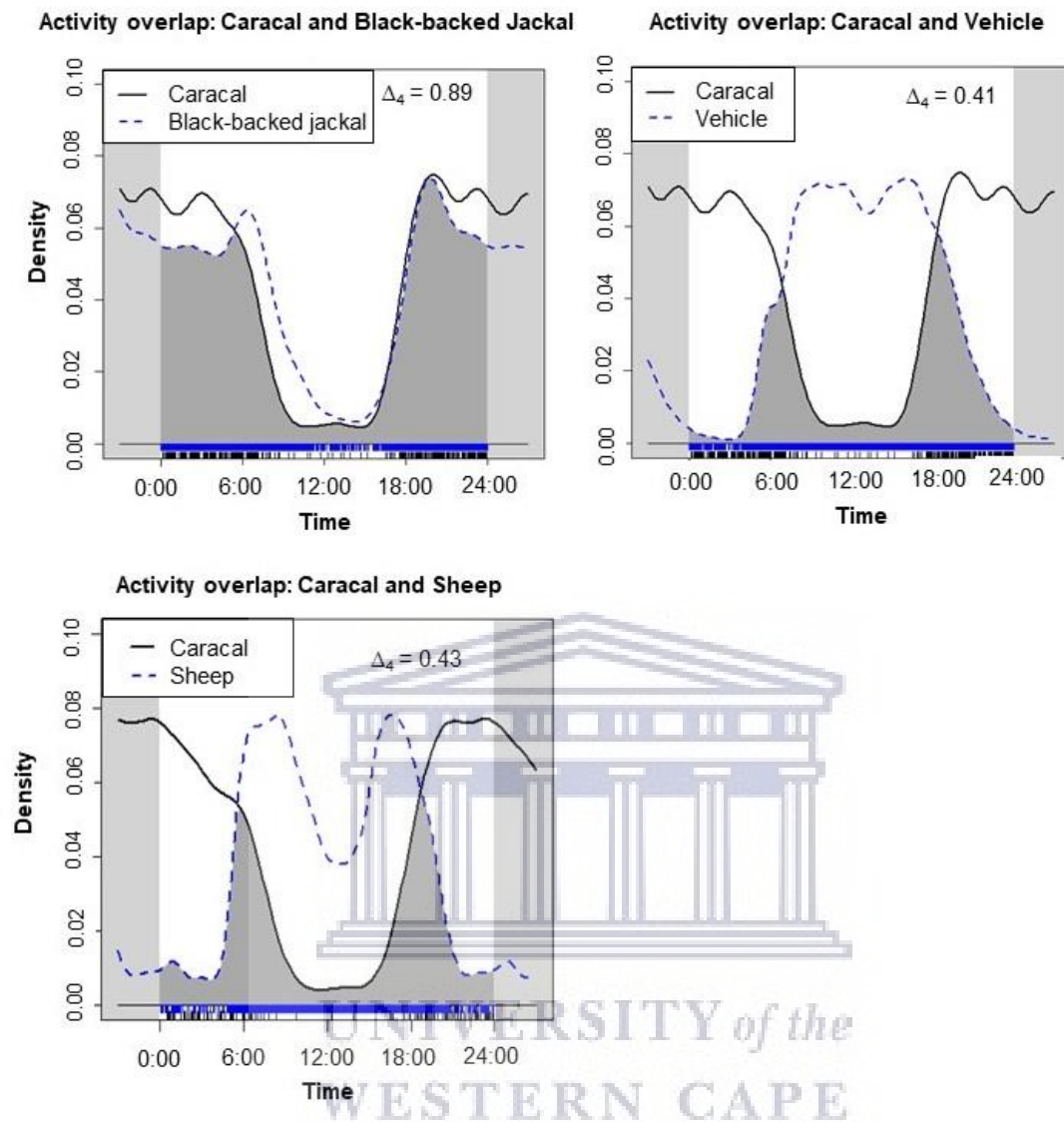


Figure 3.4 Density estimates of daily activity patterns of caracals and their main prey, competitors, humans, and livestock based on Dhat4 (Δ_4) estimators, on a predator-friendly farm in the Karoo, South Africa. Solid lines indicate kernel density estimates of caracals and dotted lines indicate kernel density estimates of prey, competitors, humans and livestock. The dark grey shaded region represents the coefficient of overlap, while the light grey is the extension of the activity period. The blue and black “rug” marks along the x-axis represent independent photographic events. Data are based on camera trap surveys from 2015 – 2020, and from 2015 – 2017 for livestock.

Table 3.4 Number of independent camera trap records (n), estimates of coefficients of overlap with caracal based on Dhat4 (Δ_4) and the 95% confidence intervals (CI), of wild prey, competitors, vehicles (human proxy), and livestock. Data are based on camera trap surveys on a predator-friendly farm in the Karoo, South Africa from 2015 – 2020, and from 2015 – 2017 for livestock.

Species	n	Δ_4	95% CI
Black-backed jackal (<i>Canis mesomelas</i>)	2725	0.89	0.86-0.93
Red rock rabbit (<i>Pronolagus rupestris</i>)	113	0.85	0.80-0.93
Common duiker (<i>Sylvicapra grimmia</i>)	919	0.84	0.80-0.88
Scrub hare (<i>Lepus saxatilis</i>)	5096	0.83	0.79-0.88
Steenbok (<i>Raphicercus campestris</i>)	885	0.46	0.40-0.49
Sheep (<i>Ovis aries</i>)	1740	0.43	0.36-0.50
Vehicle (human proxy)	21275	0.41	0.35-0.43
Springbok (<i>Antidorcas marsupialis</i>)	2449	0.37	0.33-0.41
Rock hyrax (<i>Procavia capensis</i>)	346	0.10	0.05-0.11

3.5 Discussion

3.5.1 Habitat selection

While caracals are known to tolerate a wide range of environmental variation (Sunquist & Sunquist, 2002), I found consistency in caracal resource selection patterns, offering insight into their ability and limitations to survive in agricultural landscapes. Although the global model had the best fit to caracal habitat selection, this is likely due to the over-dispersion of variables (Boyce et al., 2002). Therefore, the resource dispersion model may

actually better explain caracal habitat selection. Specifically, scrub hare relative abundance was one of the most important factors influencing caracal habitat selection, featuring in both the global model as well as the resource dispersion model, which were both highly ranked. Prey availability is known to be a major factor in determining predator habitat selection (Guo et al., 2017; Anile et al., 2020). Scrub hares were the only prey of the selected species to correlate strongly with caracal presence. Therefore, it could be argued that this is the main prey of caracals on the non-lethal treatment farm, based on their high temporal and spatial overlap, as well as the high frequency of lagomorph remains found in caracal scats in the diet chapter of this thesis (Chapter 2). On traditionally managed farms, caracals also consumed lagomorphs, but less frequently than small mammals and rock hyraxes (Drouilly et al., 2018a; Chapter 2). Therefore, if the scrub hare population were to decline on the non-lethal farm, caracals could switch to alternative species such as small mammals and rock hyraxes; in extreme cases, they could supplement their diet with livestock (Minnie et al., 2018).

The environmental feature models containing abiotic factors and vegetation cover ranked similarly, within the top five models (Table 3.3). This indicates the importance of both rugged terrain and vegetation cover for caracals. Increasingly rugged terrain with higher elevations are considered to be a proxy for less disturbed areas as it provides difficult access for humans (Guo et al., 2017). This is corroborated by the models, which indicated that caracals displayed a negative correlation to less rugged terrain on the farm. Within Iran and other regions of the Karoo, similar findings were noted (Farhadinia et al., 2007; Drouilly et al., 2018b). Elevation did not feature as an important factor for caracal habitat selection on the non-lethal farm, meaning that caracals had no preference. These results contradict findings in the Drakensberg midlands, where caracal space use decreased with an increase in altitude, and within the West Coast National Park in South Africa, where caracals were found to prefer lower lying areas (Avenant & Nel, 1998; Ramesh et al., 2017). Vegetation cover is an important aspect of any environment as it provides shelter from the elements, suitable den sites, and it provides a source of both food and moisture for animals (Adibi et al., 2014). When looking at rugged terrain and vegetation in conjunction, they can provide an optimal habitat for ambush predators such as caracals (Singh et al., 2014).

Black-backed jackals and caracals are known to depress one another's population numbers (Kaunda, 2001); therefore as a result of their interspecific competition, black-backed jackal abundance was predicted to influence caracal habitat selection. Interspecific competition also had a strong fit to caracal habitat selection. Interestingly, increased black-backed jackal relative abundance seemed to have a positive effect on caracal presence. Similar to the effect of domestic dogs having a positive interaction with native carnivores such as the chilla fox (*Pseudalopex griseus*) and culpeo fox in southern Chile, this was attributed to a similarity in their habitat preferences, and not as a result of the species positively interacting (Moreira-Arce et al., 2015b). Although they occupy similar habitats and display strong temporal overlap, they could be selecting habitats that are different on a finer scale (McCarthy et al., 2015).

As caracals were historically persecuted (up until 2015) due to human-wildlife conflict on the now non-lethal treatment farm, and are still being heavily persecuted on neighbouring farms (pers. obs.), it was expected that human avoidance would still be a major factor influencing caracal habitat selection. However, as the human avoidance model ranked seventh overall, it indicates that caracal habitat selection was not strongly correlated to human activity. This is contrary to caracal behaviour on traditional farms, where caracals maintained large home range sizes to avoid humans (Marker & Dickman, 2005; Du Plessis et al., 2015; Ramesh et al., 2017). While caracals on the non-lethal farm may not have displayed spatial avoidance of humans, they could be demonstrating temporal avoidance.

The livestock model least explained caracal habitat selection. As caracals in the Karoo are considered to be problem animals, it was expected that caracals would select habitats that house livestock; however, this was not the case. In Mexico, livestock presence was shown to decrease jaguar numbers and have an effect on their habitat selection (Anile et al., 2020). This was due to the fact that livestock outcompeted wild ungulates and small mammals, leaving less prey available for the jaguars and forcing them to occupy other environments (Anile et al., 2020). This could be the case on the non-lethal farm as well.

3.5.2 Diel activity patterns of caracals, prey, competitors, humans, and livestock

Although caracals were primarily nocturnal, they displayed increased crepuscular and diurnal activity during the colder autumn and winter months (Figure 3.2 and Figure 3.3). This is likely explained by a change in temperature, which is known to affect caracal behaviour (Weisbein & Mendelssohn, 1990; Avenant & Nel, 1998). For example, along the West coast of South Africa, caracal displayed increased diurnal activity during cooler conditions (Avenant & Nel, 1998). This is similar to activity patterns of the Eurasian lynx, which displayed increased activity during winter afternoons as opposed to the freezing night times. These behaviours resulted in lower energy expenditure during extreme temperatures (Tang et al., 2019). The opposite occurs during summer, where in the Karoo, the daily temperature can reach up to 43°C (Mucina et al., 2006), close to the caracal's critical body temperature according to their weight (McNab, 1970). Therefore, changes in activity patterns are partly attributed to the change in ambient temperatures.

Predator activity generally has a strong correlation to the activity of their prey, therefore I tested whether caracal activity patterns on the non-lethal farm are as a consequence of their prey. While caracals are considered generalist predators that consume a wide variety of prey that are active at different times of the day (Sunkist & Sunkist, 2002), I found a significant temporal overlap with caracals and Smith's red rock rabbit, common duiker, and scrub hare. These three potential prey species are highly nocturnal (Stuart & Stuart, 2015), which is why they overlap as significantly as they do with caracal. In addition, I also found that caracals and rock hyraxes displayed the lowest levels of activity overlap. This is interesting as rock hyraxes make up a significant portion of caracal diet on the non-lethal farm (Chapter 2), as well as in other regions of the Karoo (Palmer & Fairall, 1988; Jansen, 2016; Drouilly et al., 2018a). This could suggest that caracal activity patterns on the non-lethal farm are not completely driven by that of their prey, as speculated (Minnie et al., 2018).

While caracal activity overlapped moderately with free-roaming sheep on the non-lethal farm, the data indicates that sheep were not an important part of either caracal habitat selection, or their diet (Chapter 2). This could be due to the better synchronisation with natural prey such as lagomorphs and common duikers. This concurs with Jansen (2016),

who noted that between caracals, black-backed jackals, and leopards (*Panthera pardus*), caracals were the least dependant on livestock.

Caracals and black-backed jackals displayed strong temporal overlap, which is expected as they occupy the same niche as mesopredators (Drouilly et al., 2018a). However, to avoid interspecific competition, I would expect some avoidance (Kaunda, 2001; Drouilly et al., 2018a). Since caracals are not spatially avoiding humans on the non-lethal farm (as demonstrated above), both caracals and black-backed jackals could both be displaying temporal avoidance of humans. Kaunda (2000) noted that the activity patterns of black-backed jackals in Mokolodi Nature Reserve in Botswana were primarily nocturnal as a result of the intense hunting pressure on the surrounding farms. This could also be the case in this study area as it too is bounded by lethal treatment farms.

3.5.3 Study limitations and future research

As camera trapping was used, it was not possible to identify sex, age, or individual caracals. This information would have contributed to understanding how social drivers, population densities and sex-related differences explain caracal habitat selection. Future studies should also consider competitor and prey habitat selection patterns, as this could allow insight into which fine-scale habitat features allow caracals and black-backed jackals to coexist. It would also be of interest to study other caracal populations in the Karoo and investigate how these patterns may differ on a lethal treatment farm.

3.6 Conclusion

Caracal biology is vastly understudied, particularly in the Karoo where they are persecuted due to human-carnivore conflict. This study has provided baseline information regarding the effect of non-lethal predator control on the ecology of caracals. Caracal habitat selection was highly influenced by a dominant food source, scrub hares. The role of environmental features such as terrain ruggedness and vegetation in providing adequate cover for ambush was also highlighted. Spatially, caracals did not appear to display human avoidance, but instead, they could be displaying temporal avoidance of humans. Some form of avoidance is expected as caracals were previously persecuted in the area and are still highly persecuted on the surrounding farms. According to the

models, the presence of free-roaming livestock was not an important consideration, once again highlighting the importance of natural prey in caracal habitat selection. Caracals on the non-lethal farm were predominantly nocturnal but became more crepuscular during the cold winter months. Caracal diel activity patterns synchronized highly with their main competitor, black-backed jackals, as well as with their prey, lagomorphs, and common duikers. Despite consuming many rock hyraxes on the non-lethal farm, caracal activity patterns overlapped with them the least. This could indicate that caracal activity patterns are not solely dictated by that of their prey, but could be as a result of temperature and human avoidance. Future research should examine the effects of conspecific presence, sex, and age on caracal activity patterns and habitat selection, and be expanded to surrounding lethal treatment farms.



Chapter 4: Synthesis

Human-wildlife conflict is an on-going issue worldwide, and South Africa is no exception. Due to widespread livestock losses as a result of predators, as well as the resulting large-scale persecution of predators, it is becoming increasingly important to find effective means of managing this threat to livestock production and a healthy ecosystem overall.

It is imperative to understand the ecology and threats of predators in order to better manage them (Mills & Schenk, 1992; Gittleman, 1996). The high levels of carnivore persecution on Karoo farmlands have led to a change in caracal behaviour, not only in terms of reproduction (Du Plessis et al., 2015; Minnie et al., 2016) but also in their feeding habits and resource selection. Therefore, by studying the diet of predators in conflict hotspots, one can estimate how extensive livestock depredation is, and if other species are important to conserve in order to reduce livestock depredation. Similarly, by studying the ecology of the predator involved, more effective anti-predation measures can be put into place when the predator is most active and in the areas that they inhabit.

The overarching aim of this study was to determine how caracal ecology and diet varies on where different farm management techniques (i.e. lethal vs non-lethal control) are employed. I used two non-invasive techniques to achieve these aims. For the dietary component, I used scat analysis on three treatment sites. Secondly, I used camera trapping to investigate the habitat selection and activity patterns of caracals on a non-lethal farm.

4.1 Caracals in the Karoo

Through this study of diet, habitat selection, and activity patterns, the dynamic nature of caracals was revealed. Caracal diet varied among the study sites, and was significantly different on the lethal and non-lethal sites. The habitat selection and activity pattern analyses on the non-lethal farm also provided interesting results.

Lagomorphs contributed strongly to both caracal diet and habitat selection. Within the dietary component of this study, caracals at all sites frequently consumed lagomorph species. Similarly, the habitat selection analysis revealed that scrub hare (*Lepus saxatilis*) presence was a major factor in determining caracal habitat selection, with their activity

patterns mirroring each other closely. Surprisingly, rock hyraxes (*Procavia capensis*), which are known to be a major component of caracal diet as seen in this and other studies in the Karoo (Palmer & Fairall, 1988; Jansen, 2016; Drouilly et al., 2018a), had the lowest temporal overlap with caracals. This could indicate that caracal activity patterns are not entirely driven by that of their prey. Therefore, I attributed caracal activity patterns on the non-lethal farm to temperature fluctuations and partially to human avoidance.

Domestic livestock depredation by caracals is known to be a pressing problem in South Africa, causing millions of Rands in losses each year (Van Niekerk, 2010). The present study found that caracals only consumed livestock on the lethal treatment farm, while on the non-lethal treatment farm, no losses were reported at the time of sampling. This could be explained through the optimal foraging theory, with the density of sheep being higher on the smaller lethal treatment farm thereby making them more abundant, as opposed to on the larger non-lethal farm. It could also be attributed to the constant presence of a human shepherd with the herd on the non-lethal treatment farm, as opposed to the livestock being kept unsupervised in a camp on the lethal treatment farm for long periods of time. Chapter 3 examined the role of livestock on caracal activity patterns. I tested if livestock were selected by caracals between October 2015 and January 2017, before shepherds were employed. During this time no deterrents nor lethal controls were employed and sheep (*Ovis aries*) were free-roaming on the farm. I found that caracals did not use livestock as an important habitat consideration, as that particular model was the least parsimonious.

Caracal diet at each of the three sites was most likely affected by the type of farming practices used. This assumption was made as due to the close proximity of the study sites, very little variation existed in terms of the terrain, vegetation, and climate. Therefore, the main differences between sites were the type of predator controls used. On the non-lethal treatment site, the natural prey base was indirectly altered through the movement of livestock by herders, which may have had some effect on the ecological community. On the lethal treatment farm, in addition to the influence of livestock, pastoralists also made use of unselective gin traps which is suspected to alter the natural prey base through the direct removal of wildlife caught in these traps. The importance of natural prey in reducing livestock losses have often been noted (Avenant & Du Plessis, 2008; Drouilly et al., 2018a), and can be seen in Chapter 2. Similarly, the provision of natural areas for

predators to reside in could promote human-carnivore coexistence. On the non-lethal treatment farm, caracals required a natural prey base, rugged terrain, and adequate vegetation cover for the hunting of prey and for shelter.

4.2 Limitations and knowledge gaps

There are several limitations to this study that need to be acknowledged. Within the diet chapter, I could not rule out that caracals killed and consumed livestock on one farm and defecated the remains on the neighbouring property. However, Jansen et al. (2019) found a relationship between scat deposition to the location of caracal kill sites through the use of GPS cluster visitations that suggested that caracals defecate near to where kills are made. Furthermore, no livestock losses were reported on the non-lethal treatment site, nor were sheep remains found in scats collected on the control and non-lethal treatment sites. The properties, although adjacent, were separated by jackal-proof fencing, which could also provide a physical barrier to caracal movement between farms. Furthermore, in order to make this dietary study more rigorous, one could also include a prey availability component to the study through the use of both camera and Sherman trapping in order to get a clearer picture of caracal prey preference at each site.

For the habitat selection chapter, future studies would do well to include information on small mammals, as this category of prey was highly ranked in caracal diet, but was not represented in the camera trap data. It would provide greater insight into the importance of rodents in caracal habitat selection and whether caracal activity patterns mirror that of small mammals. I would also extend the study to compare activity patterns and habitat selection of caracals to those on lethal treatment farms to understand how that type of predator control affects their behaviour. This was limited by a lack of resources and access to other lethal treatment farms in the area, with access to other properties only granted towards the end of this research. This also highlights the importance of developing relationships with landowners and encouraging farmers to be part of carnivore research projects. This may also promote tolerance towards predators.

4.3 Management implications

As the consumption of livestock by caracals seems to be an artefact of lethal treatments being put into effect on livestock farms, and the importance of natural prey to caracal diet,

I would recommend the use of non-lethal predator controls by pastoralists, as this could result in fewer livestock losses by predators. Furthermore, by allowing areas of natural veld to persist on the farm, it would support more potential natural prey for mesopredators. Similarly, by impeding lethal predator controls, structured populations will establish which could result in the exclusion of young and transient individuals from settling into the area, therefore there would be less predators occupying the area and potentially killing livestock (Minnie et al., 2016).

4.4 Conclusion

This study has served to provide baseline information that was lacking regarding caracal ecology on livestock farms in the Karoo. In this case, I found that the use of two non-invasive sampling techniques was adequate for the assessment of the diet and ecology of elusive caracals on farmlands in the Karoo. Throughout the thesis, the importance of natural prey to caracals has been highlighted, in terms of both their diet as well as presence in the habitats they select. Therefore, through the persistence of a natural prey base, the removal of unselective lethal predator controls, the conservation of natural lands, and the hands-on management of livestock, conflict resolution is possible.



UNIVERSITY of the
WESTERN CAPE

References

- ADIBI, M.A., KARAMI, M. & KABOLI, M. (2014) Study of seasonal changes in habitat suitability of *Caracal caracal schmitzi* (Maschie 1812) in the central desert of Iran. *Journal of Biodiversity and Environmental Sciences*, 5, 95–106.
- ALLAN, D.G. (1989) Strychnine poison and the conservation of avian scavengers in the Karoo, South Africa. *South African Journal of Wildlife Research*, 19, 102–106.
- ALLEN, M.L., PETERSON, B. & KROFEL, M. (2018) No respect for apex carnivores: distribution and activity patterns of honey badgers in the Serengeti. *Mammalian Biology*, 89, 90–94.
- ANILE, S., GREENSPAN, E. & NIELSEN, C.K. (2020) Determinants of jaguar occupancy at the northern range edge. *Mammal Research*, 65, 667–677.
- APOLLONI, N., GRÜEBLER, M.U., ARLETTAZ, R., GOTTSCHALK, T.K. & NAEF-DAENZER, B. (2018) Habitat selection and range use of little owls in relation to habitat patterns at three spatial scales. *Animal Conservation*, 21, 65–75.
- AVENANT, N.L. & NEL, J.A.J. (1997) Prey use by four syntopic carnivores in a strandveld ecosystem. *African Journal of Wildlife Research*, 27, 86–93.
- AVENANT, N.L. & NEL, J.A.J. (1998) Home-range use, activity, and density of caracal in relation to prey density. *African Journal of Ecology*, 36, 347–359.
- AVENANT, N.L. & NEL, J.A.J. (2002) Among habitat variation in prey availability and use by caracal *Felis caracal*. *Mammalian Biology*, 67, 18–33.
- 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.
- AVGAN, B., HENSCHER, P. & GHODDOUSI, A. (2016) *Caracal caracal* (errata version published in 2016). *The IUCN Red List of Threatened Species 2016*, 8235, e.T3847A102424310.
- BACON, M.M., BECIC, G.M., EPP, M.T. & BOYCE, M.S. (2011) Do GPS clusters really work? Carnivore diet from scat analysis and GPS telemetry methods. *Wildlife Society Bulletin*, 35, 409–415.
- BAKER, L.A., WARREN, R.J. & JAMES, W.E. (1993) Bobcat prey digestibility and representation

- in scats. In *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* pp. 71–79.
- BATES, D., MAECHLER, M., BOLKER, B., WALKER, S., CHRISTIENSEN, R.H.B., SINGMANN, H., ET AL. (2020) Package ‘lme4’. Retrieved from: <https://github.com/lme4/lme4/>.
- BERGMAN, D.L., BODENCHUK, M. & MARLOW, M.C. (2013) The need to address black-backed jackal and caracal predation in South Africa. In *Proceedings of the 15th Wildlife Damage Management Conference* pp. 86–94.
- BISSETT, C., PARKER, D.M., BERNARD, R.T.F. & PERRY, T.W. (2015) Management-induced niche shift? The activity of cheetahs in the presence of lions. *African Journal of Wildlife Research*, 45, 197–203.
- BOLKER, B.M., BROOKS, M.E., CLARK, C.J., GEANGE, S.W., POULSEN, J.R., STEVENS, M.H.H., ET AL. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution*, 24, 127–135.
- BOOYSEN, J. & ROWSWELL, D.I. (1983) The drought problem in the Karoo areas. In *Proceedings of the Annual Congresses of the Grassland Society of Southern Africa* pp. 40–45.
- BOTHMA, J.D.P. (1965) Random observations on the food habits of certain Carnivora (Mammalia) in southern Africa. *Fauna & Flora*, 16, 16–22.
- BOTHMA, J.D.P. (1966) Notes on the stomach contents of certain Carnivora (mammalia) from the Kalahari Gemsbok Park. *Koedoe*, 9, 37–39.
- BOTHMA, J.D.P. (2012) Literature review of the ecology and control of the black-backed jackal and caracal in South Africa. Retrieved from: <http://www.capenature.co.za/wp-content/uploads/2014/02/Literature-Review-of-the-Ecology-and-Control-of-black-backed-jackal-and-caracal-Bothma-2012.pdf> in April 2018.
- BOTHMA, J.D.P. & LE RICHE, E.A.N. (1994) Range use by an adult male caracal in the southern Kalahari. *Koedoe*, 37, 105–108.
- BOWKETT, A.E., ROVERO, F. & MARSHALL, A.R. (2008) The use of camera-trap data to model habitat use by antelope species in the Udzungwa Mountain forests, Tanzania. *African Journal of Ecology*, 46, 479–487.

- BOYCE, M.S., VERNIER, P.R., NIELSEN, S.E. & SCHMIEGELOW, F.K.A. (2002) Evaluating resource selection functions. *Ecological Modelling*, 157, 281–300.
- BRACZKOWSKI, A., WATSON, L., COULSON, D., LUCAS, J., PEISER, B. & ROSSI, M. (2012) The diet of caracal, *Caracal caracal*, in two areas of the southern Cape, South Africa as determined by scat analysis. *South African Journal of Wildlife Research*, 42, 111–116.
- BRODIE, J.F. (2009) Felidae as a global case study. *Biodiversity and Conservation*, 18, 2927–2939.
- BROWN, J.S., KOTLER, B.P., SMITH, R.J. & WIRTZ, W.O. (1988) The effects of owl predation on the foraging behavior of heteromyid rodents. *Oecologia*, 76, 408–415.
- BROWN, K.J. & DOWNS, C.T. (2005) Seasonal behavioural patterns of free-living rock hyrax (*Procavia capensis*). *Journal of Zoology*, 265, 311–326.
- BURNHAM, K.P., ANDERSON, D.R. & HUYVAERT, K.P. (2011) AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*, 65, 23–35.
- BUTLER, J.F. (2000) The economic costs of wildlife predation on livestock in Gokwe communal land, Zimbabwe. *African Journal of Ecology*, 38, 23–30.
- BUYS, D. & KEOGH, H.J. (1984) Notes on the microstructure of hair of the Orycteropodidae, Elephantidae, Equidae, Suidae and Giraffidae. *South African Journal of Wildlife Research*, 14, 111–119.
- CARBONE, C., CHRISTIE, S., CONFORTI, K., COULSON, T., FRANKLIN, N., GINSBERG, J.R., ET AL. (2001) The use of photographic rates to estimate densities of tigers and other cryptic mammals. *Animal Conservation*, 4, 75–79.
- COLWELL, R.K. (2013) EstimateS: Statistical estimation of species richness and shared species from samples. Retrieved from: <http://purl.oclc.org/estimates>.
- CREEL, S. (2001) Four factors modifying the effect of competition on carnivore population dynamics as illustrated by African wild dogs. *Conservation Biology*, 15, 271–274.
- CREEL, S. & CREEL, N.M. (1996) Limitation of African wild dogs by competition with larger carnivores. *Conservation Biology*, 10, 526–538.

- CUMMING, G.S. (2000) Using between-model comparisons to fine-tune linear models of species ranges. *Journal of Biogeography*, 27, 441–455.
- DE GRAAF, G. (1981) *The Rodents of Southern Africa*. Butterworths, Durban, South Africa.
- DELLINGER, J.A., PROCTOR, C., STEURY, T.D., KELLY, M.J. & VAUGHAN, M.R. (2013) Habitat selection of a large carnivore, the red wolf, in a human-altered landscape. *Biological Conservation*, 157, 324–330.
- DEPARTMENT OF AGRICULTURE FORESTRY AND FISHERIES (2017) *Abstract of Agricultural Statistics*. Department of Agriculture, Forestry and Fisheries, Pretoria, South Africa.
- DIAMOND, J. (2002) Evolution, consequences and future of plant and animal domestication. *Nature*, 418, 700–702.
- DIGIKAM TEAM (2020) digiKam. Retrieved from: www.digikam.org.
- DISTEFANO, E. (2005) *Human-wildlife conflict worldwide: collection of case studies, analysis of management strategies and good practices*. Food and Agricultural Organization of the United Nations (FAO), Sustainable Agriculture and Rural Development (SARD). Rome, Italy. Retrieved from: http://www.fao.org/sard/common/ecg/1357/en/hwc_final.pdf in April 2018.
- DOLMAN, P.M. (2012) *Mechanisms and processes underlying landscape structure effects on bird populations*. Cambridge University Press, Cambridge, UK.
- DONOVAN, T.M. & WELDEN, C. (2001) *Spreadsheet Exercises in Ecology and Evolution*. Sinauer Associates inc, Sunderland, USA.
- DORRESTEIJN, I., SCHULTNER, J., NIMMO, D.G., FISCHER, J., HANSPACH, J., KUEMMERLE, T., ET AL. (2015) Incorporating anthropogenic effects into trophic ecology: predator-prey interactions in a human-dominated landscape. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20151602.
- DREYER, J.H. (1966) A study of hair morphology in the family bovidae. *Onderstepoort Journal of Veterinary Research*, 379–472.
- DROUILLY, M., NATTRASS, N. & O’RIAIN, M.J. (2018a) Dietary niche relationships among

- predators on farmland and a protected area. *Journal of Wildlife Management*, 82, 507–518.
- DROUILLY, M., TAFANI, M., NATTRASS, N. & O’RIAIN, J. (2018b) Spatial, temporal and attitudinal dimensions of conflict between predators and small-livestock farmers in the Central Karoo. *African Journal of Range and Forage Science*, 35, 245–255.
- DROUILLY, M., NATTRASS, N. & O’RIAIN, M.J. (2020) Global positioning system location clusters vs. scats: comparing dietary estimates to determine mesopredator diet in a conflict framework. *Journal of Zoology*, 310, 83–94.
- DUNHAM, K.M., GHIURGI, A., CUMBI, R. & URBANO, F. (2010) Human-wildlife conflict in Mozambique: a national perspective, with emphasis on wildlife attacks on humans. *Oryx*, 44, 185–193.
- DU PLESSIS, J.J. (2013) *Towards the Development of a Sustainable Management Strategy for Canis mesomelas and Caracal on Rangeland*. PhD thesis. University of the Free State, Bloemfontein, South Africa.
- DU PLESSIS, J.J., AVENANT, N.L., BOTHA, A., MKHIZE, N.R., MÜLLER, L., MZILENI, N., ET AL. (2018) Past and current management of predation on livestock. In *Livestock Predation and its Management in South Africa: A Scientific Assessment* (eds G.I.H. Kerley, S.L. Wilson & D. Balfour), pp. 125–177. Centre for African Conservation Ecology, Nelson Mandela University, Port Elizabeth, South Africa.
- 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? *African Journal of Wildlife Research*, 45, 138–157.
- DURANT, S.M. (2000) Living with the enemy: avoidance of hyenas and lions by cheetahs in the Serengeti. *Behavioral Ecology*, 11, 624–632.
- ECCARD, J.A., PUSENIUS, J., SUNDELL, J., HALLE, S. & YLÖNEN, H. (2008) Foraging patterns of voles at heterogeneous avian and uniform mustelid predation risk. *Oecologia*, 157, 725–734.
- ENDLER, J.A. (1986) Defense against predators. In *Predator-Prey Relationships: Perspective and Approaches from the Study of Lower Vertebrates* (eds M.E. Federand & G. V. Lauder), pp. 109–134. University of Chicago Press, Chicago, Illinois.

- FARHADINIA, M.S., BEHESHTI, M., SADEGHI, A. & AKBARI, H. (2007) Ecology and status of the caracal, *caracal caracal*, (Carnivora: Felidae), in the Abbasabad Naein Reserve, Iran. *Zoology in the Middle East*, 41, 5–10.
- FERNÁNDEZ, N., DELIBES, M. & PALOMARES, F. (2007) Habitat-related heterogeneity in breeding in a metapopulation of the Iberian lynx. *Ecography*, 30, 431–439.
- FOLEY, J.A., DEFRIES, R., ASNER, G.P., BARFORD, C., BONAN, G., CARPENTER, S.R., ET AL. (2005) Global consequences of land use. *Science*, 309, 570–574.
- FRANK, L.G. & WOODROFFE, R. (2001) Behaviour of carnivores in exploited and controlled populations. In *Carnivore Conservation* (eds J.L. Gittleman, S.M. Funk, D. Macdonald & R.K. Wayne), pp. 419–442. Cambridge University Press, Cambridge, UK.
- FUNGO, B. (2011) A review crop raiding around protected areas: nature, control and research gaps. *Environmental Research Journal*, 5, 87–92.
- GARVEY, P.M., GLEN, A.S. & PECH, R.P. (2015) Foraging ermine avoid risk: behavioural responses of a mesopredator to its interspecific competitors in a mammalian guild. *Biological Invasions*, 17, 1771–1783.
- GAYNOR, K.M., HOJNOWSKI, C.E., CARTER, N.H. & BRASHARES, J.S. (2018) The influence of human disturbance on wildlife nocturnality. *Science*, 360, 1232–1235.
- GEIST, H.J. & LAMBIN, E.F. (2002) Proximate causes and underlying driving forces of tropical deforestation. *BioScience*, 52, 143–150.
- GERBER, B.D., KARPANTY, S.M. & RANDRIANANTENAINA, J. (2012) Activity patterns of carnivores in the rain forests of Madagascar: implications for species coexistence. *Journal of Mammalogy*, 93, 667–676.
- GIPSON, P.S. (1975) Efficiency of trapping in capturing offending coyotes. *The Journal of Wildlife Management*, 39, 45–47.
- GITTLEMAN, J.L. (1996) Ecology introduction. In *Carnivore Behaviour, Ecology, and Evolution* (ed J.L. Gittleman), pp. 219–221. Cornell University Press, New York, USA.
- GLIWICZ, J. & DĄBROWSKI, M.J. (2008) Ecological factors affecting the diel activity of voles in a multi-species community. *Annales Zoologici Fennici*, 45, 242–247.

- GONZÁLEZ-SOLÍS, J., ORO, D., JOVER, L., RUIZ, X. & PEDROCCHI, V. (1997) Trophic niche width and overlap of two sympatric gulls in the southwestern Mediterranean. *Oecologia*, 112, 75–80.
- GORDON, C.E., ELDRIDGE, D.J., RIPPLE, W.J., CROWTHER, M.S., MOORE, B.D. & LETNIC, M. (2017) Shrub encroachment is linked to extirpation of an apex predator. *Journal of Animal Ecology*, 86, 147–157.
- GORDON, C.E., FEIT, A., GRÜBER, J. & LETNIC, M. (2015) Mesopredator suppression by an apex predator alleviates the risk of predation perceived by small prey. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20142870.
- GORMAN, M.L., MILLS, M.G., RAATH, J.P. & SPEAKMAN, J.R. (1998) High hunting costs make African wild dogs vulnerable to kleptoparasitism by hyaenas. *Nature*, 391, 479–481.
- GORMAN, M.L. & TROWBRIDGE, B.J. (1989) The role of odor in the social lives of carnivores. In *Carnivore Behaviour, Ecology, and Evolution* (ed J.L. Gittleman), pp. 57–88. Chapman & Hall, New York, USA.
- GRAHAM, K., BECKERMAN, A.P. & THIRGOOD, S. (2005) Human-predator-prey conflicts: ecological correlates, prey losses and patterns of management. *Biological Conservation*, 122, 159–171.
- GROBLER, J.H. (1981) Feeding behaviour of the caracal *Felis caracal* Schreber 1776 in the Mountain Zebra National Park. *South African Journal of Zoology*, 16, 259–262.
- GUO, K., LIU, H., BAO, H., HU, J., WANG, S., ZHANG, W., ET AL. (2017) Habitat selection and their interspecific interactions for mammal assemblage in the Greater Khingan Mountains, northeastern China. *Wildlife Biology*, 2017, wlb.00261.
- 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.
- HARPER, G.A. (2007) Habitat selection of feral cats (*Felis catus*) on a temperate, forested island. *Austral Ecology*, 32, 305–314.
- HARVEY, P. (2015) ExifTool: read, write and edit meta information. Retrieved from: <https://exiftool.org/>.

- HAYWARD, M.W. & KERLEY, G.I.H. (2008) Prey preferences and dietary overlap amongst Africa's large predators. *African Journal of Wildlife Research*, 38, 93–108.
- HEURICH, M., HILGER, A., KÜCHENHOFF, H., ANDRÉN, H., BUFKA, L., KROFEL, M., ET AL. (2014) Activity patterns of Eurasian lynx are modulated by light regime and individual traits over a wide latitudinal range. *PLoS ONE*, 9, 1–20.
- 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 Journal of Zoology*, 135, 91–96.
- HORSTMAN, L.P. & GUNSON, J.R. (1982) Black bear predation on livestock in Alberta. *Wildlife Society Bulletin*, 10, 34–39.
- HUMPHRIES, B.D., RAMESH, T. & DOWNS, C.T. (2016). Diet of black-backed jackals (*Canis mesomelas*) on farmlands in the KwaZulu-Natal Midlands, South Africa. *Mammalia*, 80, 405–412.
- HUTTO, R.L. (1985) Habitat selection by nonbreeding migratory land birds. In *Habitat Selection in Birds* (ed M.L. Cody), pp. 455–476. Academic Press, Orlando, Florida, USA.
- IBM CORP (2015) IBM SPSS Statistics for Windows. Armonk, New York.
- JANSEN, C. (2016) *Diet of Key Predators Responsible for Livestock Conflict in Namaqualand, South Africa*. MSc Thesis. Stellenbosch University, Stellenbosch, South Africa.
- JANSEN, C., LESLIE, A.J., CRISTESCU, B., TEICHMAN, K.J. & MARTINS, Q. (2019) Determining the diet of an African mesocarnivore, the caracal: scat or GPS cluster analysis? *Wildlife Biology*, wlb.00579.
- JENKS, K.E., CHANTEAP, P., DAMRONGCHAINARONG, K., CUTTER, P., CUTTER, P., REDFORD, T., ET AL. (2011) Using relative abundance indices from camera-trapping to test wildlife conservation hypotheses - an example from Khao Yai National Park, Thailand. *Tropical Conservation Science*, 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. *Animal Conservation*, 5, 119–120.

- JORGENSEN, C.J., CONLEY, R.H., HAMILTON, R.J. & SANDERS, O.T. (1978) In *Proceedings of the Eastern workshop on black bear management and research* pp. 297–321.
- KAMLER, J.F., LOVERIDGE, A.J., O'DONNELL, H. & MACDONALD, D.W. (2020) Effects of humans and large carnivores on the survival of black-backed jackals. *African Journal of Ecology*, 58, 557–562.
- KARANTH, K.U. & MADHUSUDAN, M.D. (2002) Mitigating human-wildlife conflicts in southern Asia. In *Making Parks Work: Identifying Key Factors to Implementing Parks in the Tropics* (eds J. Terborgh, C.P. Van Schaik, M. Rao & L.C. Davenport), pp. 250–264. Island Press, Covelo, California, USA.
- KAUNDA, S.K.K. (2000) Activity patterns of black-backed jackals at Mokolodi Nature Reserve, Botswana. *African Journal of Wildlife Research*, 30, 157–162.
- KAUNDA, S.K.K. (2001) Spatial utilization by black-backed jackals in southeastern Botswana. *African Zoology*, 36, 143–152.
- KAUNDA, S.K.K. & SKINNER, J.D. (2003) Black-backed jackal diet at Mokolodi Nature Reserve, Botswana. *African Journal of Ecology*, 41, 39–46.
- KELLERT, S.R. (1985) Public perceptions of predators, particularly the wolf and coyote. *Biological Conservation*, 31, 167–189.
- KEOGH, H. (1979) *An Atlas of Hair from Southern African Mammal Species with Reference to its Taxonomic and Ecological Significance*. PhD thesis. University of Pretoria, Pretoria, South Africa.
- KEOGH, H.J. (1983) A photographic reference system of the microstructure of the hair of southern African bovids. *South African Journal of Wildlife Research*, 13, 89–131.
- 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 Journal of Wildlife Research*, 15, 109–159.
- KERLEY, G.I.H., BEHRENS, K.G., CARRUTHERS, J., DIEMONT, M., DU PLESSIS, J., MINNIE, L., ET AL. (2017) Livestock predation in South Africa: the need for and value of a scientific assessment. *South African Journal of Science*, 113, 3–3.

- KITCHEN, A.M., GESE, E.M. & SCHAUSTER, E.R. (2000) Changes in coyote activity patterns due to reduced exposure to human persecution. *Canadian Journal of Zoology*, 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. *Mammal Review*, 41, 294–312.
- KLARE, U., KAMLER, J.F., STENKEWITZ, U. & MACDONALD, D.W. (2010) Diet, prey selection, and predation impact of black-backed jackals in South Africa. *Journal of Wildlife Management*, 74, 1030–1042.
- KOK, O.B. & NEL, J.A.J. (2004) Convergence and divergence in prey of sympatric canids and felids: opportunism or phylogenetic constraint? *Biological Journal of the Linnean Society*, 83, 527–538.
- KREBS, J.R. & DAVIES, N.B. (2009) *Behavioural Ecology: An Evolutionary Approach*. Blackwell Scientific, Oxford, UK.
- KRUUK, H. (1980) *The Effects of Large Carnivores on Livestock and Animal Husbandry in Marsabit District, Kenya*. UNEP-MAB Integrated Project in Arid Lands. IPAL Technical Report, 1–52.
- KRUUK, H. (2002) *Hunter and Hunted: Relationships Between Carnivores and People*. Cambridge University Press, Cambridge, UK.
- LENSING, J.E. & JOUBERT, E. (1976) Intensity distribution patterns for five species of problem animals in South West Africa. *Madoqua*, 10, 131–141.
- LESUR, J., HILDEBRAND, E.A., ABAWA, G. & GUTHERZ, X. (2014) The advent of herding in the Horn of Africa: new data from Ethiopia, Djibouti and Somaliland. *Quaternary International*, 343, 148–158.
- LEVINS, R. (1968) *Evolution in Changing Environments: Some Theoretical Explorations*. Princeton University Press, New Jersey, USA.
- LEWIS, P.M., BURNS, G.L. & JONES, D. (2017) Response and responsibility: humans as apex predators and ethical actors in a changing societal environment. *Food Webs*, 12, 49–55.
- LI, X., BUZZARD, P., CHEN, Y. & JIANG, X. (2013). Patterns of livestock predation by carnivores:

- human–wildlife conflict in Northwest Yunnan, China. *Environmental Management*, 52, 1334–1340.
- LINNELL, J.D.C., ODDEN, J., SMITH, M.E., AANES, R. & SWENSON, J.E. (1999) Large carnivores that kill livestock: do ‘problem individuals’ really exist? *Wildlife Society Bulletin*, 27, 698–705.
- LOW, A.B. & REBELO, A.G. (1996) *Vegetation of South Africa, Lesotho and Swaziland*. Department of Environmental Affairs and Tourism, Pretoria, South Africa.
- MACDONALD, D.W. (1983) The ecology of carnivore social behaviour. *Nature*, 301, 379–384.
- MACKENZIE, D.I. & ROYLE, J.A. (2005) Designing occupancy studies: general advice and allocating survey effort. *Journal of Applied Ecology*, 42, 1105–1114.
- MADDEN, F. (2004) Creating coexistence between humans and wildlife: global perspectives on local efforts to address human–wildlife conflict. *Human Dimensions of Wildlife*, 9, 247–257.
- MANOA, D.O. & MWAURA, F. (2016) Predator-proof bomas as a tool in mitigating human–predator conflict in Loitokitok Sub-County Amboseli Region of Kenya. *Natural Resources*, 7, 28–39.
- MARKER, L. & DICKMAN, A. (2005) Notes on the spatial ecology of caracals (*Felis caracal*), with particular reference to Namibian farmlands. *African Journal of Ecology*, 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. *Conservation Biology*, 17, 1290–1298.
- MARTÍN-DÍAZ, P., GIL-SÁNCHEZ, J.M., BALLESTEROS-DUPERÓN, E., BAREA-AZCÓN, J.M., VIRGÓS, E., PARDAVILA, X., ET AL. (2018) Integrating space and time in predator-prey studies: the case of wildcats and rabbits in SE Spain. *Mammalian Biology*, 88, 114–122.
- MARTIN, E.H., CAVADA, N., NDIBALEMA, V.G. & ROVERO, F. (2015) Modelling fine-scale habitat associations of medium-to-large forest mammals in the Udzungwa Mountains of Tanzania using camera trapping. *Tropical Zoology*, 28, 137–151.
- MAZEROLLE, M. (2019) Model Selection and Multimodel Inference Based on (Q)AIC(c)

Retrieved from: <https://cran.r-project.org/web/packages/AICcmodavg/AICcmodavg.pdf>.

- MCCARTHY, J.L., WIBISONO, H.T., MCCARTHY, K.P., FULLER, T.K. & ANDAYANI, N. (2015) Assessing the distribution and habitat use of four felid species in Bukit Barisan Selatan National Park, Sumatra, Indonesia. *Global Ecology and Conservation*, 3, 210–221.
- MCMANUS, J.S., DICKMAN, A.J., GAYNOR, D., SMUTS, B.H. & MACDONALD, D.W. (2015) Dead or alive? Comparing costs and benefits of lethal and non-lethal human-wildlife conflict mitigation on livestock farms. *Oryx*, 49, 687–695.
- MCMANUS, J., GOETS, S.A., BOND, W.J., HENSCHER, J.R., SMUTS, B. & MILTON, S.J. (2018) Effects of short-term intensive trampling on Karoo vegetation. *African Journal of Range and Forage Science*, 35, 311–318.
- MCNAB, B.K. (1970) Body weight and the energetics of temperature regulation: a re-examination. *Journal of Experimental Biology*, 53, 329–348.
- MELVILLE, H.I.A.S., BOTHMA, J.D.P. & MILLS, M.G.L. (2004) Prey selection by caracal in the Kgalagadi Transfrontier Park. *African Journal of Wildlife Research*, 34, 67–75.
- MELVILLE, H.I.A.S. & BOTHMA, J.D.P. (2006a) Using spoor counts to analyse the effect of small stock farming in Namibia on caracal density in the neighbouring Kgalagadi Transfrontier Park. *Journal of Arid Environments*, 64, 436–447.
- MELVILLE, H.I.A.S. & BOTHMA, J.P. (2006b) Possible optimal foraging for Brants's whistling rats by caracals in the Kgalagadi Transfrontier Park. *African Zoology*, 41, 134–136.
- MEREDITH, M. & RIDOUT, M. (2016) Overview of the overlap package. R Project 1–9.
- MEREDITH, M. & RIDOUT, M. (2018) Estimates of coefficient of overlapping for animal activity patterns. Retrieved from: <https://cran.r-project.org/package=overlap>.
- METZ, C.E. (1979) Applications of ROC analysis in diagnostic image evaluation. In *The Physics of Medical Imaging* (ed A.G. Haus), pp. 283–298. American Institute of Physics, New York, USA.
- MEYER, A.F. (undated) *Camera Trapping Table Mountain and Constantiaberg. Larger Terrestrial Mammals Approaching Metropolitan Cape Town, South Africa*. PhD thesis. University of Cape Town, Cape Town, South Africa.

- MILLS, M.G.L. & SCHENK, T.M. (1992) Predator-prey relationships: the impact of lion predation on wildebeest and zebra. *Journal of Animal Ecology*, 61, 693–702.
- MINNIE, L., AVENANT, N.L., DROUILLY, M. & SAMUELS, I. (2018) Biology and ecology of the black-backed jackal and caracal. In *Livestock Predation and its Management in South Africa: A Scientific Assessment* (eds G.I.H. Kerley, S.L. Wilson & D. Balfour), pp. 178–204. Centre for African Conservation Ecology, Nelson Mandela University, Port Elizabeth, South Africa.
- MINNIE, L., GAYLARD, A. & KERLEY, G.I.H. (2016) Compensatory life-history responses of a mesopredator may undermine carnivore management efforts. *Journal of Applied Ecology*, 53, 379–387.
- MISHRA, C. (1997) Livestock depredation by large carnivores in the Indian trans-Himalaya: conflict perceptions and conservation prospects. *Environmental Conservation*, 24, 338–343.
- MIZUTANI, F. (1993) Home range of leopards and their impact on livestock in Kenyan ranches. In *Mammals as Predators* (eds N. Dunstone & M.L. Gorman), pp. 425–439. Clarendon Press, Oxford, UK.
- MOLEWA, B.E.E. (2010) National Environmental Management: Biodiversity Act, 2004: Act 10 of 2004 (ed Department of Environmental Affairs). Draft norms and standards for the management of damage-causing animals in South Africa. *Government Gazette* 33806. Cape Town, South Africa.
- MONADJEM, A., TAYLOR, P.J., DENYS, C. & COTTERILL, F.P. (2015) *Rodents of Sub-Saharan Africa: A Biogeographic and Taxonomic Synthesis*. de Gruyter, Berlin, Germany.
- MONTERROSO, P., ALVES, P.C. & FERRERAS, P. (2013) Catch me if you can: diel activity patterns of mammalian prey and predators. *Ethology*, 119, 1044–1056.
- MOOLMAN, L.C. (1984) 'n Vergelyking van die voedingsgewoontes van die Rooikat *Felis caracal* binne en buite die Bergkwagga Nasionale Park. *Koedoe*, 27, 121–129.
- MOOLMAN, L.C. (1986) *Aspekte van die Ekologie en Gedrag van die Rooikat Felis caracal, Shreber, 1776 in die Bergkwagga Nasionale Park en op die Omliggende Plase*. MSc Thesis. University of Pretoria, Pretoria, South Africa.

- MOREIRA-ARCE, D., VERGARA, P.M., BOUTIN, S., SIMONETTI, J.A., BRICEÑO, C. & ACOSTA-JAMETT, G. (2015a) Native forest replacement by exotic plantations triggers changes in prey selection of mesocarnivores. *Biological Conservation*, 192, 258–267.
- MOREIRA-ARCE, D., VERGARA, P.M. & BOUTIN, S. (2015b) Diurnal human activity and introduced species affect occurrence of carnivores in a human-dominated landscape. *PLoS ONE*, 10, 1–19.
- MUCINA, L., RUTHERFORD, M.C., PALMER, A.R., MILTON, S.J., SCOTT, L., LLOYD, W.J., ET AL. (2006) Nama-Karoo Biome. In *The Vegetation of South Africa, Lesotho and Swaziland* (eds L. Mucina & M.C. Rutherford), pp. 325–347. South African National Biodiversity Institute, Pretoria, South Africa.
- MUHLI, T.B., HEBBLEWHITE, M., PATON, D., PITT, J.A., BOYCE, M.S. & MUSIANI, M. (2013) Humans strengthen bottom-up effects and weaken trophic cascades in a terrestrial food web. *PLoS ONE*, 8, e64311.
- NATTRASS, N. & CONRADIE, B. (2018) Predators, livestock losses and poison in the South African Karoo. *Journal of Cleaner Production*, 194, 777–785.
- NATTRASS, N., CONRADIE, B. & CONRADIE, I. (2015) The Koup fencing project: community-led job creation in the Karoo. *African Journal of Agricultural and Resource Economics*, 10, 131–145.
- NATTRASS, N., CONRADIE, B., DROUILLY, M. & O'RAIN, M.J. (2017) A brief history of predators, sheep farmers and government in the Western Cape, South Africa. *CSSR Working Paper no 398*. Centre for Social Science Research Unit, University of Cape Town, Cape Town, South Africa.
- NEILS, A.M. (2018) *Caracals in a Heterogeneous Landscape: Resolutions for Human-Carnivore Conflicts*. PhD thesis. University of Arizona, Arizona, USA.
- NIEDBALLA, J., COURTIOL, A., SOLLMANN, R., MATHAI, J., WONG, S.T., NGUYEN, A.T.T., ET AL. (2020) Package 'camtrapR'. Retrieved from: <https://github.com/jniedballa/camtrapR>.
- NORTON, P.M. (1986) Historical changes in the distribution of leopards in the Cape Province, South Africa. *Bontebok*, 5, 1–9.
- NORTON, P.M. & LAWSON, A.B. (1985) Radio tracking of leopards and caracals in the

- Stellenbosch area, Cape Province. *South African Journal of Wildlife Research*, 15, 17–24.
- NOWELL, K. & JACKSON, P. (1996) *Wild Cats: Status Survey and Conservation Action Plan*. Gland, IUCN.
- O'BRIEN, T.G. & KINNAIRD, M.F. (2011) Density estimation of sympatric carnivores using spatially explicit capture-recapture methods and standard trapping grid. *Ecological Applications*, 21, 2908–2916.
- O'BRIEN, T.G., KINNAIRD, M.F. & WIBISONO, H.T. (2003) Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. *Animal Conservation*, 6, 131–139.
- O'CONNELL, A.F., NICHOLS, J.D. & KARANTH, K.U. (2011) *Camera Traps in Animal Ecology: Methods and Analyses*. Springer, New York, USA.
- 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. *European Journal of Wildlife Research*, 52, 237–244.
- OGADA, D.L. (2014) The power of poison: pesticide poisoning of Africa's wildlife. *Annals of the New York Academy of Sciences*, 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. *Conservation Biology*, 17, 1521–1530.
- 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. *Biological Conservation*, 68, 63–68.
- ORDIZ, A., BISCHOF, R. & SWENSON, J.E. (2013) Saving large carnivores, but losing the apex predator? *Biological Conservation*, 168, 128–133.
- OTT, T., KERLEY, G.I.H. & BOSHOFF, A.F. (2007) Preliminary observations on the diet of leopards (*Panthera pardus*) from a conservation area and adjacent rangelands in the Baviaanskloof region, South Africa. *African Zoology*, 42, 31–37.

- PALMER, R. & FAIRALL, N. (1988) Caracal and African wild cat diet in the Karoo National Park and the implications thereof for hyrax. *South African Journal of Wildlife Research*, 18, 30–34.
- PERRIN, M.R. & CAMPBELL, B.S. (1980) 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 Journal of Wildlife Research*, 10, 1–14.
- POHL, C.F. (2015) *The Diet of Caracal (Caracal caracal) in the Southern Free State*. MSc thesis. University of the Free State, Bloemfontein, South Africa.
- PRINGLE, J.A. & PRINGLE, V.L. (1979) Observations on the lynx *Felis caracal* in the Bedford district. *South African Journal of Zoology*, 14, 1–4.
- PRUGH, L.R., STONER, C.J., EPPS, C.W., BEAN, W.T., RIPPLE, W.J., LALIBERTE, A.S., ET AL. (2009) The rise of the mesopredator. *BioScience*, 59, 779–791.
- PYKE, G.H. (1984) Optimal foraging theory: a critical review. *Annual Review of Ecology and Systematics*, 15, 523–575.
- QGIS DEVELOPMENT TEAM (2018) QGIS Geographic Information System. Open Source Geospatial Foundation. Retrieved from: <https://www.qgis.org>.
- R CORE TEAM (2016) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.
- RAMESH, T., KALLE, R. & DOWNS, C.T. (2017) Space use in a South African agriculture landscape by the caracal (*Caracal caracal*). *European Journal of Wildlife Research*, 63, 1–11.
- RASMUSSEN, G.S.A. (1999) Livestock predation by the painted hunting dog *Lycaon pictus* in a cattle ranching region of Zimbabwe: a case study. *Biological Conservation*, 88, 133–139.
- REDPATH, S.M., BHATIA, S. & YOUNG, J. (2015) Tilting at wildlife: reconsidering human-wildlife conflict. *Oryx*, 49, 222–225.
- 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. *Journal of Applied Ecology*, 53, 1225–1235.
- RIDOUT, M.S. & LINKIE, M. (2009) Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics*, 14, 322–337.

- RITCHIE, E.G. & JOHNSON, C.N. (2009) Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, 12, 982–998.
- ROBIN, X., TURCK, N., HAINARD, A., TIBERTI, N., LISACEK, F., SANCHEZ, J.C., ET AL. (2011) pROC: an open-source package for R and S+ to analyze and compare ROC curves. *BMC Bioinformatics*, 8, 12–77.
- ROCHLITZ, I., PEARCE, G.P. & BROOM, D.M. (2010) *The Impact of Snares on Animal Welfare*. Cambridge University Press, Cambridge, UK.
- RODRIGUEZ, S.L. (2007) *Perceptions and Attitudes of a Maasai Community Regarding Wildlife-Damage Compensation, Conservation, and the Predators that Prey on their Livestock*. PhD thesis. School for International Training in Brattleboro, USA.
- ROMERO-MUÑOZ, A., MAFFEI, L., CUÉLLAR, E. & NOSS, A.J. (2010) Temporal separation between jaguar and puma in the dry forests of southern Bolivia. *Journal of Tropical Ecology*, 26, 303–311.
- ROVERO, F., COLLETT, L., RICCI, S., MARTIN, E. & SPITALE, D. (2013) Distribution, occupancy, and habitat associations of the gray-faced sengi (*Rhynchocyon udzungwensis*) as revealed by camera traps. *Journal of Mammalogy*, 94, 792–800.
- ROVERO, F. & MARSHALL, A.R. (2009) Camera trapping photographic rate as an index of density in forest ungulates. *Journal of Applied Ecology*, 46, 1011–1017.
- ROVERO, F., OWEN, N. & JONES, T. (2017) Camera trapping surveys of forest mammal communities in the Eastern Arc Mountains reveal generalized habitat and human disturbance responses. *Biodiversity and Conservation*, 26, 1103–1119.
- ROWCLIFFE, J.M., KAYS, R., KRANSTAUBER, B., CARBONE, C. & JANSEN, P.A. (2014) Quantifying levels of animal activity using camera trap data. *Methods in Ecology and Evolution*, 5, 1170–1179.
- SACKS, B.N., JAEGER, M.M., NEALE, J.C. & MCCULLOUGH, D.R. (1999) Territoriality and breeding status of coyotes relative to sheep predation. *Journal of Wildlife Management*, 63, 593–605.
- SAJ, T.L., SICOTTE, P. & PATERSON, J.D. (2001) The conflict between vervet monkeys and farmers at the forest edge in Entebbe, Uganda. *African Journal of Ecology*, 39, 195–199.

- SCHIESS-MEIER, M., RAMSAUER, S., GABANAPELO, T. & KOENIG, B. (2007) Livestock predation-insights from problem animal control registers in Botswana. *Journal of Wildlife Management*, 71, 1267–1274.
- SCHNEIDER, M.F. & BURAMUGE, V.A. (2006) Atlas of the microscopic hair structure of Southern African Shrews, Hedgehogs, Golden Moles and Elephant-shrews (Mammalia). *Bonner Zoologische Beiträge*, 54, 103–172.
- SEILER, N. (2010) SEM-Atlas of hair structures of South-African mammals. *Mammalia*, 74, 281–290.
- SELVAN, K.M., KRISHNAKUMAR, B.M., RAMASAMY, P. & THINESH, T. (2019) Diel activity pattern of meso-carnivores in the suburban tropical dry evergreen forest of the Coromandel Coast, India. *Journal of Threatened Taxa*, 11, 13960–13966.
- SHRADER, A.M., BROWN, J.S., KERLEY, G.I.H. & KOTLER, B.P. (2008) Do free-ranging domestic goats show ‘landscapes of fear’? Patch use in response to habitat features and predator cues. *Journal of Arid Environments*, 72, 1811–1819.
- SILLERO-ZUBIRI, C. & LAURENSEN, K. (2001) Interactions between carnivores and local communities: conflict or co-existence? In *Carnivore conservation* (eds J. Gittleman, S.M. Funk, D.W. Macdonald & R.K. Wayne), pp 282–312. Cambridge University Press, Cambridge, UK.
- 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*, 103, 92–95.
- SKINNER, J.D. & CHIMIMBA, C.T. (2005) *The Mammals of the Southern African Sub-Region*. Cambridge University Press, Cape Town, South Africa.
- SOYUMERT, A., ERTÜRK, A. & TAVŞANOĞLU, Ç. (2019) The importance of lagomorphs for the Eurasian lynx in western Asia: results from a large scale camera-trapping survey in Turkey. *Mammalian Biology*, 95, 18–25.
- SPEELMAN, S.R. (1939) Feeding dogs. In *Food and Life/Yearbook of Agriculture* pp. 856–870.
- STORM, D.J., NIELSON, C.K., SHAUBER, E.M. & WOOLF, A. (2007) Deer-human conflict and hunter access in an exurban landscape. *Human-Wildlife Conflicts*, 1, 53–59.

- STUART, C.T. (1982) *Aspects of the Biology of the Caracal (Felis caracal Schreber 1776) in the Cape Province, South Africa*. MSc thesis. University of Natal, Pietermaritzburg, South Africa.
- STUART, C.T. & HICKMAN, G.C. (1991) Prey of caracal *Felis caracal* in two areas of Cape Province, South Africa [stomach content analysis]. *Journal of African Zoology*, 105, 373–381.
- STUART, C. & STUART, M. (2015) *Stuarts' Field Guide to Mammals of Southern Africa, Including Angola, Zambia & Malawi*. Struik Nature, Penguin Random House, Cape Town, South Africa.
- STUART, C. & STUART, T. (1994) *Tracks and Signs of southern and east African Wildlife*. Southern Book Publishers, Cape Town, South Africa.
- SUNQUIST, M.E. & SUNQUIST, F. (2002) *Wild Cats of the World*. University of Chicago Press, Chicago, USA.
- SWANEPOEL, J. (2016) Habits of the hunters: the biopolitics of combatting predation amongst small stock farmers in southern Namibia. *Journal of Contemporary African Studies*, 34, 129–146.
- SWARNA NANTHA, H. & TISDELL, C. (2009) The orangutan-oil palm conflict: economic constraints and opportunities for conservation. *Biodiversity and Conservation*, 18, 487–502.
- TANG, X., TANG, S., LI, X., MENGHE, D., BAO, W., XIANG, C., ET AL. (2019) A study of population size and activity patterns and their relationship to the prey species of the eurasian lynx using a camera trapping approach. *Animals*, 9, 864–906.
- TARU, P. & BACKWELL, L.R. (2014) Hair morphology of some artiodactyls from southern Africa. *Annals of the Ditsong National Museum of Natural History*, 4, 26–32.
- THORN, M., GREEN, M., DALERUM, F., BATEMAN, P.W. & SCOTT, D.M. (2012) What drives human-carnivore conflict in the North West Province of South Africa? *Biological Conservation*, 150, 23–32.
- TREVES, A. (2002) Wolf justice: managing human-carnivore conflict in the 21st century. *Wolf Print*, 13, 6–9.

- TREVES, A. & KARANTH, K.U. (2003) Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology*, 17, 1491–1499.
- TREVES, A., KROFEL, M. & MCMANUS, J. (2015) Predator control should not be a shot in the dark. *Frontiers in Ecology and the Environment*, 14, 380–388.
- TREVES, A., NAUGHTON-TREVES, L., HARPER, E.K., MLADENOFF, D.J., ROSE, R.A., SICKLEY, T.A., ET AL. (2004) Predicting human-carnivore conflict: a spatial model derived from 25 years of data on wolf predation on livestock. *Conservation Biology*, 18, 114–125.
- TURPIE, J.K. & BABATOPIE, A. (2018) The socio-economic impacts of livestock predation and its prevention in South Africa. In *Livestock Predation and its Management in South Africa: A Scientific Assessment* (eds G.I.H. Kerley, S.L. Wilson & D. Balfour), pp. 53–81. Centre for African Conservation Ecology, Nelson Mandela University, Port Elizabeth, South Africa.
- VAN HEEZIK, Y.M. & SEDDON, P.J. (1998) Range size and habitat use of an adult male caracal in northern Saudi Arabia. *Journal of Arid Environments*, 40, 109–112.
- VAN NIEKERK, H.N. (2010) *The Cost of Predation on Small Livestock in South Africa by Medium-Sized Predators*. MSc thesis. University of the Free State, Bloemfontein, South Africa.
- WATKEYS, M.K. (1999) Soils of the arid south-western zone of Africa. In *The Karoo: Ecological Patterns and Processes* (eds W.R.J. Dean & S.J. Milton), pp. 17–26. Cambridge University Press, Cambridge, UK.
- WEISBEIN, Y. & MENDELSSOHN, H. (1990) The biology and ecology of the caracal *Felis caracal* in the northern Arava valley of Israel. *Cat News*, 12, 20–22.
- WOODROFFE, R. (2000) Predators and people: using human densities to interpret declines of large carnivores. *Animal Conservation*, 3, 165–173.
- WORTHY, F.R. & FOGGIN, J.M. (2008) Conflicts between local villagers and Tibetan brown bears threaten conservation of bears in a remote region of the Tibetan Plateau. *Human-Wildlife Conflicts*, 2, 200–205.
- ZARCO-GONZÁLEZ, M.M. & MONROY-VILCHIS, O. (2014) Effectiveness of low-cost deterrents in decreasing livestock predation by felids: a case in Central Mexico. *Animal Conservation*, 17, 371–378.

Appendices

Appendix 1 Prey items recorded in caracal scat collected at the control site, just outside of Beaufort West, Western Cape, South Africa. Frequency of occurrence (%) was calculated as the number of occurrences of each prey item divided by the total number of occurrences (n = 124). The corrected frequency of occurrence (%) was calculated as the number of occurrences per scat divided by the total number of scats collected at that site (n = 58).

Prey	Number of occurrences (prey items) n = 124	Frequency of occurrence	Frequency of occurrence (%)	Number of occurrences (per scat) n = 58	Corrected frequency of occurrence	Corrected frequency of occurrence (%)
Invertebrates	16	0.13	12.90	6.28	0.11	10.90
Coleoptera	15	0.12	12.10	5.95	0.10	10.32
Orthoptera	0	0.00	0.00	0.00	0.00	0.00
Scorpionida	1	0.01	0.81	0.33	0.01	0.58
Hemiptera	0	0.00	0.00	0.00	0.00	0.00
Reptiles	3	0.02	2.42	0.78	0.01	1.36
Squamates	3	0.02	2.42	0.78	0.01	1.36
Karoo tent tortoise (<i>Psammobates tentorius</i>)	0	0.00	0.00	0.00	0.00	0.00
Birds	0	0.00	0.00	0.00	0.00	0.00

Mammals	68	0.55	54.84	35.32	0.61	61.24
Wild ungulates	15	0.12	12.10	6.83	0.12	11.85
Springbok (<i>Antidorcas marsupialis</i>)	6	0.05	4.84	2.33	0.04	4.05
Cape grysbok (<i>Raphicerus melanotis</i>)	3	0.02	2.42	1.50	0.03	2.60
Common duiker (<i>Sylvicapra grimmia</i>)	3	0.02	2.42	1.00	0.02	1.73
Klipspringer (<i>Oreotragus oreotragus</i>)	0	0.00	0.00	0.00	0.00	0.00
Steenbok (<i>Raphicerus campestris</i>)	3	0.02	2.42	2.00	0.03	3.47
Bush pig (<i>Potamochoerus larvatus</i>)	0	0.00	0.00	0.00	0.00	0.00
Carnivores	5	0.04	4.03	1.62	0.03	2.80
Meerkat (<i>Suricata suricatta</i>)	2	0.02	1.61	0.67	0.01	1.16
African wild cat (<i>Felis silvestris lybica</i>)	3	0.02	2.42	0.95	0.02	1.65
Striped polecat (<i>Ictonyx striatus</i>)	0	0.00	0.00	0.00	0.00	0.00
African weasel (<i>Poecilogale albinucha</i>)	0	0.00	0.00	0.00	0.00	0.00
Small-spotted genet (<i>Genetta genetta</i>)	0	0.00	0.00	0.00	0.00	0.00
Mongoose	0	0.00	0.00	0.00	0.00	0.00
Domestic sheep (<i>Ovis aries</i>)	0	0.00	0.00	0.00	0.00	0.00
Small mammals	20	0.16	16.13	12.70	0.22	22.02
Bush Karoo rat (<i>Myotomys unisulcatus</i>)	8	0.06	6.45	4.37	0.08	7.57
Hairy-footed gerbil (<i>Gerbillurus paebe</i>)	6	0.05	4.84	2.33	0.04	4.05
Cape gerbil (<i>Gerbilliscus afra</i>)	1	0.01	0.81	0.33	0.01	0.58
Brant's whistling rat (<i>Parotomys brantsii</i>)	3	0.02	2.42	2.33	0.04	4.05

Namaqua rock mouse (<i>Micaelamys namaquensis</i>)	1	0.01	0.81	0.33	0.01	0.58
Kreb's fat mouse (<i>Steatomys krebsii</i>)	1	0.01	0.81	1.00	0.02	1.73
Four-striped mouse (<i>Rhabdomys pumilio</i>)	0	0.00	0.00	0.00	0.00	0.00
Cape spiny mouse (<i>Acomys subspinosus</i>)	0	0.00	0.00	0.00	0.00	0.00
Pouched mouse (<i>Saccostomus campestris</i>)	0	0.00	0.00	0.00	0.00	0.00
Grey climbing mouse (<i>Dendromus melanotis</i>)	0	0.00	0.00	0.00	0.00	0.00
Shrews	0	0.00	0.00	2.00	0.03	3.47
Rock hyraxes (<i>Procavia capensis</i>)	10	0.08	8.06	4.50	0.08	7.80
Lagomorpha	12	0.10	9.68	7.50	0.13	13.01
Other mammals	2	0.02	1.61	1.17	0.02	2.02
Cape mole rat (<i>Georchus capensis</i>)	0	0.00	0.00	0.00	0.00	0.00
Cape ground squirrel (<i>Xerus inauris</i>)	2	0.02	1.61	1.17	0.02	2.02
Anthropogenic items	0	0.00	0.00	0.00	0.00	0.00
Vegetation	37	0.30	29.84	15.28	0.27	26.50
Total	124	1	100	57.67	1	100

Appendix 2 Prey items recorded in caracal scat collected at the lethal treatment site, just outside of Beaufort West, Western Cape, South Africa. Frequency of occurrence (%) was calculated as the number of occurrences of each prey item divided by the total number of occurrences (n = 181). The corrected frequency of occurrence (%) was calculated as the number of occurrences per scat divided by the total number of scats collected at that site (n = 88).

Prey	Number of occurrences (prey items) n = 181	Frequency of occurrence	Frequency of occurrence (%)	Number of occurrences (per scat) n = 88	Corrected frequency of occurrence	Corrected frequency of occurrence (%)
Invertebrates	10	0.06	5.52	2.45	0.03	2.79
Coleoptera	10	0.06	5.52	2.45	0.03	2.79
Orthoptera	0	0.00	0.00	0.00	0.00	0.00
Scorpionida	0	0.00	0.00	0.00	0.00	0.00
Hemiptera	0	0.00	0.00	0.00	0.00	0.00
Reptiles	3	0.02	1.66	1.17	0.01	1.33
Squamates	3	0.02	1.66	1.17	0.01	1.33
Karoo tent tortoise (<i>Psammobates tentorius</i>)	0	0.00	0.00	0.00	0.00	0.00
Birds	1	0.01	0.55	0.50	0.01	0.57
Mammals	111	0.61	61.33	58.32	0.67	66.52
Wild ungulates	22	0.12	12.15	12.08	0.14	13.78
Springbok (<i>Antidorcas marsupialis</i>)	5	0.03	2.76	2.33	0.03	2.66

Cape grysbok (<i>Raphicerus melanotis</i>)	3	0.02	1.66	1.08	0.01	1.24
Common duiker (<i>Sylvicapra grimmia</i>)	6	0.03	3.31	3.83	0.04	4.37
Klipspringer (<i>Oreotragus oreotragus</i>)	0	0.00	0.00	0.00	0.00	0.00
Steenbok (<i>Raphicerus campestris</i>)	3	0.02	1.66	1.83	0.02	2.09
Bush pig (<i>Potamochoerus larvatus</i>)	5	0.03	2.76	3.00	0.03	3.42
Carnivores	4	0.02	2.21	2.00	0.02	2.28
Meerkat (<i>Suricata suricatta</i>)	2	0.01	1.10	1.00	0.01	1.14
African wild cat (<i>Felis silvestris lybica</i>)	0	0.00	0.00	0.00	0.00	0.00
Striped polecat (<i>Ictonyx striatus</i>)	1	0.01	0.55	0.50	0.01	0.57
African weasel (<i>Poecilogale albinucha</i>)	0	0.00	0.00	0.00	0.00	0.00
Honey badger (<i>Mellivora capensis</i>)	0	0.00	0.00	0.00	0.00	0.00
Small-spotted genet (<i>Genetta genetta</i>)	0	0.00	0.00	0.00	0.00	0.00
Mongoose	1	0.01	0.55	0.50	0.01	0.57
Domestic sheep (<i>Ovis aries</i>)	5	0.03	2.76	2.50	0.03	2.85
Small mammals	31	0.17	17.13	15.72	0.18	17.93
Bush Karoo rat (<i>Myotomys unisulcatus</i>)	6	0.03	3.31	2.95	0.03	3.37
Hairy-footed gerbil (<i>Gerbillurus paeba</i>)	2	0.01	1.10	1.20	0.01	1.37
Cape gerbil (<i>Gerbilliscus afra</i>)	0	0.00	0.00	0.00	0.00	0.00
Brant's whistling rat (<i>Parotomys brantsii</i>)	5	0.03	2.76	2.33	0.03	2.66
Namaqua rock mouse (<i>Micaelamys namaquensis</i>)	8	0.04	4.42	3.78	0.04	4.32
Kreb's fat mouse (<i>Steatomys krebsii</i>)	0	0.00	0.00	0.00	0.00	0.00

Four-striped mouse (<i>Rhabdomys pumilio</i>)	2	0.01	1.10	0.45	0.01	0.51
Cape spiny mouse (<i>Acomys subspinosus</i>)	1	0.01	0.55	0.25	0.00	0.29
Pouched mouse (<i>Saccostomus campestris</i>)	1	0.01	0.55	1.00	0.01	1.14
Grey climbing mouse (<i>Dendromus melanotis</i>)	1	0.01	0.55	0.50	0.01	0.57
Shrews	5	0.03	2.76	3.25	0.04	3.71
Rock hyraxes (<i>Procavia capensis</i>)	26	0.14	14.36	11.65	0.13	13.29
Lagomorpha	20	0.11	11.05	10.37	0.12	11.83
Other mammals	2	0.01	1.10	1.50	0.02	1.71
Cape mole rat (<i>Georchus capensis</i>)	0	0.00	0.00	0.00	0.00	0.00
Cape ground squirrel (<i>Xerus inauris</i>)	2	0.01	1.10	1.50	0.02	1.71
Anthropogenic items	3	0.02	1.66	1.75	0.02	2.00
Vegetation	53	0.29	29.28	23.48	0.27	26.79
Total	181	1	100	87.67	1	100

UNIVERSITY of the
WESTERN CAPE

Appendix 3 Prey items recorded in caracal scat collected at the non-lethal treatment site, just outside of Beaufort West, Western Cape, South Africa. Frequency of occurrence (%) was calculated as the number of occurrences of each prey item divided by the total number of occurrences (n = 205). The corrected frequency of occurrence (%) was calculated as the number of occurrences per scat divided by the total number of scats collected at that site (n = 96).

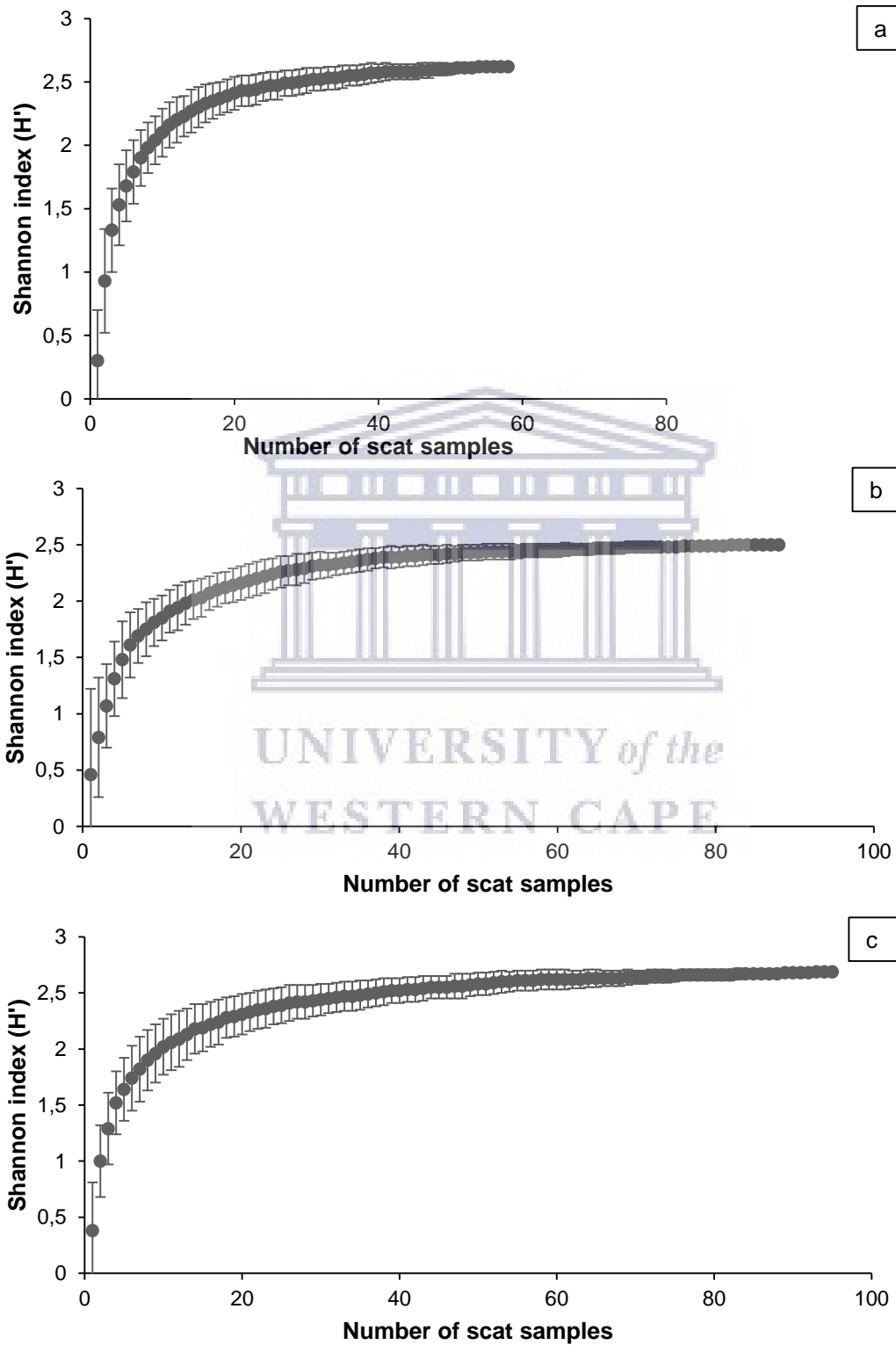
Prey	Number of occurrences (prey items) n = 205	Frequency of occurrence	Frequency of occurrence (%)	Number of occurrences (per scat) n = 96	Corrected frequency of occurrence	Corrected frequency of occurrence (%)
Invertebrates	30	0.15	14.63	10.35	0.11	11.03
Coleoptera	28	0.14	13.66	9.90	0.11	10.55
Orthoptera	1	0.00	0.49	0.20	0.00	0.21
Scorpionida	0	0.00	0.00	0.00	0.00	0.00
Hemiptera	1	0.00	0.49	0.25	0.00	0.27
Reptiles	6	0.03	2.93	1.92	0.02	2.04
Squamates	5	0.02	2.44	1.58	0.02	1.69
Karoo tent tortoise (<i>Psammobates tentorius</i>)	1	0.00	0.49	0.33	0.00	0.36
Birds	2	0.01	0.98	0.58	0.01	0.62
Mammals	116	0.57	56.59	59.58	0.63	63.50
Wild ungulates	18	0.09	8.78	9.28	0.10	9.89
Springbok (<i>Antidorcas marsupialis</i>)	4	0.02	1.95	1.83	0.02	1.95

Cape grysbok (<i>Raphicerus melanotis</i>)	2	0.01	0.98	1.25	0.01	1.33
Common duiker (<i>Sylvicapra grimmia</i>)	3	0.01	1.46	1.70	0.02	1.81
Klipspringer (<i>Oreotragus oreotragus</i>)	2	0.01	0.98	1.00	0.01	1.07
Steenbok (<i>Raphicerus campestris</i>)	6	0.03	2.93	3.00	0.03	3.20
Bush pig (<i>Potamochoerus larvatus</i>)	1	0.00	0.49	0.50	0.01	0.53
Carnivores	7	0.03	3.41	3.33	0.04	3.55
Meerkat (<i>Suricata suricatta</i>)	1	0.00	0.49	0.33	0.00	0.36
African wild cat (<i>Felis silvestris lybica</i>)	1	0.00	0.49	0.33	0.00	0.36
Striped polecat (<i>Ictonyx striatus</i>)	0	0.00	0.00	0.00	0.00	0.00
African weasel (<i>Poecilogale albinucha</i>)	1	0.00	0.49	0.33	0.00	0.36
Honey badger (<i>Mellivora capensis</i>)	1	0.00	0.49	0.50	0.01	0.53
Small-spotted genet (<i>Genetta genetta</i>)	1	0.00	0.49	0.50	0.01	0.53
Mongoose	2	0.01	0.98	1.33	0.01	1.42
Domestic sheep (<i>Ovis aries</i>)	0	0.00	0.00	0.00	0.00	0.00
Small mammals	29	0.14	14.15	15.78	0.17	16.82
Bush Karoo rat (<i>Myotomys unisulcatus</i>)	4	0.02	1.95	1.03	0.01	1.10
Hairy-footed gerbil (<i>Gerbillurus paeba</i>)	8	0.04	3.90	3.08	0.03	3.29
Cape gerbil (<i>Gerbilliscus afra</i>)	1	0.00	0.49	1.00	0.01	1.07
Brant's whistling rat (<i>Parotomys brantsii</i>)	1	0.00	0.49	0.50	0.01	0.53
Namaqua rock mouse (<i>Micaelamys namaquensis</i>)	5	0.02	2.44	2.83	0.03	3.02
Kreb's fat mouse (<i>Steatomys krebsii</i>)	0	0.00	0.00	0.00	0.00	0.00

Four-striped mouse (<i>Rhabdomys pumilio</i>)	1	0.00	0.49	1.00	0.01	1.07
Cape spiny mouse (<i>Acomys subspinosus</i>)	0	0.00	0.00	0.00	0.00	0.00
Pouched mouse (<i>Saccostomus campestris</i>)	3	0.01	1.46	2.50	0.03	2.66
Grey climbing mouse (<i>Dendromus melanotis</i>)	4	0.02	1.95	2.83	0.03	3.02
Shrews	2	0.01	0.98	1.00	0.01	1.07
Rock hyraxes (<i>Procavia capensis</i>)	30	0.15	14.63	14.48	0.15	15.44
Lagomorpha	26	0.13	12.68	15.20	0.16	16.20
Other mammals	2	0.01	0.98	1.00	0.01	1.07
Cape mole rat (<i>Georchus capensis</i>)	1	0.00	0.49	0.50	0.01	0.53
Cape ground squirrel (<i>Xerus inauris</i>)	1	0.00	0.49	0.50	0.01	0.53
Anthropogenic items	0	0.00	0.00	0.00	0.00	0.00
Vegetation	51	0.25	24.88	21.40	0.23	22.81
Total	205	1	100	93.83	1	100

UNIVERSITY of the
WESTERN CAPE

Appendix 4 The cumulative dietary Shannon diversity index against the increasing number of scats for the control (a), lethal (b) and non-lethal (c) treatment sites in the Karoo, South Africa.



Appendix 5 Biomass consumed, as calculated from caracal scat (n = 58) collected at the control site, just outside of Beaufort West, Western Cape, South Africa. Both the biomass consumed and the total biomass consumed is presented.

Prey	Prey weight (kg) ¹	Correction factor (kg/scat) ²	Number of occurrences (n = 64)	Prey item occurrence (FO)	% FO	Biomass consumed (kg) ³	Total biomass consumed (kg) ⁴	Relative biomass consumed	Relative biomass consumed (%)
Wild ungulates	151.00	162.00	15	0.23	23.44	355.50	6.33	0.26	25.97
Springbok (<i>Antidorcas marsupialis</i>)	39.00	27.00	6	0.09	9.38	234.00	2.53	0.10	10.39
Cape grysbok (<i>Raphicerus melanotis</i>)	10.00	27.00	3	0.05	4.69	30.00	1.27	0.05	5.19
Common duiker (<i>Sylvicapra grimmia</i>)	19.50	27.00	3	0.05	4.69	58.50	1.27	0.05	5.19
Klipspringer (<i>Oreotragus oreotragus</i>)	11.50	27.00	0	0.00	0.00	0.00	0.00	0.00	0.00
Steenbok (<i>Raphicerus campestris</i>)	11.00	27.00	3	0.05	4.69	33.00	1.27	0.05	5.19
Bush pig (<i>Potamochoerus larvatus</i>)	60.00	27.00	0	0.00	0.00	0.00	0.00	0.00	0.00
Carnivores	20.21	165.15	5	0.08	7.81	14.33	2.22	0.09	9.09
Meerkat (<i>Suricata suricatta</i>)	0.79	19.87	2	0.03	3.13	1.58	0.62	0.03	2.55

African wild cat (<i>Felis silvestris lybica</i>)	4.25	34.01	3	0.05	4.69	12.75	1.59	0.07	6.54
Striped polecat (<i>Ictonyx striatus</i>)	0.95	20.72	0	0.00	0.00	0.00	0.00	0.00	0.00
African weasel (<i>Poecilogale albinucha</i>)	0.29	17.82	0	0.00	0.00	0.00	0.00	0.00	0.00
Honey badger (<i>Mellivora capensis</i>)	11.00	27.00	0	0.00	0.00	0.00	0.00	0.00	0.00
Small-spotted genet (<i>Genetta genetta</i>)	2.05	25.01	0	0.00	0.00	0.00	0.00	0.00	0.00
Mongoose	0.88	20.72	0	0.00	0.00	0.00	0.00	0.00	0.00
Domestic sheep (<i>Ovis aries</i>)	40.00	27.00	0	0.00	0.00	0.00	0.00	0.00	0.00
Small mammals	0.68	169.08	20	0.31	31.25	1.77	5.31	0.22	21.79
Bush Karoo rat (<i>Myotomys unisulcatus</i>)	0.13	17.14	8	0.13	12.50	1.00	2.14	0.09	8.79
Hairy-footed gerbil (<i>Gerbillurus paeba</i>)	0.03	16.73	6	0.09	9.38	0.15	1.57	0.06	6.44
Cape gerbil (<i>Gerbilliscus afra</i>)	0.10	17.04	1	0.02	1.56	0.10	0.27	0.01	1.09
Brant's whistling rat (<i>Parotomys brantsii</i>)	0.15	17.24	3	0.05	4.69	0.45	0.81	0.03	3.32

Namaqua rock mouse (<i>Micaelamys namaquensis</i>)	0.05	16.83	1	0.02	1.56	0.05	0.26	0.01	1.08
Kreb's fat mouse (<i>Steatomys krebsii</i>)	0.02	16.73	1	0.02	1.56	0.02	0.26	0.01	1.07
Four-striped mouse (<i>Rhabdomys pumilio</i>)	0.06	16.87	0	0.00	0.00	0.00	0.00	0.00	0.00
Cape spiny mouse (<i>Acomys subspinosus</i>)	0.02	16.72	0	0.00	0.00	0.00	0.00	0.00	0.00
Pouched mouse (<i>Saccostomus campestris</i>)	0.05	16.81	0	0.00	0.00	0.00	0.00	0.00	0.00
Grey climbing mouse (<i>Dendromus melanotis</i>)	0.08	16.96	0	0.00	0.00	0.00	0.00	0.00	0.00
Shrews	0.01	16.68	0	0.00	0.00	0.00	0.00	0.00	0.00
Rock hyraxes (<i>Procavia capensis</i>)	3.75	31.97	10	0.16	15.63	37.50	4.99	0.20	20.49
Lagomorpha	3.25	26.24	12	0.19	18.75	39.00	4.92	0.20	20.19
Other mammals	0.83	36.65	2	0.03	3.13	1.30	0.60	0.02	2.47
Cape molerat (<i>Georychus capensis</i>)	0.18	17.37	0	0.00	0.00	0.00	0.00	0.00	0.00
Cape ground squirrel (<i>Xerus inauris</i>)	0.65	19.29	2	0.03	3.13	1.30	0.60	0.02	2.47
Total			64	1.00	100.00	449.41	24.37	1	100

¹ From Stuart & Stuart (2015)

² From Baker et al. (1993), $y = 16.63 + 4.09 x$; only for prey < 4.5kg

³ Prey weight x Number of occurrences

⁴ Correction factor x Prey items occurrence



UNIVERSITY *of the*
WESTERN CAPE

Appendix 6 Biomass consumed, as calculated from caracal scat (n = 88) collected at the lethal treatment site, just outside of Beaufort West, Western Cape, South Africa. Both the biomass consumed and the total biomass consumed is presented.

Prey	Prey weight (kg) ¹	Correction factor (kg/scat) ²	Number of occurrences (n = 110)	Prey item occurrence (FO)	% FO	Biomass consumed (kg) ³	Total biomass consumed (kg) ⁴	Relative biomass consumed	Relative biomass consumed (%)
Wild ungulates	151.00	162.00	22	0.20	20.00	675.00	5.40	0.22	21.76
Springbok (<i>Antidorcas marsupialis</i>)	39.00	27.00	5	0.05	4.55	195.00	1.23	0.05	4.95
Cape grysbok (<i>Raphicerus melanotis</i>)	10.00	27.00	3	0.03	2.73	30.00	0.74	0.03	2.97
Common duiker (<i>Sylvicapra grimmia</i>)	19.50	27.00	6	0.05	5.45	117.00	1.47	0.06	5.94
Klipspringer (<i>Oreotragus oreotragus</i>)	11.50	27.00	0	0.00	0.00	0.00	0.00	0.00	0.00
Steenbok (<i>Raphicerus campestris</i>)	11.00	27.00	3	0.03	2.73	33.00	0.74	0.03	2.97
Bush pig (<i>Potamochoerus larvatus</i>)	60.00	27.00	5	0.05	4.55	300.00	1.23	0.05	4.95
Carnivores	20.21	165.15	4	0.04	3.64	3.41	0.74	0.03	2.97

Meerkat (<i>Suricata suricatta</i>)	0.79	19.87	2	0.02	1.82	1.58	0.36	0.01	1.46
African wild cat (<i>Felis silvestris lybica</i>)	4.25	34.01	0	0.00	0.00	0.00	0.00	0.00	0.00
Striped polecat (<i>Ictonyx striatus</i>)	0.95	20.72	1	0.01	0.91	0.95	0.19	0.01	0.76
African weasel (<i>Poecilogale albinucha</i>)	0.29	17.82	0	0.00	0.00	0.00	0.00	0.00	0.00
Honey badger (<i>Mellivora capensis</i>)	11.00	27.00	0	0.00	0.00	0.00	0.00	0.00	0.00
Small-spotted genet (<i>Genetta genetta</i>)	2.05	25.01	0	0.00	0.00	0.00	0.00	0.00	0.00
Mongoose	0.88	20.72	1	0.01	0.91	0.88	0.19	0.01	0.76
Domestic sheep (<i>Ovis aries</i>)	40.00	27.00	5	0.05	4.55	200.00	1.23	0.05	4.95
Small mammals	0.68	169.08	26	0.24	23.64	2.21	4.01	0.16	16.17
Bush Karoo rat (<i>Myotomys unisulcatus</i>)	0.13	17.14	6	0.05	5.45	0.75	0.93	0.04	3.77
Hairy-footed gerbil (<i>Gerbillurus paeba</i>)	0.03	16.73	2	0.02	1.82	0.05	0.30	0.01	1.23
Cape gerbil (<i>Gerbilliscus afra</i>)	0.10	17.04	0	0.00	0.00	0.00	0.00	0.00	0.00

Brant's whistling rat (<i>Parotomys brantsii</i>)	0.15	17.24	5	0.05	4.55	0.75	0.78	0.03	3.16
Namaqua rock mouse (<i>Micaelamys namaquensis</i>)	0.05	16.83	8	0.07	7.27	0.40	1.22	0.05	4.93
Kreb's fat mouse (<i>Steatomys krebsii</i>)	0.02	16.73	0	0.00	0.00	0.00	0.00	0.00	0.00
Four-striped mouse (<i>Rhabdomys pumilio</i>)	0.06	16.87	2	0.02	1.82	0.12	0.31	0.01	1.24
Cape spiny mouse (<i>Acomys subspinosus</i>)	0.02	16.72	1	0.01	0.91	0.02	0.15	0.01	0.61
Pouched mouse (<i>Saccostomus campestris</i>)	0.05	16.81	1	0.01	0.91	0.05	0.15	0.01	0.62
Grey climbing mouse (<i>Dendromus melanotis</i>)	0.08	16.96	1	0.01	0.91	0.08	0.15	0.01	0.62
Shrews	0.01	16.68	5	0.05	4.55	0.06	0.76	0.03	3.06
Rock hyraxes (<i>Procavia capensis</i>)	3.75	31.97	26	0.24	23.64	97.50	7.56	0.30	30.45
Lagomorpha	3.25	26.24	20	0.18	18.18	65.00	4.77	0.19	19.23
Other mammals	0.83	36.65	2	0.02	1.82	1.30	0.35	0.01	1.41
Cape molerat (<i>Georychus capensis</i>)	0.18	17.37	0	0.00	0.00	0.00	0.00	0.00	0.00

Cape ground squirrel (<i>Xerus inauris</i>)	0.65	19.29	2	0.02	1.82	1.30	0.35	0.01	1.41
Total			110	1	100	1044.48	24.81	1	100

¹ From Stuart & Stuart (2015)

² From Baker et al. (1993), $y = 16.63 + 4.09 x$; only for prey < 4.5kg

³ Prey weight x Number of occurrences

⁴ Correction factor x Prey items occurrence



UNIVERSITY *of the*
WESTERN CAPE

Appendix 7 Biomass consumed, as calculated from caracal scat (n = 96) collected at the non-lethal treatment site, just outside of Beaufort West, Western Cape, South Africa. Both the biomass consumed and the total biomass consumed is presented.

Prey	Prey weight (kg) ¹	Correction factor (kg/scat) ²	Number of occurrences (n = 112)	Prey item occurrence (FO)	% FO	Biomass consumed (kg) ³	Total biomass consumed (kg) ⁴	Relative biomass consumed	Relative biomass consumed (%)
Wild ungulates	151.00	162.00	18.00	0.16	16.07	383.50	4.34	0.17	17.24
Springbok (<i>Antidorcas marsupialis</i>)	39.00	27.00	4.00	0.04	3.57	156.00	0.96	0.04	3.83
Cape grysbok (<i>Raphicerus melanotis</i>)	10.00	27.00	2.00	0.02	1.79	20.00	0.48	0.02	1.92
Common duiker (<i>Sylvicapra grimmia</i>)	19.50	27.00	3.00	0.03	2.68	58.50	0.72	0.03	2.87
Klipspringer (<i>Oreotragus oreotragus</i>)	11.50	27.00	2.00	0.02	1.79	23.00	0.48	0.02	1.92
Steenbok (<i>Raphicerus campestris</i>)	11.00	27.00	6.00	0.05	5.36	66.00	1.45	0.06	5.75
Bush pig (<i>Potamochoerus larvatus</i>)	60.00	27.00	1.00	0.01	0.89	60.00	0.24	0.01	0.96
Carnivores	20.21	165.15	7.00	0.06	6.25	20.13	1.47	0.06	5.86

Meerkat (<i>Suricata suricatta</i>)	0.79	19.87	1.00	0.01	0.89	0.79	0.18	0.01	0.70
African wild cat (<i>Felis silvestris lybica</i>)	4.25	34.01	1.00	0.01	0.89	4.25	0.30	0.01	1.21
Striped polecat (<i>Ictonyx striatus</i>)	0.95	20.72	0.00	0.00	0.00	0.00	0.00	0.00	0.00
African weasel (<i>Poecilogale albinucha</i>)	0.29	17.82	1.00	0.01	0.89	0.29	0.16	0.01	0.63
Honey badger (<i>Mellivora capensis</i>)	11.00	27.00	1.00	0.01	0.89	11.00	0.24	0.01	0.96
Small-spotted genet (<i>Genetta genetta</i>)	2.05	25.01	1.00	0.01	0.89	2.05	0.22	0.01	0.89
Mongoose	0.88	20.72	2.00	0.02	1.79	1.75	0.37	0.01	1.47
Domestic sheep (<i>Ovis aries</i>)	40.00	27.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Small mammals	0.68	169.08	27.00	0.24	24.11	1.71	4.07	0.16	16.18
Bush Karoo rat (<i>Myotomys unisulcatus</i>)	0.13	17.14	4.00	0.04	3.57	0.50	0.61	0.02	2.43
Hairy-footed gerbil (<i>Gerbillurus paeba</i>)	0.03	16.73	8.00	0.07	7.14	0.20	1.20	0.05	4.75
Cape gerbil (<i>Gerbilliscus afra</i>)	0.10	17.04	1.00	0.01	0.89	0.10	0.15	0.01	0.60

Brant's whistling rat (<i>Parotomys brantsii</i>)	0.15	17.24	1.00	0.01	0.89	0.15	0.15	0.01	0.61
Namaqua rock mouse (<i>Micaelamys namaquensis</i>)	0.05	16.83	5.00	0.04	4.46	0.25	0.75	0.03	2.99
Kreb's fat mouse (<i>Steatomys krebsii</i>)	0.02	16.73	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Four-striped mouse (<i>Rhabdomys pumilio</i>)	0.06	16.87	1.00	0.01	0.89	0.06	0.15	0.01	0.60
Cape spiny mouse (<i>Acomys subspinosus</i>)	0.02	16.72	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pouched mouse (<i>Saccostomus campestris</i>)	0.05	16.81	3.00	0.03	2.68	0.14	0.45	0.02	1.79
Grey climbing mouse (<i>Dendromus melanotis</i>)	0.08	16.96	4.00	0.04	3.57	0.32	0.61	0.02	2.41
Shrews	0.01	16.68	2.00	0.02	1.79	0.03	0.30	0.01	1.18
Rock hyraxes (<i>Procavia capensis</i>)	3.75	31.97	30.00	0.27	26.79	112.50	8.56	0.34	34.03
Lagomorpha	3.25	26.24	26.00	0.23	23.21	84.50	6.09	0.24	24.21
Other mammals	0.83	36.65	2.00	0.02	1.79	0.83	0.33	0.01	1.30
Cape molerat (<i>Georychus capensis</i>)	0.18	17.37	1.00	0.01	0.89	0.18	0.16	0.01	0.62

Cape ground squirrel (<i>Xerus inauris</i>)	0.65	19.29	1.00	0.01	0.89	0.65	0.17	0.01	0.68
Total			112.00	1	100	603.20	25.17	1	100

¹ From Stuart & Stuart (2015)

² From Baker et al. (1993), $y = 16.63 + 4.09 x$; only for prey < 4.5kg

³ Prey weight x Number of occurrences

⁴ Correction factor x Prey items occurrence



UNIVERSITY *of the*
WESTERN CAPE

Appendix 8 Probability values associated with each adjusted residual calculated in the Chi-square diet analysis against the associated Bonferroni adjusted alpha values. Significant *p*-values are indicated in bold.

Prey categories	Control and Lethal¹	Control and Non-lethal²	Lethal and Non-lethal³
Invertebrates	0.023	0.661	0.003
Reptiles	0.638	0.784	0.410
Birds	0.407	0.270	0.637
Wild mammals	0.519	0.757	0.695
Domestic sheep	0.062		0.017
Vegetation	0.917	0.325	0.330
Anthropogenic items	0.150		0.064

¹ Bonferroni adjusted alpha value = 0.04

² Bonferroni adjusted alpha value = 0.05

³ Bonferroni adjusted alpha value = 0.04



Appendix 9 Description and locations of camera trap stations on a non-lethal farm just outside of Beaufort West, Western Cape, South Africa.

Station	Latitude	Longitude	Description
01 - Nooitgedacht Road	-32.090231	22.8404	Next to road with relatively flat-topped mountain in centre. Overlooking road in flat with
02 - Nooitgedacht Gate	-32.073503	22.829306	mountains in background (one large; taking up half of the width of picture).
03 - House River	-32.019461	22.865175	Looking at road crossing stream.
04 - Gorge Burrow	-32.011825	22.876808	Looking at sandy patch in front of bush with hill in background.
05 - Gorge	-32.006522	22.876172	Looking down at an angle at grassy spot in river bed, sand and rocks in background.
06 - House Camp River	-32.022236	22.874775	Road through riverbed, koppie heading up to top left corner. Looking across dry river bed, trees filling top half of picture.
07 - Tree Camera	-32.043933	22.861547	Looking over flat area with scattered shrubs; rugged koppie on horizon on right side.
08 - Kale Gate	-32.036136	22.880425	Looking along road that turns sharply to left directly in front of peak of conical koppie; slope ending at right edge of picture
09 - Kale Ant Mound	-32.029944	22.893089	Close to road with hill sloping from right, filling picture to top.
10 - Langleegte	-32.028806	22.925503	In riverbed with koppie in background.
11 - Wild Camp 3	-32.06195	22.932992	Overlooking ephemeral river with dense vegetation on opposite bank.
12 - Wild Camp 2	-32.071275	22.915844	Looking along road running through dry streambed.

13 - Wild Camp 1	-32.090317	22.908242	Looking along road in large flat section with few termite mounds nearby; mountain visible on horizon on left edge.
14 - Die Yard	-32.060669	22.90425	Road in foreground, koppie in background; slightly different view than later setup.
15 - Big Dam	-32.059844	22.881014	Overlooking dam with mountains in background, with ridgeline coming from right in front of conical mountain.
16 - Die Bad	-32.062808	22.859569	In riverbed with road in centre view with dense growth behind.
17 - Wilgebos	-32.038458	22.823978	Looking along rocky section of dry riverbed.
18 - Nooitgedacht SE	-32.117458	22.873875	Next to road with large bush filling left half of picture; mountain range far on horizon.
19 - Plateau South	-32.140833	22.829967	Flat open area with single conical koppie in right half of picture.
20 - Fence East of Koppie	-32.117981	22.833272	Next to road with foot of hill in background.
21 - Bolangleegte	-32.099408	22.807392	Road in foreground, large bush on left edge and small one towards right edge.
22 - Stilhoek Hek	-32.122625	22.792822	Looking along road with small koppie in background on right edge of picture.
23 - Stilhoek Plateau	-32.132806	22.792178	Next to road overlooking edge of plateau.
24 - Rondfontein Berg	-32.101236	22.785325	Flat region with nearby road; low koppie towards back right.
25 - Witfontein Hek	-32.082517	22.791972	Flat region with nearby road; flat horizon with single mountain in centre. Looking at road intersection

			with large mountain sloping from right edge to middle of picture; single conical peak in middle of left half of picture.
26 - Main Road	-32.063917	22.806117	Next to road with low hill in background; large bush nearby in right side of picture.
27 - Saalman Road	-32.012083	22.84775	On roadside with mountains far in background; two relatively solitary mountains in centre.
28 - Saalman Dam	-32.011325	22.824958	Overlooking dam with rocks in foreground, trees on other side.
29 - Saalman Stream	-32.004364	22.812258	Looking at rocky foothill.
30 - Saalman Ant Burrow	-32.013222	22.816389	Next to road with nearby koppie filling width of picture.
31 - Solar Pump	-32.043689	22.799439	Set low next to road in rocky area; next to foot of hill.



UNIVERSITY of the
WESTERN CAPE