THE EFFECTS OF LAND USE CHANGE, FROM SMALL LIVESTOCK FARMING TO PROTECTED AREA, ON VEGETATION AND MAMMAL COMMUNITIES IN THE SKA REGION OF THE KAROO, SOUTH AFRICA

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ABSTRACT

Land-use change, particularly agriculture, has been identified as one of the major drivers of biodiversity loss worldwide. Meeting global biodiversity targets requires both the establishment of protected areas (PAs) and learning to coexist with wildlife in human-modified landscapes, particularly extensive rangelands. In the semi-arid regions of the Karoo, South Africa, small livestock production has been the primary land use for more than 350 years. This extensive agricultural activity has allowed much of the native flora and fauna to persist leading to a complex interplay between vegetation, livestock, humans and wildlife. Most farmers strive to optimise livestock production and thus actively seek to reduce or eradicate wild predators and competitors of livestock. It is against this background that the recent establishment of a large (131 000 ha) protected area within a well-established small livestock farming region in the Karoo represents a rather unprecedented event with clear benefits for biodiversity and both real and perceived costs to the farming community. This landscape level shift in land use from farming to protected area provided a unique opportunity to design a Before-After-Control-Intervention (BACI) study investigating how a cessation in farming activity impacts both natural vegetation and wildlife. I hypothesised that this change would positively impact vegetation, and small and medium/large mammals. To test this, I compared biota using standard surveys on farms before and after the cessation of farming (core, n = 3) and compared this to both neighbouring farms (edge, n = 3) that are likely to be impacted by the land use change and farms at least 50 km from the new PA (control, n = 3). I also explored the condition, maintenance levels and success of fences between the core and edge farms at preventing the movement of wildlife onto edge farms. Before the cessation of farming activities on the core, species richness and the abundance of vegetation, small mammals and medium/large mammals were similar across all farm types. After the cessation of farming activities forb cover and grass height increased slightly on core farms, while small and medium/large mammal richness and abundance remained constant. Daily activity patterns for several medium sized mammals shifted on the core farms from almost exclusively nocturnal to more diurnal. Both caracal and black-backed jackal naïve occupancy remained constant on all farm types over the study period. Despite this, edge farmers (as well as control farmers) complained of increased predator numbers and livestock losses and their attitudes to predators and the PA worsened over the study period. These perceived changes may well have been attributed to the extreme drought conditions that prevailed during the study. Most farmers resorted to food provisioning which concentrates livestock at feeding sites and around farm buildings both increasing the detection of livestock by predators and the detection of predators by farmers. Well maintained fences significantly reduced wildlife movement in general and predator movement from the core to edge farms. Poor quality and poorly maintained fences had a higher incidence of mammal movement along the fence line and a higher frequency of hole utilisation, particularly by small and medium sized herbivores. Overall, my results support expert predictions that the recovery of both flora and fauna in the Karoo following cessation of sustained livestock farming will be slow and dependent on rainfall. The drought conditions that prevailed during the study may well have dampened a resurgence in primary productivity on core farms and with that the recovery of small mammals and medium sized herbivores, followed by their predators. It will be important to continue monitoring these farms over the medium/long term to better understand the relative impacts of farmers and livestock on the flora and fauna of the Karoo and the recovery of biota within this newly proclaimed PA especially where abiotic factors such as variability of rainfall may confound these influences. In the interim improving relationships between farmers and managers of the PA is essential and will largely depend on the quality and maintenance of the fence line that separates these different land uses.

PLAGIARISM DECLARATION

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

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

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This research complied with protocols approved by the Science Faculty Animal Ethics Committee (SFAEC) of the University of Cape Town (Permit reference: 2017/V17/O'Riain) and adhered to South African legal requirements. All research methods were approved and conducted with permission and relevant permits from the Department of Agriculture, Forestry and Fisheries (DAFF) (Permit references: FAUNA 0088/2017 and FLORA 1233/2017).

DEDICATION

I dedicate this work to my family, who never stopped believing in me, my partner who never stopped supporting me and my anxiety whom I never let defeat me.

Standing in front of the most well-travelled and anxiety-provoking dirt road, between Losberg and Lovedale, on the last day I would ever travel upon it.

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My love for nature and conservation started when I was 10 years old travelling to Botswana with my family for our first major camping trip. Since then I have been fascinated, inspired and awestruck by the intricacy and beauty of the natural world. I didn't know it then, but that trip was the beginning of an incredibly academic journey and solidified my want to conserve the natural world. I have faced a tremendous number of challenges during the last four years: many, many punctures along the hard dusty Karoo roads (15 to be exact), countless 4 am mornings, sheep herding, vehicles getting stuck in the mud, lunging puff adders, missing field assistants, more punctures, and relentless Karoo heat. However, nothing compared to the internal challenge I faced due to crippling anxiety and seasonal depression. I have been dealing with some form of anxiety most of my life, but these last four year have challenged me in way I did not think possible. I have overcome huge hurdles in my head, partly thanks to my incredible support system, but mostly through an internal battle that has left some scars. I was pushed to the edge, but having come out the other side, I am grateful for the tools I hopefully developed during this time. Constantly reminding myself of my love for nature, and my deep desire to make a meaningful contribution towards its conservation has been my saving grace, and I hope this will continue to drive me in the future.

While my determination and passion for conservation pushed me through most of this PhD, I would not have made it through the darkest of times without some key players, and for them I am truly grateful.

To my field assistants and the iCWildlings

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TABLE OF CONTENTS

ABSTRACT *ii*
PLAGIARISM DECLARATION *iii*
DEDICATION *iv*
ACKNOWLEDGEMENTS *v*

CHAPTER 1: INTRODUCTION **1**
Impacts of land-use change on biodiversity with specific focus on semi-arid and arid regions 2
Human-wildlife interactions in semi-arid and arid regions 3
Relationship between protected areas and agricultural land 5
Predator conflict in semi-arid and arid regions 7
Mesopredator conflict in semi-arid region of South Africa: the Karoo as a case study 7
The story of the Square Kilometre Array (SKA) 9
Background to the SKA in South Africa 10
Establishing a protected area in the SKA core 11
Current biodiversity status of the SKA core 13
Importance of understanding the ecological and sociological impact of the SKA and a newly formed protected area 13
Thesis outline 16
Before-After Control-Intervention experimental design 16
Aims and objectives 17
Thesis design 18

CHAPTER 2: DESCRIPTION OF STUDY AREA **20**
General site description 21
Climate 21
Vegetation, status and threats 24
Past and present fauna 27
Description of farm types 29
Study farm selection 31
Core farms 31
Edge farms 33
Control farms 34

CHAPTER 3: VARIATION IN VEGETATION AND SMALL MAMMAL COMMUNITIES BEFORE AND AFTER THE CESSATION OF FARMING ACTIVITIES IN THE SKA **37**
Abstract 38
Introduction 39
Methods 45
Study site 45
Vegetation surveys 46
Broad-scale sensing 47
Fine scale vegetation surveys 47
Estimating species richness and relative abundance of small mammals 48
Small mammal trapping 48
Small mammal processing 50

Data analyses 51
Small mammal species accumulation and rarefaction analyses 51
Univariate analyses 52
Multivariate analyses 54
Results 57
Vegetation and environmental characteristics of core, edge and control farms 57
Vegetation diversity measures 62
Small mammals on core, edge and control farms 64
Taxonomic diversity and inventory completeness 68
Spatiotemporal trends in small mammal abundances 73
Multivariate analyses of abundance trends 78
Small mammals 78
Vegetation 82
Canonical correspondence analysis of small mammal and vegetation community structure 84
2017 survey 84
2019 survey 85
Discussion 88
How did the vegetation of farm types change? 89
Did small mammal diversity and community composition change? 92
Conclusions 95
Appendix 3: Small mammal and vegetation appendices 98

CHAPTER 4: ESTIMATING SPECIES RICHNESS AND RELATIVE ABUNDANCE OF MEDIUM AND LARGE MAMMALS BEFORE AND AFTER THE CESSATION OF SMALL LIVESTOCK FARMING **107**
Abstract 108
Introduction 109
Methods 113
Camera trap placement and data collection 113
Data analyses 117
Diversity measures and rarefaction curves 118
Community composition and structure 120
Functional diversity 122
Daily activity patterns 123
Results 124
Descriptive statistics 124
Diversity measures and rarefaction curves 133
Community composition and structure 139
Functional diversity 144
Daily activity patterns 147
Discussion 151
Spatial and temporal changes in diversity measures and community composition 153
Spatial and temporal changes in species abundance and functional diversity 156
Temporal shifts in daily activity patterns 157
Conclusions 158
Appendix 4: Medium and large mammal appendices 161

CHAPTER 5: EVALUATING CHANGES IN PREDATOR ABUNDANCE, ACTIVITY PATTERNS AND LIVESTOCK LOSSES FOLLOWING THE REMOVAL OF SHEEP FROM THE SKA CORE **164**
Abstract 165
Introduction 166
Methods 174
- ***Camera trap placement and data collection*** 174
- ***Data analysis*** 175
  - *Independent captures, naïve occupancy and photographic rates (RAI) for predators* 175
  - *Functional diversity* 175
  - *Daily activity patterns* 177
  - *Longitudinal surveys and landowner questionnaires* 178

Results 179
- *Predator photographic rates (RAI), naïve occupancy and distribution* 179
- *Daily activity patterns* 184
- *Functional diversity* 191
- *Farmer perceptions of livestock and attitudes to predators* 193

Discussion 195
- *Spatial and temporal changes in predator abundance and distribution* 196
- *Temporal shifts in predator daily activity pattern* 199
- *Spatial and temporal changes in predator-prey functional diversity* 200
- *Patterns in livestock losses, hunting and farmer perceptions towards predators* 201

Conclusions 203
Appendix 5: Predator population appendices 204

CHAPTER 6: EVALUATING FENCE QUALITY, MAINTENANCE AND THE USE OF HOLES BY WILDLIFE ON CORE AND EDGE FARMS **207**
Abstract 208
Introduction 209
Methods 214
- ***Survey design and data collection*** 214
  - *Fence quality and maintenance* 215
  - *Camera trap placement* 217
- ***Data analyses*** 219
  - *Species richness along fences* 219
  - *Species abundance along fences* 220
  - *Species utilisation of holes and direction of movement* 221

Results 223
- *Fence characteristics and quality* 223
- *Species richness along fences* 226
- *Relative abundance of mammal species detected along fences* 230
- *Species utilisation of holes and direction of movement* 233

Discussion 241
- *Fence quality and permeability* 242
- *Shifts in species richness relative to fence section and year* 242
- *Mammal interaction with fences and shifts in fence utilisation* 243
- *Hole utilisation and direction of movement* 245

Conclusion and implications for future fence management 247
Appendix 6: Mammal utilisation of fence appendices 249

CHAPTER 7: SYNTHESIS **253**
An important baseline database of vegetation and mammals in the SKA 255
Slow recovery in Karoo systems 258
The importance of rainfall and vegetation for mammal recovery 260
Impacts of human disturbance on wildlife 261
Perceived versus observed threat of changes in predator abundance 262
Study limitations 265
Implications for management and future research 266
Suggested future research 268
Appendix 7: Synthesis appendices 272

REFERENCES **273**

LIST OF TABLES **335**

LIST OF FIGURES **339**

LIST OF APPENDICES **345**

CHAPTER 1

INTRODUCTION

Typical Karoo landscape (sandy substrate with “driedoringbos” shrubs) (top), and dorper sheep gathering around my research vehicle (typical rocky substrate) in the hopes of receiving additional feed during a drought (bottom) (© Michelle Blanckenberg).

Impacts of land-use change on biodiversity with a specific focus on semi-arid and arid regions

Land-use change is expected to have the single largest negative effect on biodiversity across multiple biomes in the next century (Sala *et al.* 2000, Reidsma *et al.* 2006). Increasing human populations are driving the conversion of land from natural to urban or agricultural uses over large geographic areas (Foley *et al.* 2005, Carrete *et al.* 2009). Decreases in natural habitat impacts adversely on ecosystem functioning resulting in higher risks of vertebrate species decline and/or extinction (Newbold *et al*. 2015). While global trends indicate that human-dominated areas have negative effects on species richness and abundance, these patterns are typically observed for the global status of a species (Newbold *et al.* 2015). The functioning of ecosystems, however, is thought to be linked more with local diversity and the context specific trends in richness and abundance (Newbold *et al.* 2015). Understanding the context specific impacts of land-use change on biodiversity is thus essential for developing adaptive approaches to conservation and management (Haines-Young 2009, Newbold *et al.* 2015).

Ecosystem functioning (Costanza 2012) is strongly linked to plant diversity and structure (Haddad *et al.* 2011, Naeem *et al*. 2012). Experimental studies have shown that changes in plant diversity can strongly affect ecosystem functioning through “upward” cascades where higher trophic levels are impacted by changes in plant diversity and structure (Scherber *et al.* 2010, Zavaleta *et al.* 2010). Semi-arid and arid regions (also referred to as drylands) have seen a decrease in plant productivity worldwide because of both direct and indirect impacts of human disturbance (Tilman 1998, Williams *et al*. 2005, Wittig *et al.* 2007, Muposhi *et al.* 2016, Zhao *et al*. 2019). Direct impacts of human disturbance are highlighted largely through poor land management which has degraded natural plant diversity and structure (ca. 70% of all rangelands are degraded) (Darkoh 1998, Seymour *et al.* 2010, Kiage 2013, Pulido & Bocco 2014, Adenle *et al.* 2020). Where drylands are associated with livestock overstocking there is often a resultant reduction in vegetation cover, increased soil compaction and changes in soil condition (Anderson & Hoffman 2007, Seymour *et al.* 2010). While natural drought cycles are a major contributing factor to the degradation of these rangelands (Hoffman *et al.* 2009, Seymour *et al.* 2010, Saayman *et al.* 2016) droughts linked to climate change have exacerbated the impacts of human disturbance (Berglund 2003, Wittig *et al.* 2007).

Increasing need for food to support a growing population and the preference for animal products has resulted in the livestock systems being the fastest growing agricultural sub-sector in developing countries (Steinfeld *et al.* 2006, Ilea 2009). Livestock production is one of the main contributors to land use change across the globe (Steinfeld *et al.* 2006, Ilea 2009, Thornton 2010), requiring large amounts of land and water to be profitable. Increased land degradation and pollution associated with livestock has resulted in this sector being one of the biggest contributors to environmental degradation and biodiversity loss (Ilea 2009). For example, approximately 15% of the Amazon forest has been converted to agricultural land, specifically pastures, while areas in Cerrado, Brazil are being converted to agricultural land that focuses on providing animal feed (FAO 2006, Ilea 2009). Understanding the relationship between livestock production and both land degradation and biodiversity loss is essential for future conservation of threatened habitats and the species they sustain (Haines-Young 2009, Ilea 2009). Restoration of agriculturally degraded land has the potential to be a major contributor to improving landscape functionality and increasing biodiversity (Benayas & Bullock 2015). Land degradation has proved to be reversible in several examples of active reforestation (Davy 2002, Lemenih 2004, Benayas & Bullock 2015, Mugwedi *et al.* 2017), rangeland restoration (Kimiti *et al.* 2016, Bourne *et al.* 2017), and in some cases where degradation is limited, passive restoration has seen increases in biodiversity (Zahawi *et al.* 2014).

Human-wildlife interactions in semi-arid and arid regions

Agricultural practices in semi-arid and arid regions may have overall negative impacts on plant diversity and structure however, these practices have both positive and negative impacts on wildlife, evident across the globe (Stephens *et al.* 2001, Tabeni & Ojeda 2003, Legge *et al.* 2011, Gordon 2018). The impact of livestock production, for example, on medium and large sized mammals is complex. Livestock production greatly affects food availability (through changes in vegetation) (Öllerer *et al.* 2019), however how wildlife response depends on the species and ecosystem (Schieltz & Rubenstein 2016). Medium and large herbivore species for example are often negatively impacted by the presence of livestock as a result of competitive exclusion (livestock decreasing the quantity of available food) (Olff *et al*. 2002, Kartzinel *et al*. 2015). However, smaller herbivore species may benefit from the presence of livestock through facilitation as several studies have suggested that while livestock reduces the quantity of vegetation it may improve the quality proving beneficial to smaller herbivores (Alpe *et al.* 1999, Arsenault & Owen-Smith 2002, Bakker *et al.* 2009, Hopcraft *et al.* 2012). The varying responses of prey species (typically affected by changes in vegetation) will further have varying impacts on predator species (Ruscoe *et al.* 2006, Norbury 2017, Travers *et al.* 2020). For example where livestock are removed from a landscape small mammal species may benefit from increased vegetation cover which provides protection from predators (Sinclair *et al.* 2003). While, restored vegetation could further provide refuge for medium-sized mammals whose cryptic nature relies on more complex vegetation (e.g., common duiker *Sylvicapra grimmia*) (Joubert & Ryan 1999, Legge *et al.* 2011). This however, may put pressure on small and medium predator populations as prey populations become more cryptic (Eccard *et al.* 2000). Predator diversity and abundance is closely linked to the health and abundance of prey populations and therefore partially dependent on the complex impacts of livestock on their respective prey (Sandom *et al.* 2013).

Additionally the presence of livestock is tied to the presence of humans (i.e., human settlements, man-made infrastructure and hunting) and while typically, the relationship between agriculture and wildlife has focused on the impacts of livestock directly, the indirect effects of human disturbance on wildlife are increasingly important. For example, linear features (i.e., roads, fences and powerlines) are common infrastructure elements within agricultural landscapes (Goosem 2004, Gadd 2012, DeMars & Boutin 2017, Jakes *et al.* 2018) that fragment natural landscapes impacting the movement of wildlife (Blake *et al.* 2008). Furthermore, increased human disturbance along these features may have negative impacts on the behaviour and area use of certain species (Laurance *et al.* 2006). Wildlife will typically avoid humans, and therefore increased human activity at linear features may result in species changing behaviours to avoid peak human activity areas or times (Laurance *et al.* 2008). Again, these behavioural changes may have knock on effects at other trophic levels depending on the specific species response (e.g., increased species activity at night to avoid humans may increase predation risk for nocturnal prey species).

Similarly, a common feature associated with livestock and human settlements in semi-arid regions is increased access to artificial watering points. Artificial watering points have been associated with intense localised habitat degradation (de Leeuw *et al.* 2001). In many protected areas (e.g., Kruger National Park and Amboseli National Park) there is an increase in the number and abundance of wild grazing species around artificial water points, while browsing species are more associated with rivers (Western 1975, Owen-Smith 1996, James *et al.* 1999, de Leeuw *et al.* 2001, Smit *et al.* 2007). However, research on the impacts of livestock and water points on wild herbivore species in Kenya have shown that artificial water points found on farms or rangelands have a negative correlation with wild herbivores (de Leeuw *et al.* 2001). Wild grazing species had lower densities nearer to water points because of increased grazing competition with livestock and the greater presence of farmers (Verlinden *et al.* 1998, Prins 2000, de Leeuw *et al.* 2001). Where water points are sparsely distributed livestock dominate areas around water points while wildlife occupied the areas in between (de Leeuw *et al.* 2001). Interestingly, while wildlife tends to avoid human activity (i.e., farmers and their artificial water points), the paucity of natural water bodies in semi-arid regions forces obligate drinkers to move where artificial water points occur suggesting these species would have to avoid humans through changes in activity times (increased activity at water points when human activity decreases) rather than changes in spatial distribution (Smit *et al.* 2007, Ogutu *et al.* 2010). Wildlife also avoid humans that engage in hunting (recreational or wildlife management) (Fa & Brown 2009, Lone *et al.* 2015, Harrison *et al.* 2016), a common practice associated with humans in agricultural landscapes. Hunting may reduce the abundance and species richness of wildlife on agricultural landscapes but also has more subtle impacts such as, behavioural changes (Laurance *et al.* 2008, Kays *et al.* 2017) which can alter foraging behaviour and fitness of wildlife (Proffitt *et al.* 2010, Lone *et al.* 2015).

The impact of disturbances in the landscape associated with livestock (i.e., reduction of vegetation cover, desertification, soil compaction and human disturbance) on medium-sized mammals is difficult to predict due to the diverse response of different species (Hopcraft *et al.* 2010, Legge *et al.* 2011). Furthermore, these responses may not necessarily manifest through changes in abundance or diversity (at a local or community level), but rather through changes in wildlife behaviour (e.g., daily active patterns, diet selectively and use of an area), and population demographics (e.g., sex ratios or age structure) (Schieltz & Rubenstein 2016). Understanding the complexities of human, as well as livestock, impacts on wildlife is essential for long term conservation of these wildlife species outside of protected areas.

Relationship between protected areas and agricultural land

Historically protected areas (PA) have been the most common conservation tool used to protect natural biodiversity from the impacts of anthropogenic practices (Kleijn *et al.* 2011, Geldmann *et al.* 2013, Gray *et al.* 2016). However, several studies have suggested that many PAs are comprised of rugged and remote landscapes with poor potential for agricultural productivity which naturally have low levels of biodiversity (Rouget *et al.* 2003) and therefore are also inadequate for achieving their primary goal of preserving biodiversity (Norton 2000, Scott *et* *al.* 2001, Gallo *et al.* 2009, Veach *et al.* 2017, Drouilly *et al.* 2018a). Consequently, increasing evidence suggests that agricultural lands play an important role in the conservation of a large proportion of global diversity (Scott *et al.* 2001, Western *et al.* 2009, Kiffner *et al.* 2015, Moore *et al.* 2016, Drouilly *et al.* 2018a) as agricultural lands often fall within biodiversity hotspots (due to the overlapping preference of good land condition) (Scott *et al.* 2001). Future conservation goals have therefore focused on the role of agricultural land in protecting biodiversity, as well as the potential for targeting protected area placement within these more productive landscapes. However, as a result of the expansion of agricultural practices and the increased targeted placement of PAs in more productive land, the proportion of PA edges bordering farms has increased (DeFries *et al.* 2007). The result is that some form of human land use is evident within PA boundaries of almost all protected areas globally (DeFries *et al.* 2007). As such not only is it essential to understand the role of agricultural lands in conservation but so too the impacts of neighbouring land use on the ability of PAs to achieve their conservation goals (Wells & McShane 2004, Htun *et al.* 2012).

As protected areas become isolated within agricultural landscape there needs to be a balance between maintaining ecological functioning and human land use needs (e.g., socio-economic benefits and access to resources) (DeFries *et al.* 2007, DeFries *et al.* 2010). A major challenge to maintaining this balance is the actual and perceived conflict between landowners and wildlife within protected areas (Treves 2009). Landowners are less likely to support conservation and protected areas if there are negative perceptions and attitudes towards sharing a landscape with wildlife (Alkan *et al*. 2009). Negative interactions between humans and wildlife typically occur over shared resources (e.g., crop raiding by pest species), however these can extend to hunting and poaching inside or outside protected areas (Treves *et al*. 2006). Historically where wildlife deleteriously intersects with human activities, humans respond with lethal measures or transformation of wild habitats (Karanth & Madhusudan 2002). However, with increasing conservation efforts, lethal responses have become socially discouraged making conflicts with wildlife not only a direct competitive relationship but a socio-political issue (Knight 2000, Hill 2004, Treves & Naughton-Treves 2005). Understanding the impact of wildlife on livelihoods and the subsequent perception of landowners towards wildlife and natural spaces is crucial for sustained conflict resolution between agricultural and wild landscapes (Treves *et al.* 2006, Treves 2009, Drouilly *et al.* 2018b).

Predator conflict in semi-arid and arid regions

Predators remain an important element of any ecosystem, influencing landscapes through top-down control and affecting the distribution and abundance of other species (Estes *et al*. 2011, Ripple *et al.* 2014, Newsome *et al.* 2017). As discussed above the increasing intersection between wildlife and human populations, as well as habitat fragmentation has resulted in increased spatial overlap and ultimately negative interactions between humans and predators (Loveridge *et al.* 2010, Pooley *et al.* 2016). Livestock depredation and in some cases threats to human lives are the most prevalent negative interactions, particularly for felid and canid species (Dar *et al.* 2009, Boast 2014, Redpath *et al.* 2015, Bhatia *et al.* 2020). Livestock depredation may threaten human livelihoods resulting in retaliatory killings and increasing support for lethal management of predators (Jędrzejewski *et al.* 2017, van Eeden *et al.* 2018, LeFlore *et al.* 2019, Merson *et al.* 2019). Research concerning human-wildlife conflict typically focuses on the ecological impacts of predator removal (Graham *et al.* 2005, Johnson *et al.* 2006) but more recently researchers have called for the incorporation of human dimensions to better understand these conflicts (Knight 2000, Dickman *et al*. 2013, Drouilly *et al.* 2018b).

Lethal management of predators has resulted in various deleterious ecological consequences such as declines in predator abundance and trophic cascades (Loveridge *et al.* 2017, Miller & Schmitz 2019). Furthermore, a growing body of evidence suggests that lethal methods are ineffective at producing long-term reductions in the negative impacts of predators on farms (Redpath *et al.* 2015, Treves *et al.* 2016, Lennox *et al.* 2018) and may even exacerbate conflict between predators and humans (Bailey & Conradie 2013, Nattrass *et al.* 2020). Non-lethal predator management has been advocated as a better alternative with the prospect of improved ecological integrity (van Bommel & Johnson 2014), but acceptance of this approach is often low amongst farmers and critics note that non-lethal management is only as effective as the human buy-in to ensure that stated conservation goals are met (Baruch-Mordo *et al.* 2009, Kansky *et al.* 2014). Understanding the context specific human dimension surrounding large- and small-scale predator conflict issues is therefore essential for long term management (Redpath *et al.* 2013).

Mesopredator conflict in semi-arid regions of South Africa: the Karoo as a case study

The history of livestock farming in the Karoo is characterised by poor rangeland management (Dean *et al.* 1995, Dean & Milton 1999, Saaed *et al.* 2018) and extensive mesopredator conflict

(Du Plessis *et al.* 2015, Drouilly *et al.* 2018b). Black-backed jackal (*Canis mesomelas*) and caracal (*Caracal caracal*) have been heavily persecuted by livestock farmers due to perceived and actual livestock losses (Drouilly *et al.* 2018b, Nattrass *et al.* 2020). Recorded persecution of predators and predator management dates to early colonial times (ca. 1670) when domestic animal farming expanded with the first European settlers (Nattrass & Conradie 2015, Nattrass *et al.* 2017a). Predator conflict with pastoralists however, pre-dates colonial periods with records showing that KhoiKhoi herders actively protected flocks from predators (mostly jackals) (Nattrass *et al.* 2017b). The first record of proactive, rather than reactive, predator control was the process of placing bounties on the head of "problem" predators in 1815 (Nattrass & Conradie 2015, PMF 2016). Expanding farmlands in the Karoo saw the removal of large apex predators, such a lion (*Panthera leo*) and leopard (*Panthera pardus*) with associated increases in mesopredator abundance (Nattrass & Conradie 2015, PMF 2016). These predators were soon classified as "vermin" and by the early 20th century government began to subsidise lethal predator management under the 'Vermin Control Ordinance', mainly through hunting clubs and night hunts (Nattrass *et al.* 2017a). The 'fence and clean-up' approach was adopted, with farms preventing immigration through jackal-proof fencing and then hunting within fenced areas to eliminate jackals from individual farms (Nattrass & Conradie 2015, PMF 2016). By the mid-1900s caracal persecution and lethal management had increased, as fencing was not adequate protection against this more agile species (Bergman *et al.* 2013, Nattrass & Conradie 2015). Through subsidised hunting and fencing Karoo farmers were able to locally control predator populations, reducing livestock losses attributed to depredation (Bailey & Conradie 2013, Drouilly *et al.* 2018b, Nattrass *et al.* 2020).

The shift from bounties to financially aiding hunt clubs only occurred late in the 20th century, as farmers realised the importance of regional co-operation in managing predators (Bailey & Conradie 2013). By the mid-1950s the ecological importance of mesopredators (especially following the removal of apex predators) was highlighted (Ritchie *et al.* 2012), and with that, opposition to previous attempts at the total removal of all predators from farmland (Lennox *et al.* 2018). Predators were still considered "well-controlled" within this period owing largely to state financial support however, after the democratic elections in 1994 financial aid to hunt clubs and farmers for predator control declined as policy priorities shifted away from white farmers (Nattrass & Conradie 2015).

It is suggested that because of reduced subsidy from the government and the increase of both state and private game reserves in the Karoo, jackal numbers began to increase from the mid-1990s (Nattrass & Conradie 2015). The Red Meat Producer's Organisation and National Woolgrowers Association assumed the role of providing support to farmers for predator control, albeit largely through expert advice and workshops (PMF 2016). While most farmers include lethal management in their approach to predators, non-lethal methods are increasingly being explored as farmers seek more sustainable and broadly acceptable solutions to livestock depredation (McManus *et al.* 2015, Drouilly 2019, du Plessis *et al.* 2018).

Currently predator management falls into two broad camps, one which supports the systematic "fence and clean-up" approach to eradicate predators on farms (which they consider was shown to have been successful historically with government support) and a second group that is more ecologically minded advocating lethal management only for so-called 'super-jackals' and caracals that circumvent non-lethal methods (Bergman *et al.* 2013, Doherty & Ritchie 2017, Nattrass *et al.* 2020). The two groups are often in conflict over their different approaches with both blaming the other for perceived increases in predator numbers and livestock losses (Du Plessis *et al.* 2015). More recently evidence in support of Bailey & Conradie's (2013) somewhat paradoxical finding that depredation increases after block hunts, has come from Nattrass *et al.* (2020) who found a similar pattern of increased losses after systematic culling. Importantly these findings remain correlative in the absence of appropriate research that includes before and after data with controls performed at the appropriate scale and with replicates (du Plessis 2013, Doherty & Ritchie 2017). Until such data are provided the conflict amongst stakeholders of the relative merits of lethal versus non-lethal methods will remain high and farmers will continue using a combination of these methods based on diverse personal, cultural and professional experiences and input (du Plessis 2013).

The story of the Square Kilometre Array (SKA)

The complexity of top-down and bottom-up influences on the responses of an ecosystem to a significant land-use change, as well as socio-political complexities that may arise, is apparent and means predicting the impact of these changes is difficult. Land use changes associated with the establishment of the Square Kilometer Array (SKA) in the northern Karoo, South Africa provides a unique opportunity to investigate the complex responses of flora and fauna to shifts in agricultural activities, as well as how different stakeholder may respond to these shifts.

Background to the SKA in South Africa

Astronomy in South Africa has been a major focus for the Department of Science and Technology (DST) and development within this field has been identified as one of five major science goals for the country (Dewdney *et al.* 2015). To achieve this goal and to support the National Research Development Strategy for South Africa, two major radio telescope arrays (KAT-7 and MeerKAT) were built to investigate how the universe evolved and to answer major questions around galaxy formation and dark matter (Dewdney *et al.* 2015). A pre-requisite for this type of research is extremely low levels of radio interference, suggesting only radio "quite" areas of the country can be used for such research (Dewdney *et al.* 2015). The Northern Cape of South Africa is characterised by low radio interference thanks largely to its remoteness, providing South Africa with an astronomical advantage for radio telescope research (Dewdney *et al.* 2015). The Astronomy Geographic Advantage Act (Act No. 21 of 2007) was developed accordingly and protects this region of the Karoo from future radio interference (Dewdney *et al.* 2015). The act protects three major "Advantage Areas", the first of which is the largest (123 456 km^2) and contains the KAT-7 and MeerKAT telescope arrays (CSIR 2016b). The KAT-7 array forms part of the larger MeerKAT telescope array which consists of 64 interlinked mid-frequency receptors. The MeerKAT telescopes were established in 2009 and are located on two farms (Losberg and Meysdam) in the Karoo approximately 70 km north-west of Carnarvon (CSIR 2016b). The land is currently owned by the National Research Foundation (NRF) and is co-managed with DST (Dewdney *et al.* 2015, CSIR 2016b).

The establishments of the Astronomy Geographic Advantage Act strengthened South Africa's bid to host the Square Kilometre Array (SKA) program. The SKA is a collaborative international initiative to develop and improve global astronomical observational research. The program aims to build the largest, most sensitive radio telescope array in the world (Dewdney *et al.* 2015). In 2012, the SKA Advisory Committee declared South Africa as the major host and the Karoo region in the Northern Cape as the preferred site for the SKAs main "mid-frequency dish array" (Dewdney *et al.* 2015). Development of the SKA will be phased, with phase 1 construction having begun in 2018 with a proposed finishing date of 2023. SKA Phase 1, which includes the already established MeerKAT telescope array (64 dishes), will host an additional 133 mid-frequency dishes that will work in conjunction with an array of low-frequency telescopes located in Australia (Dewdney *et al.* 2015). The area covered by SKA Phase 1 consists of a core area, comprising 38 existing farms (including Losberg and Meysdam) covering 131 000 ha, and three spiralled arms which collectively consist of 131 farms covering ca. 496 657 ha (Figure 1.1) (Dewdney *et al.* 2015). Farms within the core area will be owned and co-managed by DST with NRF, while farms within the spiral arms will remain privately owned with various servitude agreements with NRF and landowners to allow for construction of dishes on relevant farms (Dewdney *et al.* 2015, Milton *et al.* 2016).

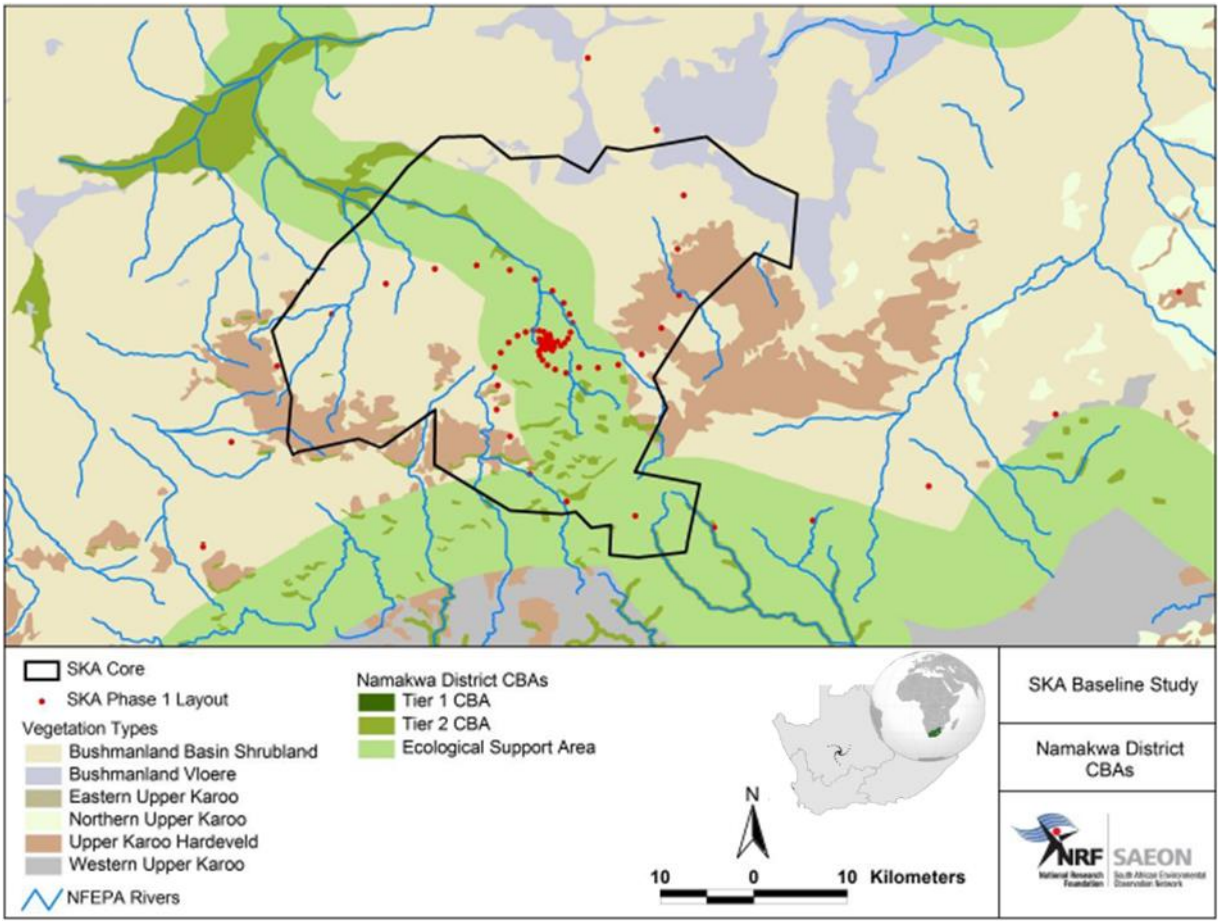


Figure 1.1: Potential ecological support areas (light green areas) found within the SKA region in relation to current critical biodiversity areas (dark green areas) (sourced from Milton *et al.* 2016). Red dots indicate the position of individual telescopes (current and future) and the black polygon shows the border of the SKA core area.

Establishing a protected area in the SKA core

The SKA core area contains the highest concentration of dish-antenna (Dewdney *et al.* 2015) and thus access is limited to research and environmental monitoring activities (Dewdney *et al.* 2015). The land within the core is owned by DST and required a shift from livestock practices (sheep farming) to a more natural 'quieter' state (Dewdney *et al.* 2015, CSIR 2016a & 2016b). It is the responsibility of DST and NRF to manage the land within the core and therefore an application was made to declare the SKA core as a formal Protected Area (PA) that would be comanaged with South African National Parks (SANParks). The SKA core will form part of the national protected areas network under the National Environmental Management: Protected Areas Amendment Act 31 of 2004 (NEMPAA) with the goal being to allow relevant research and to “protect highly sensitive ecosystems, species, geographic or physical features in an area” under the National Environmental Management Act (NEMA) of 1998 (CSIR 2016a & 2016b, Milton *et al.* 2016, Todd & Henschel 2016).

Within the Karoo there are other established protected parks and/or reserves including Tankwa-Karoo National Park, Karoo National Park and Augrabies Falls National Park (Milton *et al.* 2016, Todd & Henschel 2016) however, the Karoo region where the SKA is situated has very poor protection status (CSIR 2016a & 2016b, Milton *et al.* 2016, Todd & Henschel 2016) (Figure 1.2). The National Protected Areas Expansion Strategy (NPAES) identified a similar Karoo site southwest of the SKA core as a priority focus area for protection status expansion (Milton *et al.* 2016, Todd & Henschel 2016). However, several reports by NRF and SAEON have suggested that the SKA core contains similar habitats and attributes to this NPAES area (CSIR 2016a & 2016b, Milton *et al.* 2016, Todd & Henschel 2016). Shifting the NPAES area to include the SKA will ensure that 41% of the national goal for protecting the Upper Karoo region will have been realised (Milton *et al.* 2016, Todd & Henschel 2016).

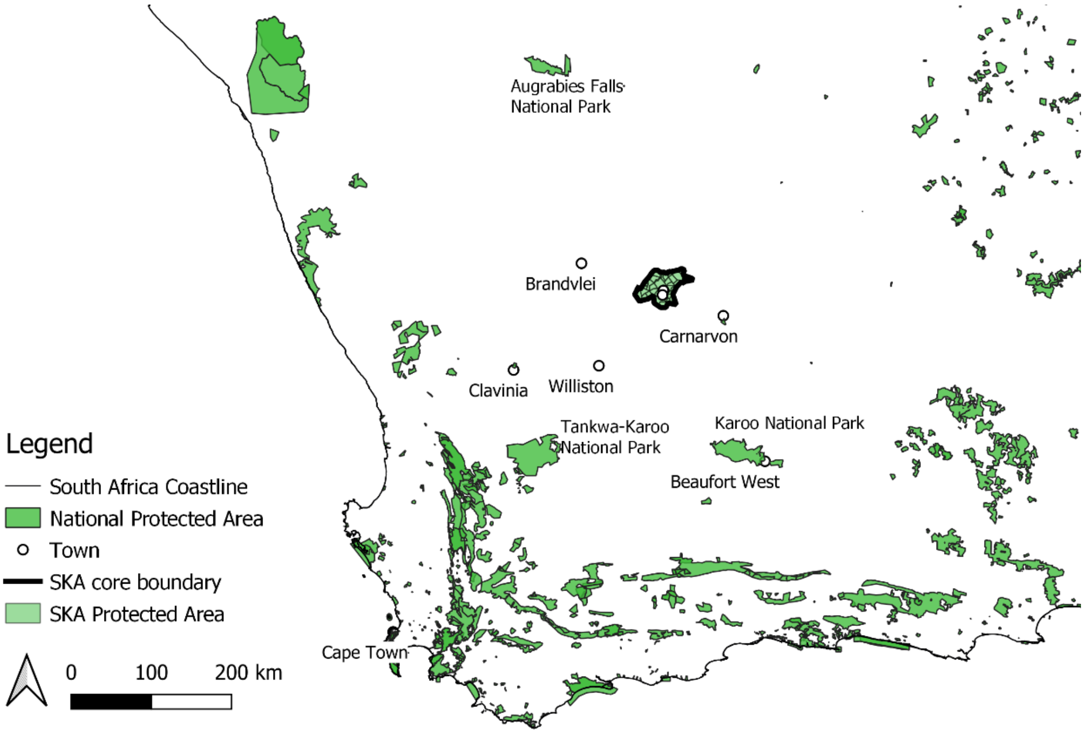


Figure 1.2: Square Kilometre Array Protected Area (black polygon) within the Karoo region in relation to the current South African protected areas network (green polygons), specifically Augrabies Falls National Park, Tankwa-Karoo National Park and Karoo National Park. White dots indicate major cities relevant to the study.

Current biodiversity status of the SKA core

Several plant and animal species within the greater Astronomy Advantage Area have been highlighted as conservation concerns (Milton *et al.* 2016, Todd & Henschel 2016). These include three plant species which are either vulnerable or declining (*Vachellia erioloba*, *Aloe dichotoma* and *Hoodia gordonii)*, and one animal species, the Near Threatened Karoo Padloper (*Homopus boulengeri)* (Milton *et al.* 2016, Todd & Henschel 2016). However, there has been no extensive survey of plant or animal species within the region and most of the information in the area is from preliminary surveys by SAEON and the NRF as part of a Strategic Environmental Assessment (SEA) prior to the construction of SKA Phase 1 telescopes and infrastructure (CSIR 2016a & 2016b, Milton *et al.* 2016, Todd & Henschel 2016). Most critical biodiversity areas (CBAs) in the region fall outside the SKA core, however the south-facing slopes in the central portion of the core have been identified as important “climate change buffering” zones (Milton *et al.* 2016, Todd & Henschel 2016).

Importance of understanding the ecological and sociological impact of the SKA and a newly formed protected area

The Upper Karoo region is considered heavily degraded due to past and current land-use practices (Milton *et al.* 2016, Todd & Henschel 2016). There is over 350 years of recorded pastoral grazing history within the Karoo region, with relatively recent focus placed on ranching with a few specific domesticated animals (Dean *et al.* 1995, Meadows & Hoffman 2002, Kraaij & Milton 2006, Milton *et al.* 2016, Todd & Henschel 2016). The combination of sheep grazing and soil compaction from livestock hooves has resulted in a shift in plant communities and the reproductive output and seedling establishment of non-forage species (Anderson & Hoffman 2007, Rutherford & Powrie 2010). As a result, the Karoo is considered heavily degraded, with plant communities dominated by ephemerals and unpalatable species (Meadows & Hoffman 2002, Anderson & Hoffman 2007). As a result, primary productivity within the area has decreased (Beukes & Cowling 2003, Hoffman *et al.* 2009, Saayman *et al.* 2016).

The farms within the SKA core have a similar history suggesting the shift from livestock farming to a PA from 2018 onwards will likely see a shift in vegetation composition (Dewdney *et al*. 2015, Todd & Henschel 2016) linked to a recovery of select flora (Dean *et al.* 1995, Kraaij & Milton 2006, Hoffman *et al.* 2009, Saayman *et al.* 2016). For example, in the Karoo

National Park, a 10-year study (sampling occurring each year at the end of the growing season from 1995 to 2004) showed that vegetation condition improved, and species richness increased over the study period after the removal of small livestock species (Kraaij & Milton 2006). The recovery in the SKA core will be passive, as SANParks have no plans to actively restore vegetation or reintroduce wild fauna (pers. comm.). Several studies, however, have highlighted the constraints to this type of recovery (Milton & Hoffman 1994, Stokes 1994, Beukes & Cowling 2003, Visser *et al.* 2004). The legacy of high levels of soil compaction and shifts in plant communities from overgrazing suggests that there is likely an inadequate supply of seeds reflecting typical Karoo plants to allow for a purely passive recovery (Milton & Hoffman 1994, Stokes 1994, Beukes & Cowling 2003, Visser *et al.* 2004). Furthermore, the lack of availability of suitable microsites and altered soil properties may result in delayed recovery of these systems despite decreased grazing (Milton & Hoffman 1994, Stokes 1994, Beukes & Cowling 2003, Visser *et al.* 2004). A 20-year survey in the Sandrivier Valley of the Karoo showed that while the biomass of some palatable species recovered in exclusion plots certain species did not re-establish through passive recovery alone (Seymour *et al.* 2010). This suggests that degradation through overgrazing can significantly hinder the recovery of the land if relying solely on passive restoration. Despite this, an increase in vegetation cover post livestock removal was evident in the first few years (Eccard *et al.* 2000, van Rooyen *et al.* 2015). Van Rooyen *et al.* (2015) stated that while passive recovery is slow, degradation as a result of overgrazing is reversible over long temporal scales (40 years +). Full recovery of the SKA core area may thus take more than 40 years if restoration relies on livestock exclusion alone. Active rangeland restoration may further improve species richness and abundance of palatable plant species and therefore improve the grazing potential of the land for wild grazers to re-establish within a shorter period (Seymour *et al.* 2010).

Poor vegetation conditions linked to sustained livestock grazing are likely to have impacted adversely on the vertebrate biodiversity within the Karoo region (Eccard *et al.* 2000, Hoffman *et al.* 2018). Both Drouilly *et al*. (2018a) and Woodgate *et al.* (2018) provide evidence of a cosmopolitan group of small to medium sized generalist species persisting on farmland throughout the Karoo. Except for greater kudu (*Tragelaphus strepsiceros*) few large mammals including large predators are found outside of protected areas in the Karoo (Carruthers & Nattrass 2018). Very little information on the current distribution, relative abundance and species richness of various vertebrate groups has been collected for the SKA region (Milton *et al.* 2016, Schumann *et al.* 2016, Todd & Henschel 2016). Species richness and abundance is predicted to be lower than areas with little to no livestock farming (i.e., Karoo National Park) (Schumann *et al.* 2016, Todd & Henschel 2016). There are currently no large apex predators within the Upper Karoo, as most carnivores were eradicated in early colonial times (Milton *et al.* 2016, Schumann *et al.* 2016, Todd & Henschel 2016). Medium-sized carnivores or mesopredators such as the black-backed jackal and caracal, have however reportedly increased in numbers over the last century (Drouilly & O'Riain 2019) and become the dominant predator within the Karoo (Milton *et al.* 2016, Schumann *et al.* 2016, Todd & Henschel 2016).

The lack of extensive biodiversity surveying within the Karoo and SKA regions suggests that the impact of sheep removal, and the cessation of farming activities in general, on biodiversity is unknown. The removal of sheep from the SKA core area will relieve grazing pressure, presenting the opportunity for the vegetation to recover. Recovery is predicted to be associated with increased vegetation cover, a shift from ephemeral to perennial plant species, as well as an increase in more palatable plant species (Todd & Hoffman 1999, van Rooyen *et al.* 2015, van der Merwe 2020). Passive recovery of vegetation is likely to have bottom-up influences on higher trophic levels (Read *et al.* 2011, Beltran *et al.* 2014), however abiotic factors such as variability of rainfall may confound these influences (Cuevas *et al*. 2020). Furthermore, the cessation of farming activities may relax top-down influences on wildlife, assuming that humans are associated with a certain degree of predation risk for both prey and predator species (Smith *et al.* 2017, Suraci *et al.* 2019). The land use changes occurring within the SKA core presents a unique opportunity to establish a baseline for long term monitoring of the recovery of the site as well as, to test the potentially complex impacts of a cessation in farming activities.

Predator management within and adjacent to the SKA has been hotly debated (Terblanche 2020). Landowners surrounding the newly formed core have expressed concern that this protected area will act as a refuge and hence source for predators in the region and that this will ultimately result in increased livestock losses. Farmers have therefore called for culling within the SKA despite little research on predator populations and how they may respond to the changes in land use. Several researchers have suggested culling may not provide the best long-term solution for predator management as culling does not necessarily prevent livestock losses (Baker & Harris 2005, Lennox *et al.* 2018, Smith & Appleby 2018) and may even exacerbate it (Bailey & Conradie 2013, Nattrass *et al.* 2020). Furthermore, several studies have shown that the removal of predators within a semi-natural system can lead to deleterious trophic cascades resulting in an overall negative impact on the landscape (Glen *et al*. 2007, Ritchie & Johnson

2009, Ritchie *et al.* 2012, Morris & Letnic 2017). Understanding how predators respond to the formation of a protected area and the removal of humans as apex predators is important given the controversy over the value of lethal methods for controlling predator numbers and reducing livestock losses on farms. Furthermore, determining whether predators actively track livestock in the landscape by emigrating out of the core area onto neighbouring farms is important for managing both PAs within farming regions and livestock losses for farms adjacent to PAs.

Thesis outline

Biological surveys of the SKA core will provide important information concerning the recovery of plants and animals following a reduction in human activities including the removal of sheep, a cessation in hunting and a reduction in water provisioning. Surveys will further provide the first robust mammalian biodiversity assessment of the region which is currently limited to presence or absence surveys that were both limited in extent and duration (Todd & Henschel 2016, Milton *et al.* 2016). Together these data will provide an important baseline for comparing long term future impacts including climate change in the Karoo. The study will also provide valuable information on how predator populations respond to the change in land use from sheep farming to protected area and whether farmers adjacent to the core area have valid concerns that predators will leave the core to feed on their sheep, and then return to seek refuge from persecution. Ideally one should capture and collar predators with satellite collars to understand land use and movement patterns of predators but this and other such activities requiring electronic equipment are not possible within the ‘radio quiet zone’ of the SKA.

Before-After Control-Intervention experimental design

Where the efficacy of management interventions including restoration needs to be measured it is essential to ensure that the study design includes replication (Underwood 1992, Conner *et al*. 2016). Site availability in the SKA and therefore replication of ‘intervention’ is however limited due to cost and physical site restrictions (Conner *et al.* 2016). Before-After-Control-Intervention (BACI) designs allow evaluation of these interventions on a temporal scale, comparing a specific site over time, eliminating the need for extensive spatial replication which may only give a snapshot view of any intervention (Conquest 2000, Smith 2002, Torres *et al.* 2011, Conner *et al*. 2016). The formation of the SKA protected area presents a unique opportunity to design a BACI research program for the long-term monitoring of ecological responses to land-use change, particularly in the Upper Karoo which historically is a poorly studied system in South Africa (Kraaij & Milton 2006). A BACI design allows an assessment of the intervention compared to natural variation in the control sites, eliminating natural temporal variation as a confounding variable (Underwood 1992, Smith 2002, Conner *et al.* 2016, Muller *et al.* 2016). Using BACI designs are particularly valuable when measuring passive restoration following a change in land use, as often changes in the ecosystem are only apparent several years after intervention (Smith 2002, Torres *et al.* 2011, Conner *et al.* 2016, Muller *et al.* 2016). For example, Muller *et al.* (2016) showed that an 8-year BACI design was effective at revealing the restoration of riparian zones after livestock exclusion. The ability to access multiple farms (i.e., sites) within the SKA allows for both spatial replicates and, while the scope of a PhD precludes long-term monitoring, temporal replicates too. Long term monitoring of select sites in this study will be continued by the South African Environmental Observation Network (SAEON).

This study includes the opportunity to explore the impact of edge effects linked to the change in land use on both treatment as well as edge farms. Edge effects typically occur where there is a zone that connects two areas of abrupt changes (i.e., two adjacent areas with different land uses) (Harris 1988, Laurance & Yensen 1991, Laurance *et al.* 2007, Ries *et al.* 2017). Edges present complex and context specific responses, and thus understanding how edges may specifically influence ecological processes at a local scale is important (Donovan *et al.* 1997, Ries *et al.* 2004, Ries *et al.* 2017). Pairing edge sites that fall adjacent to treatment sites will provide insight into the edge effects that may arise from the specific change in land use namely, from commercial small livestock farming to protected area. These data are important to both farmers and PA managers in the Karoo who have had and will continue to have a difficult relationship given the conflicting objectives of their respective land uses.

Aims and objectives

The main aim of this study is to provide baseline data for select mammalian biodiversity in this poorly studied region of the Karoo and to investigate how landscape scale land use change influences both plants and mammal occurrence and abundance using a Before-After-Control-Intervention (BACI) design. A secondary aim is to understand how the cessation of farming activities, particularly the removal of small livestock, impacts mesopredator presence, abundance, activity patterns and the use of holes in the fence separating active livestock farms (referred to as edge farms) from the newly created core PA (referred to as core farms). These aims will be achieved by addressing three main objectives:

1. Measuring changes to vegetation and small mammals on the core, edge and control farms before and after a change in land use on core farms.
2. Monitoring changes in the presence and relative abundance of medium and large mammals and the activity patterns of mesopredators and select wild prey species on core, edge and control farms, before and after a change in land use on core farms.
3. Recording movement along fences and the use of fence holes by wildlife living on core and edge farms, before and after a change in land use on core farms.

Thesis design

Chapter 2 provides a general description of my study area, including details on the layout of the Square Kilometre Array (SKA) and restrictions this layout imposed on both spatial replicates (farms) and methods for monitoring wildlife. For each data chapter I attempted to avoid unnecessary repetition, especially concerning the description of the study site, while still allowing for each chapter to be able to read independently. Reference to chapter 2 is therefore made throughout data chapters when describing the study area.

In **Chapter 3**, I explore the relationship between vegetation cover and structure and small mammal species richness and abundance using a BACI design. I hypothesize that the cessation of farming activities on core farms will positively impact vegetation recovery and small mammal populations.

In semi-arid regions, like the Karoo, medium and large mammals typically occur at low densities and have cryptic lifestyles, making detection difficult. In **Chapter 4**, I use non-invasive camera trapping surveys to investigate community level diversity and structure of medium and large terrestrial mammals in each farm type before and after the cessation of farming activities on core farms. I further use these camera trap data to study daily activity patterns of several mammal species before and after the intervention. I hypothesize that the cessation of farming activities on core farms will positively impact medium and large mammal populations, with no impacts on mammal populations on edge and control farms.

Mesopredator abundance and activity remain important considerations in carnivore ecology as well as predator management. In **Chapter 5**, I use non-invasive camera trapping to study community level diversity and structure of four mesopredator species (black-backed jackal, caracal, cape fox *Vulpes chama* and baboon *Papio ursinus*) on core, edge and control farms before and after the cessation of farming activities on core farms. Additionally, I use these data to study daily activity patterns of mesopredators and select prey species to understand how the intervention influences predators and prey and their spatio-temporal overlap. I hypothesize that the cessation of farming activities on core farms will impact meso-predator abundance and daily activity on core farms, with no impact on mesopredator populations on edge and control farms.

Predator proof fencing remains the most effective non-lethal predator management tool within the Karoo farming regions. In **Chapter 6**, I survey fence quality on the boundary between select core and edge farms and use non-invasive camera trapping at fence holes to study how fence maintenance influences the movement of medium and large mammals along fence lines and through holes that provide passage between farms. I hypothesize that fence quality will impact the presence of mammals along fences and fence hole utilisation by mammals, while cessation of farming activities on core farms will not impact the frequency of hole use or direction of movement by mammal species and mesopredators in particular.

In **Chapter 7**, I synthesise the major findings of each data chapter and place them within the broader context of understanding how small livestock production within the Karoo has influenced both plants and animals and how the cessation of this activity may influence their recovery both here and in semi-arid rangelands globally. I further explore the relevance of my findings to the conflict between farmers and protected area managers, the management of edges between their respective land uses and the impacts on livestock losses when the neighbouring land use is that of a protected area. Lastly, I provide recommendations for future monitoring of the flora and fauna in the SKA core area, and how to address conflict between farmers and PA managers concerning predators in the region.

CHAPTER 2

DESCRIPTION OF STUDY AREA

Typical karoo landscape showing the full range of topography, soil type (sandy or rocky) and gravel roads for providing access to farms (© Michelle Blanckenberg)

General site description

This study includes nine small livestock farms (i.e., sheep and goats) in the Upper Karoo region of the Northern Cape, South Africa (Figure 2.1). This region is characterised by a semi-arid climate, receiving on average less than 200 mm of rainfall annually (mean rainfall based off measures from Carnarvon, Fraserburg and Brandvlei) (Milton *et al.* 2016). The Upper Karoo substrate is dominated by mud- and sandstone with dolerite intrusions creating a landscape characterised by hard rounded dolerite hills and ridges with sandy/silty plains (Milton *et al.* 2016). The gradient of the area is on average gentle with sections of high elevation (freestanding mountains) and rivers typically draining northwards into various pans near Brandvlei (Milton *et al.* 2016).

The study site borders three main Northern Cape municipal districts, the Hantam district (includes the town of Brandvlei), the Karoo Hoogland district (includes the town of Williston) and the Kareeberg district (includes Carnarvon and the SKA core site). Combined, these districts make up 4% of the total population of the Northern Cape province (ca. 45 839 inhabitants with a density of 1 person per km^2) (Statistics South Africa 2011). The Northern Cape unemployment rate is 26% which is just below the national unemployment rate (27%) (Statistics South Africa 2019), while adult literacy rates are 72.1% which is one of the lowest for the country (Statistics South Africa 2016).

Climate

Official climate data were obtained from the South African Weather Service and from the Brandvlei and Williston weather stations located in the Upper Karoo, Northern Cape (Figure 2.1). These stations are located to the north-west and north-east sections (respectively) of the study area and were the closest stations to all nine study farms (Figure 2.1). The Upper Karoo is considered an arid or semi-arid region depending on the area, with hot summers (average maximum temperature is > 30°C) and cold winters (average minimum temperature is 0°C) (Mucina *et al*. 2006) (Figure 2.2). The study site is characterised by periodic rainfall and drought (Mucina *et al*. 2006). Rainfall typically peaks in April but can start as early as December, with sporadic winter rainfall in June/July (Palmer & Hoffman 1997, Mucina *et al*. 2006) (Figure 2.2).

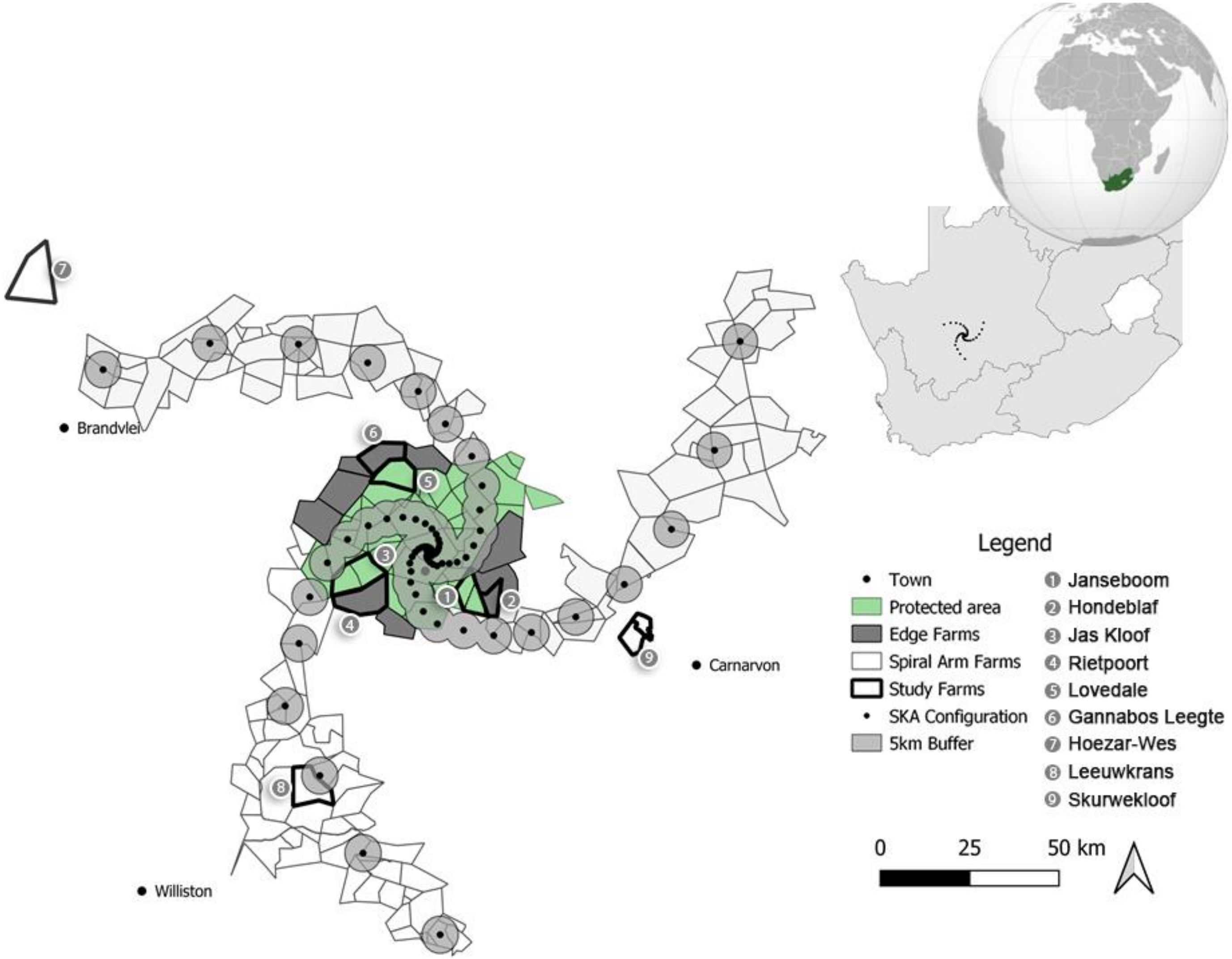


Figure 2.1: The cadastral boundaries of the farms that together comprise the core, edge and spiral arms of the Square Kilometre Array (SKA) relative to the three nearest towns (black circles), Carnarvon, Brandvlei and Williston within the Northern Cape province of South Africa. Black dots within shaded circles indicate the position of the radio dishes across the SKA with a 5 km buffer, relative to nine farms (black outline) used as individual study sites within the core (green polygons), edge (grey polygons) and spiral (white polygons) areas of the SKA zone.

Annual rainfall for the region is on average below 200 mm, however during the study period for this project the region experienced extreme drought conditions (Palmer & Hoffman 1997, Mucina *et al*. 2006) with a mean annual rainfall of 80.98 (± 17.84) mm over a three-year period (2017-2019, based off records from Brandvlei and Williston from the South African Weather service).

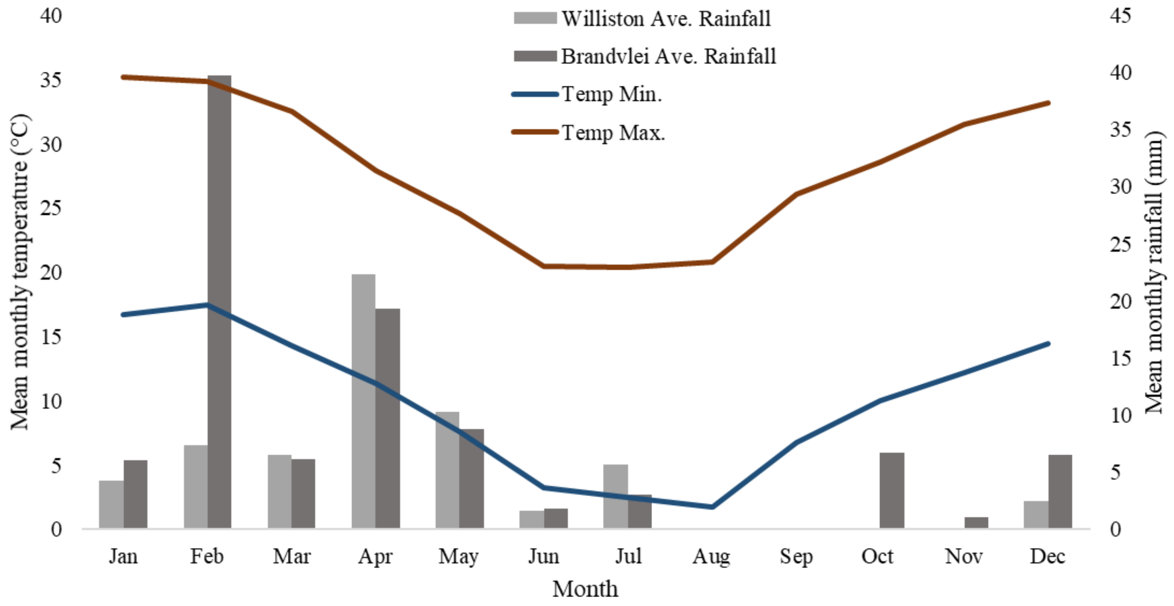


Figure 2.2: Mean monthly temperature range (°C) and mean monthly rainfall (mm) for the SKA region in the Karoo based off temperature measures taken in Brandvlei and Williston (averaged) over a three-year period (2017-2019).

Data collection for Chapter 3, 4 and 5 occurred during both dry and wet summer months (October to February) in three consecutive years (survey A, B and C) (see Table 3.1 and Table 4.2). Data collection for Chapter 6 occurred in winter months (first survey = May 2018, second survey = June 2019). During survey A (Oct 2017 – Feb 2018) rainfall data based off Brandvlei and Williston stations saw a monthly average of 14.52 mm (± 9.21), while during survey B (Nov 2018 – Feb 2019) monthly rainfall averaged 0.9 mm (± 0.79) and during survey C (Nov 2019 – Mar 2020) monthly rainfall averaged 4.5 mm (± 1.63). The average monthly rainfall during each survey period indicated that monthly rainfall was lowest during survey B. The standardised precipitation and evaporation index (SPEI) for the area highlighted the extremely hot and dry conditions that prevailed throughout the study (Figure 2.3). SPEI is a common drought index which uses both temperature and precipitation data to detect, monitor and explore drought conditions (Vicente-Serrano *et al.* 2010). Prolonged periods where the SPEI falls below 0 indicates drought conditions as seen for my study area between 2016 and 2019 (Vicente-Serrano *et al.* 2010) (Figure 2.3).

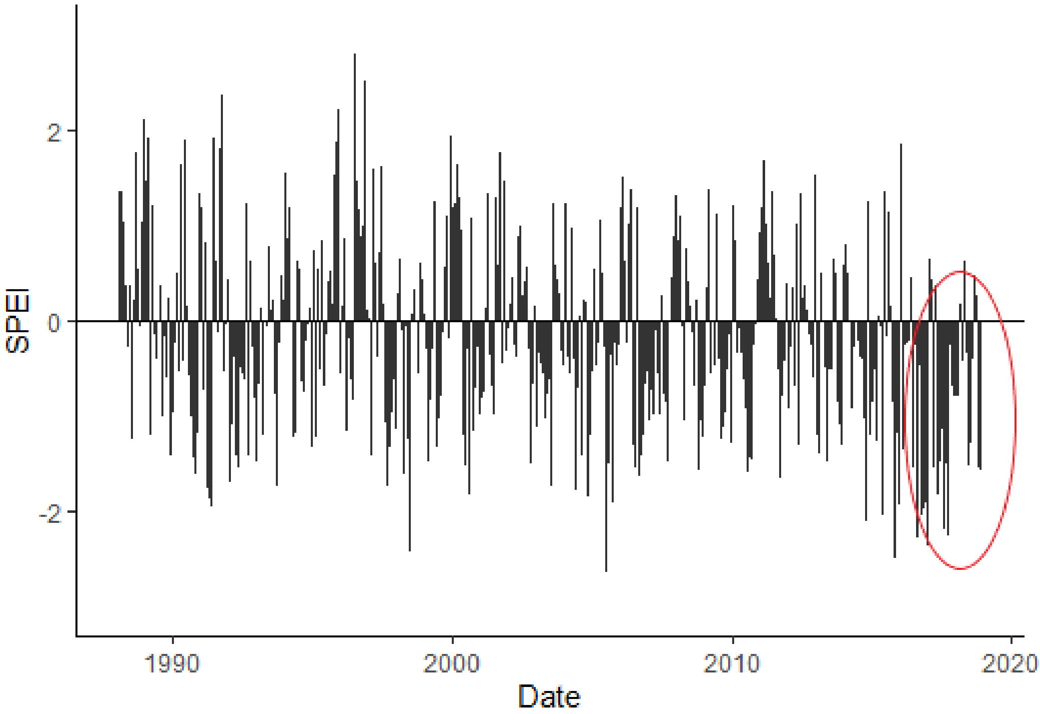


Figure 2.3: Standardised precipitation and evaporation index values for the SKA region on the Karoo between 1988 and 2019. Drought conditions between 2016 and 2018 indicated by red circle (Data sourced from Begueria *et al.* 2021).

Vegetation, status and threats

The Bushmanland bioregion vegetation dominates the northern section of the study area (68%), with Upper Karoo bioregion vegetation found mostly in the south (22%) (Figure 2.4). A small portion of the study area is made up of Inland Saline (western Upper Karoo) vegetation (5%) (Mucina *et al*. 2006). These vegetation types are classified under the Protected Areas Act of 2003 (updated 09/12/2011 in No. 34809 Government Gazette) as either ‘not protected’ or ‘poorly protected’ (Republic of South Africa 2004). While the area is not marked as a Critical Biodiversity Area (CBA), the south-facing slopes have been identified as important buffer areas from the predicted impacts of climate change (Mucina *et al.* 2006).

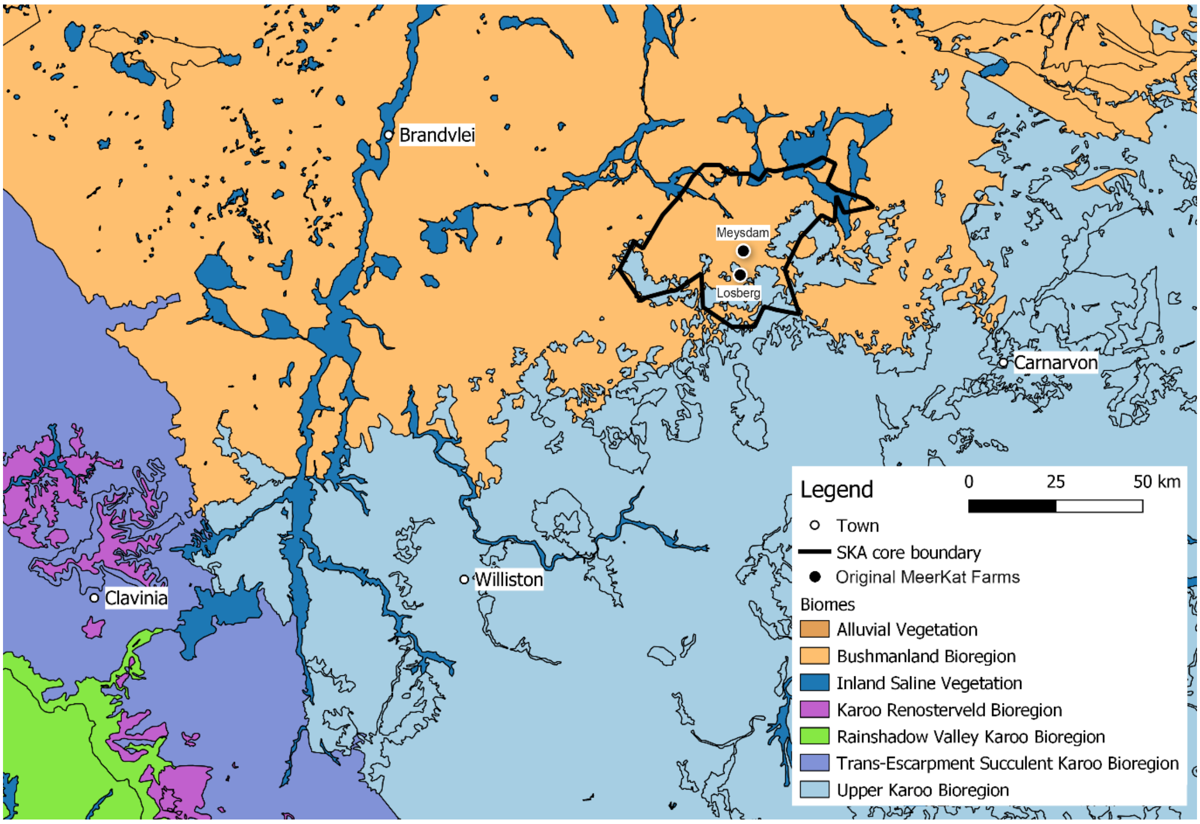


Figure 2.4: Map showing the different biomes making up the SKA core region and surrounding farmland. Labelled white dots indicate major towns (Carnarvon, Brandvlei, Williston and Calvinia), while black dots indicate original two MeerKAT farms (Losberg and Meysdam). Black polygon indicates SKA core boundary. Biome layer sourced from SANBI VEGMAP 2012.

The Bushmanland Bioregion is characterised by a mixture of low and spiny shrubs known as dwarf shrubland (*Rhigozum*, *Salsola*, *Pentzia*, *Eriocephalus*), and 'white' grasses (*Stipagrostis*) (Palmer & Hoffman 1997, Mucina *et al*. 2006) (Figure 2.5). This biome has a conservation status of 'least threatened' as there are no signs of serious land transformation therefore little to none of this bioregion is formally protected (Mucina *et al*. 2006). The Upper Karoo bioregion is characterised by similar shrubs to those in the Bushmanland bioregion, however there is a shift towards a greater range of drought resistant grasses such as *Aristida*, *Eragrostis* and *Stipagrostis* (Palmer & Hoffman 1997, Mucina *et al*. 2006). Upper Karoo bioregion features more steep slopes and boulders across the landscape creating the typical buttes and koppies of the southern section of the study area (Palmer & Hoffman 1997, Mucina *et al*. 2006) (Figure 2.5). Inland Saline (western Upper Karoo) vegetation is again characterised by drought resistant grasses however shrubs are typically more small-leaved shrubs and shrubby succulents (*Brownanthus*, *Drosanthemum*, *Ruschia*) compared to the dwarf shrubland found in the other dominant vegetation types (Palmer & Hoffman 1997, Mucina *et al*. 2006). Both Upper Karoo vegetation types have a 'least threatened' conservation status with only 3% being formally protected within the Karoo National Park and the Karoo Nature Reserve (Mucina *et al*. 2006).

Figure 2.5: Typical landscapes in the SKA core Bushmanland bioregion featuring low and spiny shrubs (*Rhigozum*, *Salsola*, *Pentzia*, *Eriocephalus)* (top left and right), rocky landscape with more small-leaved shrubs and shrubby succulents (*Brownanthus*, *Drosanthemum*, *Ruschia*) (bottom left) and dolerite boulders found scattered within the region (bottom right) (© Michelle Blanckenberg).

While the transformation of natural habitat in the study area is low, major threats to the integrity of the landscape include over-grazing, soil erosion, the spread of alien vegetation and prolonged droughts linked to climate change (Palmer & Hoffman 1997, Mucina *et al*. 2006, Walker *et al.* 2018). Over-grazing from small livestock farming in the Upper Karoo bioregion and Bushmanland bioregion has resulted in a decrease in perennial grasses and a shift to more shrubby species (Hoffman *et al.* 2018, van der Merwe 2020). The reduction in grass cover results in poor rainfall infiltration and is a likely contributor to moderate (± 60%) soil erosion across the three dominant vegetation types (Mucina *et al*. 2006). Over-grazing and soil erosion are both exacerbated by regular drought conditions in the region (Mucina *et al*. 2006). Drought is a common feature in this landscape, however with climate change the frequency, intensity and duration of drought periods are predicted to increase (Vogel 1994, Vetter 2009). This may have devastating consequences on the vegetation which is already stressed from sustained poor land management pressures (Vogel & Olivier 2019).

In the late 1880s *Prosopis* spp. trees (native to the Americas) were introduced to South Africa as a method to increase forage during drought periods as these trees are particularly drought resistant (Richardson *et al.* 2000, Ndhlovu *et al*. 2016). However, since then *Prosopis* spp. has become a major invasive plant, particularly along drainage lines, spread mostly by birds and livestock (Richardson *et al.* 2000, Mucina *et al*. 2006, Ndhlovu *et al*. 2016). *Prosopis* spp. creates dense thorny thickets, displacing native vegetation and depleting below ground water sources (Richardson *et al.* 2000, Ndhlovu *et al.* 2016). At high densities *Prosopis* spp. has been shown to increase soil erosion decreasing the environmental and economic potential of an area (Ndhlovu *et al*. 2016). *Prosopis* spp. has been targeted by the government led IAP control programme, Working for Water (WfW), which aims to clear large stands of invasive vegetation across South Africa, however *Prosopis* spp. remains a major threat to the vegetation of the Upper Karoo (Zimmermann & Pasiecznik 2005, Ndhlovu *et al.* 2016). Differences in vegetation status between farms is largely dependent on the management styles of each landowner (i.e., alien vegetation management, grazing regimes and livestock stocking practices). As a result, the degree of land degradation may have a large gradient within small areas as this gradient works within a single farm unit scale.

Past and present fauna

Historically faunal species in the karoo biomes (specifically the Nama-Karoo) originated from surrounding grassland and savanna biomes (Vernon 1999). As a result, the karoo has relatively low endemism with only one endemic mammal species (Visagie's golden mole *Chrysochloris visagiei*) and three near-endemic species (Grant's rock mouse *Micaelamys granti*, Riverine rabbit *Bunolagus monticularis*, and Shortridge's rat *Thallomys shortridgei*) out of the 83 mammal species historically found in the Nama-Karoo (Vernon 1999, Hilton-Taylor 2000). Additionally, there are only two endemic bird species (ferruginous lark *Certhilauda burra* and Sclater's lark *Spizocorys sclateri*), and 10 near-endemic reptile species with the Karoo dwarf chameleon (*Bradypodion karrooicum*) and Boulenger's Padloper (*Homopus boulengeri*) being potentially confined to the Nama-Karoo (Vernon 1999). The majority of Karoo fauna is made up of grassland species, with a large portion being birds and small to medium mammals (Vernon 1999).

The Karoo biome is defined by its ability to support large migratory ungulate species (Palmer *et al.* 1999). Historically a feature of the landscape included the movement of large herds of grazing mammals (i.e., springbok *Antidorcas marsupialis*) which moved across the landscape in response to rainfall patterns (Palmer *et al.* 1999). For example, springbok herds (often numbering in the thousands) spent the wet summer in the Bushmanland bioregion where shorter grasses dominated, migrating southwards and westwards to the succulent karoo during the winter to graze on longer tufted grasses (Palmer *et al.* 1999). These large migrations were iconic in these areas however with the increase of colonisers in the Karoo, fences and sustained hunting have halted the migration of most indigenous mammal species many of which are now limited to protected areas (Palmer *et al.* 1999).

Despite the relatively low faunal species richness in the Karoo, compared to other areas of the country, the area was able to support high species abundance (Vernon 1999). These large animal abundances were able to co-exist alongside early indigenous human groups (i.e., the Khoisan), but the arrival of colonisers over the last 350 years has dramatically altered the faunal landscape (Boshoff *et al.* 2016, Morris 2018). Competition between small livestock and indigenous grazers resulted in many landowners hunting medium to large mammals, which when coupled with increasing fences and disease outbreaks resulted in the dramatic reduction of ungulate abundance across the Karoo (Vernon 1999). Some species, including kudu (*Tragelaphus strepsiceros*), black-backed jackal (*Canis mesomelas*) and caracal (*Caracal caracal*), have managed to remain relatively abundant and widespread despite pervasive persecution from landowners either due to the threat these species pose to grazing competition or livestock predation respectively (Vernon 1999). However, the predominant pattern in the last few centuries have been a reduction in the distribution and abundance of large animal species within the Nama-Karoo (Boshoff *et al.* 2016).

Recent studies within the greater Karoo region have shown that when comparing the mammal species richness between protected areas and farmland, richness does not significantly change (Drouilly *et al.* 2018a, Woodgate *et al.* 2018, Drouilly & O'Riain 2019). However, compared to historical data, species richness, abundance and distribution has decreased as a result of anthropogenic activity (Vernon 1999, Boshoff *et al.* 2016). Large carnivores (e.g., lion, *Panthera leo*), large ungulates (e.g. zebra, eland, wildebeest sp., red hartebeest and blue antelope) and megaherbivores have all had a reduction in range and abundance in South Africa, most likely due to competition with livestock and hunting (Boshoff *et al.* 2016). Current estimates suggest that within the Karoo there are approximately 31 wild mammal species across both farmland and protected areas (Drouilly *et al*. 2018a, Drouilly & O'Riain 2019). A similar pattern to historical data was however observed when comparing the functional groups of mammals on farmland to protected areas. Farmlands favoured small-bodied species, while protected areas had more larger bodies species including larger carnivores (Drouilly & O'Riain 2019).

In 2016 a preliminary survey of the current biodiversity within the SKA core area was conducted as a requirement for the environmental impact assessment of the SKA project (CSIR 2016a & 2016b, Milton *et al.* 2016). Access to farmland was limited due to famers denying research access which limited ground truthing of key variables relevant to the survey (Milton *et al.* 2016). Consequently, information on the current species richness within the SKA core is limited, and mostly based on information provided by the *BioGaps* project and the *MammalMap* database (Todd & Henschel 2016). According to these sources there are only 25 mammal species in the area including, several small mammal species, viz., meerkat, South African ground squirrel, cape hare, steenbok, springbok, rock hyrax, bat-eared fox, black-backed jackal, caracal and African wild cat (Milton *et al.* 2016, Todd 2016). These reports also suggest the area is home to the critically endangered Riverine rabbit (Milton *et al.* 2016, Todd & Henschel 2016). During 2017 the SKA core area shifted from small livestock farming to a protected area which is characteristic of little to no human interference. The shift in land use is predicted to increase the abundance and potentially the richness of vertebrate species within the landscape. This change was predicted to be driven by increased vegetation cover, providing shelter and food for small to medium mammals (Milton *et al.* 2016, Todd & Henschel 2016).

Description of farm types

Within the SKA region of the Karoo most farms support herds of dorper sheep (a mixture of black headed and white headed dorper) (*Ovis aries*) (Figure 2.6) however, some farms also have small herds of goats and cattle. Dorper sheep are the preferred species within the Karoo as they have adapted well to areas with low and infrequent rainfall. Additionally, this species requires minimal husbandry and are often left to browse freely by farmers. Dorper are therefore an ideal small livestock species for extensive livestock production in the arid Karoo.

Figure 2.6: Adult black headed dorper sheep (left) and white headed dorper sheep lamb (right) (*Ovis aries*) typically used for small livestock production in the Karoo (© Michelle Blanckenberg).

Farm boundaries are demarcated through predator-proof fencing, with simple sheep proof wire fences dividing the interior of the farm into various camps. Camps are used to regulate the movement of sheep within the farm, and ensure that vegetation within one section of the farm is not over grazed. Camps further allow farmers to group herds into different breeding groups (based on age of lambs) to keep track of lambing and pregnant ewes. The division of farms into camps means that farmers and workers have to actively move herds between camps depending on the condition of vegetation. Water sources are typically characterised by windmills which pump groundwater into reservoirs, and from there water is gravity fed into troughs which sheep (and wildlife) can then access. In general, one windmill and reservoir system will support several troughs found in multiple camps, ensuring all camps have a permanent water source. Management of these land units therefore includes, sheep herding (between camps), maintenance of fences, maintenance of water points and road maintenance.

Major threats to lambs which are free roaming with their mothers include drought, severe cold snaps, depredation by mesopredators (particularly black-backed jackal and caracal) and theft. Interviews conducted with the landowners of my nine study farms concluded that predators were the major contributor to livestock losses within the region and perceptions towards predators was extremely negative. Consequently the preferred method of predator management for the study area was lethal focusing specifically on call and shoot hunts (most common and frequent type of hunting), block hunts (less frequent but would often cover multiple farms) and hiring of professional hunters shooting from vehicles or helicopters (infrequent due to high cost).

Study farm selection

This study compares data from nine small livestock farms divided equally into three groups: core, edge and control. Three farms within the expanded 131 000 ha core area of the SKA were paired with three farms immediately adjacent but outside the core, these were labelled as intervention (or core) and edge farms respectively (Figure 2.1). Core farms are those that will undergo a change in land use from small livestock farming to that of a protected area, while edge farms are those that potentially will undergo a change as a result of a change in land use from one of their neighbouring properties. Three control farms were selected within or near the three spiral arms that radiate out from the core area (one farm per arm) (Figure 2.1) and were selected based on their orientation to the original core farms (Losberg and Meysdam, see Figure 2.4) and distance (at least 50 km away). Control farms are assumed to not be directly influenced by the change in land use within the core area and hence provide a control for landscape level changes that may influence biotic and abiotic variables on core and edge farms that are unrelated to the cessation of small livestock farming.

Core farms

Several factors both influenced and limited the selection of core farms within the study area. Firstly, farms needed to represent the variation in topography and vegetation type in the area, specifically the two main biomes (Bushmanland bioregion and Upper Karoo bioregion) and the more rugged mountainous topography south of Losberg and Meysdam (original MeerKAT farms) compared to the flat open plains north of Losberg and Meysdam. Secondly, the farms needed to fall along the boundary of the SKA core area so that they could be paired with neighbouring edge farms to control for variation in local environmental variables (e.g., topography, climate, rainfall). Thirdly, core and edge farm pairs needed to be independent of each other such that they provided spatial replicates of the treatment (cessation in farming). Lastly, camera traps could only be set up in areas that did not interfere with the sensitive radio telescopes, therefore only farms that fell outside of a five km buffer zone of any one telescope could be sampled (Figure 2.1). These criteria limited the number of farms I could work on within the core area to three farms, Janseboom/Snelskloof (referred to as Janseboom), Jas Kloof/Saailagte (referred to as Jas Kloof) and Lovedale.

The southern core farm, Janseboom, was the smallest core farm and contained a mixture of steep rocky mountains with high elevation rocky plains. This farm is dominated by Upper

Karoo bioregion vegetation (characterised by drought resistant grasses such as *Aristida, Eragrostis* and *Stipagrostis* and large spiny *Rhigozum*, *Salsola*, *Pentzia,* and *Eriocephalus*), however to the north in the lower elevation plains there is an area which falls within the Bushmanland bioregion (characterised by large spiny *Rhigozum*, *Salsola*, *Pentzia*, and *Eriocephalus*) (Figure 2.4). This farm was one of the only farms with steep rocky cliffs suitable for providing baboons with a cliff sleeping site. Jas Kloof was the largest core farm and bordered the edge of the south west spiral arm which contained a mixture of steep buttes and koppies along the southern boundary of the farm as well as sandy low-lying plains in the north section of the farm. This core farm was dominated by Bushmanland bioregion vegetation within the sandy plains, however along the plateau of the buttes and koppies in the south the vegetation shifted to fall within the Upper Karoo bioregion vegetation (Figure 2.4). The northern core farm, Lovedale, was considered to have the flattest terrain of the three core farms. This farm lacked significant rises in elevation and contained a series of clay depressions or pans which during rain events became temporary water bodies. These depressions coincided with areas where vegetation was characterised with Inland Saline vegetation (small-leaved shrubs and shrubby succulents *Brownanthus*, *Drosanthemum*, and *Ruschia*), however most of the farm fell within the Bushmanland bioregion biome (Figure 2.4).

Prior to June 2018 all three farms were active sheep farms supporting between 600 and 700 sheep for each farm unit (Table 2.1). Janseboom and Jas Kloof followed a similar management style where farmers were permanent residents with 2-5 permanent workers. This was classified as active daily management, as there was a constant human presence on the farm. The farm Lovedale did not have any permanent residents as the original landowner was based outside of Carnarvon. Workers would only visit the farm once every two weeks. Across the three core farms, prior to sheep removal, there were 51 functioning water points (9 on Janseboom, 36 on Jas Kloof and 6 on Lovedale) between January 2017 and May 2018.

Land acquisition of the 36 core farms making up the SKA protected area or ‘core’ concluded in 2018, and all farms were vacated between October 2017 and May 2018. Each farm within the core became co-managed by SANParks and SKA from June 2018 with management shifting from daily or monthly activity to passive management (occasional visits). Passive management includes maintaining of boundary fences (i.e., fixing holes), removal of some key internal fences, closure of specific water points and maintenance of remaining water points as well as monitoring the area for poaching or unauthorised access. Currently predator management within the core area is limited to ensuring jackal proof fences are checked and maintained but occasional unofficial reports of lethal management by edge farmers in core areas were noted (per. comm.). As of June 2018, there were approximately 50 functioning water points across the three core study farms as most of the original windpumps and reservoirs were maintained.

Edge farms

Edge farms (Hondeblaf, Rietpoort and Gannabos Leegte) were selected based on each being the farm neighbouring a selected core farm (Figure 2.1). The management approach of edge farms matched the management of core farms prior to the cessation of farming activities in 2018, where two farms (Hondeblaf and Rietpoort) followed active daily management and one farm (Gannabos Leegte) followed active bi-monthly management (Table 2.1). Across the three edge farms there were approximately 43 functioning water points (5 on Hondeblaf, 13 on Gannabos Leegte and 25 on Rietpoort) between 2017 and 2020.

Hondeblaf was the smallest edge farm, as well as the smallest overall farm, and bordered the southern core farm Janseboom. This farm was predominantly flat, similar to the high elevation rocky plains of Janseboom. There was a small area of steep rocky koppie along the south-west corner of the farm. However, unlike its paired core farm, Hondeblaf was dominated by the large spiny vegetation of the Bushmanland bioregion (Figure 2.4). During 2017 the farm fell under new management, with the landowner based in Cape Town, therefore while sheep were present on the farm, management was considered passive during this time with workers only visiting the farm once a week. During 2019, sheep owned by the landowner were moved to a different property and the land was rented by a neighbouring farmer and used for his sheep herds (approximately 400 dorper sheep). While this renting farmer did not live on the property, land management became more frequent with workers visiting the farms every second day (Table 2.1).

Rietpoort was the largest edge farm and bordered the south-west core farm Jas Kloof. Along the boundary of these farms were steep buttes and koppies supporting Upper Karoo bioregion vegetation. These steep buttes continued towards the south east corner of the Rietpoort farm, extending the amount of Upper Karoo vegetation. The north-east, and south-west sections of the farm matched the low elevation sandy plains seen in Jas Kloof, and where characterised by the large spiny vegetation of the Bushmanland bioregion. The south-east section of the farm was fenced off with game-proof fencing (excluding the sheep on the farm) and used to hunt antelope such as Bontebok and Wildebeest. Throughout the study (2017 to 2020) several permanent employees lived on the farm and dorper sheep herds were actively managed on a daily basis across the entire farm. However, as drought conditions increased during 2019 and 2020, the majority of pregnant ewes and lambs were moved to two camps close to the main farmhouse in the north-east section of the farm for easy food provisioning. This was also the only farm where boundary fences were completely replaced in certain sections during the study period however, not along the section of fence sampled for Chapter 6.

Gannabos Leegte bordered the northern core farm Lovedale, and similar to the core farm had no areas of significant elevation. Soils were mostly hard shale or clay and vegetation across most of the farm was consistent with the large spiny vegetation of the Bushmanland bioregion. However, like Lovedale, the south-west section of the farm was characterised by clay depressions or pans (acting as temporary pools/marshes during rain events) and vegetation in these areas were more aligned to the small shrubby plants of the Inland Saline vegetation biome. Small livestock (dorper sheep) on this farm were allowed to roam freely within the farm boundaries, and unlike other farms in the area most gates between camps were open. During 2017 and 2018 the landowner and workers only visited this farm once every two weeks. However, by 2019 and 2020 drought conditions reduced the number of sheep supported by this farm, and the regularity of visits by workers.

Control farms

Control farms acted as an additional farming unit to help determine if changes on core or edge farms were a result of the intervention (cessation of farming activities including sheep removal) or from broadscale environmental variables (e.g., drought) influencing the entire region. The control farms had to be sufficiently far from the core area as to not be directly influenced by a change in land use but close enough to shared local environmental variability (e.g., rainfall and temperature). Control farms were thus a minimum of 50 km from the SKA core area boundary and a maximum of 100 km. Control farms were within or close to the three SKA spiral arms which represent future potential land acquisition for the SKA project (Figure 2.1).

Skurwekloof was adjacent to the south-east spiral arm, approximately 50 km from the SKA core area boundary (Figure 2.1). This was the smallest control farm, similar in size to Janseboom and Hondeblaf supporting approximately 650 dorper sheep throughout the study period. This farm was characterised by steep mountains in the north-west section of the farm, large koppies in the north-east section and a mixture of sandy and clay plains in the southern section of the farm. Skurwekloof is dominated by spiny shrubs and drought resistant grasses of the Upper Karoo bioregion, with the clay soils becoming particularly saturated during rain events. Both the landowner and workers are permanent residents on this farm with sheep herds being managed on a daily based. Near the farmhouse apricots are also grown.

Hoezar-Wes is found slightly north-west of the northern SKA spiral arm approximately 97 km from the SKA core area boundary (Figure 2.1). This farm was the largest of the control farms, as well as the largest overall study farm. The area was characterised by a mixture of rocky and sandy plains (very flat topography), with gentle koppies in the extreme southern and northern sections. In the south-west and south-east corners there were large clay pans which act as a temporary water source during rain events. Again, most vegetation was dominated by the large spiny shrubs of the Busmanland bioregion except in the pans where vegetation was dominated by Inland Saline vegetation biome (Figure 2.4). While Hoezar-Wes was mostly used for dorper sheep production, some cattle (approximately 10 animals) were kept on the farm before 2018, only being moved off the farm when drought conditions became too severe (2019 and 2020). Similar to Skurwekloof, both the landowner and workers were permanent residents on this farm with sheep herds being managed on a daily based. During 2019 and 2020 when drought conditions increased, large numbers of vulnerable sheep (pregnant ewes and lambs) were moved closed to the main farmhouse for easy food provisioning, however all camps containing sheep were provisioned with additional feed during drought conditions.

Leeuwkrans sat within the farms demarcated for the southern spiral arm approximately 50 kms from the SKA core area boundary (Figure 2.1). Similar to Hoezar-Wes this farm was characterised by flat topography with some gentle koppies in the western section of the farm. However, similar to Skurwekloof steep mountainous areas were found in the northern section of the farm. Again, like Skurwekloof, this farm was characterised exclusively by Upper Karoo bioregion vegetation (large spiny shrubs and more drought resistant grasses compared to the Bushmanland bioregion). Again, both the landowner and workers were permanent residents on this farm with sheep herds being managed on a daily based and vulnerable sheep (pregnant ewes and lambs) being moved closer to the main farmhouse during drought conditions. Across the three control farms there were approximately 33 functioning water points (9 on Leeuwkrans, 11 on Skurwekloof and 13 on Hoezar-Wes) between 2017 and 2020 (Table 2.1).

Table 2.1: Summary description of each study farm, showing farm size, major biomes, general topography, soil type, approximate number of permanent water sources (subject to change), approximate number of sheep per year (during the study period), management style and month/year of removal of sheep from core farms. All data was gathered through a series of interviews with the owners of each farm.

Farm Name	**Farm Type & Number**	**Area (ha)**	**Biome**	**Topography**	**Soil type**	**Approx. number of permanent water points**	**Approx. number of sheep (per year)**				**Management style**	**Cessation of farming activities**
							2017	*2018*	*2019*	*2020*		
Janseboom	Core 1	4440	Bushmanland bioregion/Upper Karoo bioregion	Mountainous to the north with high elevation plains to south	Hard rocky soil	8	609	0	0	0	Active, daily management	June 2018
Jas Kloof	Core 2	7343	Bushmanland bioregion/Upper Karoo bioregion	Mountainous to the south with low elevation sandy plains in the north	Combination soil, sandy and hard rocky areas	36	700	0	0	0	Active, daily management	April 2018
Lovedale	Core 3	7100	Bushmanland bioregion/Inland Saline vegetation	Flat plains with some low-lying pans	Sandy soil	6	650	0	0	0	Passive, bi-monthly management	August 2017
Hondeblaf	Edge 1	2400	Bushmanland bioregion	Low elevation plains	Hard rocky soil	5	300	300	400	400	Passive, bi-weekly management	n.a.
Rietpoort	Edge 2	8000	Bushmanland bioregion/Upper Karoo bioregion	Mountainous to the north with low elevation sandy plains in the south	Combination soil, sandy and hard rocky areas	25	700	650	600	600	Active, daily management	n.a.
Gannabos Leegte	Edge 3	7200	Bushmanland bioregion/Inland Saline vegetation	Very flat plains with some low-lying pans	Sandy soils	13	600	600	400	400	Passive, bi-monthly management	n.a.
Hoezar-Wes	Control 1	9200	Bushmanland bioregion	Flat with some gentle hills to the south	Combination soil, sandy and hard rocky areas	13	900	900	850	800	Active, daily management	n.a.
Leeuwkrans	Control 2	6359	Upper Karoo bioregion	Mostly flat with some mountains in the far north	Combination soil, sandy and hard rocky areas	9	650	650	500	400	Active, daily management	n.a.
Skruwekloof	Control 3	6200	Upper Karoo bioregion	High elevation plains to the south, mountainous in the north	Sandy soil	11	700	650	600	550	Active, daily management	n.a.

CHAPTER 3

VARIATION IN VEGETATION AND SMALL MAMMAL COMMUNITIES BEFORE AND AFTER THE CESSATION OF FARMING ACTIVITIES IN THE SKA

Hairy-footed gerbil (*Gerbilliscus paeba)* individual caught during small mammal trapping on core farm 1, this individual was placed within a measuring tube for processing before release (© Michelle Blanckenberg)

Abstract

Livestock production in semi-arid regions has reduced habitat complexity and resulted in the decrease of both plant and small mammal biodiversity and abundance worldwide. Within the Karoo historical grazing by livestock has resulted in increased unpalatable and spinescent shrub species, decreased grass cover and increased desertification. Small mammal communities, which are reliant on plants for both food and shelter, currently exhibit low species richness and abundance throughout the Karoo. The bottom-up influences of vegetation and environmental characteristics on small mammals, which have fast population turnover times, makes these species ideal bioindicators to assess ecosystem health and recovery. In this chapter I used a combination of wheel-point vegetation surveys and live trapping of small mammals to determine how elements of the flora and small mammals on small livestock farms have responded to a cessation in livestock presence. Plant functional group richness, diversity and percentage cover did not differ significantly between farm types or between survey years, however grass height did significantly increase with the removal of sheep on core farms. Overall, eight different small mammal taxa were captured across the survey period. Small mammal richness, diversity and abundance (minimum number alive, MNA) were not significantly different between farm types and survey years. There were no strong associations between small mammal MNA and environmental or vegetation gradients. Results suggest that the cessation of farming activities, specifically the removal of sheep, did not significantly impact small mammal communities or vegetation (except for grass height). The short duration of the study combined with the prolonged drought experienced throughout the study potentially dampened the recovery of vegetation and small mammal communities on core farms. These data provide an important baseline for long-term monitoring of SKA core sites with the goal of understanding both the passive recovery of vegetation and small mammals and the long term impacts of global climate change in the Northern Karoo.

Introduction

Globally the conversion of natural vegetation to agricultural lands, for either crop production or livestock farming, has resulted in the decrease of both plant and animal biodiversity (Bradshaw *et al.* 2003, Kraaij & Milton 2006, O'Farrell *et al.* 2008, Pudyatmoko 2017, Hoffman *et al.* 2018, Zungu *et al.* 2020). The relationship between increased agriculture and decreased biodiversity is typically related to a decrease in habitat complexity (Schweiger *et al.* 2000, O'Farrell *et al.* 2008). Habitat complexity refers to the degree of spatio-temporal heterogeneity within an area (plant structure and composition, soil heterogeneity, and topographic and temporal variability) (Cuddington & Yodzis 2002, Michel *et al.* 2006, Kovalenko *et al.* 2012). Extensive livestock farming has deleterious impacts on the vegetation structure (i.e., physiology and floristic composition) within an area (Eccard *et al.* 2000, Kraaij & Milton 2006, Anderson & Hoffman 2007), especially in semi-arid regions like the Upper Karoo (Dean & Milton 1999, van Rooyen *et al.* 2015, Hoffman *et al.* 2018).

Wild herbivores can markedly influence the quality, floristic composition and abundance (i.e., density, biomass or extent of plant cover) of vegetation within an area (Hempson *et al.* 2017). For example, in grasslands grazers balance the relationship between grasses and trees, helping to promote increased habitat complexity (Goheen *et al.* 2010, Hempson *et al.* 2017). Important to this relationship is the abiotic (i.e., rainfall, climate, solar energy) and biotic (e.g., disease and predation) influences that control the density and movement of wild herbivores which in turn regulates the degree of influence they have on plant communities (van de Koppel & Rietkerk 2003, Hempson *et al.* 2015). Historically, light regulated herbivory has been shown to increase plant productivity (Keesing *et al.* 2018, Young *et al.* 2018).

Wild grazers and browsers usually occur at relatively low densities within areas currently utilised for livestock production in the Karoo, owing to increased competition with domestic grazers that occur at higher densities, in addition to both hunting and fencing (Hempson *et al.* 2017). High stocking densities, coupled with restricted movement (due to increasing fencing and fixed water points) often leads to over-grazing, trampling of natural vegetation and increased soil erosion (Eccard *et al.* 2000, McManus *et al.* 2018). Such impacts affect plant richness and diversity, often leading to potential loss of habitat complexity, and may also impact animal species that rely on the resources and structure of resident plant communities (e.g., using plants for food or plant cover as refugia) (Eccard *et al.* 2000, O'Farrell *et al.* 2008, Hempson *et al.* 2017). Small mammal communities, for example, are impacted by changes in vegetation cover and structure, as well as potential shifts in competitive interactions with ants and bird granivores because of decreased plant cover from increased grazing and trampling (Kerley & Whitford 2000, Gonnet 2001, Sassi *et al.* 2006). As plant cover is reduced, surface seeds become more visible and soil temperatures increase, favouring foraging by diurnal birds (visually foragers) and ants (higher soil temperatures and activity) but limiting the foraging style of predominantly nocturnal granivorous small mammals (Kerley & Whitford 2000, Gonnet 2001, Sassi *et al.* 2006).

Several studies have investigated the relationship between habitat complexity and mammal communities, in particular small mammal communities (Joubert & Ryan 1999, Eccard *et al.* 2000, Tews *et al.* 2004, Michel *et al.* 2006, O'Farrell *et al.* 2008, Stevens & Tello 2011, Fischer *et al.* 2011, Lagesse & Thondhlana 2016). Small mammals are suitable bioindicator species to assess habitat 'integrity' (Avenant 2000, Hoffmann & Zeller 2005, Avenant & Cavallini 2007, Avenant 2011) and to monitor post-disturbance recovery of natural habitats. Owing to their small size, they have high reproductive outputs (short gestation periods, large litter sizes and rapid maturation), and fast population turnover rates (short longevity), so they respond rapidly to environmental changes. They can also survive in small areas of fragmented natural vegetation that serve as refugia in landscapes transformed by agriculture (Avenant 2000, Avenant 2011, Rebelo *et al.* 2019). These characteristics make small mammals ideal bioindicator species (Avenant 2000, Avenant 2011). Small mammals are highly influenced by bottom-up (environmental) processes determining small mammal diversity and abundance (Rebelo *et al.* 2019). Changes in ground cover, habitat heterogeneity and vertical variation in habitat structure are all important determinants of small mammal communities as these environmental characteristics influence forage availability and the amount of refugia available (Shanker 2001, Keller & Schradin 2008, Merritt 2010, Rebelo *et al.* 2019). Processes that influence these characteristics, namely changing fire regimes, rainfall, elevation and proximity to waterbodies, also determine landscape-level variation in small mammal communities, often resulting in different small mammal diversity and abundance along spatial and temporal scales (Lyra-Jorge *et al.* 2001, Yarnell *et al.* 2007, Rebelo *et al.* 2019).

The close relationship between small mammal communities and environmental factors is mostly due to their direct dependence on vegetation for survival (providing food and shelter) (Avenant 2000, Avenant 2011). Avenant (2000) suggests that any change in a habitat (i.e., decreased rainfall) will result in changes in small mammal diversity, while ecological disturbance (e.g., over-grazing) results in a decrease in small mammal richness. In both cases small mammal succession is determined by vegetation density rather than time since disturbance (Monamy & Fox 2008). The diversity, community structure and abundances of small mammals is determined by bottom-up abiotic and vegetation characteristics (Schweiger *et al.* 2000, Fox *et al.* 2003, Monamy & Fox 2008); therefore, by monitoring small mammal communities we can potentially assess ecosystem 'health' and ecosystem recovery from disturbance (Hoffman & Zeller 2005, Gaukler *et al.* 2020). According to the productivity-biodiversity hypothesis, small mammal biodiversity is primarily patterned by ecosystem productivity (Oindo *et al.* 2000, Nieto *et al*. 2015). Here the prediction is that plant productivity ultimately limits the number of species within that ecosystem (Nieto *et al.* 2015). Within the Karoo, the normalized difference vegetation index (NDVI) is on average low compared to more productive ecosystems (e.g., Afro-montane forest) (Hoffman *et al*. 2018), therefore one would expect low species richness as well as slower vegetation recovery, resulting in slow small mammal succession after disturbance events (e.g., sustained livestock overgrazing).

Ecosystems can also be regulated by small mammals through top-down effects such as herbivory (Dulamsuren *et al.* 2008), seed predation (i.e., granivory) (Kelt *et al.* 2004, Peters *et al.* 2004, Lobo 2014), pollination (Payne *et al.* 2016, Zoeller *et al.* 2016), as well as small mammals dispersing materials (such as seeds or mycorrhizal fungi) (Bricker *et al.* 2010, Lobo 2014, Mortelliti *et al.* 2019). Through these mechanisms, small mammals can alter/regulate vegetation communities, which in turn affects the pathways of nutrient cycling for both plants and animals within a landscape (Mortelliti *et al.* 2019). Granivory by small mammals is ubiquitous in arid regions where rainfall and plant productivity are low and unpredictable, but seeds provide an important food source that is more reliable throughout the year. However, within the semi-arid Karoo, most small mammals are omnivorous (Kelt *et al.* 1996, Kelt *et al.* 2004, Sassi *et al.* 2005, Kelt 2011, Fox 2011). This is contrary to dryland small mammal communities in the northern hemisphere, were granivory is dominant within communities (Kelt *et al.* 1996, Kelt *et al.* 2004, Sassi *et al.* 2005, Kelt 2011, Fox 2011). This is likely a result of temporal changes in resource reliability between the two hemispheres (Fox 2011). Disturbances, such as periods of extremely low rainfall because of natural ENSO cycles (Baudoin *et al.* 2017), or climate change (Dai 2011), fire and domestic grazing, are common factors within the southern hemisphere, more so than the northern hemisphere, and have influenced the reliability of seed production within these systems (Kelt *et al.* 2004, Kelt 2011, Fox 2011). The greater fluctuation in these disturbance regimes in the southern hemisphere has resulted in small mammal communities tending away from granivory in the southern hemisphere, and more towards omnivory which allows greater breath in diet, decreasing the impact of unreliable seed production (Kelt *et al.* 1996, Kelt *et al.* 2004, Kelt 2011, Fox 2011). Within systems with high climatic disturbance (i.e., the Karoo) this type of strategy would be more adaptive. As a result, small mammal communities within the Karoo are likely to impact not only vegetation through seed predation, but also through herbivory and predation on important insect pollinators.

Additional to the top-down effects on vegetation, small mammals may also exert bottom-up control on the diversity, abundance, and population dynamics of small to medium sized predators (birds, reptiles and mammals) that rely on them as prey (Lima 2002, Lima *et al.* 2002, Byrom *et al*. 2014, Hurst *et al.* 2014). For generalist mammal mesopredators (e.g., black-backed jackal *Canis mesomelas* and caracal *Caracal caracal*), small mammals may comprise between 25% and 80% of an individual's diet (O'Farrell *et al.* 2008, Šálek *et al*. 2010, Drouilly *et al*. 2018c). Drouilly *et al.* (2018c) showed that in a protected area within the Karoo small mammals made up most of the diet for jackals and caracals. However, in areas with high numbers of livestock the proportion of small mammals in predators' diets decreases, with livestock predominating (Drouilly *et al.* 2018c). This may be the result of either livestock being easier targets, or a decrease in natural small mammal prey owing to trampling and overgrazing, forcing predators to target livestock (Drouilly *et al.* 2018c). O'Farrell *et al.* (2008) found that landowners experiencing high livestock predation believe that if alternative prey populations (e.g., small mammals) were increased on farms there would be less predator pressure on livestock. Drouilly *et al.* (2018c) found that for caracal on farmlands, wild prey would typically be selected over livestock, suggesting that where livestock predation by caracal is observed, wild prey populations are likely limited by livestock grazing and trampling (Hoffman *et al.* 2005, Muck & Zeller 2006, Torre *et al*. 2007). Therefore, the relationship between vegetation and small mammal populations is important to understanding the potential impacts of changing habitat complexity on higher trophic levels (O'Farrell *et al.* 2008).

The semi-arid areas of southern Africa are naturally low in plant productivity and are therefore often utilised for livestock farming as opposed to crop production (Dean & Milton 1999). Historically, plant communities within these areas were regulated by two main factors, rainfall (bottom-up processes) and herbivory (top-down processes) (Todd & Hoffman 1999). Low rainfall coupled with low wildlife densities has resulted in a landscape dominated by a combination of low, spiny shrubs and perennial grasses, with a high diversity of ground and shrubby succulents (see Chapter 2). However, with the introduction of livestock, increased herbivory and year-round trampling (due to limited seasonal migration) has seen a significant shift in plant communities (Todd & Hoffman 1999, Kraaij & Milton 2006, Hoffman *et al.* 2018, Nenzhelele *et al.* 2018). Wild and domestic herbivores favour palatable plant species when grazing resulting in a decrease of these species, while unpalatable plant species are typically avoided and therefore tend to dominate landscapes where grazing pressure is high (du Toit *et al*. 2018, Hoffman *et al.* 2018, Nenzhelele *et al.* 2018). This was highlighted in the Karoo where Hoffman *et al.* (2018) reported shifts in plant communities tending toward more toxic and unpalatable woody species, as well as a decrease in perennial species resulting in decreased plant abundance during drier periods. The study found that while overall vegetation cover in the Karoo has remained stable (or slightly increased) over several decades, the combination of high stocking rates and both low and unpredictable rainfall resulted in increased rangeland degradation at local scales (Hoffman *et al.* 2018). Additionally, an increase in alien tree species (*Prosopis* spp.), while suggesting increased vegetation cover, has shifted the historic habitat structure of the area and decreased vegetation cover of native plant species (see Chapter 2) (Hoffman *et al.* 2018). With the loss of natural vegetation cover, habitat complexity and forage are lost within the system having major consequences on animal communities (Tews *et al.* 2004, O'Farrell et al. 2008). However, removal or reduction of domestic grazing pressure can have rehabilitative effects on vegetation and the reliant animal communities (Beltran *et al.* 2014, Lezama *et al.* 2014, Hoffman *et al.* 2018, Condon *et al.* 2020.

To date the relationship between vegetation and livestock has mostly been investigated through comparing vegetation and/or animal communities between "natural" (e.g., protected areas) and agricultural regions (Todd & Hoffman 1999, Hoffman *et al.* 2000, Drouilly *et al.* 2018a, Nenzhelele *et al.* 2018). No studies have tracked the impacts of land-use change over short increments of time (e.g., one year, two years, three years, etc.) both before and after the shift in land use. Rather studies focus on differences over long increments of time (Todd & Hoffman 1999, Hoffman *et al.* 2000, Kraaij & Milton 2006, Nenzhelele *et al.* 2018). Short time increments however, are essential for understanding the short-term impacts of small livestock removal on landscape vegetation and small mammal communities. Understanding the response of both vegetation and small mammals is essential for understanding how higher trophic levels may respond to the removal of top-down effects caused by livestock, and compensatory bottom-up processes determined by vegetation and small mammals respectively.

In this chapter I aimed to investigate how the cessation of farming activities within the SKA core region impacts both plant and small mammal communities. Owing to the interdependence of vegetation and small mammal communities, I hypothesized that the removal of sheep would result in a complex interaction of knock-on effects measurable through changes in both vegetation and small mammal populations. I therefore tested the hypothesis that in a semi-arid region like the Karoo, changes in land-use over time (cessation of farming activity to form a protected area) would impact vegetation cover, habitat complexity and community structure (hypothesis 1, H1) on core farms, but not edge and control farms. I further hypothesised that the cessation of farming activities will impact the community dynamics of small mammals (H2) (namely species richness, community diversity and abundances) on core farms, but not edge and control farms.

I predicted that vegetation characteristics and small mammal communities would be similar between the farm types during 2017 however vegetation cover and NDVI would increase on core farms after sheep are removed, specifically grass cover which is closely linked to grazing pressure (prediction 1, P1). Vegetation diversity and effective number of plant functional groups, however, were predicted to remain the same between survey years due to the slow vegetation turnover rate within the Karoo (P2). I further predicted that once farming activities ceased on core farms, small mammal species richness would increase as would community diversity and small mammal standing biomass as a result of increased food available from recovering vegetation (P3). However, small mammal abundances on core farms after cessation of farming activities may be closely linked to predator abundance (namely black-backed jackal and caracal) and the absence of livestock as a prey source, therefore small mammal abundances may potentially remain constant if predator abundance increased over the survey period (P4). I assumed that increased predator abundance would be a valid proxy for increased predation on small mammals, and that while pressure from livestock might ameliorate potentially increasing small mammal abundance this would be offset by increased predation. I predicted that small mammal communities on edge farms would also show lower species richness, diversity and abundance compared to core farms owing to mesopredator immigration while control farm small mammal communities remained constant over the years (P5).

Methods

Study design

Small mammal and vegetation surveys were undertaken on nine farms within the Northern Cape of South Africa (Figure 3.1). These nine farms represent three major farm types: 1) three core farms now within the newly established SKA protected area, 2) three edge farms immediately adjacent to the SKA protected area and 3) three control farms more than 50 km away from the SKA protected area (see Chapter 2). A full description of these areas is presented in Chapter 2. Surveys were carried out both before the cessation of farming activities on core farms when sheep were present on all farm types (2017) and 18 months after the cessation of farming activities on core farms where sheep were removed from core farms but remained present on edge and control farms (2019) (see Table 3.1 for specific dates).

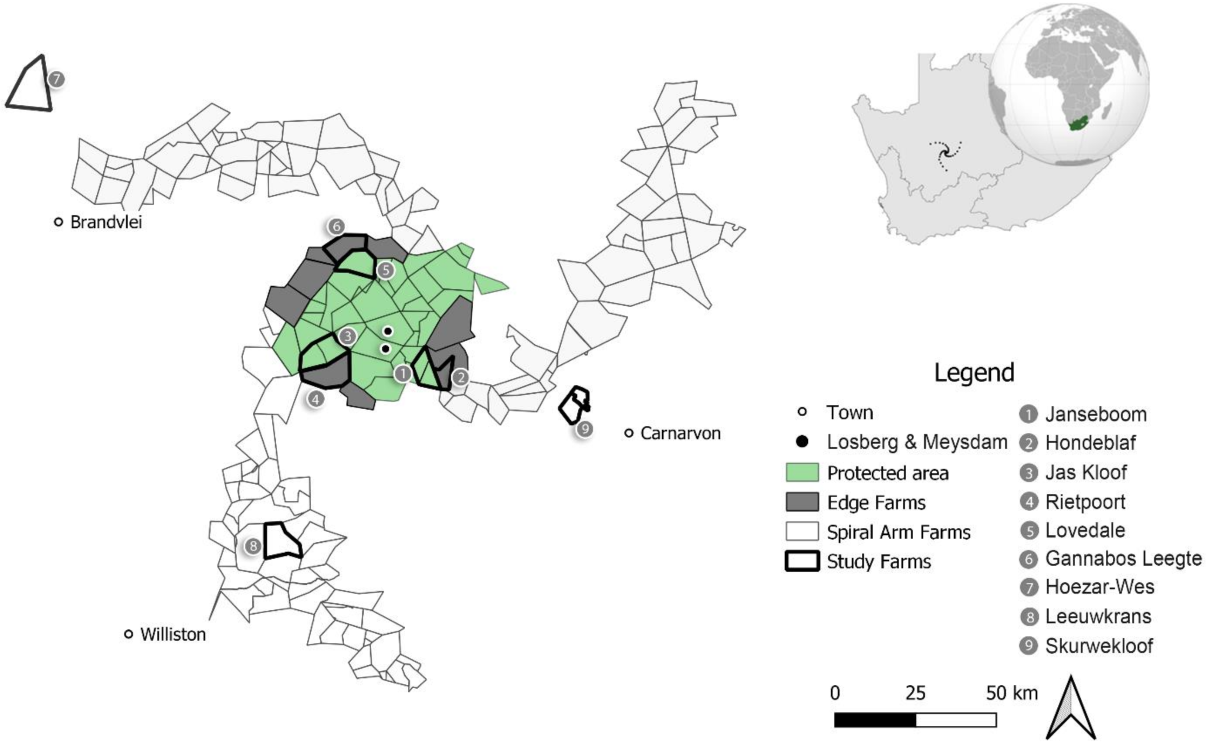


Figure 3.1: The cadastral boundaries of the farms that together comprise the core, edge and spiral arms of the Square Kilometre Array (SKA) relative to the three nearest towns (black circles), Carnarvon, Brandvlei and Williston within the Northern Cape province of South Africa. Study farms (bold black outline) represent the nine farms used as individual study sites within the core (green polygons), edge (grey polygons) and spiral (white polygons) areas of the SKA zone.

On each farm four small mammal transects and three vegetation transects were sampled. Logistical constraints including the number of small mammal traps demanded that I rotated traps between farms over a series of weeks. Transects were set at least 500 m from each other (but sometimes 5 km apart), with one transect placed in each of the three major habitat types (rocks, plains and riverbeds) in the study area. A fourth transect was placed within any obviously different ecotone and/or alternate microhabitat on each farm. Transects ran both north to south and east to west to account for effects of aspect. Transects were also selected to provide ease of access from roads and to be in proximity of one another to reduce total time for trap checking and hence ensure the welfare of small mammals sampled (Figure 3.2).

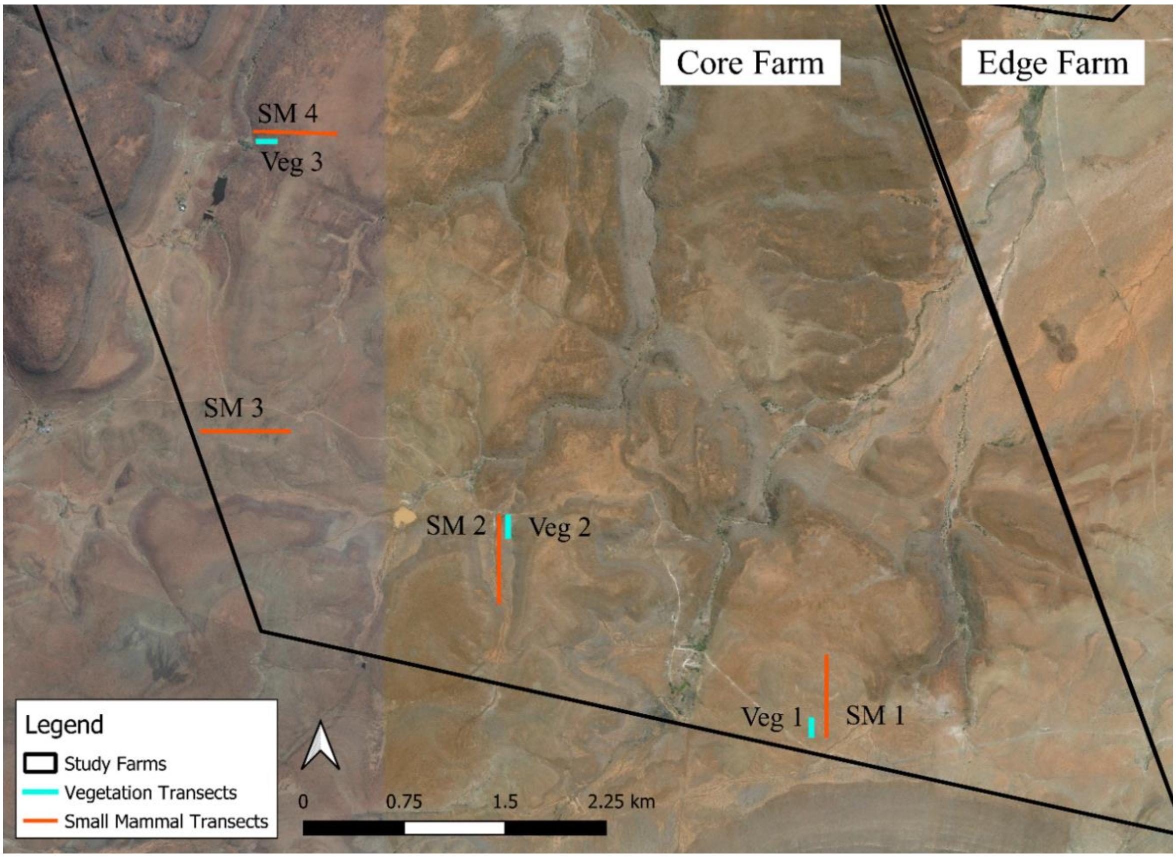


Figure 3.2: Example of the distribution of small mammal and vegetation transects on one of the core farms within the SKA protected area. SM indicates small mammal transect, while Veg indicates vegetation transect. SM 1 and Veg 1 are located in ‘plains’ habitat, SM 2 and Veg 2 in ‘river’ habitat, SM 3 within an interesting ecotone (scree landscape with small to large bushes) and SM 4 and Veg 3 are located in ‘rock’ habitat. Orange lines are ~ 600 m long while blue lines are 100 m long.

Vegetation surveys

Vegetation surveys were carried out in the same fieldtrip as small mammal trapping. I assessed vegetation parameters using two approaches: 1) broad scale remote sensing (i.e., NDVI measures), and 2) fine scale vegetation survey using the wheel-point method. Each farm had a fixed vegetation sampling area for both survey years and plots were sampled at the same time each year to limit seasonal biases. On each farm three transects, running adjacent to the nearest small mammal transects, were randomly selected to measure changes in vegetation through fine scale surveys.

Broad-scale sensing

Seasonal, spatial and temporal (year to year) changes in vegetation cover and productivity before and after land use change were assessed over the study period (2017 – 2019) and to compare (where possible) with historical vegetation status (prior to 2017). Southern Africa has an extensive record of AVHRR Normalised Difference Vegetation Index (NDVI) data. For my study we used MOD13A1 Modis Terra+ Aqua data set values as the Normalised Differential Vegetation Index (NDVI) values for analysis. This data set represents values at a 16-day global 500 m scale and NDVI values for each site in both 2017 and 2019 were calculated using the "raster" (Hijmans 2020) and "rgdal" packages (Bivand *et al.* 2021) in RStudio v3.5.3 (RStudio Team 2019).

Fine scale vegetation surveys

A quantitative estimate of vegetation cover and species composition was done using the wheel-point method. The wheel-point method was originally outlined by Tidmarsh and Havenga (1955) and is frequently used in the Karoo and similar landscapes to measure the compositional changes in vegetation after a disturbance (e.g., rainfall, livestock grazing) (Hoffman and Cowling 1990, Masubelele *et al.* 2014). On each of the nine study farms three 100 m transects were sampled during 2017 and 2019. At every meter along the transect the presence or absence of vegetation was recorded. Where vegetation was present the plant functional group, height (cm) and basal width (cm) of each individual plant as well as overall cover (%) within a one m^2 quadrat was recorded (Figure 3.3). Plant functional groups (PFGs) were identified based on growth form and for this study grouped into either 'grass', 'forb', 'shrub', 'succulent' or 'tree'. Plant species were identified in the field to the lowest possible taxonomic level, however due to limited identifiable features (most plants were dormant) full species level identification was limited. Consequently, my analyses used plant functional groups as the major classification variable but where possible I refer to common and easily identifiable species. I also noted if plants at the one-meter mark were dead (determined by breaking a large stem and observing the presence or absence of green), whether a plant had green leaves or flowers, or whether there was dead leaf litter covering bare ground. Dead leaf litter was important to note as this could still provide shelter and habitat complexity for small mammals within the area.

Where no vegetation was seen at the meter mark, the substrate was identified and recorded as either bare ground, rock or scree. ‘Bare ground’ was defined as any area with no vegetation, rock or leaf litter. ‘Rock’ was noted when the entire one m^2 area was covered by a single large boulder or multiple small boulders, while ‘scree’ was defined as any point where bare ground was visible but was coupled with multiple small rocks and stones, similar to a scree slope.

Figure 3.3: Photograph of myself taking measurements of a shrub species for a vegetation survey. Both the width and the height were recorded, as well as percentage cover of an individual within a one m^2 quadrat (© Michelle Blanckenberg).

Estimating species richness and relative abundance of small mammals

Small mammal trapping

Small mammal trapping took place in spring (from October to December) when more temperate ambient temperatures reduced the probability of mortality in traps from thermal extremes. Small mammals were defined as any terrestrial mammal less than 100 grams and excluded bat species (bat detectors were prohibited within the SKA) and subterranean species (which would require setting tunnel traps). Trapping took place over two distinct periods (referred to as surveys), representing the period before the cessation of farming activities on core farms (Oct – Dec 2017) and 18 months after the cessation of farming activities on core farms (Oct – Dec 2019, where the official cessation date being June 2018). Four 600 m transects, consisting of 60 traps per line, were set for four consecutive nights on each of the nine study farms, resulting in 240 traps set per night on each farm, with approximately 60 traps per habitat type or 960 trap nights. For each farm type (core, edge and control) there were between 2 400 and 2 900 trap nights per survey, with a total of 7 046 trap nights for the 2017 survey and 6 924 trap nights for the 2019 survey (excluding trap failures, which refer to traps sprung without captures due to wind or rain and accounts for the variation in trap nights between farm type and survey years) (Table 3.1).

Table 3.1: Summary of total trap nights, trap failures and trap nights per habitat for nine study farms within three farm type (core, edge and control) during the 2017 small mammal trapping survey. Values in bold indicate totals within a column.

Dates	**Farm Type/** *Farm Name*	**Total trap nights** (excl. trap failures)	**Trap failures**	**Trap nights per habitat** (incl. trap failures)		
				Riverbed	**Plains**	**Rocky Slope**
		2017				
	Core	**2850**	**250**	**1140**	**1180**	**780**
09/10 – 15/10	Core 1 - *Janseboom*	1180	80	300	580	300
24/10 – 28/10	Core 2 - *Jas Kloof*	960	75	360	360	240
07/11 – 11/11	Core 3 - *Lovedale*	865	95	480	240	240
	Edge	**2582**	**258**	**960**	**1200**	**680**
18/10 – 22/10	Edge 1 - *Hondeblaf*	882	38	240	480	240
31/10 – 04/11	Edge 2 - *Rietpoort*	828	120	468	240	200
23/11 – 27/11	Edge 3 - *Gannabos Leegte*	860	100	252	480	240
	Control	**2497**	**375**	**1080**	**1076**	**716**
16/11 – 20/11	Control 1 - *Hoezar-Wes*	830	130	360	356	236
01/12 – 05/12	Control 2 - *Leeuwkrans*	825	135	460	240	240
06/12 – 10/12	Control 3 - *Skurwekloof*	850	110	260	480	240
		2019				
	Core	**2603**	**277**	**1080**	**1080**	**720**
29/10 – 02/11	Core 1 - *Janseboom*	890	70	240	480	240
07/11 – 11/11	Core 2 - *Jas Kloof*	909	51	360	360	240
16/11 – 20/11	Core 3 - *Lovedale*	804	156	480	240	240
	Edge	**2689**	**191**	**960**	**1200**	**720**
02/11 – 06/11	Edge 1 - *Hondeblaf*	910	50	240	480	240
11/11 – 15/11	Edge 2 - *Rietpoort*	892	68	480	240	240
16/11 – 20/11	Edge 3 - *Gannabos Leegte*	887	73	240	480	240
	Control	**2490**	**390**	**1080**	**1080**	**720**
02/12 – 06/12	Control 1 - *Hoezar-Wes*	817	143	360	360	240
27/11 – 01/12	Control 2 - *Leeuwkrans*	835	125	480	240	240
22/11 – 26/11	Control 3 - *Skurwekloof*	838	122	240	480	240

For all transects standard Sherman live traps (LFA-TDG, 7.5 x 9 x 23 cm; H.B. Sherman Traps Inc, Florida) were used with a 10 – 12 m interval between traps (Figure 3.4). Each trap was baited with a mixture of rolled oats, chicken feed, peanut butter, oil, Bovril, raisins and apples, as this provided both moisture and nutrients for any trapped mammal reducing the physiological stress on the animal while in the trap (Bösing *et al.* 2014). Bait was removed and replaced after each trap night to reduce infestation of traps by ants. Aerothane trap covers were used to insulate traps against thermal extremes. Traps were baited within two-hours before sunset (between 17:30 pm and 19:30 pm) and checked the following morning within two-hours after sunrise (between 5:30 am and 7:30 am). Bösing *et al.* (2014) states that this period ensures both diurnal and nocturnal species are targeted with reduced mortality risk from overheating during the day.

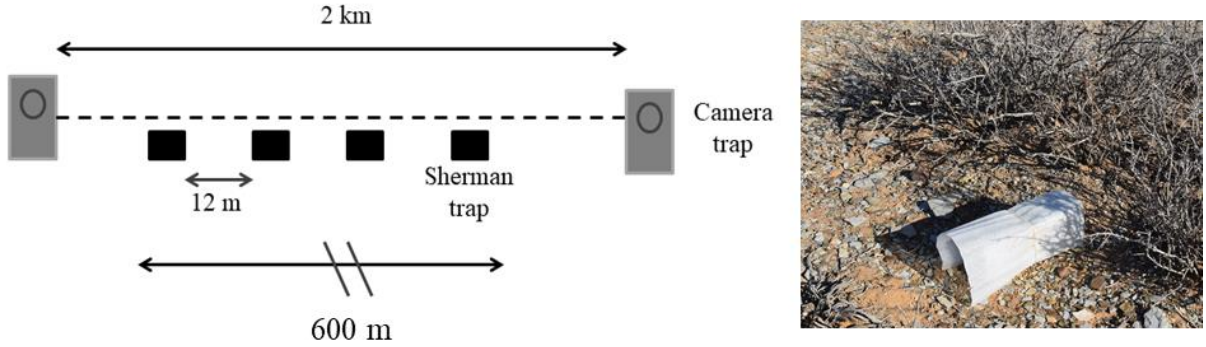


Figure 3.4: A schematic of the small mammal trapping survey in a given habitat type. Transects were 600 meters long with 12-meter intervals between adjacent Sherman traps (see image on the right) (© Michelle Blanckenberg). Transects were situated between two camera stations on the 2 x 2 km camera grid (see Chapter 4) to facilitate the location of the transect.

Small mammal processing

Each captured individual was transferred into a small mesh (potato) bag to help with rapid processing (Figure 3.5) (Hoffmann *et al.* 2010). Individuals were identified to species level (Stuart & Stuart 2007) and the sex and body mass was recorded. Each individual was uniquely marked by cutting a small portion of hair on its rump to help identify previously captured individuals (Hoffmann *et al.* 2010). Recaptured individuals were identified and released without further processing. Once processed each individual was released next to the trap in which it was caught to minimise disorientation (Hoffmann *et al.* 2010). During the 2017 survey, tissue samples (ear clippings) were collected for two cryptic small mammal taxa, *Micaelamys* (n=41) and Macroscelididae (n=14) that are known to include morphologically indistinguishable cryptic species. Samples were stored in 100% ethanol and sent for genetic analyses at the University of Johannesburg, as part of an independent research project on Karoo small mammals (see Main *et al.* 2019) (see permit numbers on page *iii*).

Figure 3.5: Example of small mesh (potato) bag used during small mammal processing, the image on the left is of a hairy-footed gerbil while the image on the right is a short-tailed gerbil (© Michelle Blanckenberg).

Data analyses

Statistical analyses were conducted using a combination of RStudio version v3.5.3 (RStudio Team 2019), QGIS v3.12.0 (QGIS Development Team 2019), EstimateS v9.1.0 (Colwell 2013) and MVSP v3.22 (Kovach 2007). Small mammal analyses included abundance and diversity measures of various community parameters across both spatial and temporal scales, while vegetation analyses focused on NDVI, overall vegetation cover, plant functional group richness and cover as well as habitat complexity on both a spatial and temporal scale.

Small mammal species accumulation and rarefaction analyses

Species accumulation and sample-based (abundance data based on the number of individuals in a sample) rarefaction curves were used to assess small mammal trapping effort for each farm type (core, edge and control) in each survey (before - 2017 and after - 2019), with data combined for all habitats. Observed species richness (S_{obs}), the non-parametric Chao-1 estimator and Coleman rarefaction estimates were used as species richness estimators. Individual-based rarefaction curves (based on Chao-1 estimates) were created using the ‘iNEXT’ package (Chao *et al.* 2014, Hsieh *et al.* 2016, Hsieh *et al.* 2020) in RStudio Version 3.5.3 (RStudio Team 2019), while EstimateS Version 9.1.0 (Colwell 2013) was used to determine S_{obs} and the Coleman rarefaction curves. Chao-1 estimators upweight the occurrence of rare species (singletons versus doubletons) and are widely used to predict the actual species richness with incomplete data sets, as opposed to S_{obs} which simply reflects observed species richness (Chao 1987). Following Rautenbach *et al.* (2013) and Delcross *et al.* (2015), taxonomic completeness (i.e., species sampling or inventory completeness) was calculated by dividing S_{obs} by the Chao-1 estimates.

Univariate analyses

Analyses for vegetation datasets focused on plant functional groups (PFG), vegetation cover (plant abundance and basal cover), habitat complexity and NDVI. Plant functional groups included grass, forb, shrub, succulent and tree and these groups acted as a proxy for plant species richness. As vegetation surveys were carried out during drier summer months under drought conditions most plant species lacked defining characteristics to accurately identify to genus or species level. Hence my reliance on the use of functional groups which group plants according to their response to environmental and abiotic factors rather than traditional phylogenetic groupings (Ramsey *et al.* 2000). Plant functional groups have been shown to provide meaningful patterns in plant responses to both anthropogenic and ecological processes while acting as proxies for plant species richness (Ramsey *et al.* 2000). Basal cover, as well as total plant abundance, were used for each PFG to determine changes in vegetation cover between farm types and over time. Basal cover was determined using average basal width (measured at the base of each plant ca. 2.5 cm from the ground) per plant group. Habitat complexity was estimated as the effective number of microhabitats (i.e., rocks, dead plant litter, shrubs, trees and grasses) identified along a transect. Microhabitats are important resources for small mammals providing refugia from environmental extremes and predators (Kerley, 1992a).

To assess patterns of variation in the abundances of small mammals among the farm types and habitats (within farm types), I used simple enumeration, i.e., the number of individuals per taxon, commonly referred to as the Minimum Number Alive (MNA) (Pocock *et al.* 2004). I then pooled the MNA and present it as the number of individuals captured per 1000 trap nights for each transect on each farm. While this conservative index underestimates the true number of individuals, it is commonly used for limited duration surveys, and is less prone to statistical assumptions of more sophisticated estimation methods (Bronner 1987, Slade & Blair 2000). Shannon-Wiener diversity (H') estimates were calculated for each farm type (core, edge and control) within both survey years.

$$H' = -\sum_{i=1}^{R} pi \ln pi$$

Where p_i is the proportion of individual within the *i*th species. From these values the effective number of species (e^H), also known as Hill numbers, and Pielou's evenness (J') were calculated.

$$J' = H'/\log(\alpha)$$

Where α = alpha diversity or S_{obs} (observed) species richness.

Shannon-Wiener diversity index and Pielou's evenness were chosen as primary measures of diversity. While Shannon-Wiener indices are particularly useful as they account for both species richness and the dispersion of individuals across species (evenness), these indices are open-ended making them difficult to interpret and compare with other studies, and they do not scale linearly with increasing species richness even if there is complete evenness (Jost 2006, Chao *et al.* 2014). To account for this, Hill numbers, or the effective number of species, which are increasingly recognised as a more accurate measure of community diversity (Chao *et al.* 2014) were also calculated. Where available data were averaged to indicate single values per farm types, the coefficient of variation (CV) was also calculated. The CV provides an indication of variation between samples free from scale effects and can help determine whether analyses may represent Type 1/2 statistical errors (Conquest 1983, Brown 1998, Pélobon *et al.* 2020). CV values exceeding 0.30 indicate high levels of variation within a data set (Brown 1998).

I used multiple Linear Mixed Effect Models (LMER for normal distribution or GLMER with a Poisson (link = log) distribution for non-normal datasets) within the "vegan" (Oksanen *et al.* 2019) and "lme4" packages (Bates *et al.* 2015) to test for differences in diversity of small mammals (e^H, H' and J') and vegetation (PFGs, H' and J'), small mammal abundance, trap success, recapture rate, standing biomass and habitat complexity. Farm replicates were used as a random effect variable to account for replication within farm sites. Post-hoc Tukey tests were used to determine specific differences in small mammal and vegetation variables between farm types within a specific survey (i.e., before cessation of farming activities on core farms) as well as within a specific farm type between surveys (i.e., core farms before versus after cessation of farming activities). Significance level was set *a priori* at p = 0.05.

Multivariate analyses

Univariate testing highlighted two response variables for further investigation, namely small mammal MNA per taxa and vegetation cover per PFG. Generalised linear models (GLM) were used to test differences between small mammal relative abundances and vegetation cover (per PFG). Small mammal relative abundance per species was calculated at two landscape levels: 1) MNA per taxa were pooled per farm and standardised to 1000 trap nights to determine general trends in abundance between farm types and surveys; 2) abundances were pooled per habitat type within each farm and standardised to 300 trap nights to determine the community composition between habitats within each farm type and survey. Vegetation measurements were pooled per farm type resulting in 300 points per farm, which is the recommended survey size for the wheel point method to adequately sample vegetation within arid sites (Hoffman and Cowling 1990, Masubelele *et al.* 2013). As shrubs were the dominant plant type, this PFG was further split into different height categories (< 0.5m, between 0.5 and 1m, between 1 and 1.5m and between 1.5 and 2m) to provide a more nuanced analysis of the impacts of shrubs on small mammals. Ideally grasses should also be spilt into height categories however grass height was consistent between all transects creating only one height category referred henceforth simply as "grass". For both response variables a series of categorical, abiotic and biotic predictor variables were used (Table 3.2). Predictor variables were tested for autocorrelation using the Pearson's correlation coefficient (r) for continuous data produced via the 'MuMIn' (Barton 2020) and 'GGally' (Schloerke *et al.* 2020) packages in RStudio version v3.5.3 (RStudio Team 2019) (see Appendix App 3.1 and 3.2). Variables were considered strongly correlated if the Pearson's correlation coefficient was greater than 0.6 or less than -0.6. Habitat complexity and PFGs were found to be strongly correlated ($r = 0.60$, $p = 0.05$), as well as rock cover and bare ground ($r = -0.91$, $p = 0.03$), and shrub cover and shrub basal cover ($r > 0.60$, $p = 0.04$). These variables were subsequently modelled separately.

GLMs were executed using the *manyglm* function within the 'mvabund' package (Wang *et al.* 2020) in RStudio version v3.5.3 (RStudio Team 2019). The 'mvabund' package is a relatively new method of modelling and visualising multivariate abundance data. Unlike previous methods (i.e., ANOSIM and PERMANOVA) the 'mvabund' package is more powerful and better with dealing with a range of abundance data types (count, presence/absence, etc.) (Wang *et al.* 2012, Warton *et al.* 2012). The *manyglm* function fits separate GLM models to each species within a data set using a common set of environmental or predictor variables (Wang *et* *al.* 2012, Warton *et al.* 2012). Therefore, summary statistics for the model (using the *anova* function from the 'stats' package, R Core Team 2020) provides information for both multivariate variables (i.e., the effect of an environmental variable on the entire dataset) as well as univariate variables (looking at the effect of predictor variables on individual species) (Wang *et al.* 2012, Warton *et al.* 2012). This ensures the model takes correlation between species into account which is not possible with other GLM tools (Wang *et al.* 2012, Warton *et al.* 2012).

Table 3.2: Description of landscape-level environmental covariates and site-specific vegetation predictor variables used to assess differences in small mammal communities within the SKA region of the Karoo. The predicted effect (+/-) describes how we predict each variable to affect small mammal abundance and vegetation, positively, negatively or no effect (na). SM = small mammal, NDVI = normalised difference vegetation index.

Predictor category	**Variable**	**Predicted effect**		**Source**
		SM abundance	*Vegetation*	
Categorical variables	Farm Type	+	+	Field data
	Habitat	+/-	+/-	Field data
	Domestic livestock presence	-	-	Field data
Local environmental variables	Longitude	na	na	Field data
	Latitude	na	na	Field data
	NDVI	+/-	+/-	MOD13A1 Modis Terra+ Aqua data set values (https://earthdata.nasa.gov/)
	Monthly Precipitation (Dec 2017 – Dec 2019)	+	+	BIOCLIM (worldclim.org); field data; South African Weather Service
Local vegetation variables	PFGs (proxy for species richness)	+	na	Field data
	Fine vegetation cover (abundance)	+	na	Field data
	Habitat complexity	+	na	Field data
	Bare ground	-	na	Field data
	Rock cover	+	na	Field data
	Grass cover	+	na	Field data
	Grass basal cover	+	na	Field data
	Forb cover	na	na	Field data
	Shrub cover	+	na	Field data
	Shrub basal cover	+	na	Field data
	Tree cover	na	na	Field data

GLMs were fitted with a negative binomial distribution which is typical for count data where mean-variance is quadratic rather than linear (Wang *et al.* 2012). Full diagnostic plots were further run on each model and showed signs of non-constant variance suggesting appropriate model fit for the data sets (see App 3.3, 3.4 and 3.5). Model selection was determined using the *drop1* function from the 'stats' package (R Core Team 2020) based on the Akaike Information criterion (AIC) to select the most parsimonious model (Crawley 2007). Predictor covariates with an AIC below the <none> AIC generated through the *drop1* function were removed from the model, and only approximate covariates were reported in the final model (Crawley 2007) (Table 3.3). The *anova.manyglm* function was used to determine p-values for each predictor covariate, and both the multivariate and univariate results were reported for each model. This showed both the general effect of covariates on the response variable but also the effects of each covariate on individual species. To visualise the patterns in small mammal abundance among sites a non-metric multidimensional scaling (nMDS) ordination plot was constructed using the 'vegan' package (Oksanen *et al.* 2019). I used a Jaccard (presence/absence) similarity index to determine groupings and examine similarities within small mammal communities. Contour environmental variables were determined using the *ordisurf* function from the 'vegan' package (Oksanen *et al.* 2019) to show how continuous variables may affect the community patterns. The *ordisurf* function uses generalised additive models (GAM) to fit smooth surfaces or contours to the ordination space (Oksanen *et al.* 2018).

Table 3.3: Description of most parsimonious models based on the Akaike Information criterion (AIC) (with negative binomial distributions) used for three response variables small mammal abundance (per farm type), small mammal abundance (per farm type and habitat) and vegetation cover. Covariates include survey year, farm type, sheep presence (presence/absence), habitat type, NDVI, rock cover, shrub cover and shrub basal cover.

Response Variable	**Covariates**
Small mammal abundance ~ (per farm type)	Null
	Survey + Farm Type + Sheep presence
Small mammal abundance ~ (per farm type and habitat)	Null
	Survey + Farm Type + Sheep presence + Habitat + NDVI + Vegetation cover + Rock cover + Shrub (> 0.5m) cover + Shrub (0.5 < 1m) cover + Shrub basal cover (1.5 < 2m)
Vegetation cover ~	Null
	Survey + Farm Type + Habitat

I used the *veg.dist* function from the 'vegan' package (Oksanen et al. 2019) to calculate a dissimilarity matrix to visually display any potential community compositional clustering for small mammal communities as well as vegetation. I used the Jaccard dissimilarity index method to create the dissimilarity matrix for each farm per farm type in each survey year (Faith *et al.* 1987). I then applied hierarchical cluster analysis (complete linkage clustering) to the dissimilarity matrix to produce a cluster dendrogram which visually represents the degree of similarity between specific communities, in this case each farm per farm type within a specific year (e.g. Core 1, 2 or 3 within 2017 and 2019).

To assess environmental correlates of small mammal community composition (based on abundances) I used canonical correspondence analysis (CCA), using MVSP version 3.22 (Kovach 2007). Relative abundance values (i.e., MNA) were used as an index of small mammal species abundances. Axes extraction followed Kaiser's Rule, with the Hill reciprocal averaging algorithm used to scale eigenvectors. Overall, the first two axes explained most of the variance among species and sites (2017 = 84.87% and 2019 = 82.34%), however there was significant multi-collinearity among vegetation variables such that only nine variables (NDVI, habitat complexity, percentage rock cover, percentage bare ground, percentage grass cover, percentage forb cover, percentage shrub cover, percentage succulent cover and percentage tree cover) were used for the final ordinations (see App 3.6).

Results

Vegetation and environmental characteristics of core, edge and control farms

Shrubs were the dominant plant functional group across all farm types and survey years, with grasses being the second most abundant (Table 3.4). The dominant large shrub species was *Rhigozum trichotomum* (known as driedoringbos) and the dominant small shrub species was *Salsola aphylla* (known as gannabos) despite *Salsola aphylla* typically being taller than *Rhigozum trichotomum*. Dominant grass species included *Stipagrostis ciliata* and *Stipagrostis obtusa*, but these species were often observed as small, dried tufts. The invasive mesquite/prosopis (*Prosopis* spp.) was the dominant tree species found across all farm types and survey years. Forb and succulent species were low in abundance, with *Aloe* spp. being most common.

Vegetation cover on all three farm types was similar within the 2017 and 2019 surveys (Figure 3.6). However, the CV values for each vegetation variable (excluding bare ground cover and forb cover) showed considerable spatial variability within farm types in both years (Table 3.4). During the 2017 survey, vegetation cover was lowest on core sites (27.2 ± 4.3 %), and highest on control sites (35 ± 4.6 %) (Figure 3.6 and Table 3.4). However, vegetation cover was more consistently similar across the three farm types during the 2019 survey. For each farm type total vegetation cover did not differ significantly within a specific farm type between the 2017 and 2019 surveys (Table 3.5). There was a slight increase in vegetation cover on both the core and edge sites between 2017 and 2019, but this increase was not significant (Figure 3.6 and Table 3.5).

A similar pattern was evident for grass and shrub cover (Table 3.4 and App 3.7). There was a slight increase in forb cover on core and edge farms between 2017 and 2019 (Table 3.4). Overall shrub cover decreased slightly on edge farms between 2017 and 2019, but this change was not significant (Table 3.5). Both grass and shrub cover remained similar between farm types with no significant changes within a specific survey year between farm types (Table 3.6). Grass cover was similar within each farm type between 2017 and 2019 (e.g., core 2017 vs. core 2019) (Tables 3.5).

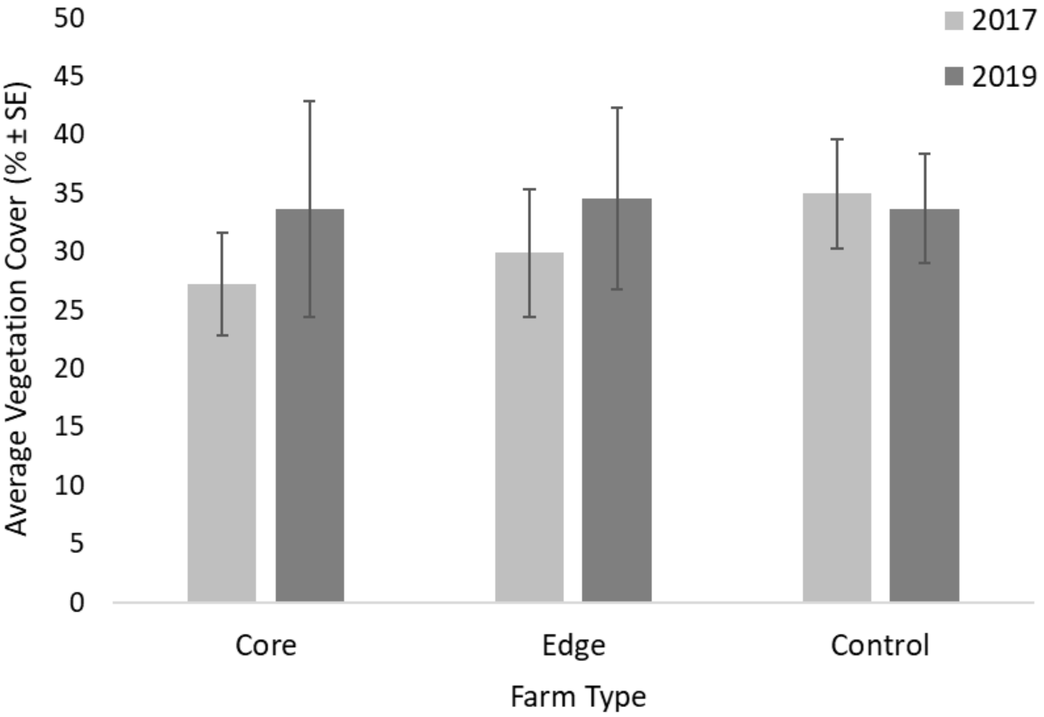


Figure 3.6: Average vegetation percentage cover per farm type over two survey years, 2017 before sheep are removed from farms and 2019 after sheep are removed from the core. Error bars indicate standard error.

Table 3.4: Summary of environmental and PFG parameters (% ± standard error) per farm type over two survey years, 2017 (before cessation of farming activities on the core) and 2019 (after cessation of farming activities on the core). Both total cover as well as cover for each plant functional group is reported. Cover indicates abundance or count of a particular plant functional group expressed as a percentage. Coefficient of variation (CV = sd/mean) indicated by [ ] and italicised. CV ≥ 0.3 indicates a relatively high variation and is highlighted in bold.

Survey	Farm Type	Total veg cover	Bare	Rock/Scree	Grass	Forb	Shrub	Succulent	Tree
2017	Core	27.22 (± 4.37)	58.44 (± 6.03)	13.89 (± 6.11)	4.44 (± 2.40)	0	22.33 (± 2.18)	0.22 (± 0.22)	0.22 (± 0.11)
		[0.27]	*[0.17]*	***[0.76]***	***[0.93]***	-	*[0.16]*	***[1.73]***	***[0.86]***
	Edge	29.89 (± 5.44)	46.67 (± 3.97)	23.33 (± 1.73)	0.78 (± 0.61)	0	28.67 (± 4.82)	0	0.44 (± 0.22)
		[0.31]	*[0.14]*	*[0.12]*	***[1.37]***	-	*[0.29]*	-	***[0.86]***
	Control	35.00 (± 4.66)	49.11 (± 7.06)	17 (± 8.52)	1.56 (± 1.39)	0	33.33 (± 4.16)	0	0.11 (± 0.11)
		[0.23]	*[0.24]*	***[0.86]***	***[1.55]***	-	*[0.21]*	-	***[1.73]***
2019	Core	33.67(± 9.26)	49.78 (± 5.61)	15.78 (± 5.22)	5.67 (± 2.66)	1.44 (± 0.72)	25.67 (± 6.85)	0.11 (± 0.11)	0.78 (± 0.61)
		[0.47]	*[0.19]*	***[0.57]***	***[0.81]***	*[0.00]*	***[0.46]***	***[1.73]***	***[1.37]***
	Edge	34.56 (± 7.73)	46.44 (± 7.66)	19.33(± 1.64)	2.33 (± 1.26)	0.33 (± 0.33)	31.67 (± 7.39)	0	0.22 (± 0.22)
		[0.38]	*[0.28]*	*[0.14]*	***[0.93]***	*[0.00]*	***[0.40]***	-	***[1.73]***
	Control	33.67 (± 4.66)	41.44 (± 4.49)	25.22 (± 2.78)	1.78 (± 1.45)	0	31.67 (± 3.79)	0	0.22 (± 0.22)
		[0.24]	*[0.18]*	*[0.19]*	***[1.41]***	-	*[0.20]*	-	***[1.73]***

Table 3.5: Summary statistics for post-hoc Tukey tests comparing total vegetation cover, grass cover and shrub cover within each farm type (core, edge and control) between 2017 (before cessation of farming activities on core farms) and 2019 (after cessation of farming activities on core farms). For each comparison n = 9. 'Est.' indicates model output estimate with standard error.

Comparison	Treatment	Variable	Est. (± SE)	z value	p.adjust
2019 vs. 2017	***Core***	Total veg cover	6.16 (5.43)	1.13	0.84
		Grass cover	-0.02 (0.26)	-0.09	1.00
		Shrub cover	4.17 (5.21)	0.80	0.96
	Edge	Total veg cover	4.66 (4.74)	0.98	0.91
		Grass cover	1.09 (0.42)	2.56	0.07
		Shrub cover	3.00 (4.65)	0.64	0.98
	Control	Total veg cover	-1.33 (4.74)	-0.28	1.00
		Grass cover	0.13 (0.35)	0.37	0.99
		Shrub cover	-1.66 (4.65)	-0.35	0.99

Table 3.6: Summary statistics for post-hoc Tukey tests comparing total vegetation cover, grass cover and shrub cover between farm types (core, edge and control) within 2017 (before cessation of farming activities on core farms) and 2019 (after cessation of farming activities on core farms). For each comparison n = 9. 'Est.' indicates model output estimate with standard error.

Survey	Variable	Comparison	Est. (± SE)	z value	p.adjust
2017	***Total veg cover***	Core – Control	-7.98 (8.54)	-0.93	0.92
		Edge - Control	-5.11 (8.81)	-0.58	0.99
		Edge - Core	2.86 (8.54)	0.33	0.99
	Grass cover	Core – Control	1.85 (1.23)	1.49	0.58
		Edge - Control	-0.27 (13.6)	-0.20	0.99
		Edge - Core	-2.12 (1.24)	-1.70	0.44
	Shrub Cover	Core – Control	-0.12 (7.25)	-1.67	0.52
		Edge - Control	-4.66 (7.40)	-0.63	0.98
		Edge - Core	7.48 (7.25)	1.03	0.89
2019	***Total veg cover***	Core – Control	-0.47 (8.54)	-0.56	1.00
		Edge - Control	0.88 (8.81)	0.10	1.00
		Edge - Core	1.36 (8.54)	0.16	1.00
	Grass cover	Core – Control	1.69 (1.23)	1.37	0.67
		Edge - Control	0.68 (1.32)	0.52	0.99
		Edge - Core	-1.00 (1.20)	-0.83	0.94
	Shrub Cover	Core – Control	-6.30 (7.25)	-0.87	0.94
		Edge - Control	0.00 (7.40)	0.00	1.00
		Edge - Core	6.30 (7.25)	0.87	0.94

Grass height coefficient of variation (CV) showed marked variation between farms in each farm type for 2017 (core CV = 0.74; edge CV = 1.40; control CV = 0.65) and for 2019 (core CV = 0.76; edge CV = 0.67; control CV = 0.78). During 2017 mean grass height did not differ significantly between farm types ($H_{(2)} = 1.33$, $p = 0.51$) (Figure 3.7). During 2019 grass height was significantly different between the three farm types ($H_{(2)} = 43.5$, $p < 0.001$). Grass height on core farms was significantly higher than edge ($p < 0.001$) and control ($p < 0.001$) farms, while there was no significant difference in grass height between edge and control farms ($p = 0.07$) (Figure 3.7). Grass height was significantly different between 2017 and 2019 ($H_{(1)} = 3.71$, $p = 0.05$) with core sites showing a significant increase in grass height between 2017 and 2019 ($p < 0.001$), while edge and control sites showed significant decreases ($p = 0.05$ and $p = 0.01$ respectively) (Figure 3.7).

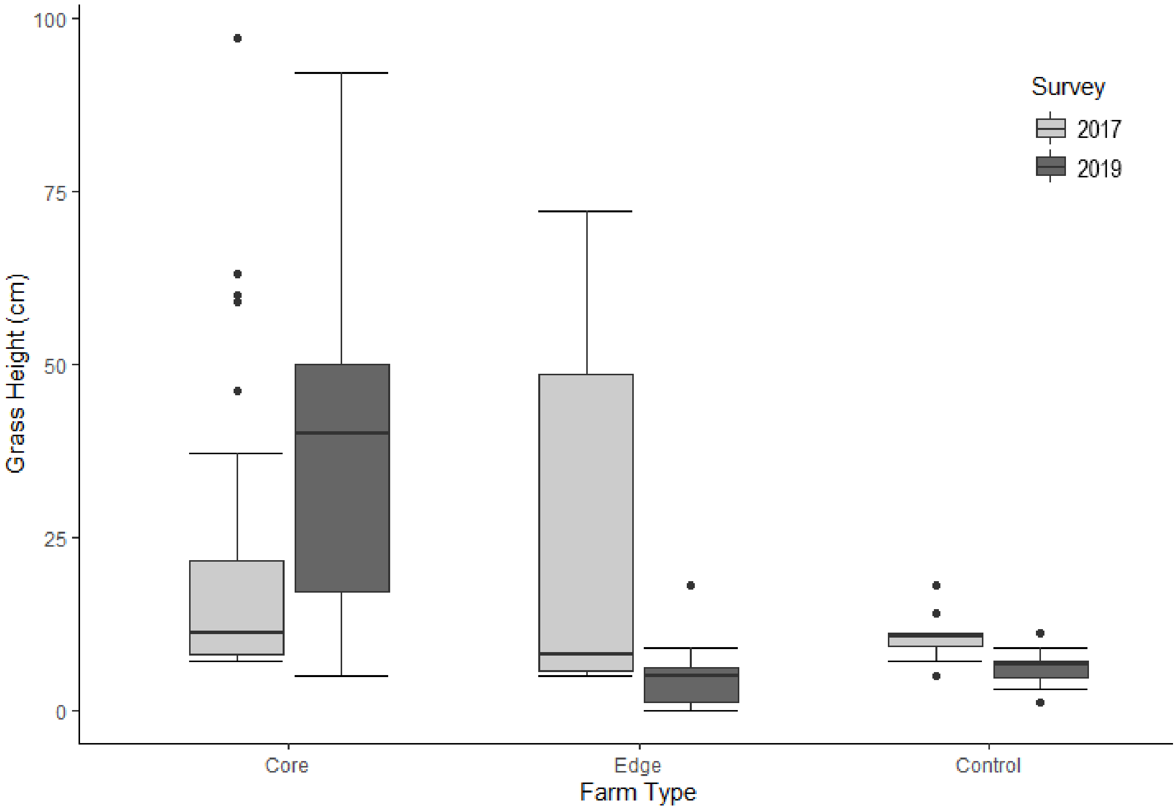


Figure 3.7: Boxplots representing mean grass height (cm) for three farm types (core, edge and control) between two survey years (2017 survey, before cessation of farming activities on the core, 2019 survey, after cessation of farming activities on core farms). Shaded boxes indicate lower quartile, median (thick black line) and upper quartile for grass height, while black dot indicates mean grass height with error bars representing standard error.

Vegetation diversity measures

The average effective number of plant functional groups (ENPFG) during the 2017 survey ranged from 1.61 (± 0.26) to 1.18 (± 0.12), while during the 2019 survey ENPFG ranged from 1.21 (± 0.13) to 1.96 (± 0.50) (Table 3.7). PFG Shannon-Weiner diversity (H') increased slightly from 2017 to 2019 on all farm types (Table 3.7), but such increases were not statistically significantly (Table 3.8 and 3.9). Core farm H' showed the greatest increase between survey years from 0.44 (± 0.18) to 0.60 (± 0.27) (Table 3.7), but this increase was not significant (Table 3.8). A similar pattern was evident for Pielou's evenness between 2017 and 2018, with core and edge sites showing the greatest average increase between the two survey years (Table 3.7), albeit non-significantly (Table 3.8). Habitat complexity and NDVI remained fairly consistent between edge farms and between survey years (Table 3.7). There were no significant differences in Pielou's evenness, habitat complexity or NDVI between survey years within a specific farm type (Table 3.8) or between farm types within a specific year (Table 3.9). Coefficients of variation were consistently high for some variables (H' and J') for all farm types and surveys (Table 3.7). The CV values were high for effective number of PFGs among core farms in 2019 and for habitat complexity among control farms in 2017 (Table 3.9).

Table 3.7: Vegetation diversity measures averaged (± standard error) for each farm type during two different surveys, 2017 (before sheep removed) and 2019 (after sheep were removed) Diversity values include alpha diversity (observed PFG richness), effective number of species (e^H), Shannon-Wiener diversity index (H'), Pielou's evenness (J'), habitat complexity (Hab. comp) and NDVI. Coefficient of variation (CV = sd/mean) indicated by [ ] and italicised. CV ≥ 0.3 indicates a relatively high variation and is highlighted in bold.

Survey	**Site**	**Alpha diversity**	**e^H**	**H'**	**J'**	**Hab. Comp**	**NDVI**
2017	Core	4	1.61 (± 0.26)	0.44 (± 0.18)	0.37 (± 0.13)	1.10 (± 0.08)	0.12 (± 0.005)
			[0.28]	***[0.71]***	***[0.61]***	*[0.13]*	*[0.08]*
	Edge	3	1.18 (± 0.08)	0.16 (± 0.06)	0.18 (± 0.04)	0.88 (± 0.08)	0.12 (± 0.002)
			[0.11]	***[0.69]***	***[0.46]***	*[0.16]*	*[0.03]*
	Control	2	1.18 (± 0.12)	0.15 (± 0.09)	0.22 (± 0.13)	0.63 (± 0.27)	0.09 (± 0.01)
			[0.17]	***[1.07]***	***[1.07]***	***[0.76]***	*[0.18]*
2019	Core	5	1.96 (± 0.50)	0.60 (± 0.27)	0.42 (± 0.15)	1.00 (± 0.16)	0.12 (± 0.005)
			[0.44]	***[0.80]***	***[0.63]***	*[0.29]*	*[0.08]*
	Edge	3	1.36 (± 0.21)	0.28 (± 0.15)	0.25 (± 0.14)	0.85 (± 0.10)	0.12 (± 0.007)
			[0.27]	***[0.96]***	***[0.96]***	*[0.22]*	*[0.11]*
	Control	3	1.21 (± 0.13)	0.18 (± 0.10)	0.23 (± 0.15)	0.83 (± 0.06)	0.10 (± 0.008)
			[0.19]	***[1.02]***	***[1.19]***	*[0.14]*	*[0.15]*

Table 3.8: Summary statistics for post-hoc Tukey tests comparing effective number of PFGs (e^H), Shannon-Wiener diversity index (H'), Pielou's evenness (J') and habitat complexity (Hab. comp) within each farm type (core, edge and control) between 2017 (before cessation of farming activities on core farms) and 2019 (after cessation of farming activities on core farms). 'Est.' indicates model output estimate with standard error.

Comparison	Farm Type	Variable	Est. (± SE)	z value	p.adjust
2019 vs. 2017	***Core***	e^H	0.58 (0.60)	0.97	0.92
		H'	0.07 (0.14)	0.55	0.99
		J'	0.005 (0.12)	0.04	1.00
		Hab. comp	-0.12 (0.18)	-0.65	0.98
	Edge	e^H	0.00 (0.54)	0.00	1.00
		H'	0.12 (0.12)	0.97	0.91
		J'	0.07 (0.11)	0.64	0.98
		Hab. comp	-0.02 (0.17)	-0.17	1.00
	Control	e^H	0.00 (0.54)	0.00	1.00
		H'	0.02 (012)	0.22	1.00
		J'	0.008 (0.11)	0.07	1.00
		Hab. comp	0.20 (0.17)	1.17	0.84

Table 3.9: Summary statistics post-hoc Tukey tests comparing effective number of PFGs (e^H), Shannon-Wiener diversity index (H'), Pielou's evenness (J') and habitat complexity (Hab. comp) between farm types (core, edge and control) within 2017 (before cessation of farming activities on core farms) and 2019 (after cessation of farming activities on core farms). 'Est.' indicates model output estimate with standard error.

Survey	Variable	Comparison	Est. (± SE)	z value	p.adjust
2017	***e^H***	Core – Control	1.22 (0.81)	1.50	0.64
		Edge - Control	0.33 (0.82)	0.40	0.99
		Edge - Core	-0.88 (0.81)	-1.09	0.87
	H'	Core – Control	0.39 (0.22)	1.71	0.48
		Edge - Control	0.007 (0.23)	0.03	1.00
		Edge - Core	-0.38 (0.22)	-1.67	0.50
	J'	Core – Control	0.20 (0.18)	1.09	0.87
		Edge - Control	-0.03 (0.18)	-0.20	1.00
		Edge - Core	-0.24 (0.18)	-1.30	0.76
	Hab. comp	Core – Control	0.50 (0.21)	2.37	0.16
		Edge - Control	0.25 (0.21)	1.20	0.83
		Edge - Core	-0.24 (0.21)	-1.16	0.84
2019	***e^H***	Core – Control	1.81 (0.81)	2.23	0.20
		Edge - Control	0.33 (0.82)	0.40	0.99
		Edge - Core	-1.47 (0.81)	-1.82	0.42
	H'	Core – Control	0.44 (0.22)	1.93	0.34
		Edge - Control	0.10 (0.23)	0.42	0.99
		Edge - Core	-0.34 (0.22)	-1.49	0.63
	J'	Core – Control	0.19 (0.18)	1.07	0.88
		Edge - Control	0.02 (0.18)	0.14	1.00
		Edge - Core	-0.17 (0.18)	-0.93	0.93
	Hab. comp	Core – Control	0.17 (0.21)	0.82	0.96
		Edge - Control	0.01 (0.21)	0.08	1.00
		Edge - Core	-0.15 (0.21)	-0.73	0.97

Small mammals on core, edge and control farms

Trapping over 7 046 nights in 2017 resulted in 325 captures of 222 individuals giving a trapping success of 4.61%, while 6 924 trap nights in 2019 resulted in 258 captures of 256 individuals giving a trapping success of 3.72% (Table 3.10). The same five morphotaxa were caught on all farm types during both the 2017 and 2019 surveys (Table 3.11), namely, *Gerbilliscus paeba* (hairy-footed gerbil), *Desmodillus auricularis* (short-tailed gerbil), *Rhabdomys pumilio* (four-striped field mouse), *Micaelamys* spp. (rock rat spp.) and Macroscelididae spp. (rock sengi spp.). It was difficult to accurately assign individuals of *Micaelamys* spp. and Macroscelididae spp. to species level due to the presence of cryptic species in these taxa. Genetic data obtained during the 2017 survey (see Methods) showed that within the subset of individuals sampled from these two groups there were five distinct species (*Micaelamys namaquensis*, *Micaelamys granti*, *Macroscelides proboscideus*, *Elephantulus rupestris* and *Elephantulus pilicaudus*), but not all samples could be amplified and sequenced using the 2 mtDNA markers used (see Main *et al*. 2019). As a result, all captures of the *Micaelamys* species were classified to genus level and all captures of the Macroscelididae species were classified to family level.

Of the 55 samples collected in 2017 that were sent for genetic analyses, only 38 (69 %) could be amplified and sequenced (Control Region and Cytochrome-b) to species level (Main *et al.* 2019). Plans for genetic processing of 2019 samples were prevented by Covid-19 lockdowns and laboratory closures. Consequently, all analyses hereafter refer to field morphotaxa identifications. Of the 24 Macroscelididae specimens collected, only 2 *Elephantulus* spp. were identified through genetic analysis, namely *E. rupestris* and *E. pilicaudus* (App 3.8) but both were rarely sampled. Cryptic differences between these species may have resulted in underestimation of the cryptic diversity of *Elephantulus* species. While morphotaxon field identifications may underestimate the cryptic diversity of *Elephantulus* spp. and *Micaelamys granti*, this is unlikely to have significantly influenced results as these taxa were present but scarce on all farm types (App 3.8).

Recapture rates were similar across surveys (0.32 in 2017 and 0.22 in 2019), with no significant change between farm types within a specific year (Table 3.12). There was a significant decrease in recapture rates between the two surveys carried out on the core farms (0.38 in 2017 and 0.12 in 2019) (Table 3.10 and 3.12). Trapping success between farms types in 2017 ranged between 1.6 % and 5.4% but did not differ significantly (Table 3.12). Trapping success was significantly different between core (5.13 ± 1.18) and control (1.39 ± 0.30) farms during the 2017 survey (t = 3.07, df = 4, p = 0.03) (Table 3.12). Trapping success in 2019 was not significantly different from 2017, ranging from 3.01% to 5.8%, but there was a slight (albeit non-significant) increase in trap success on control farms between 2017 and 2019 (Table 3.10).

During the 2017 survey, trapping success on core and control farms was the lowest in the plain habitats (3.56% and 0.46% respectively), while on edge farms trapping success was lowest in river habitats (3.85%) (Table 3.11). Trapping success was highest in rock habitats for both core and control farm (5.26% and 3.91% respectively), while edge farms saw the highest trapping success in plain habitats (5.08%) (Table 3.11). Overall, there was no significant difference between the average number of captures between 2017 (108 ± 60.2) and 2019 (104 ± 40.4) (t = -1.3, df = 2, p = 0.99) (Table 3.10).

Table 3.10: Summary table comparing results of small mammal trapping in three different farm types (core, edge and control) over two different survey years (2017 and 2019). Values in bold indicate totals within each farm type in each year, while values in bold italics indicated averages (± standard error) for each farm type. Coefficient of variation (CV = sd/mean) indicated by [ ] and italicised. CV ≥ 0.3 indicates a relatively high variation and is highlighted in bold.

Treatment/ Site	**Number of captures (incl. recaptures)**		**Number of recaptures**		**Number of individuals /1000 trap nights** (excl. recaptures)		**Recapture rate**		**Trapping success (%)**	
	2017	*2019*	*2017*	*2019*	*2017*	*2019*	*2017*	*2019*	*2017*	*2019*
Core	**154**	**151**	**58**	**19**	***32.9 (± 5.97)*** *[0.21]*	***49.8 (± 15.2)*** ***[0.55]***	***0.35 (±0.06)*** *[0.29]*	***0.15 (±0.05)*** ***[0.64]***	***5.13 (± 1.18)*** ***[0.39]***	***5.24 (± 1.47)*** ***[0.48]***
Janseboom	33	75	8	7	21.18	76.40	0.24	0.09	2.79	7.81
Jas Kloof	63	50	24	5	40.62	49.50	0.38	0.10	6.56	5.20
Lovedale	58	26	26	7	36.99	23.63	0.45	0.27	6.04	2.70
Edge	**131**	**81**	**32**	**19**	***38.1 (± 12.2)*** ***[0.58]***	***23.05 (± 5.83)*** ***[0.43]***	***0.21 (±0.04)*** ***[0.35]***	***0.18 (±0.09)*** ***[0.85]***	***4.66 (± 1.82)*** ***[0.67]***	***2.81 (± 0.98)*** ***[0.60]***
Hondeblaf	76	23	21	1	62.35	24.17	0.28	0.04	8.26	2.39
Rietpoort	23	45	3	16	24.15	32.51	0.13	0.35	2.39	4.68
Gannabos	32	13	8	2	27.90	12.40	0.25	0.15	3.33	1.35
Control	**40**	**81**	**13**	**19**	***10.81 (± 1.38)*** *[0.22]*	***24.89 (± 11.4)*** ***[0.79]***	***0.30 (±0.06)*** ***[0.39]***	***0.19 (±0.11)*** ***[1.00]***	***1.39 (± 0.30)*** ***[0.37]***	***2.81 (± 1.23)*** ***[0.75]***
Hoezar-Wes	19	26	8	10	13.25	19.58	0.42	0.38	1.99	2.70
Leeuwkrans	10	48	3	9	8.48	46.70	0.300	0.187	1.04	5.00
Skurwekloof	11	7	2	0	10.58	8.35	0.181	0.00	1.14	0.72
Total ***(mean ± SE)***	**325** ***(108 ± 60.2)***	**258** ***(104 ± 40.4)***	**103** ***(34.3 ± 22.5)***	**57** ***(19 ± 0)***	**31.50** ***(27.6 ± 14.7)***	**29.02** ***(32.8 ± 15.4)***	**0.32** ***(0.31 ± 0.06)***	**0.22** ***(0.19 ± 0.06)***	**4.61** ***(4.02 ± 2.1)***	**3.72** ***(4.02 ± 1.5)***

Table 3.11: Summary results of the number of small mammal individuals captured per taxon (excluding recaptures, hereafter referred to MNA = Minimum Number Alive) and per habitat in three farm types (core, edge and control) over two survey years (2017 and 2019). Overall trapping success per habitat and per farm type in each survey year indicated in bold. Individuals captured was standardised per 300 trap nights per habitat type and standardised per 1000 trap nights for total captures in each farm type to account for slight variations in sampling effort.

Survey	**Taxa**	**Core**				**Edge**				**Control**			
		Rock	*River*	*Plain*	*Total*	*Rock*	*River*	*Plain*	*Total*	*Rock*	*River*	*Plain*	*Total*
2017	**Rodentia** *Gerbilliscus paeba*	5.13	34.21	15.25	34.03	8.82	21.88	33.33	35.63	1.40	6.48	4.65	5.60
	Desmodillus auricularis	0	3.51	0.85	2.80	1.47	2.08	0	1.93	6.98	2.78	0	2.00
	Micaelamys spp.	24.36	1.75	0	11.57	22.06	0	0.83	8.13	15.36	0	0	8.01
	Rhabdomys pumilio	0	0	0	0	0	6.25	0	2.32	0	0	0	0
	Macroscelididae spp.	2.56	2.63	3.39	5.61	7.35	1.04	0.83	2.71	1.40	0	0	0.40
	Trapping success	**5.26**	**6.23**	**3.56**	**5.40**	**4.85**	**3.85**	**5.08**	**5.07**	**3.91**	**1.20**	**0.46**	**1.60**
2019	**Rodentia** *Gerbilliscus paeba*	12.50	36.11	43.52	41.87	2.78	8.33	30.83	23.42	6.94	16.67	13.89	22.08
	Desmodillus auricularis	1.39	10.19	0.93	6.91	5.56	0	2.50	2.97	4.17	6.48	0.93	5.22
	Micaelamys spp.	18.06	2.78	0.93	6.53	5.56	0	0	2.23	6.94	0	1.85	3.21
	Rhabdomys pumilio	0	0.93	0	0.38	0	0	1.67	0.74	0	0	0	0
	Macroscelididae spp.	2.78	1.85	1.85	2.30	2.78	0	0	0.74	2.78	0	2.78	2.01
	Trapping success	**3.61**	**6.11**	**5.46**	**5.80**	**1.94**	**0.83**	**4.92**	**3.01**	**2.92**	**2.69**	**2.87**	**3.25**

Table 3.12: Summary statistics for unpaired and paired t-tests comparing both trapping success and recapture rate of small mammal communities between three farm types (core, edge and control) within each survey year, and within each farm type over two survey years (2017 and 2019). Significant p-values are indicated by an asterisk.

Survey	**Site**	**Trapping success**			**Recapture rate**		
		t	*df*	*p*	*t*	*df*	*p*
2017	C - E	0.21	4	0.83	1.83	4	0.14
	C - Con	3.07	4	0.03*	0.61	4	0.57
	E - Con	1.77	4	0.15	-0.99	4	0.37
2019	C - E	1.37	4	0.24	-0.27	4	0.79
	C - Con	1.26	4	0.27	-0.29	4	0.78
	E - Con	0	4	1	-0.04	4	0.96
2017 vs. 2019	Core	-0.04	2	0.96	5.08	2	0.03*
	Edge	0.78	2	0.51	0.25	2	0.82
	Control	-1.08	2	0.39	2.62	2	0.11

Taxonomic diversity and inventory completeness

When plotted against sampling effort (cumulative number of individuals caught), observed taxon richness (S_{taxa}) on both control and core farms reached an asymptote in 2017, whereas on edge farms the curve did not, suggesting that sampling effort was inadequate to detect the full set of taxa present (Figure 3.8). In contrast, (S_{taxa}) curves for all three farm types in 2019 were asymptotic suggesting that sampling effort was sufficient to accurately represent the taxonomic diversity of resident small mammals (Figure 3.8). Chao 1 rarefaction curves, indicating that predicted taxa richness (taking rare taxa into account) on all three farm types reached asymptotes in both years (Figure 3.9 A and B). Chao 1 95% CI limits overlapped with S_{taxa} indicating no significant difference between S_{taxa} and predicted taxonomic richness across farm types or between years (Cumming 2008).

Figure 3.8: Taxa incidence (S_{taxa}) of small mammals captured on three farm types (core, edge and control) during two survey years (2017, before sheep were removed for any farm and 2019, after sheep are removed from core farms).

When plotted against cumulative number of individuals, small mammal taxonomic diversity (S_{taxa}) on all three farms reached an asymptote in both 2017 (Figure 3.9C) and 2019 (Figure 3.9D). Effective number of taxa (e^H) and Shannon-Weiner diversity followed a similar pattern to the rarefaction curves. Effective number of taxa ranged between 3 (± 0.57) and 4 (± 0.57) in both 2017 and 2019 (Table 3.13). During the 2017 survey e^H was greatest on edge farms, while in 2019 e^H was greatest on core farms (Table 3.13), but there were no significant differences in e^H among farm types in either survey year, or within farm types between 2017 and 2019 (Table 3.14 and 3.15).

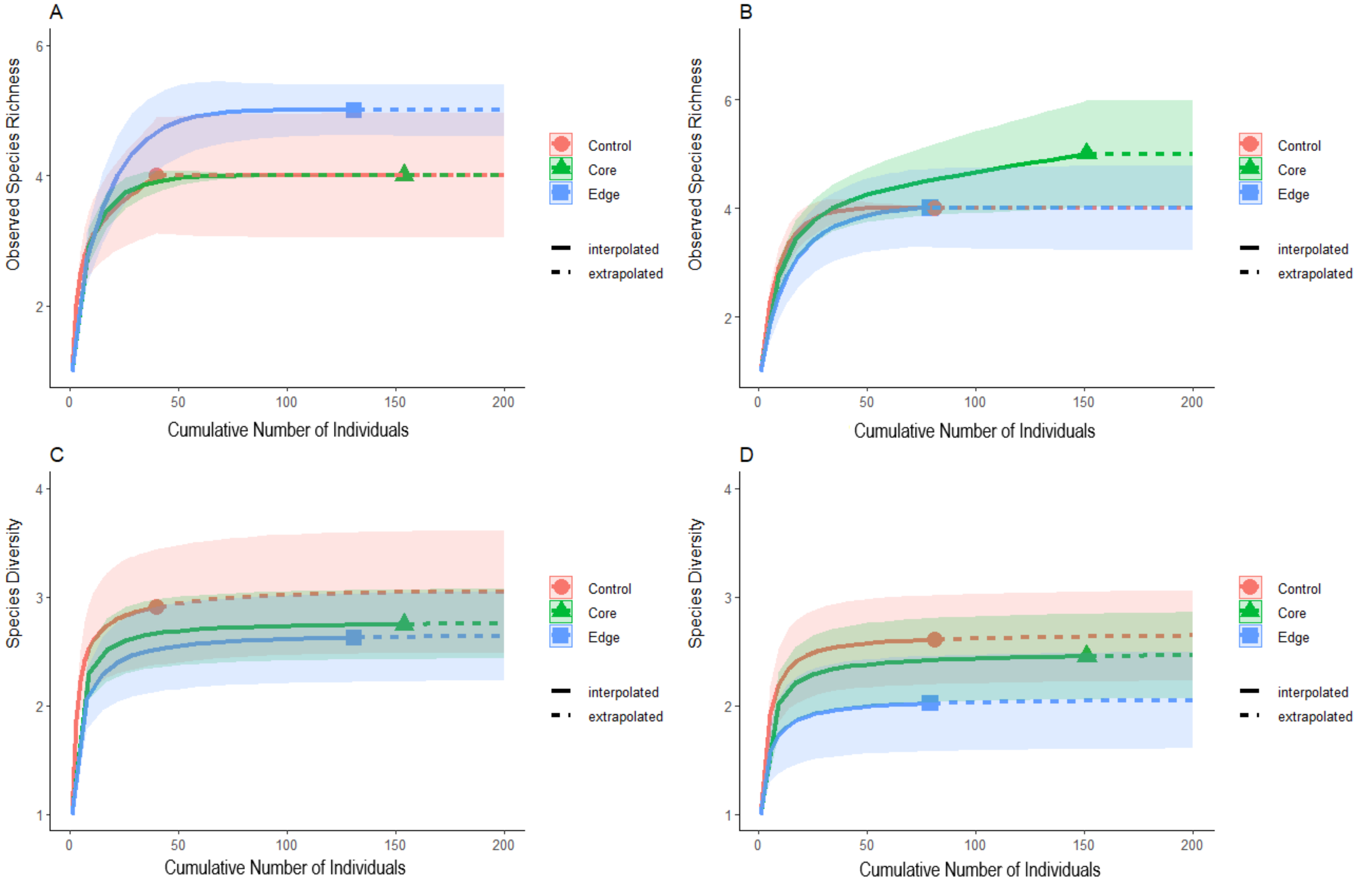


Figure 3.9: Chao 1 taxa rarefaction curves (A and B) and Shannon-Wiener taxon diversity curves (C and D) for small mammal taxa captured on three farm types (core, edge and control) over two survey years (A and C = 2017, B and D = 2019). Solid lines represent observed richness and diversity, while dotted line represent Chao 1 expected richness and diversity. Shaded polygons indicate 95% confidence intervals.

Shannon-Wiener taxon diversity (H') ranged between 0.86 (± 0.07) and 0.97 (± 0.17) in 2017, while in 2019 diversity ranged between 0.68 (± 0.14) and 0.82 (± 0.18) (Table 3.13). Overall, there was a lower diversity of small mammals in 2017 compared to 2019 (Table 3.13), but there were no significant differences in any diversity variables between survey years (App 3.2) or among farm types (Table 3.15). Pielou evenness (J') values were highest on control farms during 2017 (0.93 ± 0.03), suggesting a fairly even spread of individuals across taxa (low dominance) and was lowest on edge farms (0.65 ± 0.12) suggesting greater dominance by a few taxa (Table 3.13). A similar pattern was evident during 2019, when evenness values were highest on control farms (0.77 ± 0.07) and lowest on core farms (0.59 ± 0.13), however in this case the lowest evenness values (therefore higher dominance) was seen on edge farms (0.57 ± 0.13) not core farms (Table 3.13). Small mammal morphotaxa spread was not significantly different between survey years (Table 3.14) or between farm types within a specific year (Table 3.15).

Table 3.13: Small mammal diversity measures averaged (± standard error) for each farm type during two different surveys, 2017 (before any sheep were removed from farms) and 2019 (after sheep were removed from core farms). Diversity values include alpha diversity (observed number of taxa), Chao 1 estimates, effective number of taxa (e^H), Shannon-Wiener taxon diversity index (H'), Pielou's evenness (J'), and % inventory (taxonomic) completeness (S_{taxa}/Chao1*100).

Survey	Site	Alpha diversity	Chao 1 (± SE)	e^H (± SE)	Shannon diversity (H') (± SE)	Pielou's evenness (J') (± SE)	% Inventory (taxonomic) completeness
2017	Core	4	4 (± 0)	3.33 (± 0.33)	0.91 (± 0.13)	0.76 (± 0.11)	100
	Edge	5	5 (± 0)	4 (± 0.57)	0.86 (± 0.07)	0.65 (± 0.12)	100
	Control	4	4 (± 0.43)	3 (± 0.57)	0.97 (± 0.17)	0.93 (± 0.03)	100
2019	Core	5	5 (± 0.44)	4 (± 0.57)	0.82 (± 0.18)	0.59 (± 0.13)	100
	Edge	5	5 (± 0)	3.33 (± 0.33)	0.68 (± 0.14)	0.57 (± 0.13)	100
	Control	4	4 (± 0)	3 (± 0.57)	0.81 (± 0.14)	0.77 (± 0.07)	100

Table 3.14: Summary statistics for post-hoc Tukey tests comparing effective number of small mammal taxa (e^H), Shannon-Wiener taxon diversity index (SWI), and Pielou's evenness within each farm type (core, edge and control) between 2017 (before cessation of farming activities on core farms) and 2019 (after cessation of farming activities on core farms). 'Est.' indicates model output estimate with standard error.

Comparison	Farm Type	Variable	Est. (± SE)	z value	p.adjust
2019 vs. 2017	***Core***	e^H	0.66 (0.43)	1.54	0.61
		H'	-0.09 (0.20)	-0.46	0.99
		J'	-0.17 (0.15)	-1.16	0.85
	Edge	e^H	-0.66 (0.43)	-1.54	0.61
		H'	-0.18 (0.20)	-0.87	0.95
		J'	-0.08 (0.15)	-0.53	0.99
	Control	e^H	0.00 (0.43)	0.00	1.00
		H'	-0.16 (0.20)	-0.79	0.96
		J'	-0.15 (0.15)	-0.99	0.92

Table 3.15: Summary statistics for post-hoc Tukey tests comparing effective number of small mammal taxa (e^H), Shannon-Wiener taxon diversity index (SWI), and Pielou's evenness between farm types (core, edge and control) within 2017 (before cessation of farming activities on core farms) and 2019 (after cessation of farming activities on core farms). 'Est.' indicates model output estimate with standard error.

Survey	Variable	Comparison	Est. (± SE)	z value	p.adjust
2017	***e^H***	Core – Control	0.33 (0.63)	0.52	0.99
		Edge - Control	1.00 (0.63)	1.56	0.60
		Edge - Core	0.66 (0.63)	1.04	0.89
	H'	Core – Control	-0.06 (0.20)	-0.29	1.00
		Edge - Control	-0.11 (0.20)	-0.53	0.99
		Edge - Core	-0.04 (0.20)	-0.24	1.00
	J'	Core – Control	-0.16 (0.15)	-1.06	0.89
		Edge - Control	-0.27 (0.15)	-1.79	0.46
		Edge - Core	-0.11 (0.15)	-0.73	0.97
2019	***e^H***	Core – Control	1.00 (0.63)	1.56	0.60
		Edge - Control	0.33 (0.63)	0.52	0.99
		Edge - Core	-0.66 (0.63)	-1.04	0.89
	H'	Core – Control	0.007 (0.20)	0.03	1.00
		Edge - Control	-0.12 (0.20)	-0.61	0.99
		Edge - Core	-0.13 (0.20)	-0.65	0.98
	J'	Core – Control	-0.18 (0.15)	-1.23	0.81
		Edge - Control	-0.20 (0.15)	-1.33	0.76
		Edge - Core	-0.08 (0.15)	-0.53	0.99

Spatiotemporal trends in small mammal abundances

The minimum number alive (MNA) per 1000 trap nights, or total relative abundance of small mammals, did not differ significantly between 2017 and 2019 for all farm types (Figure 3.10 and Table 3.16). For core and control farms, mean MNA increased slightly between 2017 and 2019, and decreased on edge farms (Figure 3.10). During the 2017 survey mean MNA was not significantly different between any farm types (Figure 3.10 and Table 3.16). Relative abundance was highest on edge farms during 2017, in contrast to 2019 when the highest mean relative abundance was on core farms (Figure 3.10). There were no significant different in mean MNA between the three farms type during the 2019 survey (Figure 3.10 and Table 3.16).

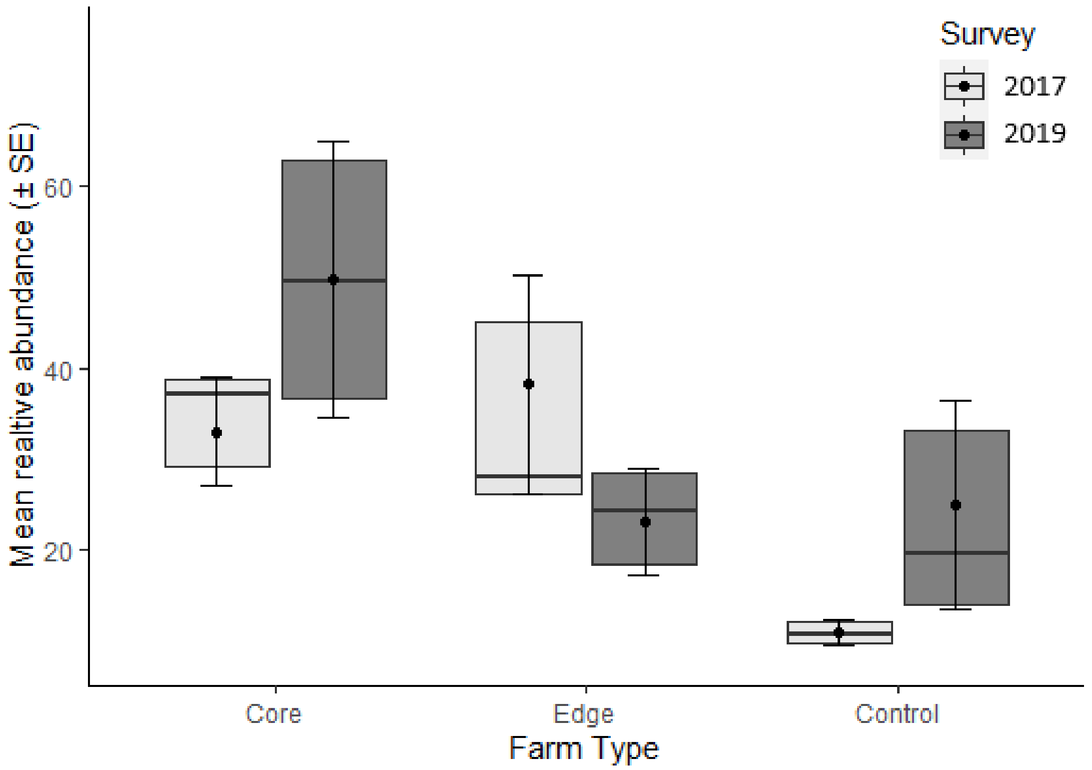


Figure 3.10: Boxplots representing small mammal mean relative abundances (per 1000 trap nights) for three farm types (core, edge and control) between two survey years (2017 survey, before cessation of farming activities on core farms, 2019 survey, after cessation of farming activities on core farms). Shaded boxes indicate lower quartile, median (thick black line) and upper quartile for relative abundance, while black dot indicates mean relative abundance with error bars representing standard error.

Table 3.16: Summary statistics for post-hoc Tukey tests comparing both relative abundance (per 1000 trap nights) and overall standing biomass (g) of small mammal communities between three farm types (core, edge and control) within a survey year, and within a farm type between two survey years (2017, before sheep were removed and 2019, after sheep were removed from core farms). 'Est.' indicates model output estimate with standard error.

Survey	**Site**	**Abundance (MNA)**			**Standing Biomass (g)**		
		Est. (± SE)	*z*	*p.adjust*	*Est. (± SE)*	*z*	*p.adjust*
2017	Core – Control	22.16 (13.91)	1.59	0.40	783.97 (469.74)	1.66	0.55
	Edge – Control	27.36 (13.91)	1.96	0.36	933.33 (469.74)	1.98	0.34
	Edge - Core	5.20 (13.91)	0.37	0.99	149.36 (469.74)	0.31	0.99
2019	Core – Control	24.96 (13.91)	1.79	0.46	1084.74 (469.74)	2.30	0.19
	Edge – Control	-1.85 (13.91)	-0.13	1.00	-11.46 (469.74)	-0.02	1.00
	Edge - Core	-26.81 (13.91)	-1.92	0.38	-1096.19 (469.74)	-2.33	0.18
2017 vs. 2019	Core	16.91 (13.91)	1.21	0.82	838.72 (469.74)	1.78	0.47
	Edge	-15.11 (13.91)	-1.08	0.88	-406.84 (469.74)	-0.86	0.95
	Control	14.10 (13.91)	1.01	0.91	537.95 (469.74)	1.14	0.86

During the 2017 survey, *G. paeba* MNA was the highest of all taxa on all farm types, followed by *D. auricularis* (Figure 3.11). *R. pumilio* was only caught on a single edge farm (Figure 3.11 *Edge 2017*). *G. paeba* and *D. auricularis* were the numerically predominant rodent species in river and plain habitats, while *Micaelamys* spp. and Macroscelididae spp. were mostly found in rock habitats (Figure 3.11).

During the 2019 survey there was a slight shift in taxa composition per habitat compared to 2017. *G. paeba* and *D. auricularis* still dominated river and plain habitats, however *D. auricularis* MNA increased in rock habitats for both core (LMER est. = 0.33 ± 0.33, z = 1, p.adjust = 0.31) and edge farms (LMER est. = 0.61 ± 0.48, z = 1.28, p.adjust = 0.19), but decreased on control farms (LMER est. = -1.00 ± 0.57, z = -1.73, p.adjust = 0.08) (Figure 3.11). *R. pumilio* was caught on both core and edge farms in 2019, but in slightly lower numbers on edge farms compared to the 2017 survey (Figure 3.11). The majority of *Micaelamys* spp. and Macroscelididae spp. individuals were captured in rock habitats for all farm types, while on core farms there was an increase in *Micaelamys* spp. MNA in river (LMER est. = 0.55 ± 1.09, z = 0.50, p.adjust = 0.61) and plain habitats (LMER est. = 0.16 ± 0.16, z = 1, p.adjust = 0.31). Macroscelididae spp. MNA decreased in these habitats in 2019 compared to 2017 (LMER est. = -0.05 ± 0.42, z = -0.13, p.adjust = 0.89 and LMER est. = -0.16 ± 0.53, z = -0.30, p.adjust = 0.76 respectively) (Figure 3.11). On edge farms both *Micaelamys* spp. and Macroscelididae spp. MNA decreased in all habitat types from 2017-2019, however on control farms *Micaelamys* spp. decreased on rock (LMER est. = -1.68 ± 1.76, z = -0.95, p.adjust = 0.33), while Macroscelididae spp. increased in rock (LMER est. = 0.43 ± 0.42, z = 1.03, p.adjust = 0.30) (Figure 3.11).

MNA for small mammal taxa was highest on core 2 during 2017 and core 1 during 2019, while on edge farms overall MNA was highest on edge 1 during 2017 and edge 2 during 2019 (App 3.9). During 2017 overall MNA for control farms was highest on control 1 but during 2019 highest MNA was on control 2 (App 3.9). For both 2017 and 2019 total MNA for all small mammal taxa was highly variable between individual farms within a specific farm type (App 3.9).

Standing biomass of small mammal taxa followed a similar pattern to relative abundance. There was no significant difference in total standing biomass between survey years (Table 3.16 and App 3.10, Figure 3.12). In 2017, total standing biomass was not significantly different between core and edge farms but differed significantly between core and control farms (t = 3.24, df = 4, p = 0.03) (Table 3.16 and App 3.10). During the 2019 survey, there were no significant differences in standing biomass among the different farm types (Table 3.16 and App 3.10). In both survey years *G. paeda* accounted for most total and average standing biomass on core and edge farms, as well as the highest total and average standing biomass on control farms in 2019 (Figure 3.12 and App 3.10). During the 2017 survey, *Micaelamys* spp. accounted for most total and average standing biomass on control farms (Figure 3.12 and App 3.10).

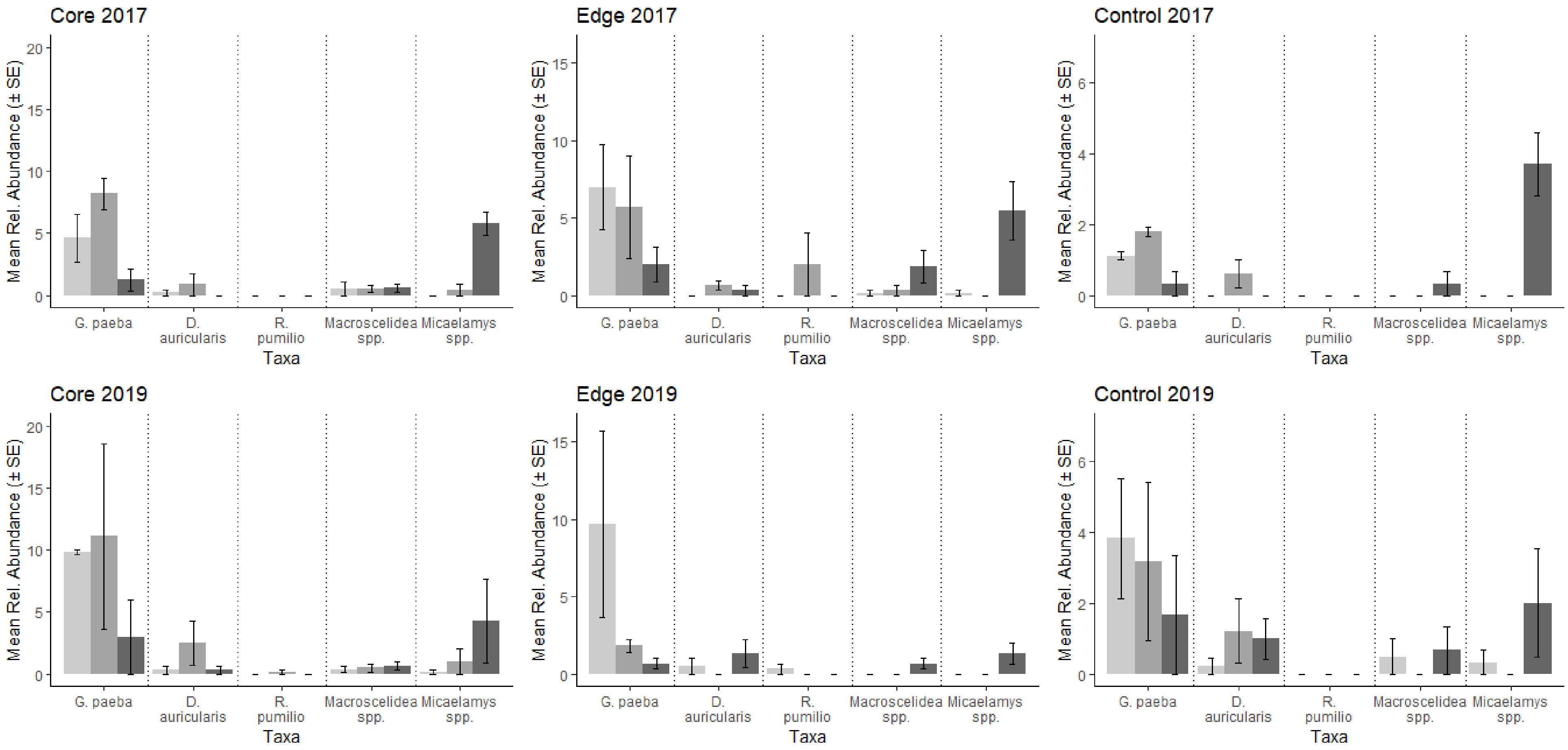


Figure 3.11: Comparison of small mammal mean relative abundance per taxon in three habitat types (plain = light grey, river = medium grey and rock = dark grey) across three farm types (core, edge and control) over two survey years. Error bars represent standard errors. Relative abundance was standardised per 300 trap nights for each habitat and pooled across farm type to account for slight variations in sampling effort.

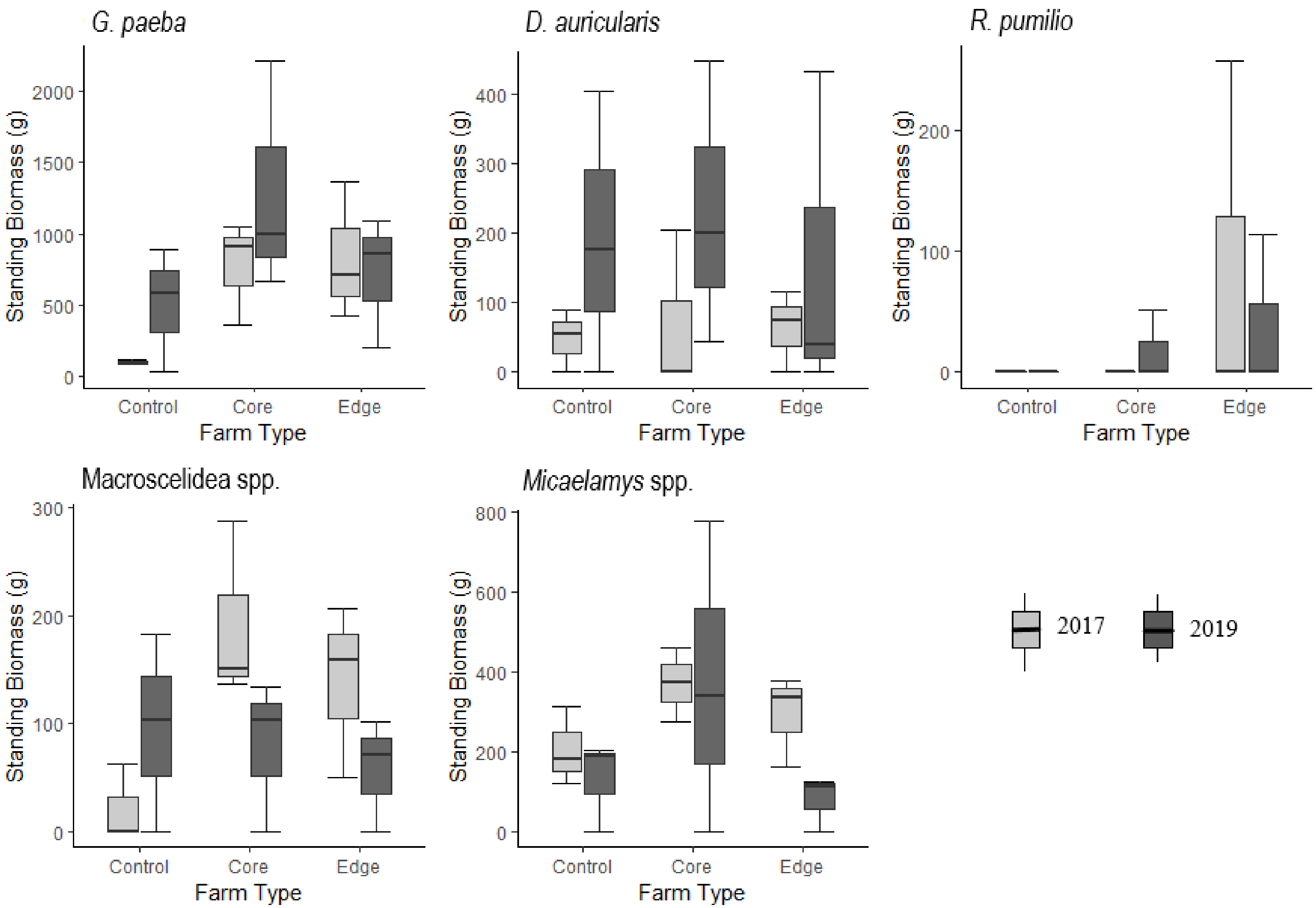


Figure 3.12: Total standing biomass (g) of small mammal taxa captured across three farm types (core, edge and control) during two surveys years. Light grey bars represent 2017 surveys, and dark grey bars represent 2019 surveys. Standing biomass was standardised per 1000 trap nights. Shaded boxes indicate lower quartile, median (thick black line) and upper quartile for standing biomass with error bars representing standard error. Note different y-axis scales.

Multivariate analyses of abundance trends

Small mammals

Multivariate GLMs showed there was no significant effects of survey year (p = 0.17), farm type (p = 0.11) or sheep presence/absence (p = 0.74) on small mammal abundances (minimum number alive, MNA) per farm (Table 3.17). There were, however, significant effects on small mammal abundances (per farm and per habitat) resulting from changes in habitat (p = 0.001), shrub (0.5 < 1m) cover (p = 0.02) and shrub (1.5 < 2m) basal cover (p = 0.03) (Table 3.17). Multivariate GLMs focusing on vegetation parameters revealed a significant effect of farm type (p = 0.02) and habitat (p = 0.006), but not of survey year (p = 0.15) on vegetation cover (Table 3.17).

Table 3.17: ANOVA table summarising statistical significance of the most parsimonious multivariate GLMs for small mammal taxon abundances and plant functional group abundances (vegetation cover). *p* values were calculated using 999 resampling. $*p \leq 0.05$; $**p \leq 0.001$.

Response variable	Covariable	Res.Df	Df.diff	Val (Dev)	Pr (> F)
Small mammal abundance (per farm)	Survey	16	1	8.62	0.17
	Farm type	14	2	18.31	0.11
	Sheep presence	13	1	3.23	0.74
Small mammal abundance (per farm and habitat)	Survey	52	1	7.12	0.25
	Farm type	50	2	17.24	0.08
	Sheep presence	49	1	1.95	0.77
	Habitat	51	2	66.58	0.001**
	NDVI	50	1	8.64	0.16
	Vegetation cover	49	1	9.66	0.17
	Rock cover	48	1	8.74	0.12
	Shrub (> 0.5m) cover	47	1	3.85	0.64
	Shrub (0.5 < 1m) cover	46	1	16.80	0.02*
	Shrub (1.5 < 2m) basal cover	45	1	14.02	0.03*
Vegetation cover (per farm and habitat)	Survey	52	1	8.98	0.15
	Farm type	50	2	23.31	0.02*
	Habitat	48	2	29.98	0.006**

Multivariate GLMs identified small mammal abundance (MNA per farm and habitat), across all farm types and surveys, as significantly associated with habitat, shrub cover and shrub basal cover (Table 3.18). Univariate statistics for specific taxa indicated that habitat had a significant effect on the abundances of *Gerbilliscus paeda* (p = 0.01) and *Micaelamys* spp. (p = 0.001).

Shrub (0.5 < 1m) cover had a significant effect on the abundance of *Rhabdomys pumilio*, while shrub (1.5 < 2m) basal cover had a significant effect on abundance of *Desmodillus auricularis* (p = 0.04) (Table 3.18). No other taxa showed significant changes in abundance according to specific covariates (Table 3.18).

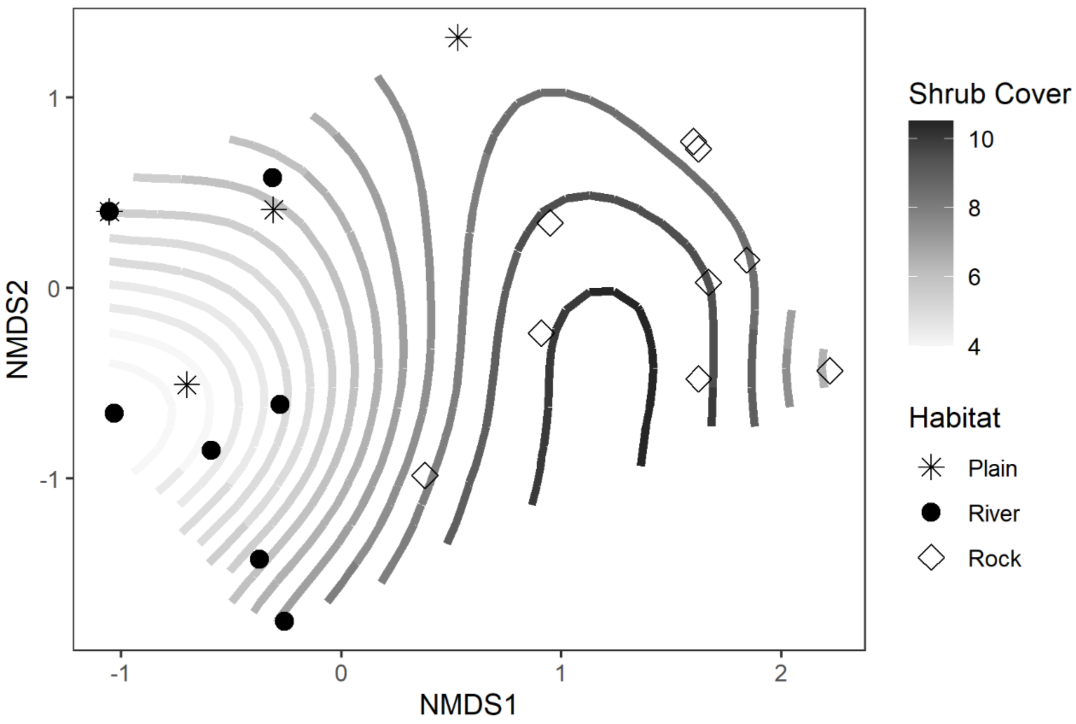
Table 3.18: Univariate statistic from multivariate GLMs for small mammal abundances (MNA) showing which specific taxa significantly influenced changes in overall abundance between different significant covariates (habitat, shrub (0.5 < 1m) cover and shrub (1.5 < 2m) basal cover). Dev = deviance explained by each taxon. $^*p \leq 0.05$; $^{**}p \leq 0.001$.

Taxa	**Habitat**		**Shrub (0.5 < 1m) cover**		**Shrub (1.5 < 2m) basal cover**	
	Dev	*p*	*Dev*	*p*	*Dev*	*p*
Macroscelididae spp.	7.38	0.09	1.19	0.76	0.48	0.75
Rhabdomys pumilio	3.67	0.21	12.81	0.009**	0	0.75
Gerbilliscus paeba	13.13	0.01*	1.26	0.76	0.62	0.75
Micaelamys spp.	36.23	0.001**	1.23	0.76	4.55	0.16
Desmodillus auricularis	6.15	0.11	0.28	0.76	8.35	0.04*

nMDS ordination plots showed significant clustering of small mammal taxa within different habitat types (Figure 3.13). Contours represent a gradient in shrub density with dark grey lines indicating high shrub cover and light grey lines indicating low shrub cover (Figure 3.13). In 2017, there was strong clustering of communities in rock habitats compared to plain and river habitats (Figure 3.13). The was a strong separation of small mammal communities along a shrub (1.5 < 2 m) cover gradient with shrub density increasing within rock habitats (Figure 3.13). There was a similar pattern of clustering in the 2019 plot, however separation of small mammal communities was not as strong as in 2017 (Figure 3.13). Strong clustering of small mammal communities was still evident for rock habitats, where there was a higher shrub density, but there was little visible clustering in plain and river habitats (Figure 3.13).

Hierarchal clustering analysis of small mammal abundances in 2017 (see Table 3.17) showed significant grouping of control sites (Control 1, 2 and 3) which separated from other farm types at the ~50% similarity level in 2017 (Figure 3.14A). There was no clear pattern of clustering among core and edge farms, although core farm 1 (south-east farm) and edge farm 2 (south-west farm) grouped with control sites rather than other core and edge sites (Figure 3.14A). During 2019 there was no strong clustering of any farm type, with core, edge and control sites displaying no discernible grouping pattern (Figure 3.14B).

2017



2019

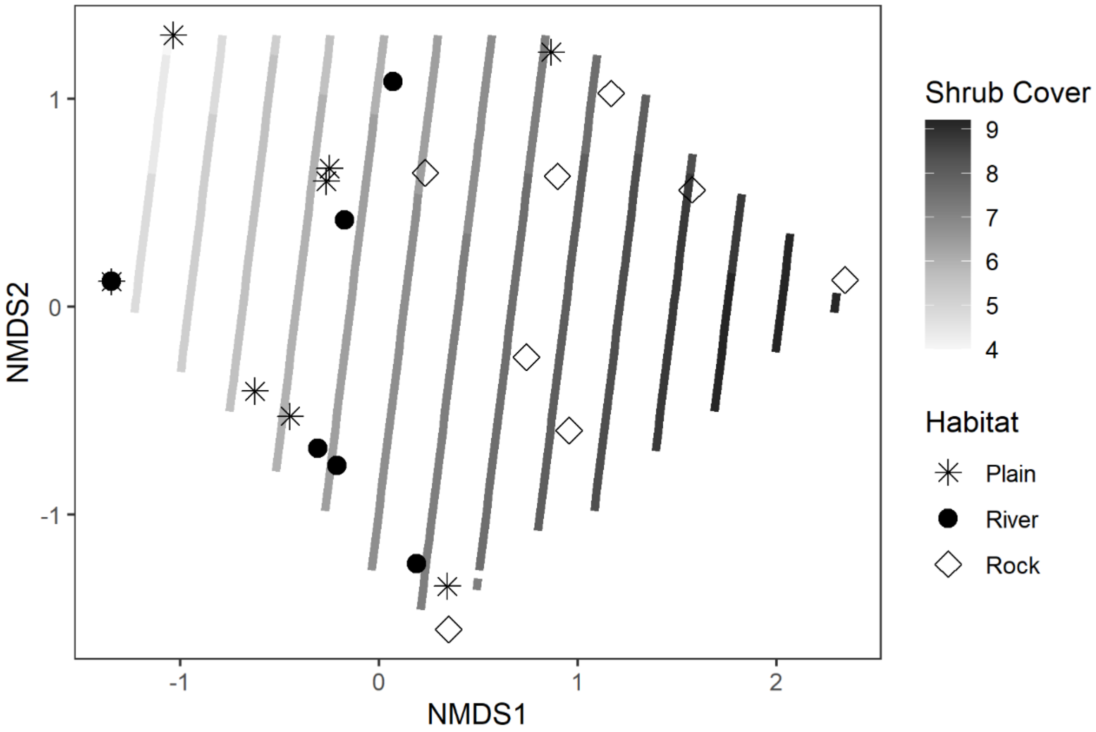


Figure 3.13: nMDS of small mammal occurrence (based off abundance) based on Jaccard-index of similarity of all nine sites for two survey years (2017 and 2019), overlaid with a fitted large shrub cover (1.5 > 2 m) surface (grey contour lines) (Stress value for 2017 = 0.072, and for 2019 = 0.100). The habitat type of each site is indicated by distinct symbols.

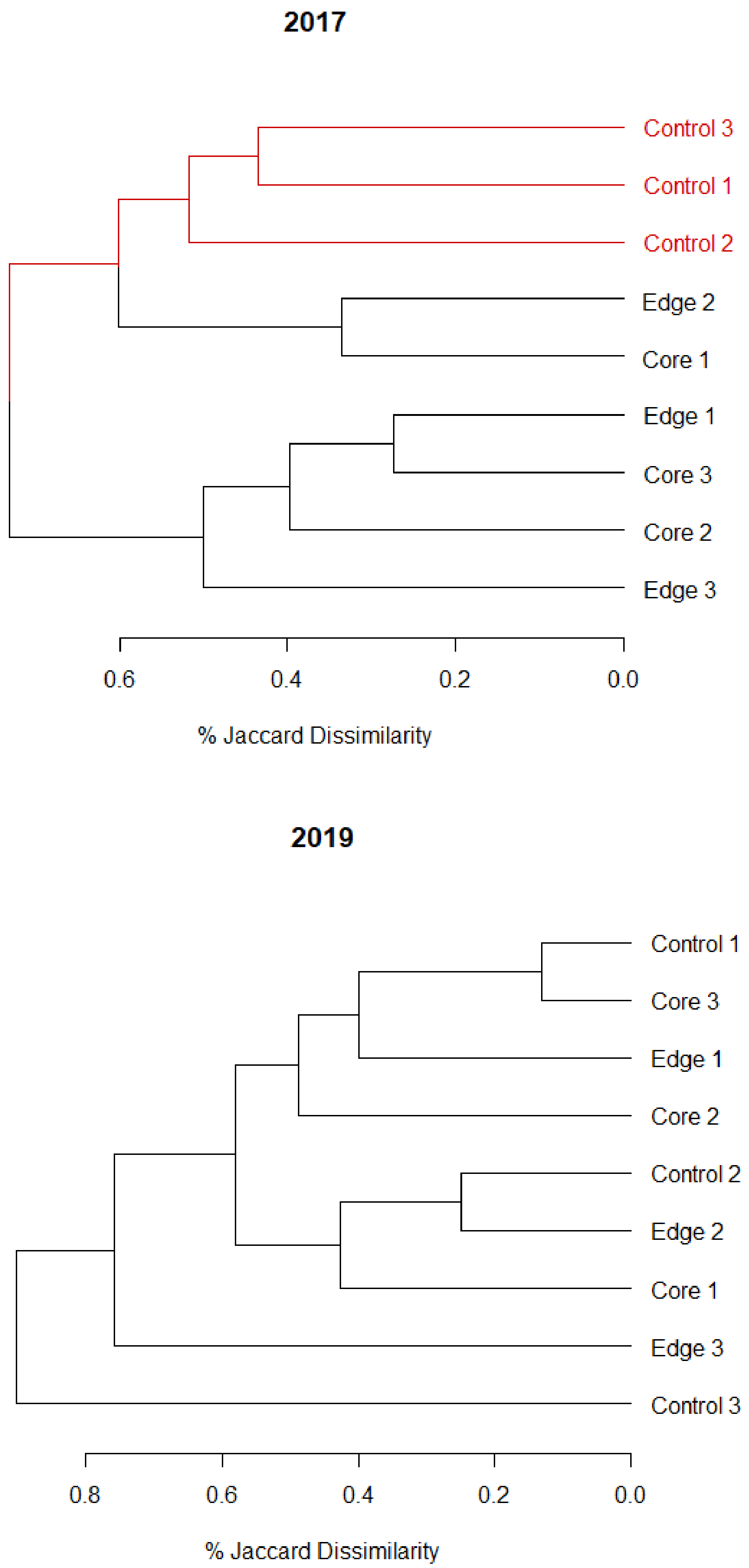


Figure 3.14: Hierarchal cluster dendrogram showing similarities in small mammal abundances among nine farms (core, edge and control) during two survey years (2017 – before the cessation of farming activities on the core and 2019 – after the cessation of farming activities on the core). Red indicates interesting groupings.

Vegetation

Multivariate GLMs based on vegetation cover identified both survey year and habitat as significant determinants of changes in PFG abundance (Table 3.17). Univariate statistics indicated that forbs relative cover significantly contributed to the changes in PFG abundance when compared to vegetation across survey years (p = 0.04) (Table 3.19). Changes in shrub abundance significantly contributed to the overall change in PFG abundance between habitats (p = 0.01) (Table 3.19).

Table 3.19: Univariate statistic from multivariate GLMs for plant functional group abundances showing which PFG contributed significantly to changes in abundance between different significant covariates (survey, farm type and habitat). Dev = deviance explained by each PFG. * $p \leq 0.05$.

PFG	**Survey**		**Farm Type**		**Habitat**	
	Dev	*p*	*Dev*	*p*	*Dev*	*p*
Grass	0.44	0.93	4.79	0.29	2.50	0.65
Forb	7.61	0.04*	6.38	0.25	2.65	0.65
Shrub	0.24	0.93	5.72	0.25	14.10	0.01*
Succulent	0.17	0.93	4.62	0.29	5.21	0.33
Tree	0.51	0.93	1.79	0.46	5.51	0.33

In hierarchal cluster analysis of vegetation communities in 2017, there was no clear pattern grouping different farm types (Figure 3.15A). Core farm 1 and 3, and control farm 3 were more similar (~30% similarity level) than the other farms which did not group in any discernible manner (Figure 3.15A). In 2019, there was again no clear pattern of grouping according to farm types.

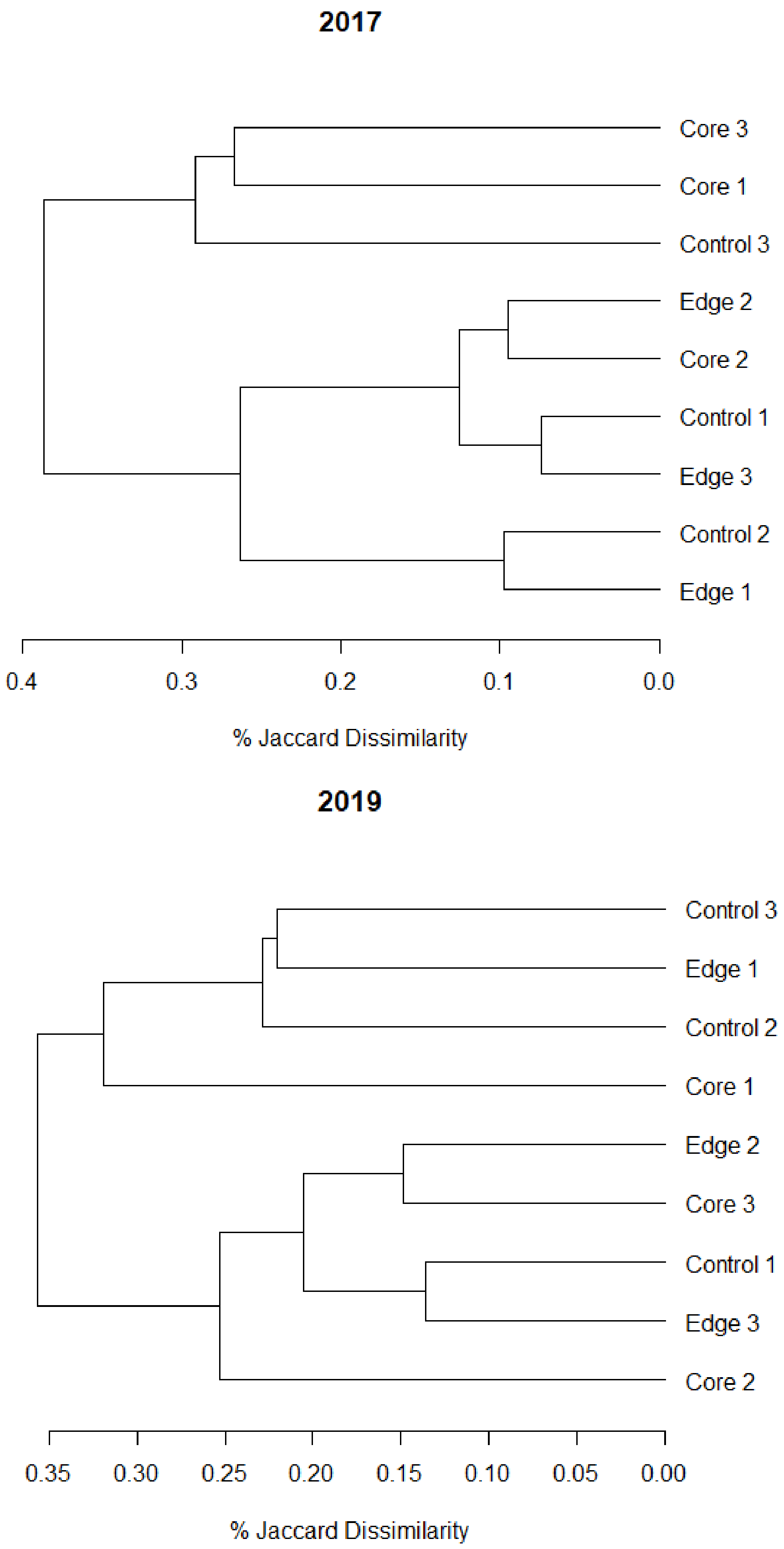


Figure 3.15: Hierarchal cluster dendrogram showing vegetation community associations among nine farms within three farm types (core, edge and control) during two survey years (2017 – before the cessation of farming activities on the core and 2019 – after the cessation of farming activities on the core).

Canonical correspondence analysis of small mammal and vegetation community structure

2017 survey

The most obvious differences in vegetation parameters between 2017 and 2019 were a lack of forb cover on all farms in 2017 (resulting in a suspect model output compared to the more definitive 2019 analysis). During 2017 the most important environmental parameters positively affecting Axis 1 were NDVI (r = 0.613), followed by % bare ground (r = 0.413), and % grass (r = 0.337; whereas % rock/scree (r = -0.763. and % succulents (r = -0.387) loaded strongly and negatively (App 3.6). % grass was strongly and positively correlated with Habitat complexity (r = 0.646), whereas %rock/scree cover was negatively and strongly correlated with percent bare ground (r = -0.691) (App 3.6). This axis therefore summarizes an environmental gradient changing (from left to right along CCA1) from less complex and productive habitats dominated by open rock/scree with more succulents, to habitats with higher NDVI, more bare ground (excluding rock) and more grass cover with a concomitant increase in habitat complexity. CCA2 was influenced most strongly by NDVI (r = 0.546) and % trees cover (r = -0.326) (App 3.6); this axis therefore summarized a gradient dominated by greater productivity as trees (most of which are invasive) became relatively more common.

During 2017 two core farms (1 and 3) and one edge farm (2) plotted to the right along CCA1 with little separation along CCA2 (Figure 3.16). This reflects higher NDVI and percent shrub cover, while most control and edge sites plotted negatively along CCA1 reflecting higher percent rock and less bare ground (Figure 3.16). Control farm 1 also plotted to the right along CCA1 reflecting greater NDVI, % grass and % bare ground. Core farm 2 plotted with edge and control farms 3 and 2 respectively along CCA1 and negatively along axis 2 which reflects higher rock/scree areas, intermediate NDVI/% grass/hab. complexity but fewer trees (Figure 3.16). Edge farm 1 plotted above all other farms along CCA2 (Figure 3.16) though this result is attributable to small mammal parameters (see below).

The only discernible grouping of farm types that was evident was for control farms 1-3, which all plotted negatively along CCA2 (which explained a low % variance) owing to greater % shrubs and % trees, intermediate % grass and NDVI, but not to the extent that this influenced clustering patterns shown in Figure 3.15,

The presence of *R. pumilio* correlated strongly with Edge farm 1 as this species was exclusively captured on this farm in 2017 (Figure 3.16). *G. paeba* and *Micaelamys* spp. plotted together close to the origin suggesting they are both ecological generalists (Figure 3.16). *D. auricularis* plotted to the left of axis 1, reflecting a preference for increased rock/scree (Figure 3.16). Macroscelididae spp. plotted more to the right of axis 1 but still close to the origin reflecting a correlation with increased vegetation cover while still exhibiting generalist traits (Figure 3.16). The relatively strong (~50%) of the control farms in Figure 3.14A reflects a tendency whereby *Gerbillus paeba* was relatively more abundant, and *Micaelamys* spp. rarer, on the control farms.

2019 survey

During 2019 the most important environmental parameters influencing CCA1 positively were % shrub cover (r = 0.683), % forbs (r = 0.466), % grass (r = 0.399) and NDVI (r = 0.366) whereas % bare ground (r = -0.658) and % rock/scree (r = -0.351) loaded negatively (App 3.6). CCA1 thus reflects a gradient from habitats with lower productivity (NDVI) but increased rock/bare ground (on the left) towards habitats with higher NDVI; more grasses, forbs and succulents and associated greater habitat complexity. CCA2 was influenced most strongly by NDVI which increased from bottom to top.

During 2019 core, edge and control farms showed less of a definitive pattern compared to 2017 (Figure 3.17). Most core farms positioned along the right side of axis 1 with core farm 1 reflecting higher % grass cover and core farm 2 reflecting higher % succulent cover (Figure 3.17). However, core farm 3 plotted positively along axis 2 which was more reflective of high % bare ground cover (Figure 3.17). Edge farm 2 plotted above all other farms along CCA2 reflecting both high % bare ground cover and higher NDVI values (Figure 3.17). this was likely attributed to high large shrub cover (associated with higher NDVI) but low grass, succulent and small shrub cover which resulted in increases bare ground between larger shrubs (Table 3.4 and B, Figure 3.17). Farms positioned along the right side of axis 1 reflective of areas with higher vegetation cover and habitat availability (Figure 3.17). The presence of *R. pumilio* correlated strongly with Edge farm 1 similar to the biplot calculated for 2017 (Figure 3.17). *G. paeba* plotted close to the origin indicating high generalist characteristics, while *Micaelamys* spp. and Macroscelididae spp. grouped together and plotted more to the right of axis 1 perhaps reflecting a preference for higher vegetation cover and habitat complexity (Figure 3.17). *D. auricularis* plotted to the left of axis 1, this was closely correlated with increased rock/scree (Figure 3.17).

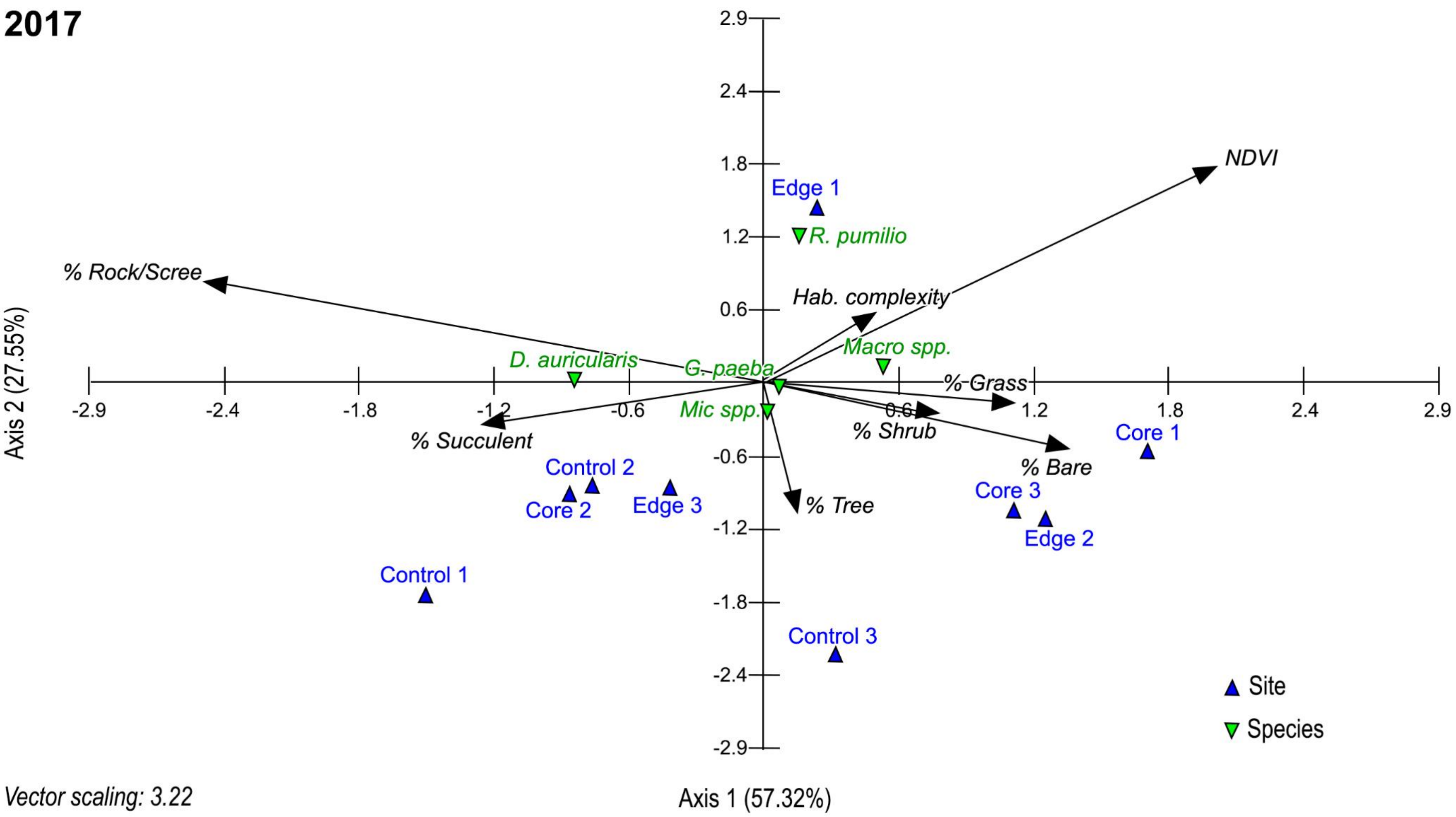


Figure 3.16: Canonical correspondence analysis biplot of the nine study sites (blue triangle; Core *x* = a specific core farm, Edge *x* = a specific edge farm and Control *x* = a specific control site) during 2017 (before sheep were removed from core farms) and five taxa (green triangle; *Desmodillus auricularis*, *Gerbilliscus paeba*, *Rhabdomys pumilio*, Macroscelididae spp. and *Micaelamys* spp.) in the SKA region of the Karoo, based on small mammal relative abundances and environmental data variables (Table 3.4 and 3.8). Arrows represent the most important environmental variables indicating direction of maximum change of that variable across the diagram. Length of arrows is proportional to the rate of change.

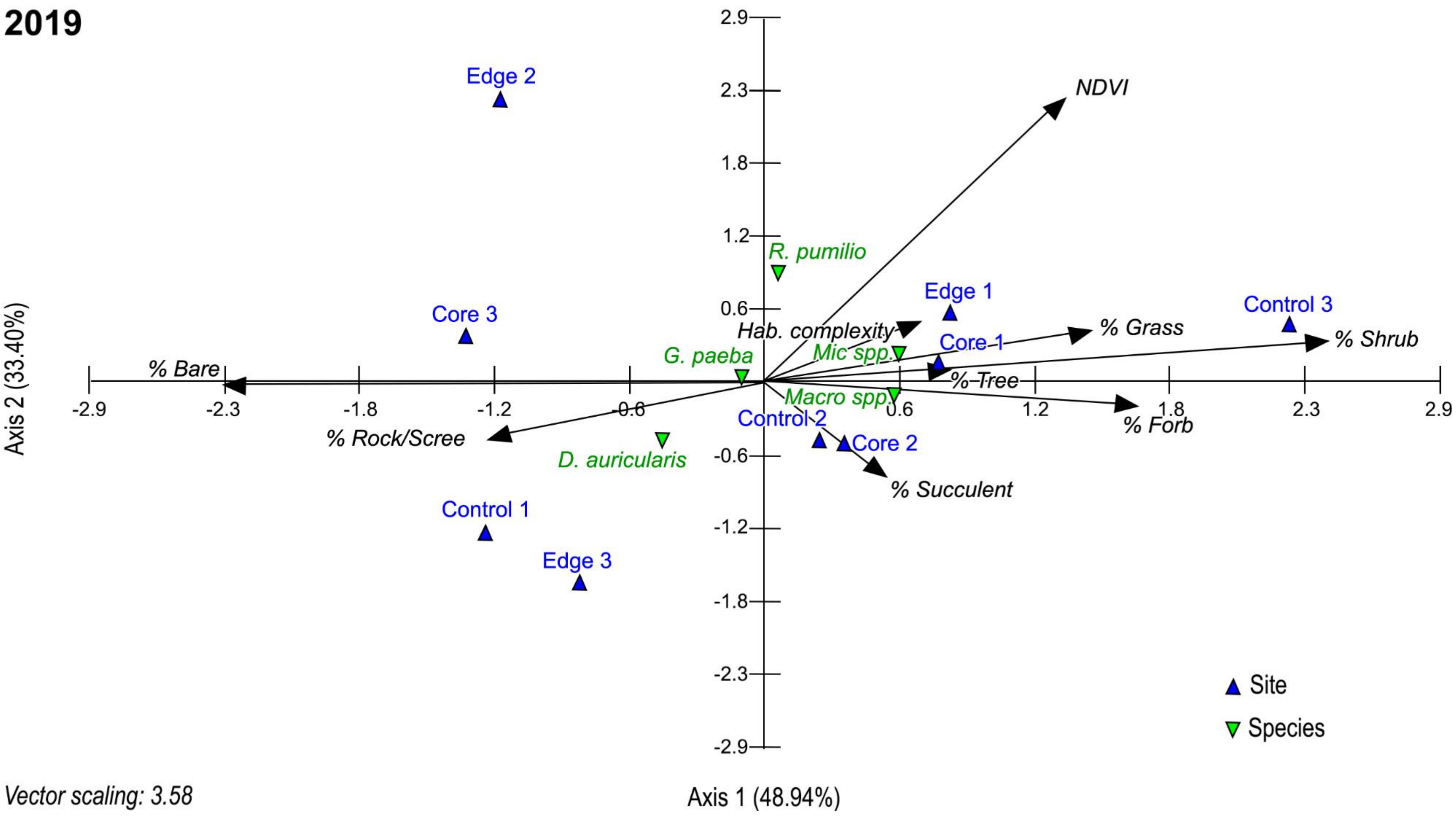


Figure 3.17: Canonical correspondence analysis biplot of the nine study sites (blue triangle; Core *x* = a specific core farm, Edge *x* = a specific edge farm and Control *x* = a specific control site) during 2019 (after sheep were removed from core farms) and five taxa (green triangle; *Desmodillus auricularis*, *Gerbilliscus paeba*, *Rhabdomys pumilio*, Macroscelididae spp. and *Micaelamys* spp.) in the SKA region of the Karoo, based on small mammal relative abundance and environmental data variables (Table 3.4 and 3.8). Arrows represent the most important environmental variables indicating direction of maximum change of that variable across the diagram. Length of arrow is proportional to the rate of change.

Discussion

Contrary to my hypotheses (H1 and H2), there were few significant changes in vegetation and small mammal communities on core farms following the cessation of farming activities. During both 2017 and 2019, when farmland transitioned to a protected area on core farms, vegetation cover, habitat complexity and overall community structure remained similar. Small mammal community attributes (specifically species richness, diversity and abundances) also did not change significantly among farm types or between surveys. These results corroborate those of other studies within the Karoo which highlight the slow recovery of both vegetation (Boardman *et al.* 2010, Rahlao *et al.* 2008, van Rooyen *et al.* 2015, McManus *et al.* 2018) and mammal communities (Kerley 1992a, Keesing 1998, Eccard *et al.* 2000, Kelly *et al.* 2013) following shifts in livestock grazing pressure.

Evidence of slow vegetation recovery within the Karoo is provided by several studies over longer time scales compared to this study (Boardman *et al.* 2010, Rahlao *et al.* 2008, van Rooyen *et al.* 2015, McManus *et al.* 2018). Hoffman *et al.* (2018) illustrated, through repeat photography analysis, that vegetation in several Karoo dryland areas remained unchanged over a 24-year period despite changes in land-use and grazing intensity. Rainfall (Hoffman *et al.* 2009, Hoffman *et al.* 2018) and grazing treatments (O'Connor & Roux 1995, du Toit & O'Connor 2020) were the main reasons for changes in vegetation cover. In particular where shifts in growth form were observed, rainfall was cited as the major determinant with changes in stocking rate of only secondary importance (van der Merwe *et al*. 2018, du Toit & O'Connor 2020). However, even minimal recorded changes in vegetation were over relatively long timescales (e.g., 24 - 27 years) suggesting that the low rainfall of the Karoo greatly influences the slow response of this region to positive land use changes (van der Merwe *et al.* 2018).

The lack of significant changes in vegetation between 2017 and 2019 further suggests that the timescale over which the study was conducted when sheep were absent may have been too brief to detect changes. Additionally, at the time of the study this region of the Karoo region was in the grip of a severe five-year drought (see Chapter 2), compounding the already known effects of low rainfall on slow recovery times (Hoffman *et al.* 2009, Kelly *et al.* 2013). Several other studies have suggested that recovery time for small mammals after livestock are removed in an area may be well over several years, as mammals within arid landscapes typically have a slower response time to major interventions (Kerley 1992a, Keesing 1998, Eccard *et al.* 2000, Kelly *et al.* 2013). Vegetation and small mammal surveys carried out in 2018 on Losberg (the original MeerKAT farm), by Jonathan Plaistowe for his B.Sc. Hons thesis (co-supervised by myself), suggested that even after seven years without sheep, small mammal communities did not differ significantly to those I recorded on core farms in 2017 despite signs of significant recovery in grasses, succulents and forbs (Plaistowe 2018). This lack of recovery after almost a decade is unexpected (Eccard *et al.* 2000, Rickart *et al.* 2013, van der Merwe & Milton 2019) and all the more noteworthy given the significant increase in effective number of PFGs (e^H), as well as grass and succulent cover in this part of the SKA core. Together these results support the idea that livestock grazing within the Karoo has a lesser influence on vegetation and small mammal communities than climate, and that recovery is primarily driven by rainfall.

How did the vegetation of farm types change?

Consistent with my prediction (P1), vegetation communities on all farm types were similar in 2017, with low total vegetation cover (27 - 35%; Table 3.4), low alpha diversity, effective number of PFGs (e^H) and Shannon-Wiener (H') diversity, and high dominance of shrubs (with few forbs and succulents) (Table 3.7). These attributes are consistent with vegetation that has been subject to the long-term impacts of small livestock in a semi-arid region. These impacts include sustained grazing (Kraaij & Milton 2006, Hempson *et al.* 2017, Hoffman *et al.* 2018, van der Merwe *et al.* 2018) and trampling (Bradshaw *et al.* 2003, Hoffman *et al.* 2018, McManus *et al.* 2018) which together lead to the degradation of plant communities and habitats in the Karoo (Hoffman *et al.* 2018, McManus *et al.* 2018).

The combination of assumed trampling (not quantified in this study) and heavy grazing likely resulted in the overall low vegetation cover and diversity during 2017. These results are further supported by the consistently low NDVI values for all farm types during 2017 (Table 3.7), which may reflect the overall low rainfall (see Chapter 2 for details on rainfall) compounding the effects of grazing and decreasing the amount of green vegetation. Over a 25-year period approximately 90% of the Karoo has shown no significant change in NDVI values despite changes in land use and livestock production (Hoffman *et al.* 2018). Where NDVI did increase (~ 10% of the Karoo) the areas were typically adjacent to higher rainfall grassland areas, not the drier regions included in this study (Hoffman *et al.* 2018). It should, however, be noted that while NDVI is a comparatively efficient measure of vegetation especially over time (as with this study), this measure replies on chlorophyll to reflect near infrared light. Karoo vegetation is highly drought resistant with minimal "greenness" visible during periods of low rainfall.

Consequently, NDVI is generally very low in the Karoo and may not accurately represent overall vegetation cover and primary productivity within the region (Hoffman *et al.* 2018).

Of the shrubs present, *Rhigozum trichotomum*, *Salsola tuberculata* and *Salsola aphylla* were the dominant species. *Rhigozum trichotomum* is a common unpalatable spinescent species typically dominant in overgrazed Karoo systems, while *Salsola tuberculata* and *Salsola aphylla* are only moderately palatable species (Hoffman 2000, O'Connor *et al.* 2014, van der Merwe 2020). Most shrubs fell within the first two height cover categories (below 0.5 m and between 0.5 and 1 m), which is also typical of woody shrubs in Karoo habitats subjected to intensive livestock herbivory (Hoffman 2000, van der Merwe 2020). Increases in percentage shrub cover largely accounted for the trend of increasing mean % vegetation cover on core farms relative to control farms in 2019 (Table 3.4 and Figure 3.6). However, changes in overall cover and shrub cover were not significantly different, and thus farm types did not separate out in multivariate clustering and ordination outputs (Figure 3.15 and 3.16). The higher % of shrubs below 0.5 m on control farms compared to other farm types in 2017 was largely the result of increased *Rhigozum trichotomum* (pers. obs.) which may indicate overgrazing, especially on sandy soils (Stafford *et al.* 2017, van der Merwe 2020).

Tree species were almost exclusively dominated by invasive *Prosopis spp.* (*P. glandulosa* and *P. velutina*, henceforth referred to as Prosopis) across all farm types. Prosopis is a major invasive species within the Karoo (Ndhlovu *et al.* 2016, van der Merwe 2020) and the subject of several government-led removal programs in the Karoo. Private landowners are also encouraged to develop their own management plans particularly within water courses (Ndhlovu *et al.* 2016). It may well be that with time the core site, which will be managed by a single body (SANParks) will begin to diverge from private neighbouring land which lacks the resources for large scale control of invasive vegetation.

Between 2017 and 2019 there were no significant changes in vegetation characteristics (diversity measures and NDVI) as well as vegetation cover. This contradicts my predictions that vegetation cover and NDVI would increase on core farms between 2017 and 2019 (P1) but supports my hypothesis that diversity measures would not change (P2). The high levels of specialisation of Karoo vegetation to arid and semi-arid climates means that richness is unlikely to change over short time periods. Consequently, researchers interested in veld recovery typically focus on changes in vegetation cover and plant functional group composition (Rutherford *et al.* 2012, Masubelele *et al.* 2014, McManus *et al.* 2018). In general, there was greater consistency in vegetation cover between farm types in 2019, but the variability between individual farms (per farm type) had increased by 2019 (Table 3.4). Shrubs remained the dominant PFG on all farms, albeit with a slight decrease in cover of shrubs below 0.5 m, and a slight increase in cover of shrubs 0.5 - 1.5 m high (App 3.7). This pattern of changes in shrub height was consistent across the farm types and not significantly different among farm types suggesting that the change is likely attributed to growth over time.

While not significant among years or farm types, forb cover increased on core farms (Table 3.19) in 2019 as did the ratio of grasses to small shrubs. Forbs typically include more palatable plant species (i.e., *Aptosimum marlothii* and *Pentzia spinescens*) and their recovery has been associated with decreased trampling in several studies (Bradshaw *et al*. 2003, Hoffman *et al.* 2018, McManus *et al*. 2018). Forb recovery may also potentially be associated with decreased livestock grazing as *Aptosimum marlothii* and *Pentzia spinescens* recovery was recorded on the original SKA core farms (Losberg and Meysdam) after livestock were removed (van der Merwe 2020). Surprisingly, there were no significant changes in grass cover between 2017 and 2019, contrary to my prediction (P1) but grass height was significantly higher on core farms relative to both edge and control farms and the average grass height decreased significantly on edge and control sites between 2017 and 2019 (Figure 3.7). Karoo grass species (i.e., *Stipagrostis namaquensis*) are fast growing and typically are the first to recover from decreased herbivory (Masubelele *et al*. 2014), especially after rainfall (du Toit *et al.* 2018). Grass height, however, has been highlighted as an important factor in determining impacts of grazing on vegetation and small mammals in semi-arid ecosystems (Landsberg *et al.* 1999, Kuiper & Parker 2013). Kuiper & Parker (2013) proposed that different levels of grazing impacted grass height (high grazing, grass height = 20.2 cm, medium grazing = 27.6 cm and low grazing = 45.3 cm) and grass height was the primary mechanism controlling differences in small mammal abundance and diversity. My results show that while livestock grazing intensity was similar across all farm types in 2017, grass height ranged between 21.6 cm and 47.9 cm which is similar to the ranges seen in Kuiper & Parker (2013) (Figure 3.7). This suggests that within Karoo systems, grass height was significantly impacted by the presence or absence of sheep with grasses being generally taller where sheep were absent (Landsberg *et al.* 1999). The lack of change in overall grass cover may be attributed to drought conditions within the region over the study period, as grasses rely heavily on rainfall to increase in abundance (du Toit *et al.* 2018).

These findings suggest that vegetation changes are apparent on core farms and are consistent with predictions for the recovery of plants following the cessation of sustained livestock grazing in the Karoo (Olff & Ritchie 1998, Bradshaw *et al.* 2003, Kraaij & Milton 2006, Hempson *et al.* 2017, Hoffman *et al.* 2018, Van der Merwe *et al.* 2018). Predictions for changes in vegetation within the Karoo have focused on the expansion of shrub cover and dominance, which is thought to be linked mostly to long term changes in climate (drier and hotter) and land use (long term livestock production) (Sala *et al.* 2000, Archer 2010, Rutherford *et al*. 2012). However, decreased livestock grazing may drive a trend towards increasing grass cover across the Nama-Karoo biome (Masubelele *et al*. 2014). Importantly future vegetation surveys should include species level identification as there is evidence that the presence of sheep has increased invasive grasses within the Karoo (Milton 2004, Snyman & Malan 2011) which may have a growth advantage (Dean *et al.* 2000) and hence outcompete local grasses (Milton 2004).

Did small mammal diversity and community composition change?

The Strategic Environmental Assessments (SEAs and CSIR 2016a) predicted that at least ten small mammal species are present within the SKA area (Todd & Henschel 2016). I recorded a total of eight small mammal species, five of which were cryptic species (*Micaelamys namaquensis*, *Micaelamys granti*, *Macroscelides proboscideus*, *Elephantulus rupestris* and *Elephantulus pilicaudus*). Sherman live-trapping is a common and effective tool for studying small mammal populations but is biased towards species that are trap prone (Harkins *et al.* 2019, Motro *et al.* 2019, Thomas *et al.* 2020). Thus, some species that were predicted to be in the study area but were not captured (e.g., Karoo bush rat *Otomys unisulcatus* and reddish-grey musk shrew *Crocidura cyanea*) may have required alternative sampling methods (e.g., targeted placement of Sherman trap near nests or along paths to nests, Vermeulen & Nel 1988). I observed both rat nests and mole-rat mounds typical of both Karoo bush rat and members of the subterranean rodent family Bathyergidae (most likely *Cryptomys hottentotus*) in both 2017 and 2019 on all three farm types. However, mole-rate (Bathyergidae) – in this case common mole-rats (*Cryptomys* spp.) – are seldom sampled with Sherman traps, and require specialized traps and sampling efforts (Hickman 1979) that were precluded by the time and logistical constraints of this study.

The small mammal morphotaxa sampled during this study are hardy ecological generalists (Eccard *et al.* 2000, Russo *et al.* 2010, Schlitter & Kerley 2016) which was supported by CCA biplots (2017 and 2019) showing that small mammal taxa tended more towards the origin point of plots consistent with generalist ecological characteristics. Specifically, *G. paeba* has been shown to favour open arid habitats and areas inhabited by livestock (i.e., increased disturbance) (Blaum *et al.* 2006, Schlitter & Kerley 2016). Definitive characteristics of hardy generalist species include r-selected life history traits (fast growing species with rapid reproduction) making these species typical pioneer species within a landscape, quickly dominating community structures (Büchi & Vuilleumier 2014). Dominance by such hardy generalists may impede ecological succession of small mammal communities (within the SKA and elsewhere) after the cessation of farming activities (where vegetation does not recover immediately) as these dominant species are already established and dominate resources within the area (Fox *et al.* 2003).

During 2017 small mammal richness and diversity were similar across farm types (Table 3.13) with *Gerbilliscus paeba* dominating. Similar results have been recorded in other recent Karoo studies (e.g., Aboul-Hassan 2020), but small mammal richness was slightly higher in this study, possibly as a result of the Aboul-Hassan (2020) study having a much broader scope with lower trapping effort per site. Arid zones are characterised by lower taxon richness and diversity (Andrews & O'Brien 2000, Eccard *et al.* 2000, Hoffman & Zeller 2005, Bosing *et al.* 2014) due to reduced available resources (i.e., vegetation cover and food availability) which may be exacerbated by overgrazing and drought conditions (Eccard *et al.* 2000, Bosing *et al.* 2014, Aboul-Hassan 2020).

The minimum number alive (MNA) also did not vary significantly among farm types within or between surveys but was lowest on control farms in 2017, which may explain why they clustered together (Figure 3.14). Control sites had similar vegetation cover to core and edge farms in 2017 but CCA biplots revealed consistently lower NDVI and higher % rock/scree cover. Lower NDVI and shrub and grass cover, typical of control sites may explain the lower MNA recorded. MNA results for individual taxa suggested control farms were dominated by *Micaelamys* spp. in 2017 but *G. paeba* in 2019 (Figure 3.11). The ability of *G. paeba* to thrive in disturbed areas may explain the higher MNA on control farms in 2019 even in worsening drought conditions (Figure 3.14).

Despite the cessation of farming activities on core farms, small mammal abundance, richness and diversity were not significantly different between surveys or, between edge or control farms in either survey (Table 3.14 and 3.14). Additionally, small mammal MNA in 2019 was more similar across farm types (Figure 3.14) than in 2017 contradicting my prediction (P3).

The increased consistency between sites in terms of small mammal communities and vegetation characteristics was apparent in CCA biplots where both farms and small mammal taxa were closer to the origin point compared to 2017. CCA biplots illustrated clear environmental variations and gradients which were relatively disparate between 2017 (gradients between NDVI and % rock/scree) and 2019 (gradients between % bare ground, % shrub cover and NDVI) (despite most univariate analysis suggesting non-significant changes). However, small mammal taxa plotted fairly consistently along those gradients during 2017 and 2019 reflecting the generalist characteristics of these species and suggesting subtle changes in environmental conditions were not reflected in small mammal communities.

Multivariate GLMs showed that both *Gerbilliscus paeda* and *Micaelamys* spp. MNA responded predictably to habitat variables according to previous descriptions (Kerley 1992a, Kerley 1992b). *G. paeda* was found significantly more in plain and river habitats, while *Micaelamys* spp. was found almost exclusively in rock habitat, consistent with previous studies (Kerley 1992a, Kerley 1992b). These patterns were consistent across farm types and survey years but less pronounced in 2019 with *G. paeda* and *D. auricularis,* being captured more often in rock habitat, possibly in response to increasing drought conditions.

Loss of habitat complexity, specifically a reduction in grass cover and increasing shrub encroachment has been linked to changes in small mammal communities in the Nama Karoo, specifically a reduction in total abundance and species richness and diversity (Hoffman & Zeller 2005). The absence of a measurable change in habitat complexity from 2017 to 2019 in my study is consistent with the similar levels of species richness and MNA of small mammals across surveys and consistent with the predictions of other studies (Kerley 1992a, Carrilho *et al.* 2017, Rebelo *et al.* 2019). Grass cover and height have also been highlighted as important determinants of changes in small mammal MNA (Hoffman & Zeller 2005, Yarnell *et al.* 2007, Kuiper & Parker 2013) and while grass height on core farms was higher in 2019 there was no significant influence on small mammal MNA. By contrast, shrub cover (with shrubs between 0.5 and 1 m in height) had a significant positive effect on both *Rhabdomys pumilio* and *Desmodillus auricularis* MNA (Table 3.18), consistent with the findings of Kerley (1992a). *Desmodillus auricularis* (Table 3.18) was also positively associated with larger shrub cover (between 1.5 and 2 m in height) in plain and river habitat (Figure 3.13). Together these results support the literature showing a strong effect of habitat on the composition of small mammal communities within an area (Kerley 1992a, Williams *et al.* 2002, Hoffman & Zeller 2005, Ceradini & Chalfoun 2017, Santos *et al.* 2017).

Top-down regulation of small mammal populations has been described for predators around the world (Miller *et al.* 2012, Prevedello *et al.* 2013, Drouilly *et al.* 2018c, Woolley *et al.* 2019, Stobo-Wilson *et al.* 2020). In the Karoo both black-backed jackal and caracal include small mammals in their diet, both on farmland (13.5% of jackal diet and 16.7% of caracal diet on farmland in the Karoo) and in the neighbouring Anysberg PA (63.7% of jackal diet and 86.2% of caracal diet) (Drouilly *et al.* 2018c). Drouilly *et al.* (2018) did not quantify small mammal abundance and thus could not infer whether small mammals were a preferred prey category in either land use. Despite this it is clear from this and other studies (van der Merwe 2009, Humphries *et al.* 2016a, Humphries *et al.* 2016b, Soe *et al.* 2017, Steenkamp 2018, Jansen *et al.* 2019) that rodents are an important component of the diet of mesopredators in agricultural landscapes, underlying my prediction that sheep removal would increase predation pressure on small mammals and result in lowered or constant MNA on core farms. It is possible therefore that for small mammals the advantages of small recoveries in vegetation and reduced trampling on core farms (i.e., improved bottom-up effects) were offset by increased predation pressure (i.e., greater top-down effects) linked to the removal of an abundant and preferred prey item viz., sheep (Drouilly *et al.* 2018c). My study design could not discern between these two processes and while I did aim to include predator diet in this study the low RAI of predators in the study area translated to too few scats to allow for a meaningful dietary analysis.

Conclusions

Vegetation surveys revealed the sustained impacts of small livestock farming on the flora including low vegetation cover, a high proportion of unpalatable (i.e., *Rhigozum trichotomum)* or moderately palatable shrub species (i.e., *Salsola tuberculata* and *Salsola aphylla*) and consistently low NDVI values (ranging between 0.09 and 0.12). The persistence of Prosopis throughout the study area further highlighted the impacts of farming within the region as planting this invasive species was historically encouraged as a good forage plant for livestock (Ndhlovu *et al.* 2016). Very little baseline data is available for vegetation within the SKA core region (now protected area) (Todd & Henschel 2016). SEA reports predicted between 200 and 500 plant species with no predictions for patterns in plant functional group cover although it was suggested that vegetation cover would be similar to the Karoo National Park (Todd & Henschel 2016). Special attention was paid to the presence of *Aloe dichotoma* which was shown to have healthy populations (Todd & Henschel 2016) however, this species was predominately found on steep slopes and highly clustered which may explain why it was not recorded during my vegetation surveys. While this study did not focus of specific plant species, vegetation cover was similar to other studies reported for Karoo farmland (Hoffman *et al.* 2018, Kraaij & Milton 2006). Grass and forb cover in my survey was markedly lower than reported on the original core farm of Losberg which has benefited from seven years of sheep exclusion (van der Merwe 2020).

Livestock grazing has been shown to increase vegetation patchiness in many semi-arid regions (Lezama *et al.* 2013, Hanke *et al.* 2014, Eldridge & Delgado-Baqueriza 2017), increasing landscape variability which compounds the effects of grazing on vegetation changes (Hendricks *et al.* 2005). The slow recovery of Karoo vegetation explains why grazing induced patchiness. Together with low rainfall and climatic unpredictability, may impact core farms despite the removal of sheep, reflected by high CV values for vegetation attributes on core farms during 2019 (Table 3.4 and Table 3.7). The close relationship between vegetation and small mammal communities (i.e., the links between shrub density and *Rhabdomys pumilio* and *Desmodillus auricularis*, Table 3.18) (Bösing *et al*. 2014) explains why this variability was carried through both vegetation and small mammal attributes. In terms of vegetation there were very few changes 18 months after the cessation of farming activities (i.e., changes in grass height and forb cover).

The small mammal taxon present in this study likely reflects many years of livestock farming activities with surviving species all being members of generalist taxa similar to other studies in the Karoo (Eccard *et al.* 2000, Aboul-Hassan 2020). I only recorded eight taxa (*Gerbilliscus paeba*, *Desmodillus auricularis*, *Rhabdomys pumilio*, *Micaelamys namaquensis*, *Micaelamys granti*, *Macroscelides proboscideus*, *Elephantulus rupestris* and *Elephantulus pilicaudus*) with clear signs of two other small mammals (Karoo rat and common mole-rat) predicted to occur in the region. These results are consistent with the predictions made in the SEA (Todd & Henschel 2016, Milton *et al.* 2016) and other recent studies in the Karoo which point to a small subset of generalist species (Plaistowe 2018, Aboul-Hassan 2020). SEA reports recorded ten small mammal species within the SKA core region and predicted more acknowledging the presence of cryptic species within rocky habitats (Todd & Henschel 2016). My study recorded a lower species richness compared to the SEA however, this could be the result of the trapping method used which excluded very large and very small trap shy species as well as subterranean species.

The dominance of *G. paeba*, which thrives in more desert like conditions (Piers *et al.* 2020), reflects not only desertification linked to overgrazing but the effects of the sustained drought conditions that prevailed throughout the study period. Despite this and the high preponderance of generalist species, small mammal communities were largely structured according to habitat type with rocky areas dominated by *Micaelamys* spp. and Macroscelididae spp.. Having a higher MNA of these more sensitive taxa was possibly because of rocky habitats being less impacted by overgrazing relative to riverbeds and open plains, or possibly the exclusion of these species by *G. paeba* which thrive in heavily grazed riverbeds and open plains.

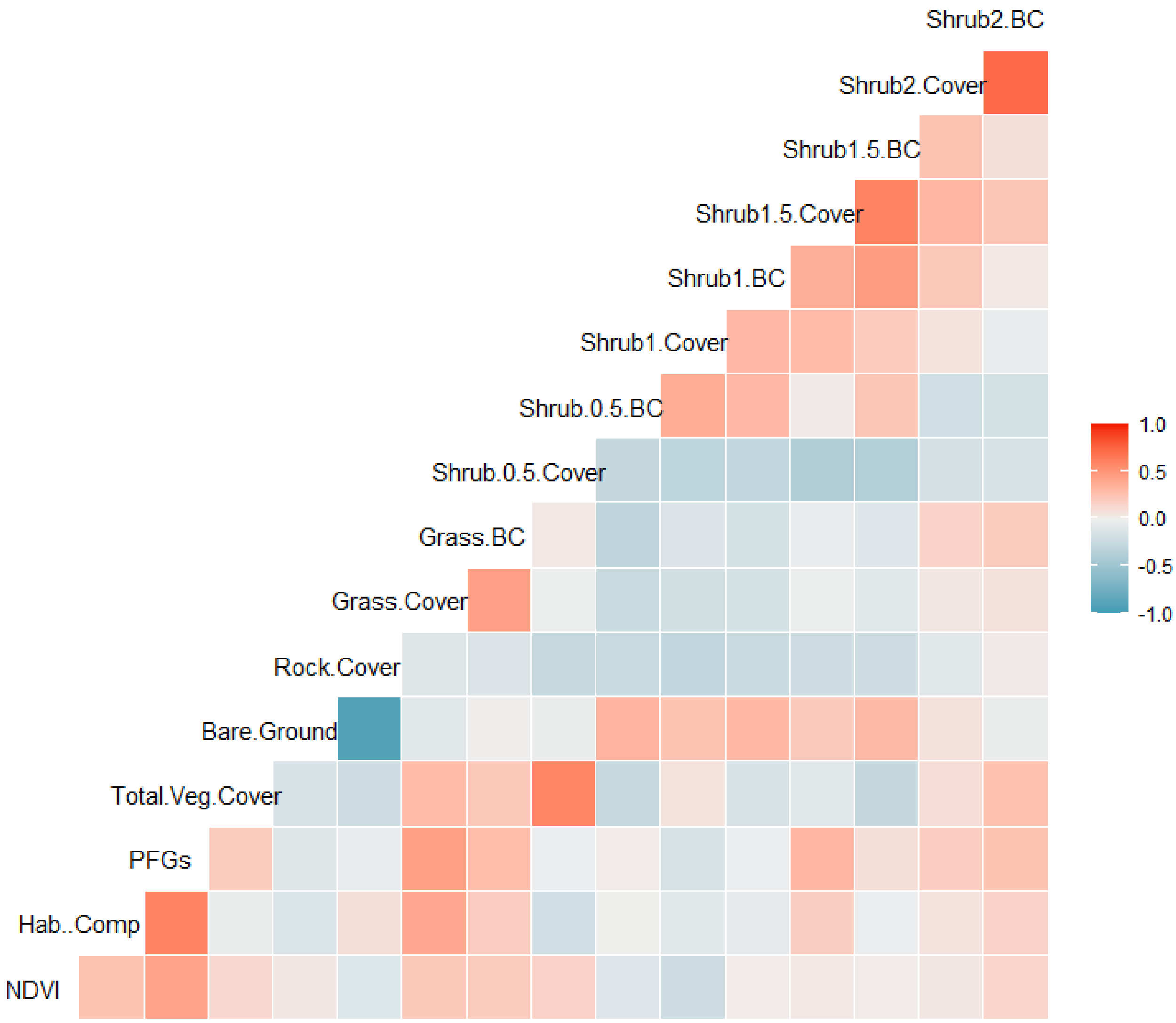
Early signs of passive recovery in the vegetation on core farms, including greater grass height and increasing forb cover, were not associated with any discernible changes in small mammal richness or abundance. Small mammals are capable of short-term responses to interventions such as changes in livestock grazing intensity (Hayward *et al.* 1997, Schmidt *et al.* 2005) but it is likely that the persistent drought conditions dampened the recovery of the vegetation (Frank *et al.* 2013, du Toit *et al.* 2018, Schmiedel & Oldeland 2018) upon which small mammals rely on for both food and refugia (Vial *et al.* 2011, Frank *et al.* 2013). Furthermore, the removal of an important prey item for predators viz., sheep from core farms may have increased predation pressure on small mammals.

Future research should focus on understanding the interaction between drought, vegetation cover and rocky habitats as this may be key in the conservation of small mammal species within the Karoo. For example, an interesting future study may look at how small mammal community structure shifts as shrub height and density increases or decreases in various habitats relative to sheep absence or presence. After ~ 350 years of extensive livestock grazing within the area the survival of only generalist taxa is not unprecedented (Eccard *et al.* 2000, Aboul-Hassan 2020). Small mammal succession has been shown to track vegetation succession in post-fire disturbed regions, where generalist species recolonise first followed by more specialised species (which should increase as vegetation density and habitat complexity increases) (Kruger & Bigalke 1984, Briani *et al.* 2004, Torre & Díaz 2004, Rebelo *et al.* 2019). Ultimately potential changes in vegetation and small mammal communities will only be determined with long term monitoring programs within the SKA sites in order to mitigate the effects of rainfall and characteristics of slow recovery apparent within the system.

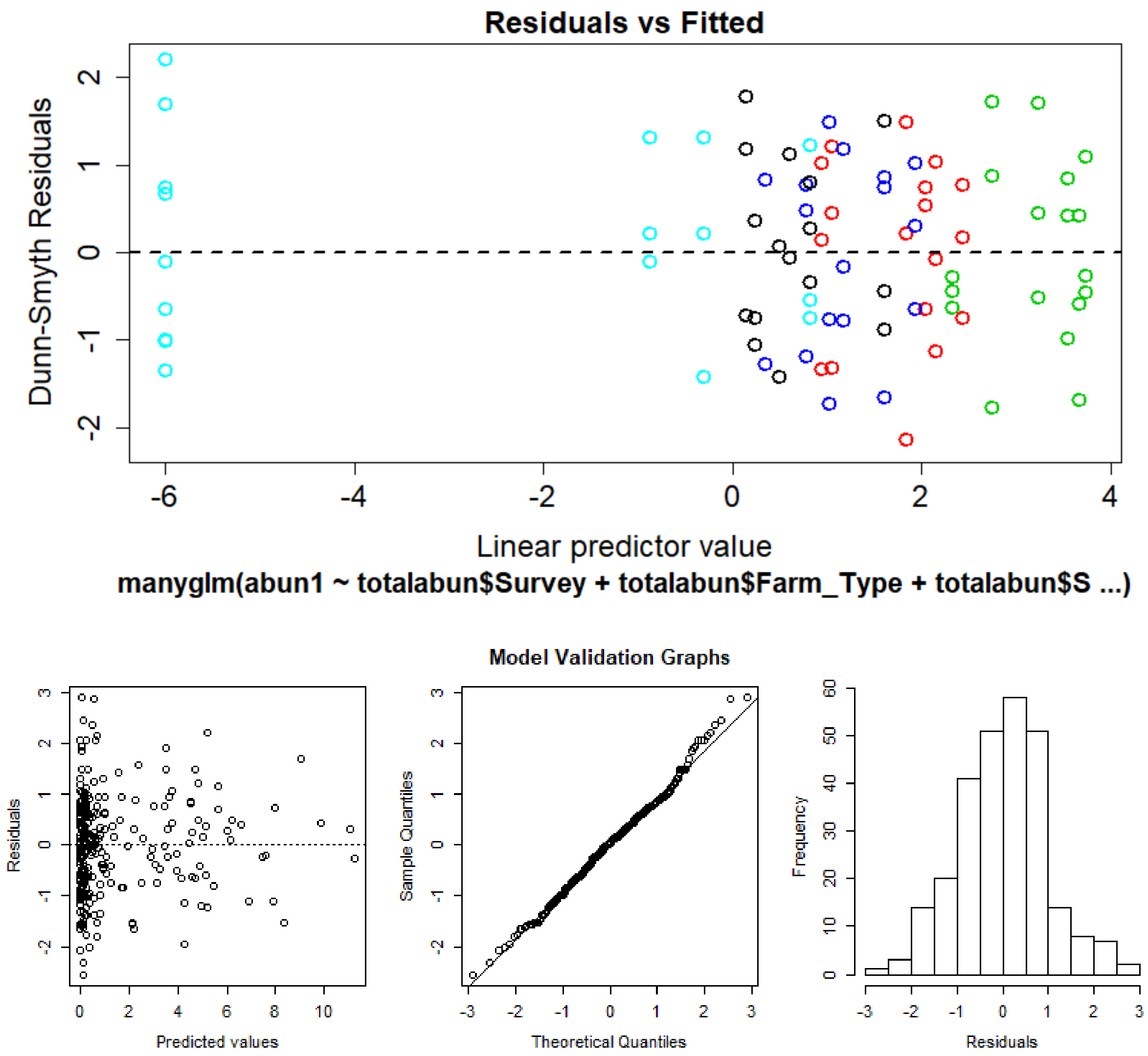
Appendix 3: Small mammal and vegetation appendices

App 3.1: Pearson's similarity coefficients between continuous environmental covariates. Grey shaded boxes indicate significant correlations (< -0.6 and > 0.6).

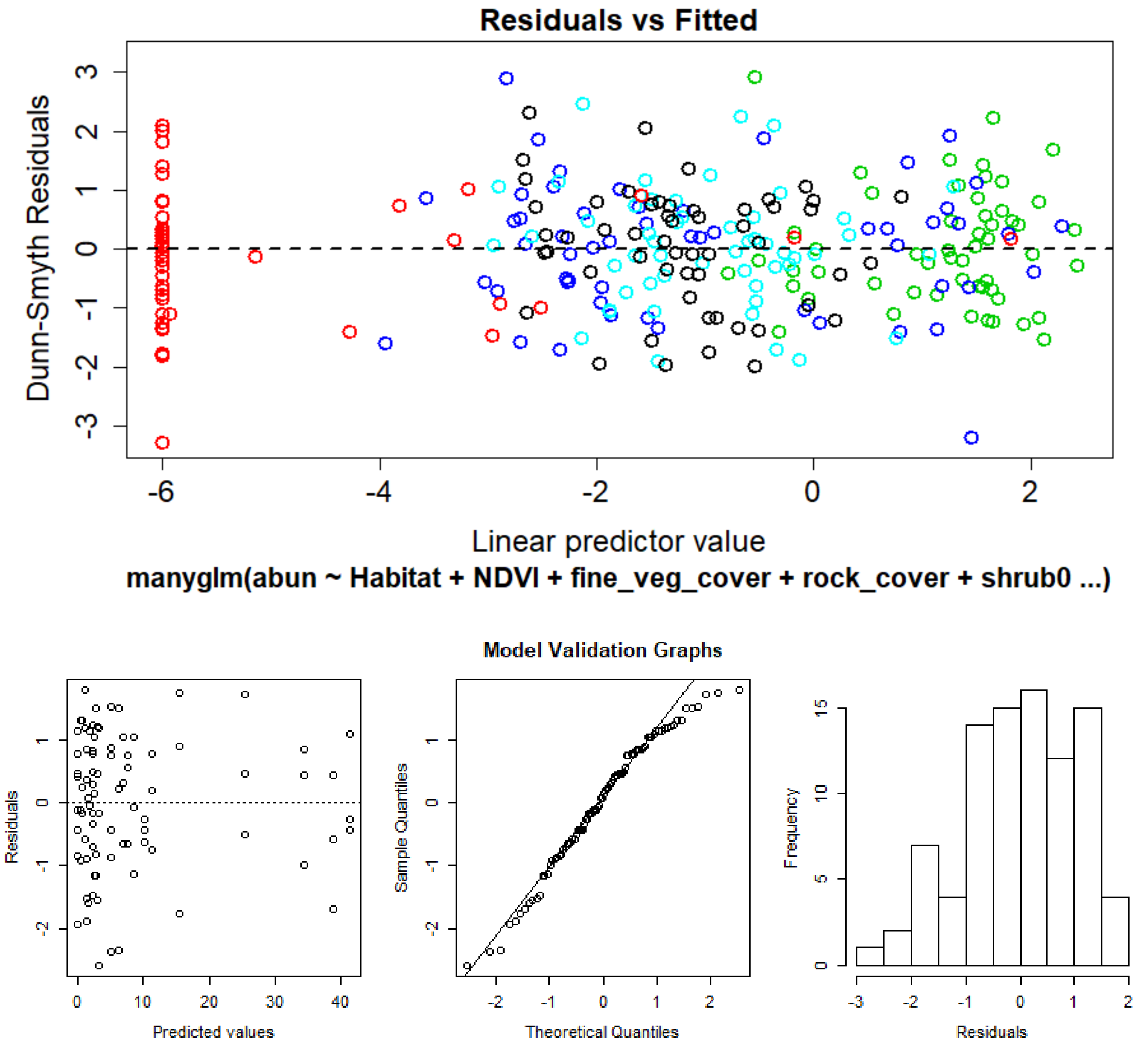
	Hab. comp	PFGs	Veg cover	Bare ground	Rock cover	Grass cover	Grass basal cover	Shrub cover (> 0.5m)	Shrub basal cover (> 0.5m)	Shrub cover (0.5 > 1m)	Shrub basal cover (0.5 > 1m)	Shrub cover (1 > 1.5m)	Shrub basal cover (1 > 1.5m)	Shrub cover (1.5 > 2m)	Shrub basal cover (1.5 > 2m)
NDVI	0.24	0.42	0.13	0.04	-0.11	0.21	0.20	0.16	-0.10	-0.21	0.02	0.03	0.02	0.04	0.14
Habitat complexity		0.60	-0.02	-0.12	0.09	0.40	0.19	-0.18	0.002	-0.07	-0.05	0.18	-0.02	0.06	0.16
PFGs			0.20	-0.10	-0.03	0.45	0.28	-0.02	0.02	-0.15	-0.02	0.32	0.09	0.19	0.24
Veg cover				-0.13	-0.20	0.29	0.21	0.59	-0.24	0.07	-0.15	-0.08	-0.25	0.09	0.26
Bare ground					-0.91	-0.08	0.01	-0.02	0.33	0.24	0.30	0.21	0.29	0.08	-0.02
Rock cover						-0.09	-0.11	-0.25	-0.22	-0.28	-0.22	-0.20	-0.21	-0.08	0.03
Grass cover							0.44	-0.01	-0.22	-0.17	-0.16	-0.01	-0.08	0.04	0.08
Grass basal cover								0.04	-0.29	-0.11	-0.16	-0.03	-0.10	0.15	0.20
Shrub cover (> 0.5m)									-0.25	-0.31	-0.27	-0.37	-0.36	-0.15	-0.15
Shrub basal cover (> 0.5m)										0.37	0.30	0.02	0.23	-0.19	-0.17
Shrub cover (0.5 > 1m)											0.30	0.29	0.20	0.06	-0.02
Shrub basal cover (0.5 > 1m)												0.36	0.46	0.22	0.03
Shrub cover (1 > 1.5m)													0.60	0.31	0.23
Shrub basal cover (1 > 1.5m)														0.25	0.09
Shrub cover (1.5 > 2m)															0.72



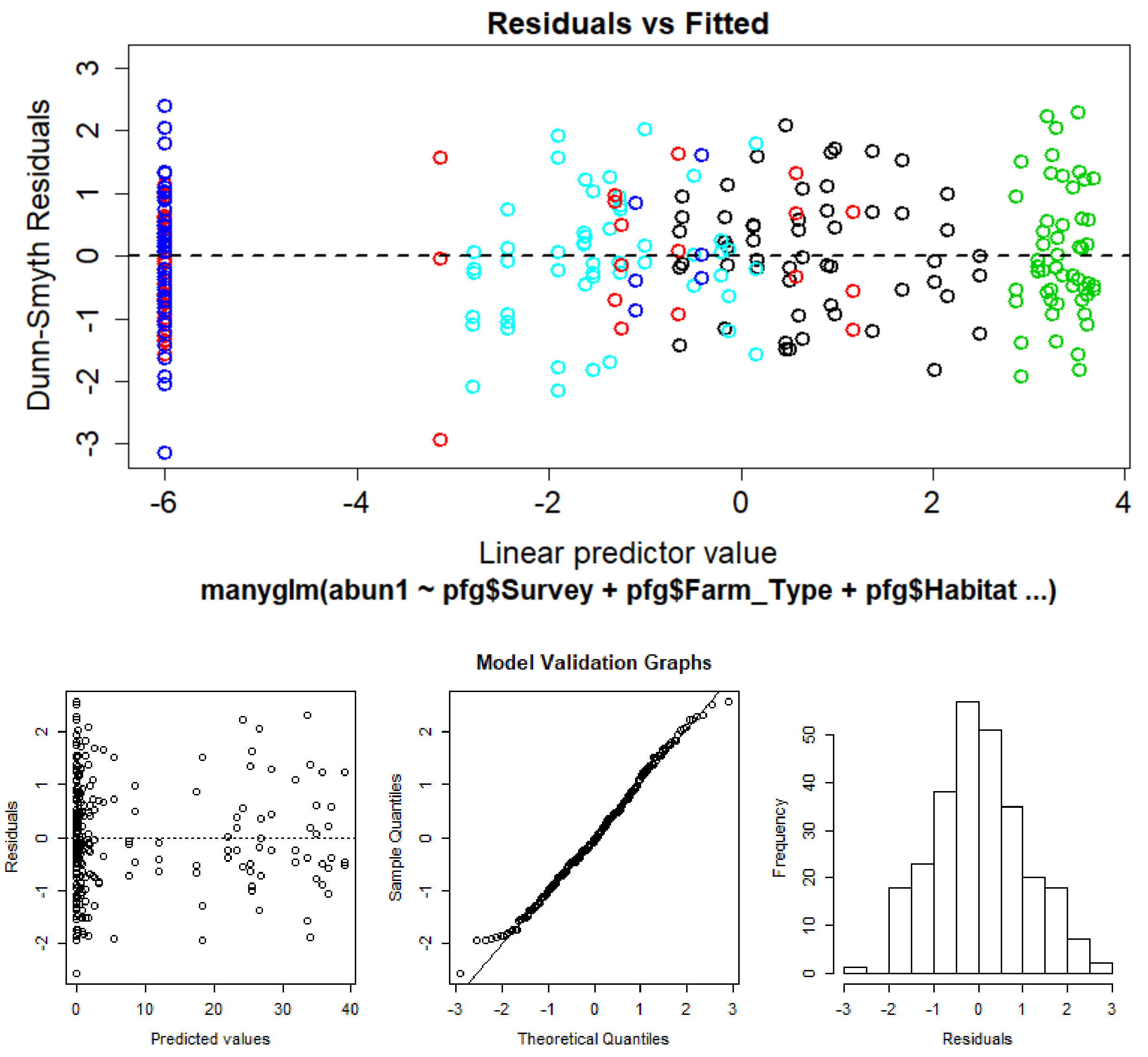
App 3.2: Visual representation of Pearson's similarity coefficients between continuous environmental covariates, dark red and blue indicate strong correlations while light red and blue indicate weaker correlations. Habitat complexity = Hab. Comp, PFGs = plant functional group richness, Total.Veg.Cover = overall vegetation cover, Shrub 0.5 = shrubs below 0.5 m in height, Shrub 1 = shrubs between 0.5 and 1 m in height, Shrub 1.5 = shrubs between 1 and 1.5 m in height, Shrub 2 = shrubs between 1.5 and 2 m in height, Cover = above ground plant cover and BC = basal plant cover.



App 3.3: Model validation graph for top small mammal abundance (per farm) model showing predicted versus fitted residuals (top graph), residual versus predicted values spread (bottom left), sample versus theoretical quantile spread (bottom middle) and distribution of data (bottom right).



App 3.4: Model validation graph for top small mammal abundance (per habitat and farm) model showing predicted versus fitted residuals (top graph), residual versus predicted values spread (bottom left), sample versus theoretical quantile spread (bottom middle) and distribution of data (bottom right).



App 3.5: Model validation graph for top vegetation model showing predicted versus fitted residuals (top graph), residual versus predicted values spread (bottom left), sample versus theoretical quantile spread (bottom middle) and distribution of data (bottom right).

App 3.6: Ordination results for the first two axes (Figure 3.16) from canonical correspondence ordination analyses to assess the environmental factors associated with differences in small mammal communities in two different survey years (2017 and 2019). Strong correlations (>±0.60) are given in boldface.

	Canonical coefficient		**Intra-set correlations**		**Correlations between environmental variables**							
2017												
Variable	***Axis 1***	***Axis 2***	***Axis 1***	***Axis 2***	***NDVI***	***Hab. complexity***	***Bare***	***Rock/Scree***	***Grass***	***Shrub***	***Succulent***	
Eigenvalue	0,120	0,060										
NDVI	0,308	0,763	**0,613**	0,546								
Hab. complexity	0,774	-0,275	0,151	0,177	0,181							
Bare	0,629	-5,719	0,413	-0,165	0,239	-0,266						
Rock/Scree	-0,359	-4,293	**-0,763**	0,259	-0,312	0,285	**-0,691**					
Grass	-0,231	-1,545	0,337	-0,050	0,251	**0,646**	-0,122	-0,248				
Shrub	0,675	-3,992	0,236	-0,082	-0,085	-0,378	-0,429	-0,261	0,005			
Succulent	-0,175	-0,442	-0,387	-0,105	0,012	0,436	-0,117	0,343	0,313	-0,467		
Tree	0,255	-1,078	0,044	-0,326	0,076	0,281	-0,355	0,327	0,115	-0,095	0,123	
2019												
Variable	***Axis 1***	***Axis 2***	***Axis 1***	***Axis 2***	***NDVI***	***Hab. complexity***	***Bare***	***Rock/Scree***	***Grass***	***Forb***	***Shrub***	***Succulent***
Eigenvalue	0,192	0,131										
NDVI	-7,505	-2,597	0,366	**0,648**								
Hab. complexity	25,448	13,500	0,191	0,141	0,448							
Bare	-3,214	-0,567	**-0,658**	-0,002	-0,146	-0,285						
Rock/Scree	-15,239	-5,716	-0,351	-0,130	**-0,619**	0,114	-0,150					
Grass	-15,539	-8,296	0,399	0,117	**0,632**	**0,788**	-0,374	-0,406				
Forb	-1,484	0,843	0,466	-0,052	**0,609**	0,543	-0,216	**-0,669**	**0,836**			
Shrub	0,000	0,000	**0,683**	0,095	0,258	-0,313	**-0,695**	-0,391	0,094	0,203		
Succulent	-5,341	-5,071	0,150	-0,217	0,224	**0,858**	-0,047	0,092	0,575	0,559	-0,463	
Tree	-3,881	-1,437	0,227	0,029	0,393	**0,885**	-0,011	-0,014	**0,633**	0,568	-0,434	**0,940**

App 3.7: Mean shrub cover (%) (± standard error) in different height categories per farm type over two survey years, 2017 (before cessation of farming activities on the core) and 2019 (after cessation of farming activities on the core). Shrub cover is divided into four height group, below 0.5 m, between 0.5 and 1 m, between 1 and 1.5 m and between 1.5 and 2 m. Cover indicates abundance or count (as a percentage) of a particular shrub height group. Coefficient of variation (CV = sd/mean) indicated by [ ] and italicised. CV ≥ 0.3 indicates a relatively high variation and is highlighted in bold.

Survey	**Farm Type**	**Shrub (< 0.5 m)**	**Shrub (0.5 > 1 m)**	**Shrub (1 > 1.5 m)**	**Shrub (1.5 > 2 m)**
2017	Core	45.3 (± 22.6) **[0.86]**	19 (± 5.5) **[0.50]**	4.5 (± 2.6) **[0.91]**	0.6 (± 0.6) **[1.73]**
	Edge	60.6 (± 13.4) **[0.38]**	20.3 (± 7.4) **[0.63]**	2.3 (± 0.6) **[0.49]**	0.3 (± 0.3) **[1.73]**
	Control	72.3 (± 19.3) **[0.46]**	21.6 (± 8.2) **[0.65]**	2.3 (± 0.8) **[0.65]**	0
2019	Core	39.6 (± 19.7) **[0.86]**	19.6 (± 4.4) **[0.38]**	9.3 (± 6.3) **[1.18]**	0.3 (± 0.3) **[1.73]**
	Edge	58 (± 15.6) **[0.46]**	27.6 (± 5.8) **[0.36]**	7 (± 2) **[0.51]**	0
	Control	68 (± 17) **[0.43]**	20.6 (± 6.1) **[0.51]**	5 (± 1) **[0.34]**	1.3 (± 1.3) **[1.73]**

App 3.8: Number of positively identified small mammal individuals per cryptic species (based on genetic identification of 2017 samples) as well as overall species richness (including cryptic species and non-cryptic species) for each farm in three different farm types (core, edge and control).

Farm type	**Farm**	***M. namaquensis***	***M. granti***	***Macro. proboscideus***	***E. rupestris***	***E. pilicaudus***	**Overall species richness**
Core	Janseboom	4	2	2	-	-	5
	Jas Kloof	6	1	1	-	-	5
	Lovedale	2	1	1	1	1	6
	Total	**12**	**4**	**4**	**2**	**2**	**7**
Edge	Hondeblaf	4	1	1	1	1	8
	Rietpoort	3	-	-	1	1	4
	Gannabos	2	1	1	-	-	5
	Total	**9**	**2**	**2**	**2**	**2**	**8**
Control	Hoezar-Wes	3	-	-	-	-	3
	Leeuwkrans	-	1	-	-	1	4
	Skurwekloof	-	3	-	-	-	2
	Total	**3**	**4**	**-**	**-**	**1**	**5**

App 3.9: Standardised MNA for small mammal taxa found on nine different farms within three farm types (core, edge and control) during two survey years (2017 = before cessation of farming activities on core farms and 2019 = after cessation of farming activities on core farms). Macroscelididae spp. = *Macro* spp., *Rhabdomys pumilio* = *R. pumilio*, *Gerbilliscus paeba* = *G. paeba*, *Micaelamys* spp. = *Mic* spp. and *Desmodillus auricularis* = *D. auricularis*.

Farm type	***Macro* spp.**	***R. pumilio***	***G. paeba***	***Mic* spp.**	***D. auricularis***	**Total**
2017						
Core 1 -*Janseboom*	9.16	0	11.66	6.66	0	27.48
Core 2 - *Jas Kloof*	2.08	0	39.58	15.62	8.33	65.61
Core 3 - *Lovedale*	3.12	0	46.87	10.41	0	60.40
Core	**14.36**	**0**	**98.11**	**32.69**	**8.33**	**153.49**
Edge 1 - *Hondeblaf*	2.5	5.00	46.66	6.66	2.50	63.32
Edge 2 - *Rietpoort*	3.12	0	11.45	9.375	0	23.94
Edge 3 - *Gannabos*	1.04	0	26.04	4.16	2.08	33.32
Edge	**6.66**	**5.00**	**84.15**	**20.195**	**4.58**	**120.58**
Control 1 - *Hoezar-Wes*	0	0	5.20	11.45	3.12	19.77
Control 2 - *Leeuwkrans*	1.04	0	4.16	3.12	2.08	10.40
Control 3 - *Skurwekloof*	0	0	5.20	6.25	0	11.45
Control	**1.04**	**0**	**14.56**	**20.82**	**5.20**	**41.62**
2019						
Core 1 -*Janseboom*	3.12	0	67.70	6.25	1.04	78.11
Core 2 - *Jas Kloof*	2.08	0	26.04	11.45	12.5	52.07
Core 3 - *Lovedale*	1.04	1.04	19.79	0	5.20	27.07
Core	**6.24**	**1.04**	**113.53**	**17.7**	**18.74**	**157.25**
Edge 1 - *Hondeblaf*	0	2.08	18.75	2.08	1.04	23.95
Edge 2 - *Rietpoort*	1.04	0	41.66	4.16	0	46.86
Edge 3 - *Gannabos*	1.04	0	5.20	0	7.29	13.53
Edge	**2.08**	**2.08**	**65.61**	**6.24**	**8.33**	**84.34**
Control 1 - *Hoezar-Wes*	0	0	20.83	0	6.25	27.08
Control 2 - *Leeuwkrans*	2.08	0	35.41	5.20	7.29	49.98
Control 3 - *Skurwekloof*	3.12	0	1.04	3.12	0	7.28
Control	**5.20**	**0**	**57.28**	**8.32**	**13.54**	**84.34**

App 3.10: Total standing biomass (g) of small mammal taxa captured during two surveys years (2017 and 2019) across three farm types (core, edge and control) as well as total standing biomass per farm type. Values in bold show average standing biomass (± standard error) (referred to as 'Ave. total') per farm type. Standing biomass was standardised per 1000 trap nights.

Survey	**Taxa**	**Standing biomass (g)**			
		Core	*Edge*	*Control*	*Total*
2017	*Gerbilliscus paeba*	1977 **(659 ± 301.6)**	2077 **(692.3 ± 395.2)**	310 **(103.3 ± 31.8)**	4364
	Desmodillus auricularis	170 **(170 ± 0)**	157 **(78.5 ± 24.7)**	158 **(79 ± 38.2)**	485
	Micaelamys spp.	944 **(314.6 ± 73.9)**	729 **(243 ± 97.5)**	601 **(200.3 ± 78.3)**	2274
	Rhabdomys pumilio	**-**	212 **(212 ± 0)**	**-**	212
	Macroscelididae spp.	496 **(165.3 ± 76.8)**	346 **(115.3 ± 66.7)**	60 **(60 ± 0)**	902
	Ave. total (± SE)	**1234.80 (± 236)**	**1384.10 (± 425)**	**450.79 (± 53.3)**	**-**
2019	*Gerbilliscus paeba*	3500 **(1166.6 ± 745.1)**	1798 **(599.3 ± 391)**	1360 **(453.3 ± 397.8)**	6658
	Desmodillus auricularis	619 **(206.3 ± 181.5)**	388 **(194 ± 227.6)**	527 **(263.5 ± 149.1)**	1534
	Micaelamys spp.	1002 **(501 ± 271.5)**	198 **(99 ± 8.4)**	335 **(167.5 ± 21.9)**	1535
	Rhabdomys pumilio	46 **(46 ± 0)**	95 **(95 ± 0)**	**-**	141
	Macroscelididae spp.	314 **(104.6 ± 15.5)**	142 **(71 ± 16.9)**	241 **(120.5 ± 37.4)**	697
	Ave. total (± SE)	**2073.50 (± 485)**	**977.28 (± 166)**	**988.74 (± 400)**	**-**

CHAPTER 4

ESTIMATING SPECIES RICHNESS AND RELATIVE ABUNDANCE OF MEDIUM AND LARGE MAMMALS BEFORE AND AFTER THE CESSATION OF SMALL LIVESTOCK FARMING

Camera trap image of a juvenile greater kudu (*Tragelaphus strepsiceros*) moving through a dry riverbed on core farm 1, taken during a 70-day camera trap survey in 2019/2020, Northern Cape, South Africa (© Michelle Blanckenberg).

Abstract

Small livestock production has significantly transformed natural land within South Africa, but the extent and nature of the impacts of this land use on biodiversity and wildlife abundance remains poorly understood. The establishment of a formal protected area (PA) within a well-established small livestock farming area in the Karoo provided a unique opportunity to investigate the response of mammal communities to the cessation of farming activities across a large area. In this chapter I used extensive camera trapping, rarefaction analysis and rank abundance within a BACI design to determine community diversity and structure of medium and large mammal communities (i.e., species richness, diversity, evenness, similarity and functional diversity) in addition to activity patterns following a change in land use from commercial sheep farming to protected area. Overall (across three surveys) I obtained 6 251 wildlife images, detecting a total 27 medium and large mammal species over 26 983 trap nights. Species richness, diversity and abundance were not significantly different between farm types and surveys years, however there were significant differences in community composition between core, edge and control farms. Daily activity patterns for several mammal species shifted significantly on core farms between surveys but remained constant on edge and control farms. Results suggest that the cessation of farming activities including the removal of sheep did not significantly impact mammal diversity and abundance in the short term. It is possible that the prolonged drought that prevailed throughout the study dampened the recovery of the vegetation and with that fauna at higher trophic levels. Long term monitoring of these sites will prove important to our understanding of the potential of land subject to prolonged livestock farming to recover and support higher levels of species richness and abundance of wildlife.

Introduction

It is estimated that approximately 77% of global agricultural land is either directly or indirectly involved with livestock production (Ilea 2009). Agricultural or arable land is often land at low elevation with highly productive soils (Ilea 2009). While protected areas (PAs) are the primary mechanism globally for preserving biodiversity they are often situated in areas with low "agricultural potential" (i.e., high elevations with poor soils) and therefore typically have naturally low biodiversity and abundance of fauna (Scott *et al.* 2001, Rouget *et al.* 2003). A large proportion of global biodiversity still persists outside of protected areas (Scott *et al*. 2001, Madhusudan 2004, Riginos *et al.* 2012, Xun *et al.* 2017, Drouilly & O'Riain 2019, Graves *et al.* 2019) and competes with diverse human land uses. It is increasingly important to understand the impacts of these land uses on biodiversity (Madhusudan 2004, Riginos *et al*. 2012) and what changes can be affected to optimise the coexistence of native fauna and flora on disturbed landscapes (Mishra *et al.* 2002, Madhusudan 2004) and ultimately either expand existing PA networks or the stewardship networks that seek coexistence with wildlife on private lands (CapeNature 2016, Drouilly 2019).

Agriculture is widely recognised as one of the primary drivers of biodiversity loss globally (Madhusudan 2004, Green 2005, Drouilly & O'Riain 2019) with intensive crop farming transforming the landscape to the point that few native species persist (McKinney & Lockwood 1999, Olden *et al.* 2004, Walker *et al*. 2004). By contrast, extensive livestock farming on natural vegetation may allow for both indigenous flora and fauna to persist albeit with marked changes in species richness and abundance (de Leeuw *et al*. 2001, O'Brien *et al.* 2003, Krausman *et al*. 2009, Schieltz & Rubenstein 2016). Overstocking remains a major threat to biodiversity (Mishra *et al.* 2001, van der Merwe *et al*. 2018) with the resultant excessive vegetation loss linked to an increased risk of desertification (particularly in semi-arid and arid regions) (Sansom 1999, Mishra *et al*. 2001, Harris 2010, van der Merwe *et al*. 2018, Ball & Tzanopoulos 2020).

Arid and semi-arid regions are particularly vulnerable to desertification from livestock with several studies investigating the role of livestock production on the reduction of vegetation cover and standing biomass and therefore the indirect impact on animal biodiversity (Olff & Ritchie 1998, Bradshaw *et al*. 2003, Kraaij & Milton 2006, Tessema *et al*. 2011, Hempson *et* *al.* 2017, Hoffman *et al.* 2018). Tessema *et al.* (2011) investigated the impacts of livestock grazing on soil nutrients, vegetation structure and plant cover in semi-arid savannah regions of Ethiopia. The authors concluded that more heavily grazed sites negatively impacted soil nutrients, plant diversity and above-ground plant biomass having an overall negative knock-on effect on the productivity of semi-arid savannah landscapes, and their ability to support biodiversity (Tessema *et al.* 2011). Van der Merwe *et al.* (2018) illustrated the effect of varying stocking rates of sheep on vegetation diversity and structure in the Karoo, concluding that even in arid regions where ecological processes like plant growth is slow, higher stocking rates still negatively impacted plant cover.

The decline in vegetation productivity of arid and semi-arid regions due to degradation caused by overgrazing is clearly evident in the Karoo (Milton & Hoffman 1994, Hempson *et al.* 2017, Hoffman *et al.* 2018, Van der Merwe *et al.* 2018). However, the direct and indirect impacts of livestock on wild animal communities is still debated (Madhusudan 2004). Competition for resources and space has been identified as the major impact livestock may have on wild animal populations, in particular wild herbivores (Mishra *et al.* 2002). On an evolutionary scale, competition is a recognised driver of resource-partitioning and niche establishment (a potentially natural and overall positive impact), however several studies have suggested that if one group has a competitive advantage over another a likely outcome will be the competitive exclusion of the poorer competitor (Bagchi *et al.* 2003, Madhusudan 2004). It can be argued that livestock have a competitive advantage over wild herbivores because of human interventions (introduction of livestock to non-native environments, buffering from environmental fluctuations through provisioning, protection from parasites and pathogens and increased protection from natural predation), which could result in a net negative impact of livestock on wild animals (Prins 2000, Mishra *et al.* 2002).

While the relationship between livestock and wild animals has been theorised there has been little adequate experimental investigation of the direct impacts of livestock competition on wild animal communities (Madhusudan 2004). Studies are often limited to the response of only a few species (e.g., Legge *et al.* 2011 only looked at the impact of livestock removal on vegetation and small mammals in Australia) or livestock are still present during the study albeit in very low numbers (Joubert & Ryan 1999, Madhusudan 2004, Hoffman & Zeller 2005, Mann 2014). Within an Indian wildlife reserve Madhusudan (2004) found a clear negative impact of livestock grazing on wild herbivore densities (namely gaur *Bos gaurus*, chitel *Axis axis* and elephant *Elephas maximus indicus*), and with the reduction in livestock densities reduced competition for grazing was associated with an increase in wild herbivore densities (Madhusudan 2004). While this type of study is beneficial for highlighting the importance of reducing livestock grazing to benefit wild animal populations, they still do not provide evidence of how wild animals would respond to the complete removal of livestock.

Several studies in the semi-arid Karoo region of South Africa have predicted the possible impact that sustained extensive livestock production has had on vegetation and wildlife, often comparing areas with and without livestock (Joubert & Ryan 1999, Todd *et al.* 2016, Mann 2014, Woodgate *et al*. 2018, Drouilly *et al.* 2018a, Nenzhelele *et al.* 2018, Drouilly & O'Riain 2019). However few studies (Krueper *et al*. 2003, Harihar *et al.* 2009, Vial *et al.* 2011, Frank *et al*. 2013) have been able to track the response of wildlife in a specific area over time from a period with livestock present to a period after livestock have been removed. The benefit of this type of experimental investigation being that one can ensure minimum bias within estimates of response variables, without making assumptions of baseline values (Block *et al.* 2001).

Medium and large mammal species (mammal species weighing more than 500 grams) represent a higher trophic level within a landscape and play a critical role within ecosystems (either as prey populations, predator populations or impacting vegetation structure) (Berger *et al*. 2001, Morrison *et al.* 2007). As a result, medium and large mammals are often sensitive to changes in habitat quantity and quality (Morrison *et al.* 2007, Ripple *et al*. 2015). As such they are good target species to act as indicators for ecosystem functioning and other lower trophic levels that may be more difficult to monitor on a large scale (Morrison *et al.* 2007, Ripple *et al*. 2015). Medium and large mammals are relatively scarce across semi-arid and arid agricultural landscapes and are typically sensitive to human presence following sustained persecution (Gompper *et al.* 2006, Long *et al.* 2007, Kelly & Holub 2008, Tobler *et al.* 2008, O'Brien *et al.* 2010). Camera traps provide a suitable non-invasive method of data collection across large areas for species that are shy and difficult to study through capture-recapture methods (Gompper *et al.* 2006, Long *et al.* 2008, Kelly & Holub 2008, O'Brien *et al*. 2010). Camera traps also provide an efficient method for surveying multiple species concurrently on a large scale, and often in areas that are difficult to work in (O'Brien *et al*. 2010). There has been an increasing trend in using large scale camera trap surveys to collect information at the community level, unlike other methods such as line transect counts or spotlight searches from cars which are often very time consuming and only provide information at a smaller local scale (Gompper *et al.* 2006, Long *et al.* 2007, Kelly & Holub 2008, O'Brien *et al.* 2010, Midlane *et al*. 2014).

Camera traps have recently been used to successfully survey medium and large mammals in both protected areas and farmland of the semi-arid Karoo region of South Africa (Drouilly *et al.* 2018, Woodgate *et al.* 2018). Camera traps were also recently used within the Square Kilometre Array (SKA) region of the Karoo as part of the Strategic Environmental Assessment (SEA) for the establishment of the SKA protected area. Together with historical data and extrapolating from other studies it was estimated that there were between 25 and 40 different wild mammal species within SKA core region (Todd & Henschel 2016, CSIR 2016a). As the core area transitions to a formally protected area, it is essential to design and run a more complete survey of species present, to assess diversity, community composition and structure of mammal populations over time.

I had two major aims for this chapter firstly, to present a more comprehensive survey of medium and large mammal species present within the SKA protected area and surrounding farms. Secondly, to investigate the short-term impact of a cessation in farming activity, including an end to hunting and the removal of sheep on wild medium and large mammal species and predators in particular. I tested the hypothesis that the removal of sheep on core sites would affect diversity, community structure and composition of medium and large wild mammals and that these effects would be magnified over time (hypothesis 1, H1).

I predicted that species richness, diversity and community structure and composition would be the same for all three farm types during the first survey (prediction 1, P1) as all three farm types lie within the same region and have been subject to small livestock farming for more than 350 years. In line with other studies comparing farmland and protected areas in semi-arid landscapes (Kinnaird & O'Brien 2012, Mann 2014, Kiffner *et al.* 2015, Drouilly *et al.* 2018a), I predicted that species richness would not change between survey years for any of the farm types despite the change in land use on the core (P2). However, during the second and third surveys I predicted that diversity would increase on core farms (P3) and that community composition would shift from baseline compositions (P4). I also predicted that the relative abundance of medium sized and large mammals would increase on core farms over the years (P5), while remaining similar on edge and control farms compared to the initial survey (P6). I further predicted that community composition and structure will remain unchanged on edge and control farms over the survey period (P7). Lastly, I predicted daily activity patterns of previously persecuted species would shift to a more even activity pattern on core farm as a result of less human disturbances (P8), while activity patterns on edge and control farms will remain constant and avoid peaks of human activity (P9).

Methods

Camera trap placement and data collection

Three separate camera trap surveys were carried out across nine small livestock farms in the Karoo, Northern Cape, South Africa. The nine small livestock farms were grouped into three categories: core (n = 3), edge (n = 3) and control (n = 3) based on their relative proximity to the SKA region of the Karoo (see Chapter 2, Figure 2.1). During survey A (summer of 2017/18) all nine farms included small livestock (predominantly sheep). In survey B (summer 2018/19) and C (summer 2019/20) livestock had been removed from the core farms for six (B) and 18 months (C) prior to the survey, respectively. Cameras were initially deployed in the summer due to logistical constraints and therefore subsequently only deployed in summer months to reduce seasonal biases that may impact comparability of detection frequencies (see Table 4.2 for specific survey dates). Bushnell Trophy CAM HD cameras (Bushnell Outdoor Products, Overland Park, Kansas, USA) were placed at 135 camera trap locations across the nine study farms (45 core camera locations, 43 edge camera locations and 52 control camera locations) (*sensu* Drouilly *et al.* 2018a). These cameras use a Passive Infra-Red (PIR) motion sensor to detect movement. Infra-red LEDs allow images to be captured at night without bright flashes potentially scaring animals passing close to the camera. These LEDs ensure camera flashes will not influence the detectability of species, especially those which are shy by nature and easily disturbed (Swann *et al.* 2004, Roberts *et al.* 2006). The Bushnell Trophy CAM HD has been used widely for detecting small and large mammals across a variety of habitats (Steenhuisen *et al.* 2015, Wang *et al.* 2015, Adila *et al.* 2017).

I had sufficient cameras to sample core, edge and control farms within the same season, but did not have sufficient resources to deploy all cameras simultaneously. Cameras were therefore deployed sequentially and collected in the same order to ensure a similar time in the field. Camera placement was according to a 2 km inter-camera distance grid pattern following Drouilly *et al.* (2018a), with the starting point for each site being randomly generated in QGIS (v3.14.16) (QGIS Development Team 2019) (Figure 4.1). The randomised grid design ensures that there is no sampling bias towards specific habitats, topography or landscape features (i.e., roads or trails), and ensures all natural and human features are sampled proportionally to their occurrence in the landscape. The spacing between camera traps can also influence the trap probability of an individual for a specific species. However different species have different characteristics that can influence this trap probability (e.g., habitat preference, diurnal versus nocturnal activity, timid nature) (O'Brien *et al.* 2010, Foster & Harmsen 2012). Different trap placement designs have therefore been used to target different species, and non-random placement is considered more effective if there is a specific target species (Foster & Harmsen 2012). During multispecies surveys, trap placement may be biased towards certain species unintentionally, resulting in varying detection probabilities for different species (O'Brien *et al.* 2010, Foster & Harmsen 2012). To limit unnecessary bias a random grid design is preferred to ensure as many species have an equal detection probability (O'Brien *et al.* 2010, Foster & Harmsen 2012).

I used a handheld Garmin GPSMAP 60Cx (Garmin International, Inc., Olathe, Kansas, USA) to find the exact position of each designated camera station. Cameras were placed within 80 m of the indicated GPS position, so that I could optimise fine scale placement (field of view, near paths or near presence of animal sign, e.g., scat or spoor) (Colyn *et al.* 2018). For each survey cameras were placed in exactly the same place facing the same direction to ensure consistency across survey years. Cameras were programmed to take three photographs if triggered (to include pairs of animals or parents and offspring) with a one-minute delay between triggers to avoid multiple photos of gregarious species (e.g., springbok or dorper sheep). The sensitivity of the infrared sensor was set on high and image size was set at 8M pixel, while LED control was set at medium and field scan was off. Cameras were attached to 10mm thick metal stakes at a height of 30 cm off the ground and typically facing outward from a bush so that they were less inconspicuous within the landscape (Figure 4.2).

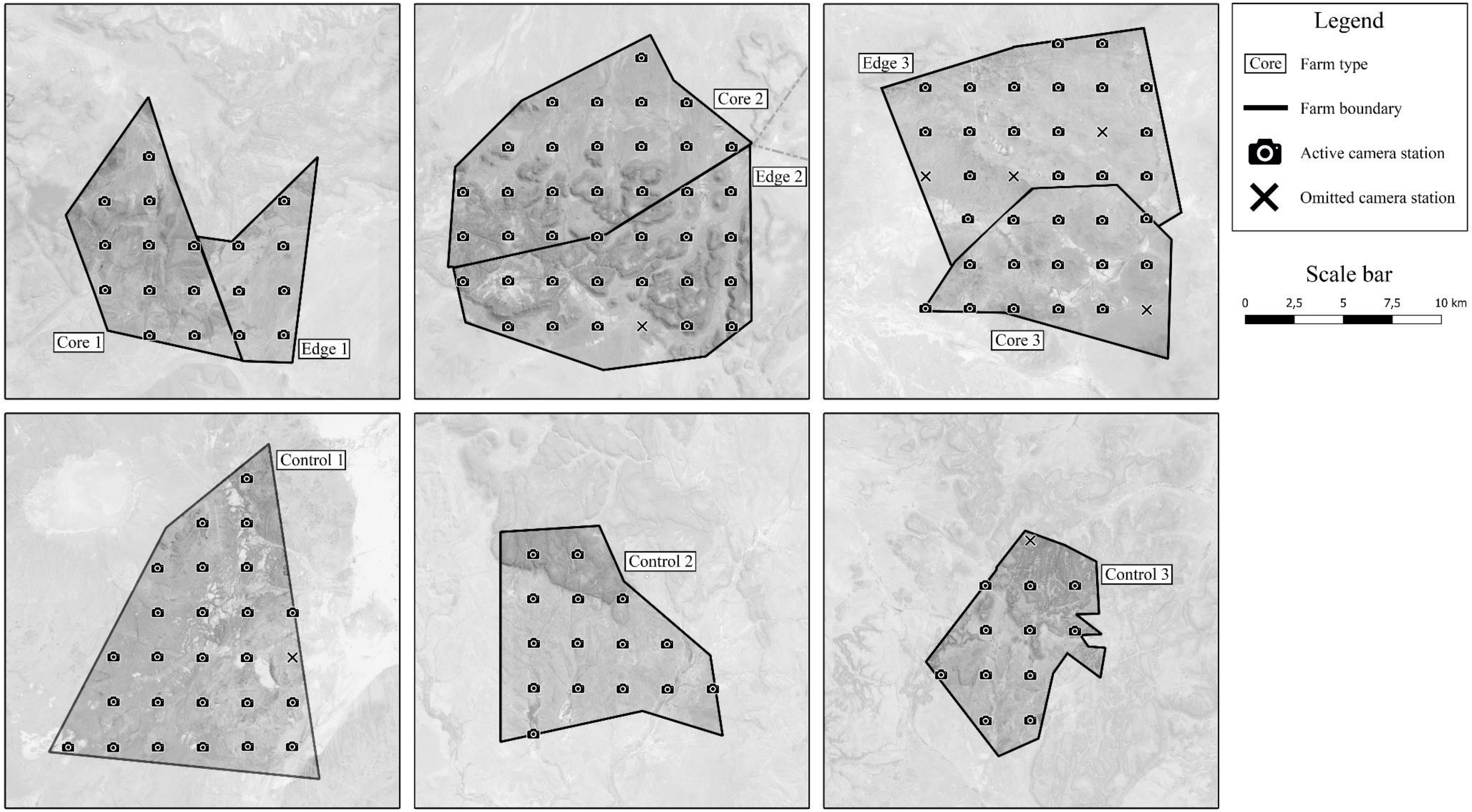


Figure 4.1: Camera trap (black camera icons) survey design across the nine small livestock farms including core (n=3 with 44 cameras), edge (n=3 with 43 cameras) and control farms (n=3 with 51 cameras). Cameras were placed at regular intervals on a randomly established 2x2 km grid. X refers to stations that were omitted because of extreme terrain and inaccessibility. Core 1 = Janseboom, Core 2 = Jas Kloof, Core 3 = Lovedale, Edge 1 = Hondeblaf, Edge 2 = Rietpoort, Edge 3 = Gannabos Leegte, Control 1 = Hoezar-Wes, Control 2 = Leeuwkrans and Control 3 = Skurwekloof.

Figure 4.2: Setting up camera traps using recycled fence droppers (A). Cameras were ideally placed with the back of the camera against a bush to provide a level of protection from the elements and camouflage (B).

Cameras were active during each survey for a minimum of 70 days to ensure all mammal species had a viable chance of being detected at any one site. Drouilly *et al.* (2018a) showed in similar landscapes a camera survey of 70 days was adequate for sampling mammal species in the Karoo. Sites were sampled for 70 – 112 days (average 75.08 days ± 2.37 standard error) during survey A (2017/18), 70 – 101 days (average 69.79 days ± 2.50 standard error) during survey B (2018/19), and 70 – 80 days (average 67.66 days ± 2.12 standard error) during survey C (2019/20). Averages that fell below 70 days were mostly due to camera failure because of premature battery failure. Battery failure was mostly linked to excessive triggers following regrowth of cleared plants (e.g., grasses) that sprouted post clearing of vegetation when establishing the camera station. Cameras which failed to capture data beyond 60 consecutive days were considered camera failures and omitted from analyses (Table 4.2). Trap nights represented a 24-hour timeframe (00:00 until 23:59). All camera data was included unless number of sampling days was below 60 days.

Camera trap data was cleaned by removing false captures (any image that did not contain an animal). I defined an independent capture if more than one image was captured 30 minutes apart. Any consecutive images of the same species within the 30 min limit were grouped and considered a single independent event to avoid auto-correlation. Images that contained individuals that were difficult to identify (e.g., night images that were over-exposed) were discarded (n = 74 in survey A, n = 40 in survey B and n = 45 in survey C) to avoid false detection during analysis. Images of domestic animals were recorded for use in sheep abundance comparisons between farm types and survey years.

Data analyses

Camera trap data is widely used to estimate the abundance or density of unmarked species within a landscape using either RAI measures or occupancy modelling. A review by Burton *et al.* (2015) of 266 camera trap studies showed that 43.6% of studies looked at relative abundance using camera trap data, while 15.4% studies focused on occupancy modelling. The major difference between the two types of analysis being the ability to account for changing species detectability (Burton *et al.* 2015, Sollmann 2018). While occupancy models are preferred when analysing camera trap data, due to their ability to estimate species occurrence while accounting for difference in detectability (resulting from species movement patterns or changes in habitat), models often perform poorly when data is either over dispersed (high prevalence of zeros) or over saturated (high prevalence of ones). Overdispersion is often assumed to result from a lack of adequate trap nights but can also occur when trapping in areas with naturally low species abundance and hence detectability (e.g., arid regions like the Karoo). Detection probabilities were incredibly low in this study with for example, naïve occupancy measures for caracal (a rare species however a main species of interest) being 0.029, and 0.156 for cape fox (a more common species) (Table 4.3). This resulted in extreme overdispersion of the data and a failure of the models to converge preventing me from being able to distinguish between true absence or low detection (MacKenzie *et al*. 2002, MacKenzie & Bailey 2004, MacKenzie *et al.* 2004). This restricted me to exploring the photographic rate (a measure of activity) of target species across survey years with standardised survey effort between surveys at the same site.

For each survey (A, B and C) and each farm type (core, edge and control) I calculated the number of independent capture events, naïve occupancy (proportion of sampled trap stations where a species was present, does not take detectability into account) and photographic rate (also known as relative abundance index, RAI) for each species. Photographic rate or RAI is calculated by dividing the total number of independent captures per farm type by the total number of trap nights all cameras were active per farm, multiplied by 100, creating a standardised species abundance per 100 trap nights for all surveys (O’Brien *et al.* 2003, Sollmann 2018). RAI does not explicitly account for detection variability within a survey therefore cannot provide true representations of abundance. Consequently, photographic rate is used here more as a measure of activity, where a given species' activity (either increasing or decreasing) at a particular site can be compared over time (Sollmann 2018). It is important to consider the effect of ecological and sampling processes when using this measure, therefore comparing like habitats spatially and temporally, as in this study, is preferred (Sollmann 2018). Photographic rate was therefore also calculated at a camera level for each species for all three surveys so that I could compare the overall change in activity. All data analyses were performed using RStudio Version 3.5.3 (RStudio Team 2019).

Diversity measures and rarefaction curves

The most used measure to describe community and regional diversity is species richness (α diversity), however calculating true species richness for an area is often impractical. Relative species richness (the proportion of species represented at a site from a regional pool of species, α diversity divided by γ diversity) helps standardise richness through sub-sampling and allows for comparisons across sites or over time. During each survey year I completed the observed species richness (S_{obs}) for each farm type, as well as the overall S_{obs} for each specific survey. I used the 'vegan' package to perform rarefaction analyses and calculate sample-based species accumulation curves that compared observed species richness between surveys (all sites pooled per year) using a 95% confidence interval based off 1000 randomisations performed with replacement. A limitation with these types of curves, however, is that they do not account for variable detectability of species and therefore may not present accurate representations of communities (not fully representing communities with rare species). Non-parametric species richness estimators were used to account for potential undetected species.

For each survey year and each farm type within a year I firstly calculated Chao 1, first-order Jackknife (Jack1) and Bootstrap estimates using the 'vegan' package (Oksanen *et al.* 2019), as well as the Chao 1 asymptotic estimate using the 'iNEXT' package (Hsieh *et al.* 2020). I then calculated the sample-based rarefaction curves for each farm type per survey year, as well as overall rarefaction curves for each survey year using the 'iNEXT' package (Hsieh *et al.* 2020). 'iNEXT' calculates hill numbers of order q ($q = 0$, species richness and $q = 1$, the exponential of Shannon entropy) and produces both rarefied and extrapolated curves against sample size and therefore shows both observed and expected species richness for a specific site (Chao *et* *al.* 2014). Hill numbers are increasingly considered more effective at measuring linear increases in species richness compared to traditional measures of diversity (Chao *et al.* 2014). Rarefaction curves in this study mainly report q = 0, however q = 1 was also reported for overall community diversity for each year. Adequate sampling to capture all species within a survey was assumed when both accumulation and rarefaction curves reached their asymptotes (Colwell *et al.* 2004).

Within each survey year for each farm type I calculated the point average farm type level species richness as well as Shannon-Weiner diversity index (H') for each community based off photographic rate (RAI) which combines species richness with relative abundance and is a more accurate representation of community diversity than α diversity. From this value I could calculate farm level Pielou's evenness (J') which quantifies the spread of species within a community. Both measures provide a standardised index for measuring diversity despite potentially unequal species sampling probabilities and are widely utilised in ecology making them comparable to other studies. From Shannon-Weiner index values I was able to calculate the effective number of species (ENS) which is the number of equally common species in a community and therefore provides a more accurate interpretation of diversity (Jost 2006) (see Chapter 3).

I used negative binomial generalized linear mixed-effects model (GLMM) (*glmer.nb* function from the 'lme4' package as these values were not normally distributed, Bates *et al.* 2015) to determine any potential changes in ENS, and Pielou's evenness and linear mixed-effects models (LMER) (*lmer* function from 'lme4' package as these values were normally distributed) to determine any potential changes in Shannon-Weiner diversity between years (set as an explanatory variable) with farm type set as a random variable (App 4.1). I further determined any potential changes between farm types using the same models with survey year set as a random variable (App 4.1). All models were run against null models, which lacked any explanatory variables, to determine if potential changes were a result of the covariable or random variable in the dataset. Where significant differences were detected, I used a Wilcox pairwise tests to determine specific difference between survey years within a specific farm type (i.e., core year A versus core year B) or between farm types (i.e., core versus edge) within a specific survey year.

Community composition and structure

While univariate diversity measures (i.e., species richness) are the more commonly used indices to explore the potential spatial and temporal differences in a community, these measures often represent an oversimplification (Avolio *et al.* 2019). Multivariate measures may help account for differences in abundance and account for how some species measures (i.e. dissimilarity indices) change through time (Collins *et al.* 2008, Avolio *et al.* 2019). Traditionally diversity measures focus more on spatial system stability or organisation however they may not provide detail on internal community "reordering" over time (Collins *et al.* 2008). I therefore used Rank Abundance Distributions (RADs) and fitted model deviance criteria to investigate the changes in community structure for each farm type across survey years (incorporating both spatial and temporal shifts) highlighting compositional shifts that could potentially be masked by a lack of change in species richness and diversity (e.g., turnover) (Whittaker 1965, Wilson 1991, Foster & Dunstan 2010, Avolio *et al.* 2019, Drouilly & O'Riain 2019). RADs are routinely used in ecology and can be grouped into two particular classes of distributions: the log-series and the lognormal (see Fig. 1 in Ulrich *et al.* 2010, Connolly *et al.* 2005, Ulrich *et al.* 2016). I therefore calculated the overall relative abundance (RAI) for each species in core, edge and control farm types for each survey year (A, B and C), and created a rank abundance distribution for each community. I then fitted null, pre-emptive, lognormal, Zipf and Zipf-Mandelbrot models to each distribution to determine if the structure of these distributions changed between farm type or year (Wilson 1991, Drouilly & O'Riain 2019). These models fall within either the log-series or lognormal distributions indicating a stabilised community influenced by many ecological factors (lognormal) or a disturbed/unstable community or early successional habitat (log-series) (Ulrich *et al.* 2010). Best fit models were determined by the minimisation of the sum of squares of the deviance between observed points and the fitted line (Wilson 1991, Drouilly & O'Riain 2019).

I further used Rank Abundance Curves (RACs) and various derived measures using the 'codyn' package (Hallett *et al.* 2020) to explore the specific complexities of community structure over time (Collins *et al.* 2008, Avolio *et al.* 2015, Hallett *et al*. 2016, Avolio *et al.* 2019). 'Codyn' is particularly suited to explore community dynamics over time and can be used across multiple replicates or treatments such as is the case in this study (Hallett *et al.* 2016). I used species RAI to track changes in community composition for each farm type between the three survey years.

The *RAC_change* function derived various measures of temporal change, including species richness, evenness, species ranks and species gains (Avolio *et al.* 2019). In this way, change in species richness (ΔS) between two time periods for a given site is calculated as:

$$\Delta S\ = (S_{t+1} - S_t)/S_{tot}$$

where St is the species richness of the survey at time t, and St+1 the richness at the same survey for time t+1. $Stot$ is the total number of species unique to both time periods. As ΔS is a proportion, richness and evenness change are bound between -1 and 1, whereby larger negative values indicate greater decreases in evenness or richness (Avolio *et al.* 2019), and rank change is bound between 0 and 0.5, where 0.5 represents the maximum rank changes possible in a community (Avolio *et al.* 2019).

I further used the *turnover* function to calculate species turnover for each farm type over the three survey years. Species turnover provides an equivalent to changes in species richness over time (Collins *et al.* 2008, Hallett *et al.* 2016). This function calculates total turnover, as well as specifically looking at species appearance and disappearance over time (Hallett *et al.* 2016). I chose to focus on disappearance turnover which represents the proportion of species lost between two survey years,

$$Disappearance\ turnover\ = \frac{species\ lost}{total\ species\ observed\ in\ both\ timepoints}$$

Turnover is bound between 0 and 1, where larger values represent a high proportion of species lost between years (Hallett *et al.* 2020). I tested for significant difference in rank abundance measures and turnover between farm types during the third survey year (Survey C) using an ANOVA test after performing a Shapiro Wilks test for normality.

I used the *dist.binary* function from the ‘ade4’ package (Dray & Dufour 2007) to calculate a dissimilarity matrix to visually display any potential community compositional clustering (Dray & Dufour 2007). I used the Jaccard Similarity index coefficient (S3 coefficient of - Gower & Legendre 1986) to create the dissimilarity matrix for each farm type in each survey year.

$$S_1 = \frac{a}{a + 2(b + c)}$$

I then applied hierarchical cluster analysis to the dissimilarity matrix to produce a cluster dendrogram which visually represents the degree of similarity between specific communities, in this case each farm type, within a specific year.

Functional diversity

To investigate potential changes in functional diversity of communities within the different farm types across the three survey years I looked at species level RAI relative to trophic level and body mass (Drouilly & O'Riain 2019). Functional diversity explores the influence of various species traits within a multidimensional space, giving insight into the functioning of an ecosystem based on the distribution of species in a niche space (Tilman 2001, Petchey & Gaston 2006, Drouilly & O'Riain 2019). I used two functional traits, trophic level (herbivore, insectivore, omnivore and carnivore) and body mass (in grams) which, as suggested by Drouilly & O'Riain (2019), represent attributes of resilience to land use change (Table 4.1). I also highlighted species experiencing different levels of persecution, with low persecution representing species that are not actively hunted by landowners, while high persecution represents species that are routinely hunted by landowners (Drouilly & O'Riain 2019). Body mass was presented as the log-transformed mean body mass in grams for both females and males for a particular species (Stuart & Stuart 2007, Drouilly & O'Riain 2019). I then calculated the functional dispersion index (FDis) for each farm type in a specific year using the *fdist* function from the 'FD' package (Laliberté & Legendre 2010). This index measures the weighted mean distance of a particular mammal species (using RAIs) in a multidimensional space, to the centroid of all species within that space (Ahumada *et al.* 2011, Laliberté & Legendre 2010, Drouilly & O'Riain 2019). I then compared the FDis between farm types within a specific year and within a specific farm type across years using an ANOVA with a post-hoc Tukey test.

Table 4.1: Trophic guild, persecution level and body mass (grams) (Stuart & Stuart 2007) for 25 wild mammal species recorded on the three farm types (core, edge and control) over three survey years in the SKA region of the Karoo, South Africa.

Species	Trophic guild	Persecution level	Body mass (grams)
Aardvark *Orycteropus afer*	Insectivore	Low	55000
Aardwolf *Proteles cristata*	Insectivore	Low	8500
African wildcat *Felis sylvestris*	Carnivore	Low	4250
Bat-eared fox *Otocyon megalotis*	Insectivore	Low	4000
Black-backed jackal *Canis mesomelas*	Carnivore	High	8000
Bontebok *Damaliscus pygargus*	Herbivore	Low	62000
Cape fox *Vulpes chama*	Carnivore	Medium	3250
Cape grey mongoose *Galerella pulverulenta*	Carnivore	Low	750
Cape ground squirrel *Xerus inauris*	Herbivore	Low	650
Cape porcupine *Hystrix africaenustralis*	Herbivore	Medium	17000
Caracal *Caracal caracal*	Carnivore	High	13000
Chacma baboon *Papio ursinus*	Omnivore	Medium	16000
Gemsbok *Oryx gazella*	Herbivore	Low	225000
Greater kudu *Tragelaphus strepsiceros*	Herbivore	Low	207500
Hare spp. *Lepus* spp.	Herbivore	Low	2950
Meerkat *Suricata suricata*	Carnivore	Low	790
Rock hyrax *Procavia capensis*	Herbivore	Low	3500
Rock rabbit spp. *Pronolagus* spp.	Herbivore	Low	1750
Small-spotted cat *Felis nigripes*	Carnivore	Low	1500
Small-spotted genet *Genetta genetta*	Carnivore	Low	2050
Springbok *Antidorcas marsupialis*	Herbivore	Low	39000
Springhare *Pedetes capensis*	Herbivore	Low	3000
Steenbok *Raphicerus campestris*	Herbivore	Low	11000
Striped polecat *Ictonyx striatus*	Carnivore	Low	950
Yellow mongoose *Cynictis penicillata*	Carnivore	Low	675

I compared species level RAI for three trophic levels (herbivore, insectivore and carnivore) between survey A and C within each farm type, as well as between farm types in Survey A and C, respectively. For this comparison I excluded survey B. Omnivores were excluded from analysis as only one species (chacma baboon) fell within this category and had very low detection rates. I used a paired Wilcox signed-rank test to compare between years, and Kruskal-Wallis tests with a post hoc pairwise wilcox test to compare between farm types within a specific year. Again, all data was tested for normality using a Shapiro wilks normality test prior to choosing an appropriate significance test.

Daily activity patterns

I used the 'overlap' package (Ridout & Linkie 2009) to determine potential shifts in the time specific species were active during different years in a particular farm type. Activity patterns can be highly variable among species with different functional traits, in different seasons or even different regions (Noor *et al.* 2017). However, at the local scale predator-prey interactions or competition can also play a role in shifting daily activity patterns (Noor *et al.* 2017). The removal of sheep from one farm type (core) may impact local interactions between species resulting in shifts in daily activity between years. I calculated the temporal overlap of 10 species which were consistently the most abundant species across farm types and survey years. Typically, temporal overlap compares the daily activity of two different species (Noor *et al.* 2017), however as I was interested in the change in daily activity for a particular species over time, I compared the temporal overlap of one species in a specific farm type over two years. I was specifically interested in how time after the cessation of farming activities would impact daily activity of wildlife therefore comparisons looked exclusively at comparing either survey A with B (six months after intervention), or survey A with C (18 months after intervention). For each comparison a coefficient of overlap, or Δ, is produced to measure the extent of overlap between two kernel density measures (in this case daily activity of one species over two years) (Noor *et al.* 2017). The Δ is bound between 0 and 1, with 0 being no overlap and 1 being complete overlap (Noor *et al.* 2017). I further obtained 95% confidence intervals using 1000 bootstrap resampling technique (Noor *et al.* 2017). As suggested by various studies a Δ coefficient below 0.70 was considered as a significant shift in daily activity patterns (Linkie & Ridout 2011, Noor *et al.* 2017, Dias *et al.* 2019). I highlighted significant shifts graphically, as well as any particular species of interest.

Results

Descriptive statistics

Over the three survey years total survey effort reached 26 983 trap nights, with 9 725 trap nights during survey A, 9 011 trap nights during survey B and 8 247 trap nights during survey C (Table 4.2). Overall, there was no significant difference in the number of trap nights between the different surveys (Table 4.2). Over the three survey years a total of 62 cameras failed (due mostly to battery deficiency before the minimum number of survey days linked to excessive triggers following regrowth of cleared plants), with 17 failing during survey A (12%), 24 failing during survey B (18%) and 21 failing during survey C (15%) (Figure 4.2).

Table 4.2: Camera trapping effort including the number of camera traps, number of trap nights and the duration of the survey on three farm types (core, edge and control) over three survey periods (A, B and C) in the SKA region of the Karoo, Northern Cape, South Africa.

Survey	Farm Type	# of camera traps	Trap nights	Sampling period	Camera failure (%)
A	Core	35	3159	Oct 2017 – Feb 2018	16
	Edge	39	3237	Oct 2017 – Feb 2018	4
	Control	42	2156	Nov 2017 – Feb 2018	16
	Total	**116**	**9725**	**Oct 2017 – Feb 2018**	**12**
B	Core	38	3192	Nov 2018 – Feb 2019	9
	Edge	36	3042	Nov 2018 – Feb 2019	12
	Control	35	2777	Nov 2018 – Feb 2019	30
	Total	**109**	**9011**	**Nov 2018 – Feb 2019**	**18**
C	Core	32	2357	Jan 2020 – Mar 2020	23
	Edge	36	2739	Jan 2020 – Mar 2020	12
	Control	44	3151	Nov 2019 – Feb 2020	12
	Total	**112**	**8247**	**Nov 2019 – Mar 2020**	**15**

Across all surveys I recorded 27 species of wild mammal (> 0.5 kg) and six species of domestic animals (dorper sheep, domestic goats, donkey, dog, domestic cat and domestic horse) (Table 4.3). Of the 27 wild mammal species two were extra limital species (typically introduced for hunting): Bontebok (*Damaliscus pygargus*) and Gemsbok (*Oryx gazella*) (Figure 4.4). Wild mammals ranged in size from the cape ground squirrel (*Xerus inauris*) with an average body mass of 650 grams, to the gemsbok (*Oryx gazella*) with an average body mass of 225 kg (Table 4.1).

Trapping rate (number of wildlife captures divided by trap nights) was consistently low across the three surveys (A = 0.23, B = 0.26 and C = 0.19), stable for core sites (0.23 for survey A and 0.24 for survey B and C), and more variable on both edge and control sites (edge ranged from 0.24 in survey A, 0.29 in survey B and 0.15 in survey C, while control ranged from 0.33 in survey A, 0.23 in survey B and 0.20 in survey C). There were no significant differences in trapping rates between farm types (ANOVA F = 1.2, p = 0.73) or survey years (ANOVA F = 2.3, p = 0.45). Sheep captures remained fairly constant on edge and control farms between the three survey years, with no to a few sheep captures in survey B and C on core farms, consistent with the agreed removal of sheep following survey A (Table 4.3).

Table 4.3: Number of wildlife captures, and number of species recorded during three extensive camera trap surveys (A = 2017/18, B = 2018/19 and C = 2019/20) across three different farm types (core, edge and control).

Survey	Farm Type	No. of mammal species	No. of independent wildlife images	No. of domestic animal species	No. of independent domestic animal images	No. of independent sheep images
A	Core	22	729	3	323	310
	Edge	23	796	2	217	215
	Control	23	733	4	690	678
	Total	**27**	**2258**	**6**	**1230**	**1203**
B	Core	22	796	2	3	0
	Edge	21	902	1	124	124
	Control	22	660	3	350	344
	Total	**24**	**2358**	**5**	**477**	**468**
C	Core	24	573	2	5	2
	Edge	18	421	4	100	92
	Control	24	641	3	432	429
	Total	**27**	**1635**	**6**	**537**	**523**

Within core farms members of the Leporidae (i.e., rabbits and hares) (total n = 852) were the most frequently captured mammal family (Table 4.4). Within edge and control farms Leporidae (edge: total n = 599, control: n = 707) was again the most frequently captured mammal family (Table 4.5 and 4.6). On core sites hare spp. (*Lepus capensis* and *Lepus saxatilis* were pooled as they are too difficult to reliably identify to species level using camera trap images) were detected at the most camera station across all three years (naïve occupancy), while in survey A caracal (*Caracal caracal*) and cape ground squirrel (*Xerus inauris*) were detected at the least camera stations (Table 4.4). During survey B on core farms aardvark (*Orycteropus afer*) was the least detected species and in survey C rock hyrax (*Procavia capensis*) and chacma baboon (*Papio ursinus*) were the least detected species (Table 4.4). On edge farms during survey A and B, hare spp. were detected at the most trap stations while during survey C bat-eared fox (*Otocyon megalotis*) was detected at the most camera trap stations (Table 4.5). During survey A, greater kudu (*Tragelaphus strepsiceros*), African wildcat (*Felis sylvestris*), small-spotted cat (*Felis nigripes*) and caracal were detected at the least camera stations, while in survey B small-spotted cat was detected least and in survey C again small-spotted cat and kudu as well as small-spotted genet (*Genetta genetta*) were detected at the least camera stations (Table 4.5). On control farms hare spp. were again detected at the most camera station across all three surveys (Table 4.6). Bontebok (*Damaliscus pygargus*), gemsbok and small-spotted genet were detected at the least camera station during survey A, while small-spotted cat was detected the least during survey B (Table 4.6). During survey C greater kudu, small-spotted cat, caracal, springhare (*Pedetes capensis*) and small-spotted genet were all equally detected at the least camera stations (Table 4.6). Small-spotted cat, chacma baboon and springhare were the rarest species captured across all survey years, with small-spotted cat and chacma baboon being detected on only two farms, and springhare only being detected once on one farm during the third survey (Table 4.4, 4.5 and 4.6).

Table 4.4: Summarised results of the number of independent captures of individual species grouped by family for three camera trap surveys (A = 2017/18, B = 2018/19 and C = 2019/20) on core farms. Species completely absent (not detected) on a specific farm type are highlighted in grey. Naïve occupancy indicates the proportion of camera stations where a species was detected, while photographic rate (also known as relative abundance index) indicates the trapping rate of a species per 100 trap nights.

Family Species	**Number of independent captures**			**Number of cameras where species was detected**			**Naïve occupancy**			**Photographic rate**		
	A	*B*	*C*	*A*	*B*	*C*	*A*	*B*	*C*	*A*	*B*	*C*
Bovidae	**107**	**63**	**188**	**29**	**22**	**17**	**0.82**	**0.57**	**0.53**	**3.38**	**1.97**	**7.97**
Bontebok *Damaliscus pygargus*	0	0	0	0	0	0	0	0	0	0	0	0
Gemsbok *Oryx gazella*	0	0	0	0	0	0	0	0	0	0	0	0
Greater kudu *Tragelaphus strepsiceros*	3	0	4	3	0	2	0.08	0	0.06	0.09	0	0.17
Springbok *Antidorcas marsupialis*	35	20	22	9	6	6	0.25	0.15	0.18	1.10	0.62	0.93
Steenbok *Raphicerus campestris*	69	43	162	21	18	11	0.60	0.47	0.34	2.18	1.34	6.87
Canidae	**83**	**103**	**94**	**28**	**21**	**19**	**0.80**	**0.55**	**0.59**	**2.62**	**3.22**	**3.98**
Black-backed jackal *Canis mesomelas*	20	18	28	10	9	9	0.28	0.23	0.28	0.63	0.56	1.18
Bat-eared fox *Otocyon megalotis*	36	58	50	13	14	12	0.37	0.36	0.37	1.14	1.81	2.12
Cape fox *Vulpes chama*	27	27	16	14	12	5	0.40	0.31	0.15	0.85	0.84	0.67
Cercopithecidae	**1**	**3**	**1**	**1**	**3**	**1**	**0.02**	**0.07**	**0.03**	**0.03**	**0.09**	**0.04**
Chacma baboon *Papio ursinus*	1	3	1	1	3	1	0.02	0.07	0.03	0.03	0.09	0.04
Felidae	**12**	**20**	**9**	**6**	**11**	**9**	**0.17**	**0.28**	**0.28**	**0.38**	**0.62**	**0.38**
African wildcat *Felis sylvestris*	11	11	4	5	6	4	0.14	0.15	0.12	0.34	0.34	0.17
Small-spotted cat *Felis nigripes*	0	0	0	0	0	0	0	0	0	0	0	0
Caracal *Caracal caracal*	1	9	5	1	5	5	0.02	0.13	0.15	0.03	0.28	0.21
Herpestidae	**46**	**32**	**18**	**20**	**20**	**8**	**0.57**	**0.52**	**0.25**	**1.45**	**1.00**	**0.76**
Cape grey mongoose *Galerella pulverulenta*	13	9	8	5	7	4	0.14	0.18	0.12	0.41	0.28	0.33
Meerkat *Suricata suricata*	15	10	0	13	9	0	0.37	0.23	0	0.47	0.31	0
Yellow mongoose *Cynictis penicillata*	18	13	10	9	9	5	0.25	0.23	0.15	0.57	0.40	0.42
Hyaenidae	**23**	**27**	**15**	**12**	**12**	**10**	**0.34**	**0.31**	**0.31**	**0.72**	**0.84**	**0.63**
Aardwolf *Proteles cristata*	23	27	15	12	12	10	0.34	0.31	0.31	0.72	0.84	0.63
Hystricidae	**23**	**26**	**24**	**6**	**9**	**12**	**0.17**	**0.23**	**0.37**	**0.72**	**0.81**	**1.01**
Cape porcupine *Hystrix africaenustralis*	23	26	24	6	9	12	0.17	0.23	0.37	0.72	0.81	1.01

Leporidae	**334**	**364**	**158**	**33**	**33**	**30**	**0.94**	**0.86**	**0.93**	**10.57**	**11.40**	**6.70**
Hare spp. *Lepus* spp.	287	326	125	32	26	24	0.91	0.68	0.75	9.08	10.21	5.30
Rock rabbit spp. *Pronolagus* spp.	47	38	33	7	9	7	0.20	0.23	0.21	1.48	1.19	1.40
Mustelidae	**27**	**27**	**13**	**11**	**12**	**10**	**0.31**	**0.31**	**0.31**	**0.85**	**0.84**	**0.55**
Striped polecat *Ictonyx striatus*	27	27	13	11	12	10	0.31	0.31	0.31	0.85	0.84	0.55
Orycteropodidae	**8**	**3**	**4**	**6**	**3**	**3**	**0.17**	**0.07**	**0.09**	**0.25**	**0.09**	**0.17**
Aardvark *Orycteropus afer*	8	3	4	6	3	3	0.17	0.07	0.09	0.25	0.09	0.17
Pedetidae	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
Springhare *Pedetes capensis*	0	0	0	0	0	0	0	0	0	0	0	0
Procaviidae	**50**	**48**	**8**	**11**	**10**	**1**	**0.31**	**0.26**	**0.03**	**1.58**	**1.50**	**0.33**
Rock hyrax *Procavia capensis*	50	48	8	11	10	1	0.31	0.26	0.03	1.58	1.50	0.33
Sciuridae	**3**	**23**	**2**	**1**	**5**	**2**	**0.02**	**0.13**	**0.06**	**0.09**	**0.72**	**0.08**
Cape ground squirrel *Xerus inauris*	3	23	2	1	5	2	0.02	0.13	0.06	0.09	0.72	0.08
Viverridae	**7**	**10**	**12**	**7**	**7**	**6**	**0.20**	**0.18**	**0.18**	**0.22**	**0.31**	**0.50**
Small-spotted genet *Genetta genetta*	7	10	12	7	7	6	0.20	0.18	0.18	0.22	0.31	0.50

Table 4.5: Summarised results of the number of independent captures of individual species grouped by family for three camera trap surveys (A = 2017/18, B = 2018/19 and C = 2019/20) on edge farms. Species completely absent (not detected) on a specific farm type are highlighted in grey. Naïve occupancy indicates the proportion of camera stations where a species was detected, while photographic rate (also known as relative abundance index) indicates the trapping rate of a species per 100 trap nights.

Family Species	**Number of independent captures**			**Number of cameras where species was detected**			**Naïve occupancy**			**Photographic rate**		
	A	*B*	*C*	*A*	*B*	*C*	*A*	*B*	*C*	*A*	*B*	*C*
Bovidae	**180**	**145**	**122**	**25**	**22**	**21**	**0.64**	**0.61**	**0.58**	**5.56**	**4.76**	**4.45**
Bontebok *Damaliscus pygargus*	0	0	0	0	0	0	0	0	0	0	0	0
Gemsbok *Oryx gazella*	0	0	0	0	0	0	0	0	0	0	0	0
Greater kudu *Tragelaphus strepsiceros*	1	0	1	1	0	1	0.02	0	0.02	0.03	0	0.03
Springbok *Antidorcas marsupialis*	132	112	89	15	13	11	0.38	0.36	0.30	4.07	3.68	3.24
Steenbok *Raphicerus campestris*	47	33	32	15	11	10	0.38	0.30	0.27	1.45	1.08	1.16
Canidae	**79**	**146**	**137**	**19**	**25**	**28**	**0.48**	**0.69**	**0.77**	**2.44**	**4.79**	**5.00**

Black-backed jackal *Canis mesomelas*	6	20	11	5	9	8	0.12	0.25	0.22	0.18	0.65	0.40
Bat-eared fox *Otocyon megalotis*	58	107	114	15	15	25	0.38	0.41	0.69	1.79	3.51	4.16
Cape fox *Vulpes chama*	15	19	12	7	10	8	0.17	0.27	0.22	0.46	0.62	0.43
Cercopithecidae	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
Chacma baboon *Papio ursinus*	0	0	0	0	0	0	0	0	0	0	0	0
Felidae	**3**	**9**	**3**	**3**	**7**	**3**	**0.07**	**0.19**	**0.08**	**0.09**	**0.29**	**0.11**
African wildcat *Felis sylvestris*	1	7	0	1	6	0	0.02	0.16	0	0.03	0.23	0
Small-spotted cat *Felis nigripes*	1	2	1	1	1	1	0.02	0.02	0.02	0.03	0.06	0.03
Caracal *Caracal caracal*	1	0	2	1	0	2	0.02	0	0.05	0.03	0	0.07
Herpestidae	**61**	**92**	**16**	**22**	**25**	**9**	**0.56**	**0.69**	**0.25**	**1.88**	**3.02**	**0.58**
Cape grey mongoose *Galerella pulverulenta*	12	18	0	7	5	0	0.17	0.13	0	0.37	0.59	0
Meerkat *Suricata suricata*	25	26	0	9	16	0	0.23	0.44	0	0.77	0.85	0
Yellow mongoose *Cynictis penicillata*	24	48	16	12	17	9	0.30	0.47	0.25	0.74	1.57	0.58
Hyaenidae	**26**	**15**	**9**	**12**	**8**	**5**	**0.30**	**0.22**	**0.13**	**0.80**	**0.49**	**0.32**
Aardwolf *Proteles cristata*	26	15	9	12	8	5	0.30	0.22	0.13	0.80	0.49	0.32
Hystricidae	**10**	**13**	**3**	**6**	**7**	**3**	**0.15**	**0.19**	**0.08**	**0.30**	**0.42**	**0.11**
Cape porcupine *Hystrix africaeaustralis*	10	13	3	6	7	3	0.15	0.19	0.08	0.30	0.42	0.11
Leporidae	**238**	**258**	**103**	**24**	**27**	**18**	**0.61**	**0.75**	**0.50**	**7.35**	**8.48**	**3.76**
Hare spp. *Lepus* spp.	227	258	101	23	27	17	0.59	0.75	0.47	7.01	8.48	3.68
Rock rabbit spp. *Pronolagus* spp.	11	0	2	2	0	2	0.05	0	0.05	0.34	0	0.07
Mustelidae	**26**	**28**	**7**	**9**	**10**	**5**	**0.23**	**0.27**	**0.13**	**0.80**	**0.92**	**0.25**
Striped polecat *Ictonyx striatus*	26	28	7	9	10	5	0.23	0.27	0.13	0.80	0.92	0.25
Orycteropodidae	**7**	**4**	**9**	**3**	**3**	**5**	**0.07**	**0.08**	**0.13**	**0.21**	**0.13**	**0.32**
Aardvark *Orycteropus afer*	7	4	9	3	3	5	0.07	0.08	0.13	0.21	0.13	0.32
Pedetidae	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
Springhare *Pedetes capensis*	0	0	0	0	0	0	0	0	0	0	0	0
Procaviidae	**129**	**83**	**0**	**8**	**6**	**0**	**0.20**	**0.16**	**0**	**3.98**	**2.72**	**0**
Rock hyrax *Procavia capensis*	129	83	0	8	6	0	0.20	0.16	0	3.98	2.72	0
Sciuridae	**2**	**28**	**10**	**2**	**8**	**6**	**0.05**	**0.22**	**0.16**	**0.06**	**0.92**	**0.36**

Cape ground squirrel *Xerus inauris*	2	28	10	2	8	6	0.05	0.22	0.16	0.06	0.92	0.36
Viverridae	**10**	**4**	**1**	**3**	**4**	**1**	**0.07**	**0.11**	**0.02**	**0.30**	**0.13**	**0.03**
Small-spotted genet *Genetta genetta*	10	4	1	3	4	1	0.07	0.11	0.02	0.30	0.13	0.03

Table 4.6: Summarised results of the number of independent captures of individual species grouped by family for three camera trap surveys (A = 2017/18, B = 2018/19 and C = 2019/20) on control farms. Species completely absent (not detected) on a specific farm type are highlighted in grey. Naïve occupancy indicates the proportion of camera stations where a species was detected, while photographic rate (also known as relative abundance index) indicates the trapping rate of a species per 100 trap nights.

Family Species	**Number of independent captures**			**Number of cameras where species was detected**			**Naïve occupancy**			**Photographic rate**		
	A	*B*	*C*	*A*	*B*	*C*	*A*	*B*	*C*	*A*	*B*	*C*
Bovidae	**99**	**92**	**36**	**26**	**10**	**10**	**0.61**	**0.28**	**0.22**	**4.59**	**3.31**	**1.14**
Bontebok *Damaliscus pygargus*	1	0	0	1	0	0	0.02	0	0	0.04	0	0
Gemsbok *Oryx gazella*	1	0	0	1	0	0	0.02	0	0	0.04	0	0
Greater kudu *Tragelaphus strepsiceros*	0	0	3	0	0	1	0	0	0.02	0	0	0.09
Springbok *Antidorcas marsupialis*	53	40	5	7	4	4	0.16	0.11	0.09	2.45	1.44	0.15
Steenbok *Raphicerus campestris*	44	52	28	23	7	7	0.54	0.20	0.15	2.04	1.87	0.88
Canidae	**186**	**99**	**144**	**34**	**30**	**34**	**0.81**	**0.85**	**0.77**	**8.62**	**3.56**	**4.57**
Black-backed jackal *Canis mesomelas*	3	8	16	3	6	10	0.07	0.17	0.22	0.13	0.28	0.50
Bat-eared fox *Otocyon megalotis*	54	40	76	19	12	22	0.45	0.34	0.50	2.50	1.44	2.41
Cape fox *Vulpes chama*	129	51	52	31	20	24	0.73	0.57	0.54	5.98	1.83	1.65
Cercopithecidae	**0**	**0**	**1**	**0**	**0**	**1**	**0**	**0**	**0.02**	**0**	**0**	**0.03**
Chacma baboon *Papio ursinus*	0	0	1	0	0	1	0	0	0.02	0	0	0.03
Felidae	**8**	**3**	**5**	**6**	**3**	**4**	**0.14**	**0.08**	**0.09**	**0.37**	**0.10**	**0.15**
African wildcat *Felis sylvestris*	5	0	2	4	0	2	0.09	0	0.04	0.23	0	0.06
Small-spotted cat *Felis nigripes*	0	1	1	0	1	1	0	0.02	0.02	0	0.03	0.03
Caracal *Caracal caracal*	3	2	2	2	2	1	0.04	0.05	0.02	0.13	0.07	0.06
Herpestidae	**60**	**30**	**41**	**23**	**13**	**23**	**0.54**	**0.37**	**0.52**	**2.78**	**1.08**	**1.30**
Cape grey mongoose *Galerella pulverulenta*	17	3	7	9	2	5	0.21	0.05	0.11	0.78	0.10	0.22
Meerkat *Suricata suricata*	10	14	10	6	8	5	0.14	0.22	0.11	0.46	0.50	0.31

Yellow mongoose *Cynictis penicillata*	33	13	24	16	8	15	0.38	0.22	0.34	1.53	0.46	0.76
Hyaenidae	**98**	**57**	**39**	**27**	**16**	**18**	**0.64**	**0.45**	**0.40**	**4.54**	**2.05**	**1.23**
Aardwolf *Proteles cristata*	98	57	39	27	16	18	0.64	0.45	0.40	4.54	2.05	1.23
Hystricidae	**7**	**5**	**19**	**4**	**2**	**10**	**0.09**	**0.05**	**0.22**	**0.32**	**0.18**	**0.60**
Cape porcupine *Hystrix africaenustralis*	7	5	19	4	2	10	0.09	0.05	0.22	0.32	0.18	0.60
Leporidae	**209**	**219**	**279**	**35**	**27**	**28**	**0.83**	**0.77**	**0.63**	**9.69**	**7.88**	**8.85**
Hare spp. *Lepus* spp.	200	213	271	32	25	25	0.76	0.71	0.56	9.27	7.67	8.60
Rock rabbit spp. *Pronolagus* spp.	9	6	8	4	2	3	0.09	0.05	0.06	0.41	0.21	0.25
Mustelidae	**7**	**4**	**8**	**7**	**3**	**6**	**0.16**	**0.08**	**0.13**	**0.32**	**0.14**	**0.25**
Striped polecat *Ictonyx striatus*	7	4	8	7	3	6	0.16	0.08	0.13	0.32	0.14	0.25
Orycteropodidae	**7**	**7**	**18**	**7**	**6**	**13**	**0.16**	**0.17**	**0.29**	**0.32**	**0.25**	**0.57**
Aardvark *Orycteropus afer*	7	7	18	7	6	13	0.16	0.17	0.29	0.32	0.25	0.57
Pedetidae	**0**	**0**	**1**	**0**	**0**	**1**	**0**	**0**	**0.02**	**0**	**0**	**0.03**
Springhare *Pedetes capensis*	0	0	1	0	0	1	0	0	0.02	0	0	0.03
Procaviidae	**33**	**27**	**25**	**7**	**4**	**5**	**0.16**	**0.11**	**0.11**	**1.53**	**0.97**	**0.79**
Rock hyrax *Procavia capensis*	33	27	25	7	4	5	0.16	0.11	0.11	1.53	0.97	0.79
Sciuridae	**16**	**33**	**9**	**4**	**2**	**4**	**0.09**	**0.05**	**0.09**	**0.74**	**1.18**	**0.28**
Cape ground squirrel *Xerus inauris*	16	33	9	4	2	4	0.09	0.05	0.09	0.74	1.18	0.28
Viverridae	**1**	**2**	**1**	**1**	**2**	**1**	**0.02**	**0.05**	**0.02**	**0.04**	**0.07**	**0.03**
Small-spotted genet *Genetta genetta*	1	2	1	1	2	1	0.02	0.05	0.02	0.04	0.07	0.03

Diversity measures and rarefaction curves

Observed species richness was highest during survey A, followed by survey C and then survey B. Chao 1, Jack 1 and Bootstrap all estimated higher species richness overall and for individual farm types during survey A and survey B, while survey B had similar observed versus estimated species richness (Table 4.7). Species accumulation curves for the pooled farm types showed survey B was the only survey where the curve levelled off (after 5 000 trap nights), while survey A and B did not reach their asymptote for the same effort (Figure 4.3).

Table 4.7: Pooled observed (S_{obs}) and estimated (± SE) species richness of wild mammals detected during three different surveys (A = 2017/18, B = 2018/19 and C = 2019/20) across three different farm types. Species richness estimates include Chao 1, first order Jackknife (Jack 1) and bootstrap. Total number of camera trap nights per year indicated by n.

Survey	S_{obs}	Chao 1	Jack 1	Bootstrap	n
A	24	29.94 (± 7.20)	27.96 (± 1.98)	25.50 (± 0.98)	9725
B	21	21 (± 0)	21 (± 0)	21.18 (± 0.40)	9011
C	23	23.24 (± 0.72)	23.99 (± 0.99)	23.66 (± 0.70)	8247

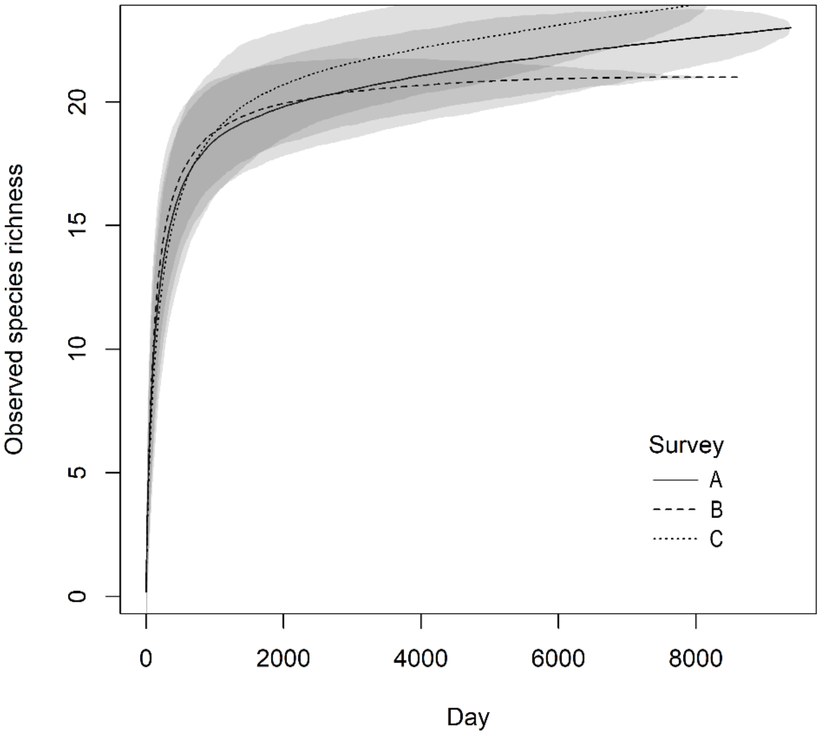


Figure 4.3: Sample-based species accumulation curves of total wild mammals pooled across three farm types (core, edge and control) during three different survey years (A = 2017/18 before intervention on core farms, B = 2018/19 six months after intervention on core farms and C = 2019/20 eighteen months after intervention). Shaded areas represent 95% confidence interval drawn from 1000 randomisations performed with replacement.

At the level of farm type, control sites during survey C had the highest observed richness (S_{obs} = 23 species), while edge sites during survey C had the lowest observed richness (S_{obs} = 17 species) (Table 4.8). Asymptotic estimates were highest overall for survey A (total = 29.95 ± 7.22) and lowest for survey B (Table 4.8). Estimates at the farm level were highest for control sites in survey C (40.64 ± 23.16) (Table 4.8).

Table 4.8: Observed (S_{obs}) and asymptotic estimated (± SE) species richness of wild mammals detected during three different surveys (A = 2017/18, B = 2018/19 and C = 2019/20) on three different farm types (core, edge and control). 95% confidence intervals drawn from 1000 randomisations performed with replacement.

Survey	Farm Type	S_{obs}	Asymptotic estimate (± SE)	95% confidence interval
A	Core	21	23.93 (± 4.47)	21.34 – 46.17
	Edge	21	24.90 (± 5.18)	21.54 – 49.12
	Control	21	25.41 (± 7.05)	21.48 – 61.15
	Total	**24**	**29.95 (± 7.22)**	**24.92 – 62.40**
B	Core	20	20.00 (± 0.33)	20.00 – 20.78
	Edge	18	18.00 (± 0.54)	18.00 – 19.56
	Control	19	19.08 (± 0.33)	19.00 – 21.24
	Total	**21**	**21.00 (± 0.40)**	**21.00 – 21.98**
C	Core	20	20.97 (± 1.83)	20.08 – 30.86
	Edge	17	19.19 (± 3.32)	17.25 - 35.65
	Control	23	40.64 (± 23.16)	25.48 – 148.50
	Total	**23**	**23.24 (± 0.72)**	**23.01 – 27.70**

Sampled-based rarefaction curves only reached a clear asymptote for all three farm types from ca. 50 active camera traps in the 2018/19 summer (Figure 4.4B). In survey periods A and C rarefaction curves never reach their asymptote (Figure 4.4A and C). Rarefaction curves pooled across farm types reached an asymptote in in survey B and C from ca. 140 active camera traps, while survey C continued to increase with effort (Figure 4.4D). Comparatively rarefaction curves representing Shannon-Weiner diversity (hill number q = 1) for all three surveys (pooled over three farm types) reached an asymptote from 100 active camera traps (Figure 4.5 - 1).

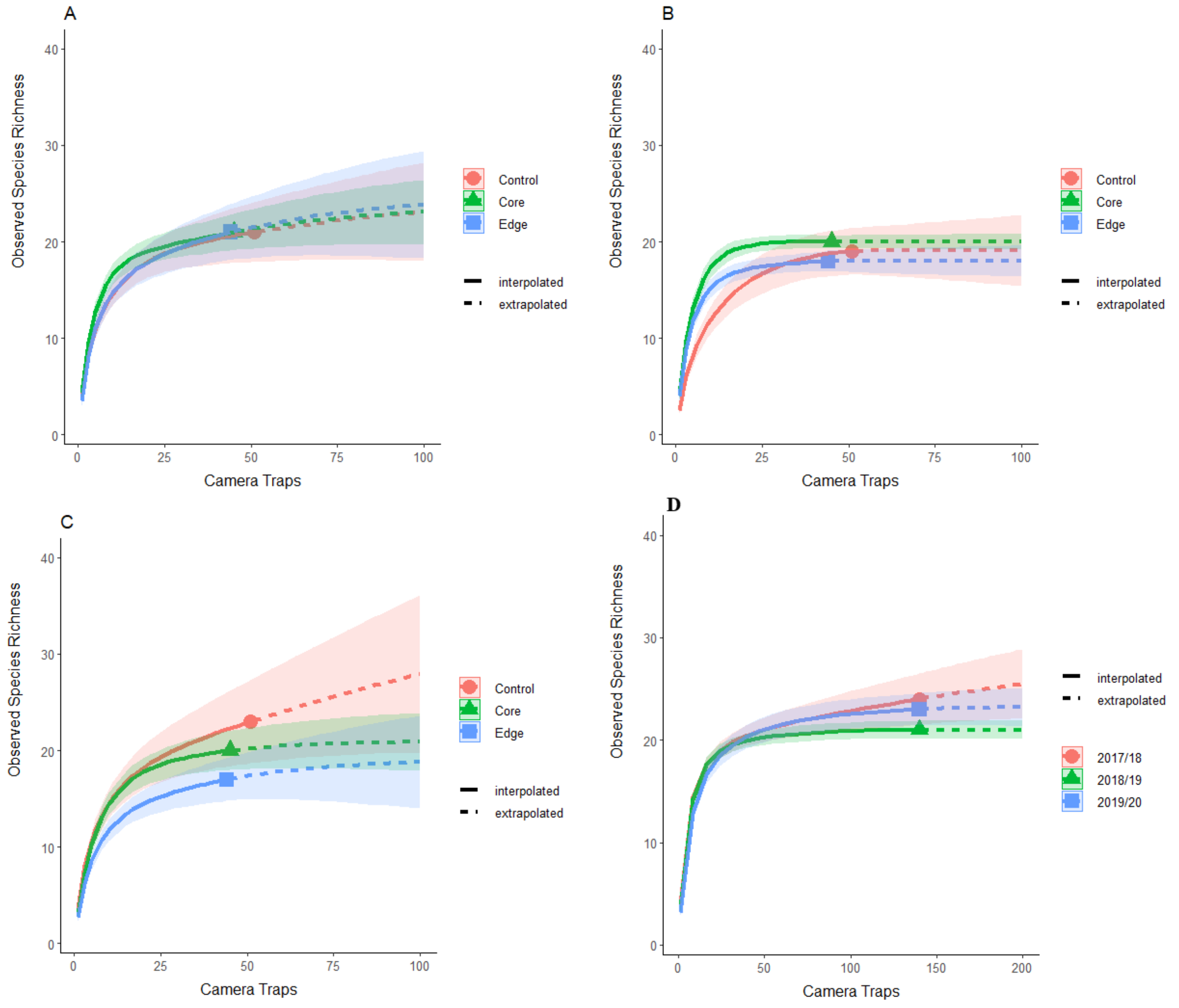


Figure 4.4: Sample-based rarefaction curves of wild mammals captured across three farm types, control farms (red line), edge farms (blue line) and core farms (green line) during three different survey years (A: 2017/18 before the intervention on core farms, B: 2018/19 six months after the intervention on core farms and C: 2019/20 eighteen months after the intervention). D shows observed species richness for data pooled across all three farm types in each of the three survey years. Shaded areas represent 95% confidence interval drawn from 1000 randomisations performed with replacement. Solid lines indicate observed richness, while dotted lines indicate expected species richness. X-axis represents number of active camera traps.

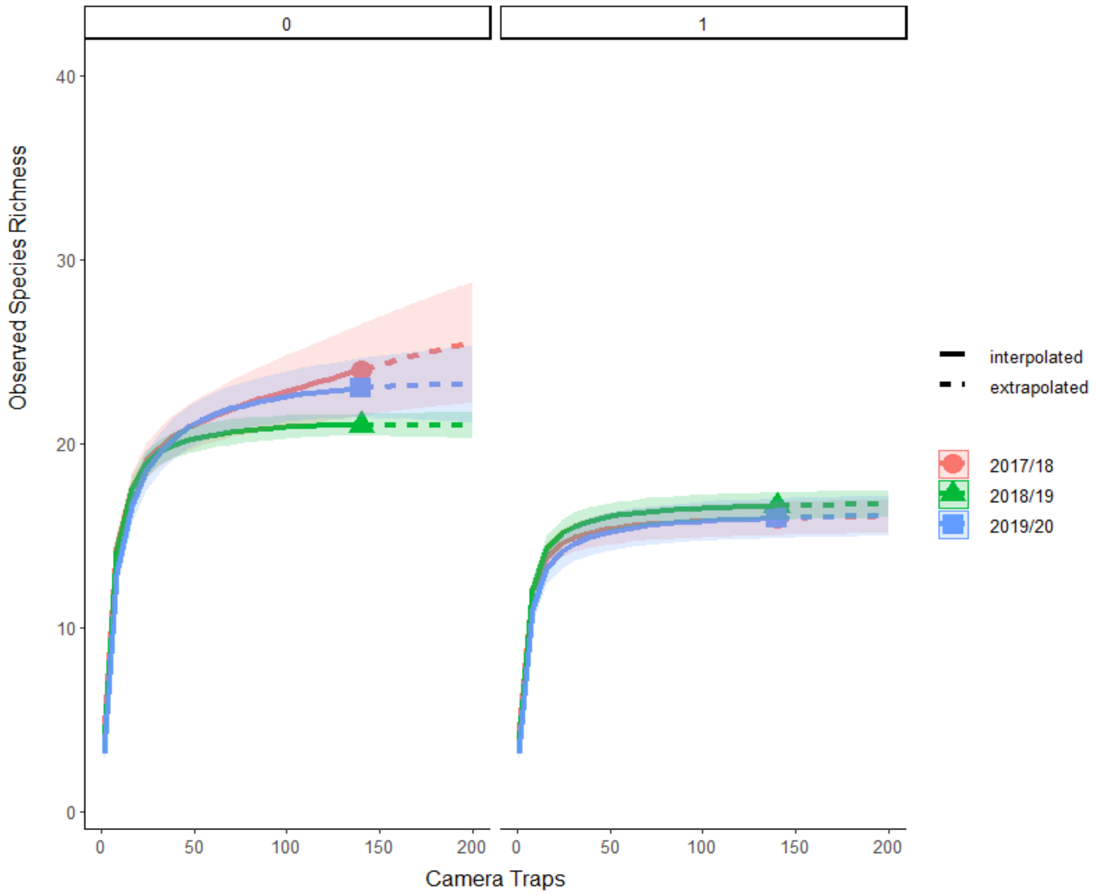


Figure 4.5: Sample-based rarefaction curves of wild mammals captured across three farm types during three different survey years (2017/18 before the intervention on core farms, 2018/19 six months after the intervention on core farms and 2019/20 eighteen months after the intervention). 0 represents overall species richness curve (hill number q = 0), and 1 indicates overall Shannon-Weiner diversity curves (hill number q = 1). Shaded areas represent 95% confidence interval drawn from 1000 randomisations performed with replacement. Solid lines indicate observed richness, while dotted lines indicate expected species richness. X-axis represents number of active camera traps.

There was a trend of decreasing effective number of species (ENS) for all farm types over the three survey years (Figure 4.6A). A similar trend was seen for Shannon-Weiner diversity however this decrease was less prominent (Figure 4.6B). Pielou’s evenness was constant for all farm types between survey’s A and B, however there was a slight decrease for all farm type during survey C (Figure 4.6C). Results for GLMER and LMER models indicated that null models for both Shannon-Wiener diversity and Pielou’s evenness had a lower AIC compared to models including covariables, indicating these models were not significant and any variation in the data was attributed to random variation (see App 4.1). GLMER models for ENS resulted in the null AIC being lower than models with covariables therefore this model was reported, and data was further investigated using pairwise tests (see App 4.1).

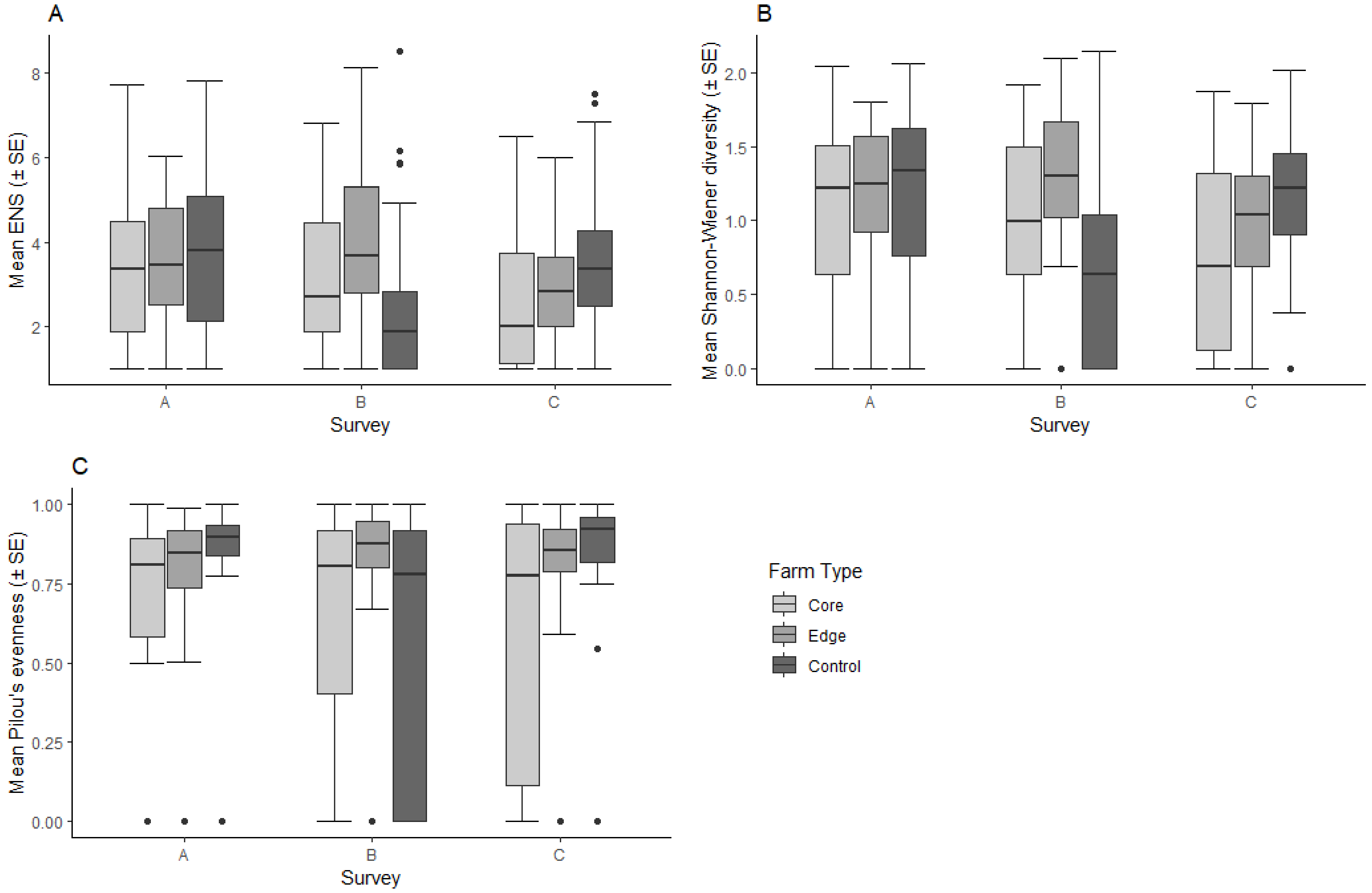


Figure 4.6: (A) Mean effective number of species (± SE), (B) mean Shannon-Weiner Diversity (± SE) and (C) mean Pielou's evenness (± SE) for three farm types (core, edge and control) between three different survey years (A = 2017/18, B = 2018/19 and C = 2019/20). Shaded boxes indicate lower quartile, median (thick black line) and upper quartile for each measure, while black dot indicates mean values with error bars representing standard error.

GLMERs indicate that survey had a significant effect on ENS across all farm types, while farm type had a slight significant effect (Table 4.9A). Univariate analysis indicated that ENS on core farms did not differ significantly between survey years (Table 4.9B). On edge farms ENS decreased significantly during survey C compared to survey A (p = 0.05) and B (p = 0.05), while there was no significant difference between survey A and B (Table 4.9B). On control farms ENS was significantly lower during survey B compared to survey A (p < 0.001) and survey C (p = 0.002), while the increase in ENS from survey B to survey C resulted in no significant difference between survey A and survey C (Table 4.9B).

There was no significant difference in ENS between any farm type during survey A (Table 4.9B). During survey B ENS for control farms was significantly lower than core (p = 0.01) and edge farms (p < 0.001), while ENS was not significantly different between core and edge farms (Table 4.9B). During survey C ENS was significantly lower on core farms compared to control farms (p = 0.03), while there was no significant difference between core and edge farms and edge and control farms (Table 4.9B).

Table 4.9A: Summary statistics for negative binomial GLMER summarising significance of survey year and farm type on changes in effective number of species (ENS). *p* values were calculated using 999 resampling, significantly different values (< 0.05) were indicated with an asterisk.

Response variable	**Covariable**	**Variance (± SD)**	**AIC**	**Fixed effect**	**Est (± SE)**	**z value**	**Pr (>|z|)**
ENS	Survey + (1|Type)	0.0002 (± 0.01)	1450.86	Survey A /Intercept	1.25 (± 0.04)	25.72	<0.001*
				Survey B	-0.15 (± 0.06)	-2.17	0.02*
				Survey C	-0.16 (± 0.07)	-2.41	0.01*
ENS	Type + (1|Survey)	0.003 (± 0.05)	1452.88	Control /Intercept	1.13 (± 0.05)	19.41	<0.001*
				Core	-0.04 (± 0.06)	-0.59	0.55
				Edge	0.09 (± 0.07)	1.33	0.18

Table 4.9B: Summary statistics for Wilcox rank sum and signed-rank tests comparing effective number of species (ENS) within core, edge and control communities between three survey years (A = 2017/18, B = 2018/19 and C = 2019/20). P-values were adjusted using the holm method, significantly different values (< 0.05) were indicated with an asterisk.

Variable	Comparison	Statistic	p.adjust
Between survey year			
	Survey A – Survey B	507	0.49
Core	Survey A – Survey C	582	0.06
	Survey B – Survey C	539	0.16
	Survey A – Survey B	214	0.23
Edge	Survey A – Survey C	428	0.05*
	Survey B – Survey C	438	0.05*
	Survey A – Survey B	687	<0.001*
Control	Survey A – Survey C	556	0.48
	Survey B – Survey C	182	0.002*
Between farm types			
	Control – Core	1147	1.00
A	Control - Edge	835	1.00
	Core - Edge	720	1.00
	Control – Core	700	0.01*
B	Control - Edge	381	<0.001*
	Core - Edge	592	0.06
	Control – Core	1347	0.03*
C	Control - Edge	950	0.33
	Core - Edge	670	0.33

Community composition and structure

Species richness estimates derived from rank abundance change measures (RAC) decreased between survey A and survey B for all three farm types (Table 4.10). However, between survey A and survey C richness only decreased in core and edge sites, while there was a slight increase in control farms (Table 4.10). Edge farms had the greatest decrease in richness in both comparisons however, all changes in richness were minor (Table 4.10). Changes in evenness were positive for all farm types between survey A and B, as well as between survey A and C (Table 4.10). Evenness changes between survey A and B were greater than the changes seen between survey A and survey C (Table 4.10). Between survey A and survey B there was a slight rank change in all three farm types, with edge farms showing the greatest species rank change (Table 4.10 and App 4.2). Rank changes increased further between survey A and survey C with edge farms again showing the greatest rank shift (Table 4.10 and App 4.2).

Control sites were the only farm type that saw a gain in species over the three survey years, species losses (expressed through turnover measures) were present in all three farm types between both survey A and B, and survey A and C (Table 4.10). Between survey A and survey B control farms had the greatest proportion of species lost, however between survey A and survey C edge farms had the greatest proportion of species loss compared to core and control farms (Table 4.10). Core farms had a consistently low proportion of species lost across all three survey years (Table 4.10).

Table 4.10: Rank abundance curve changes between year A and B and year A and C for each farm type. Richness and evenness change bound between -1 and 1 (larger values indicate greater increases or decreases). Rank change bound between 0 and 0.5 (0.5 represents the maximum rank changes allowed). Turnover bound between 0 and 1 (larger values represent a high proportion of species lost).

Survey	Farm Type	Richness changes	Evenness change	Rank change	Species gains	Turnover
A vs. B	Core	-0.04	0.15	0.09	0	0.04
	Edge	-0.14	0.13	0.11	0	0.14
	Control	-0.09	0.04	0.08	0.04	0.18
A vs. C	Core	-0.04	0.03	0.12	0	0.09
	Edge	-0.19	0.02	0.21	0	0.33
	Control	0.08	0.01	0.10	0.16	0.17

When comparing the RAC measures between farm types (after farming had ceased on core farms for 18 months) there was no significant difference in the RAC between core, edge or control sites in survey C (Table 4.11). Changes in richness and species gains between core and control farms had the lowest p-values (diff = - 0.22, p = 0.19 and diff = - 0.10, p = 0.19 respectively) (Table 4.11).

Table 4.11: ANOVA results showing the difference between rank abundance curve (RAC) change measures between farm types in survey C. All ANOVAs were tested for normality using a Shapiro-Wilk's test with all results showing a p value > 0.05, therefore assuming normality for all tests.

Comparison	Richness changes		Evenness change		Rank change		Species gains		Turnover	
	diff	*p*	*diff*	*p*	*diff*	*p*	*diff*	*p*	*diff*	*p*
Core - Control	-0.22	0.19	-0.06	0.50	0.01	0.83	-0.10	0.19	-0.03	0.91
Edge - Control	-0.20	0.24	-0.01	0.97	0.003	0.99	-0.09	0.25	0.12	0.45
Edge - Core	0.01	0.98	0.05	0.61	-0.01	0.88	0.01	0.97	0.16	0.29

Of the 27 wild mammal species detected throughout the study period, 25 species were detected at least once on all three farm types in all three survey years and therefore only these species were considered for analysis (springhare and bontebok were excluded from this analysis). Best fit models (based on deviance criteria) were variable across the survey years for each farm type (Figure 4.7 and App 4.3). For core sites, the lognormal distribution provided the best fit for observed rank abundance distribution (RAD) of species during survey A, while the Zipf and Zipf-Mandelbrot distributions provided the best fit in survey B and survey C respectively (Figure 4.7 and App 4.3). For edge and control farms, the Zipf-Mandelbrot distribution provided the best fit for RADs during survey A and survey C, however the lognormal distribution was the best fit model during survey B (Figure 4.7 and App 4.3).

Jaccard Similarity Indices (S_J) were bound between 0 and 1, with 1 representing a community with complete compositional similarity. Core and edge farms ($S_J = 0.70$) had a higher degree of similarity compared to core and control farms ($S_J = 0.58$) and edge and control farms ($S_J = 0.58$) during survey A (Figure 4.8). Similarity between core and edge farms ($S_J = 0.56$) decreased during survey B, while similarity between edge and control farms increased ($S_J = 0.61$) (Figure 4.8). During survey C edge and control farm similarity decreased ($S_J = 0.49$), as well as similarity between core and edge farms ($S_J = 0.51$) (Figure 4.8). Similarity between core and control farms increased in survey C ($S_J = 0.64$) compared to survey A (Figure 4.8).

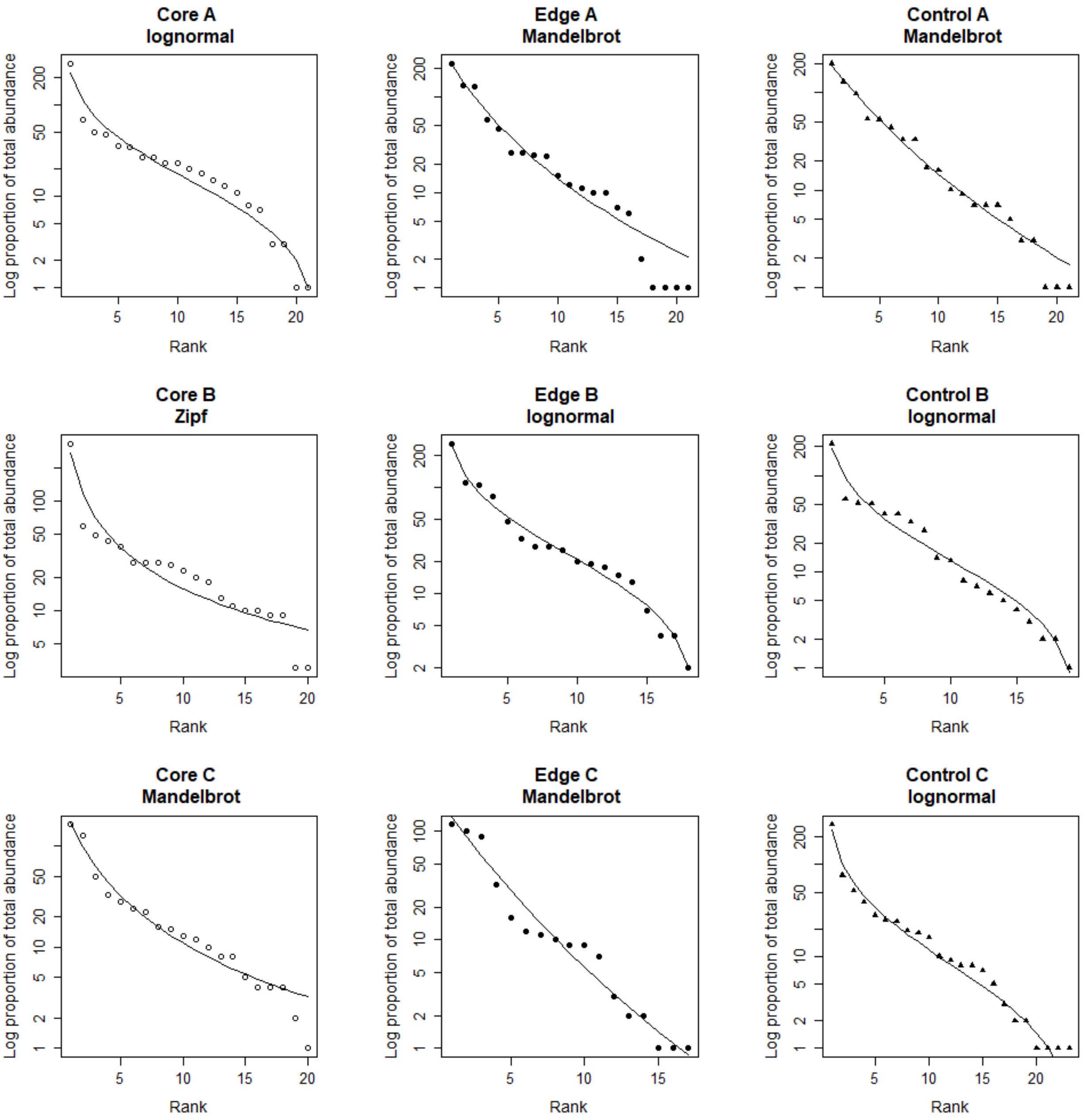
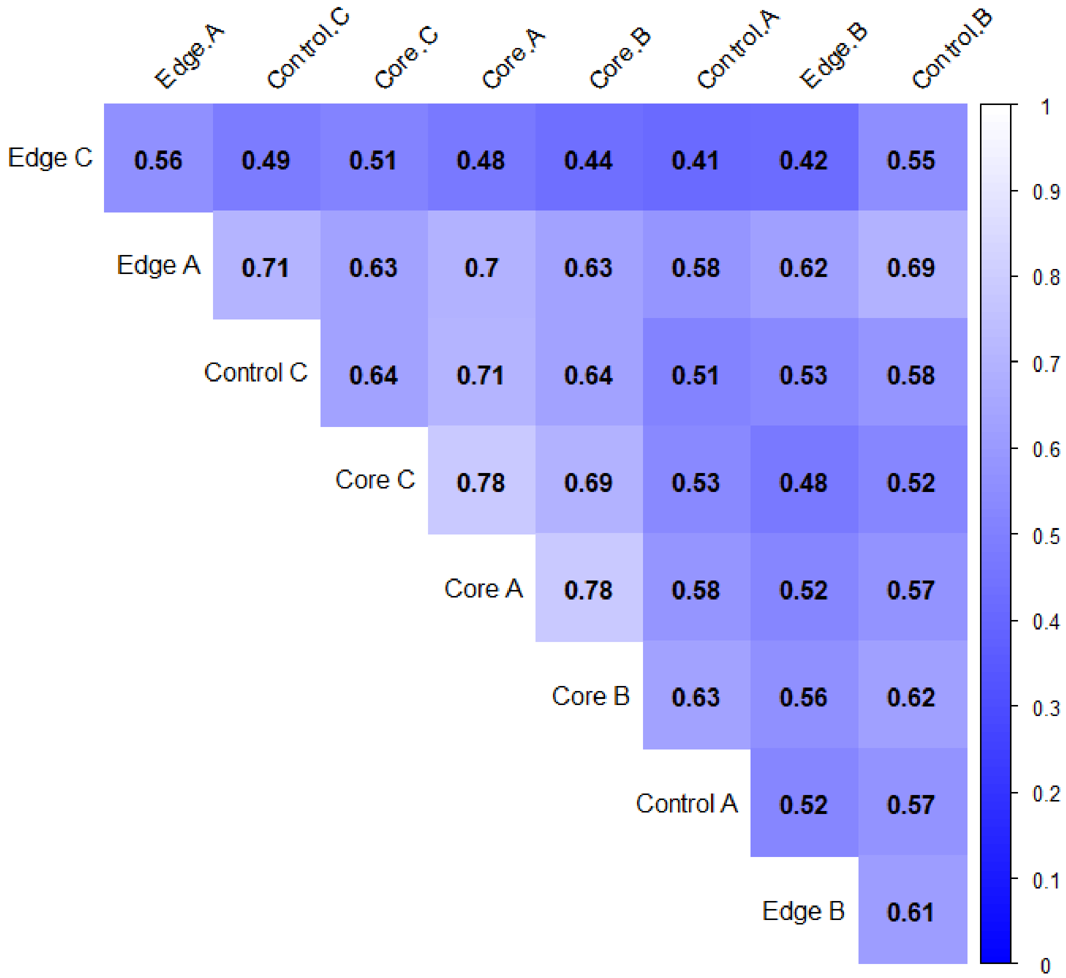


Figure 4.7: Best fit distribution models for observed rank abundance distributions of 25 selected species (springhare and bontebok excluded) constructed from farm type level RAIs on three farm types (core, edge and control) during three different survey years (A = 2017/18, B = 2018/19 and C = 2019/20).



	Edge.A	Control.C	Core.C	Core.A	Core.B	Control.A	Edge.B	Control.B
Edge C	0.56	0.49	0.51	0.48	0.44	0.41	0.42	0.55
Edge A		0.71	0.63	0.7	0.63	0.58	0.62	0.69
Control C			0.64	0.71	0.64	0.51	0.53	0.58
Core C				0.78	0.69	0.53	0.48	0.52
Core A					0.78	0.58	0.52	0.57
Core B						0.63	0.56	0.62
Control A							0.52	0.57
Edge B								0.61

Figure 4.8: Jaccard Similarity Index heatmap showing the relative similarity between communities within three farm types (core, edge and control) over three different survey years (A = 2017/18, B = 2018/19 and C = 2019/20). Index bound between 0 and 1, with 1 (white) representing greatest similarity.

Hierarchal cluster analysis showed strong grouping of core sites (core A and core B) compared to other farm types (Figure 4.9). Core sites in survey C clustered separately from survey A and B (Figure 4.9). Edge and control sites had a higher degree of clustering together than with core sites (Figure 4.9). Edge sites in survey C had an independent grouping to all other sites (Figure 4.9).

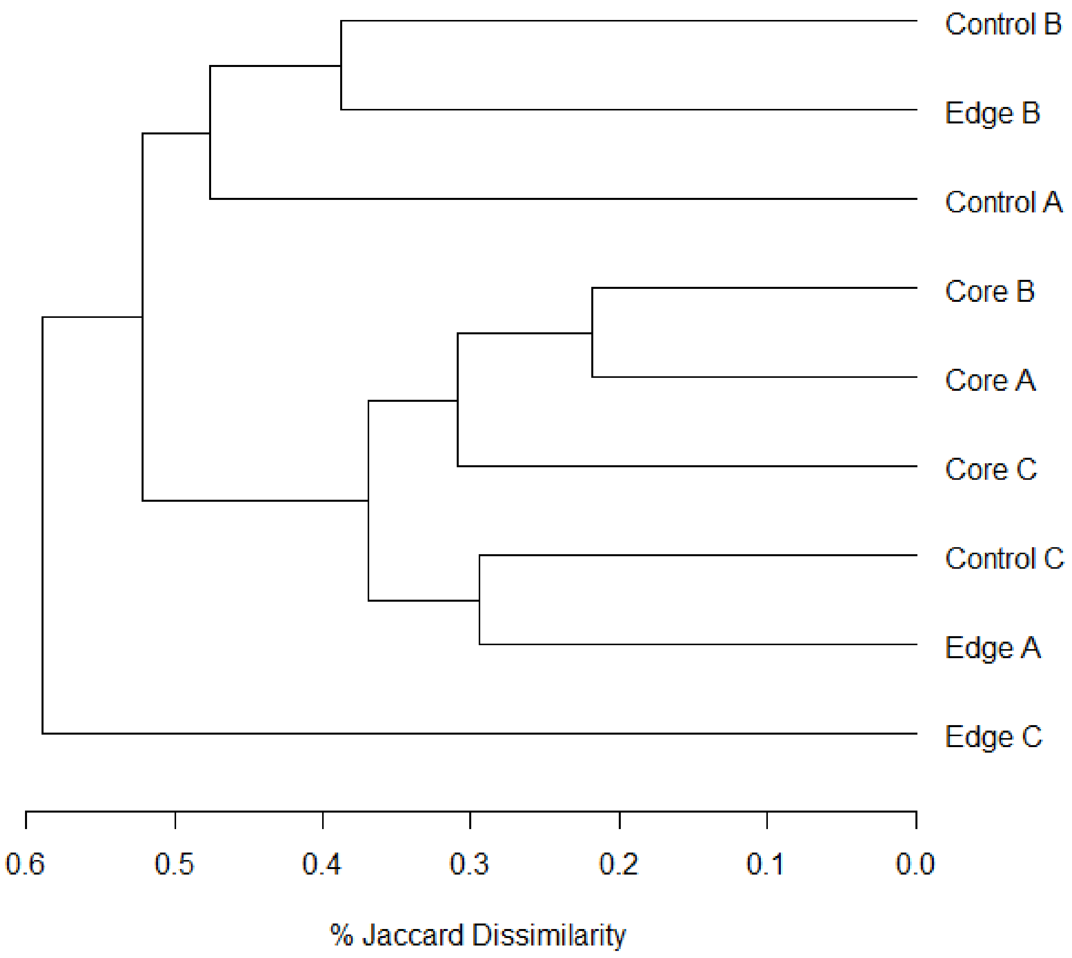


Figure 4.9: Hierarchal cluster dendrogram based off Jaccard dissimilarity matrices showing community associations between three farm types (core, edge and control) over three different survey years (A = 2017/18, B = 2018/19 and C = 2019/20).

Functional diversity

Functional structure was compared between survey A and survey C for core, edge and control communities. In core sites functional diversity and average body mass did not change significantly over time (Table 4.12 and Figure 4.10). There was no significant change in the RAIs of species between survey A and C, with no functional groups appearing or disappearing over time (Table 4.13 and Figure 4.10). In edge sites functional diversity and average body mass also did not change significantly over time (Table 4.12 and Figure 4.10). There was no significant change in the RAIs of species between survey A and C, with no functional groups appearing or disappearing over time but omnivores were completely absent from edge communities (Table 4.13 and Figure 4.10). Control sites followed the same pattern as core and edge sites, however during survey C omnivores were present despite being absent in survey A (Table 4.12 and Figure 4.10). An observed decrease in cape fox RAI is notable on control sites between survey A and survey C (Figure 4.10). In general, the distribution of herbivores was more evenly spread along the log body mass scale, while carnivores were skewed more towards a small body mass category (Figure 4.10). Functional diversity of the communities on core, edge and control farms were not significantly different between farm types within a specific year (e.g., Core A versus Edge A) (Table 4.14) or between years within a specific farm type (e.g., Core A versus Core B) (Table 4.13 and App 4.4).

Table 4.12: Functional dispersion index (FDis) indicating the weighted mean distance of a particular mammal species (using RAIs) in a multidimensional space, to the centroid of all species within that space. FDis values were calculated for each farm type (core, edge and control) in three different survey years (A = 2017/18, B = 2018/19 and C = 2019/20).

Survey	Core	Edge	Control
A	0.247	0.249	0.327
B	0.248	0.292	0.278
C	0.259	0.322	0.295

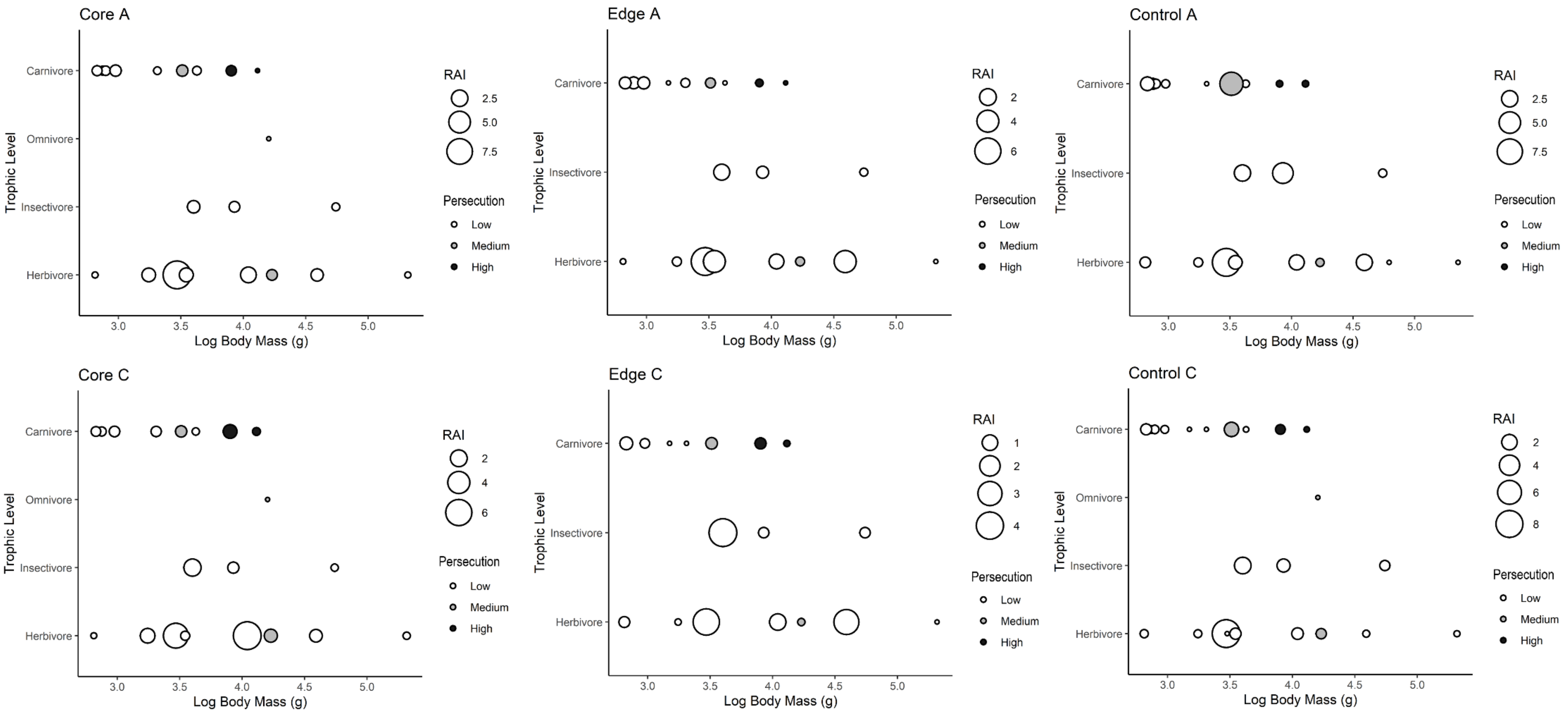


Figure 4.10: Distribution of 25 wild mammal species on three farm types (core, edge and control) across two survey years (A = 2017/18 and C = 2019/20), along two functional traits, trophic level and log body mass (g). Each circle represents a specific species within a community, while circle size is relative to photographic rate (RAI). Shading of circles indicates level of persecution with a specific farm type and year.

Table 4.13: Results from both paired Wilcox signed-rank and unpaired Wilcox rank-sum tests comparing RAIs for different trophic levels found within core, edge and control communities between survey A (2017/18) and survey C (2019/20). Comparisons are considered significantly different when p.adjust < 0.05.

Farm Type	**Comparison**	**Herbivore**			**Insectivore**			**Carnivore**		
		statistic	*n*	*p.adjust*	*statistic*	*n*	*p.adjust*	*statistic*	*n*	*p.adjust*
Core	A – C	21	11	1.00	3	3	1.00	25	10	0.81
Edge	A – C	30	11	0.32	2	3	1.00	44	10	0.07**.**
Control	A – C	55	11	0.16	4	3	1.00	46	10	0.19

Table 4.14: Results for Kruskal-Wallis test with post-hoc pairwise wilcox test comparing RAIs for different trophic levels found within survey A (2017/18) and survey B (2019/20) community between three farm types (core, edge and control). Comparisons are considered significantly different when p.adjust < 0.05.

Year	**Trophic level**	**Chi-squared**	**df**	**p**	**Comparison**	**Wilcox post hoc p value**
A	Herbivore	0.13	2	0.93	Core – Control	0.89
					Edge – Control	0.89
					Edge - Core	0.89
	Insectivore	1.68	2	0.42	Core – Control	0.60
					Edge – Control	0.60
					Edge - Core	1.00
	Carnivore	0.45	2	0.79	Core – Control	0.79
					Edge – Control	0.79
					Edge - Core	0.79
C	Herbivore	0.88	2	0.64	Core – Control	0.64
					Edge – Control	0.64
					Edge - Core	0.64
	Insectivore	0.62	2	0.73	Core – Control	1.00
					Edge – Control	1.00
					Edge - Core	1.00
	Carnivore	2.11	2	0.34	Core – Control	0.73
					Edge – Control	0.46
					Edge - Core	0.46

Daily activity patterns

Activity pattern comparisons explored the daily activity of species during survey A (2017/18 before the cessation of farming activities on the core) and compared them to activity during survey B (2018/19 six months after sheep removed on core) as well as survey C (2019/20 eighteen months after sheep are removed on the core). Focus is placed on shifts seen between survey A and survey C however, delta is reported for both comparisons (Table 4.15). Within core sites four species had a significant shift in daily activity patterns between survey A and survey C, namely: springbok (Δ = 0.66), rock hyrax (Δ = 0.31), cape fox (Δ = 0.65) and yellow mongoose (Δ = 0.64) (Table 4.15). In the case of springbok and yellow mongoose activity shifted from having two defined activity peaks in the morning and in the evening, to more evenly spread activity throughout the day (Figure 4.11). For rock hyrax there is almost a complete shift in peak activity from between 06:00 and 12:00 to between 12:00 and 18:00 (Figure 4.11). Cape fox saw a shift in activity from one activity peak in A (between 00:00 and 02:00) to three distinct activity peaks in C (04:00, 12:00 and 21:00) (Figure 4.11).

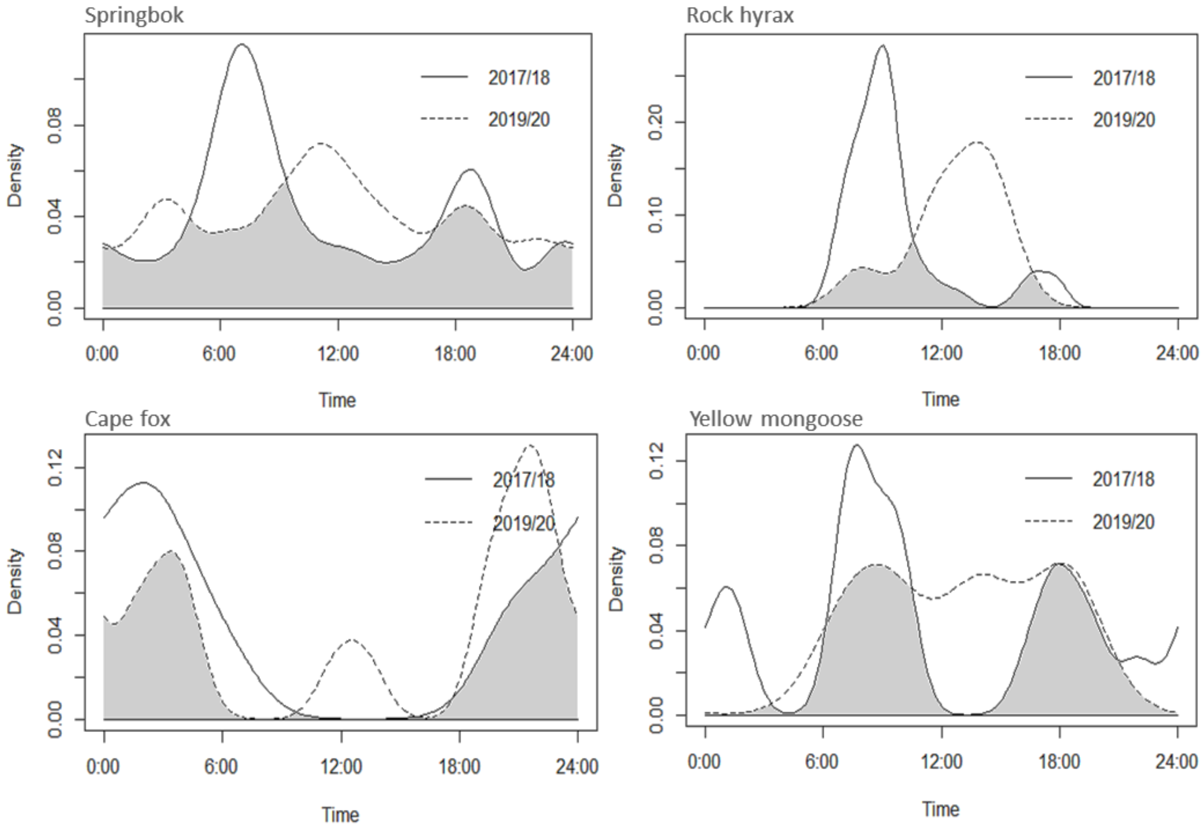


Figure 4.11: Changes in the density of time stamps for four mammal species on core sites during survey A (2017/18, solid line) and survey C (2019/20, dotted line). Grey shaded area indicates the overlap in activity between the two years (also known as delta).

Table 4.15: Overlapping coefficients (Δ) with 95% bootstrap confidence intervals for top ten most abundant mammal species across three farm types (core, edge and control) over three survey years (A = 2017/18, B = 2018/19 and C = 2019/20). Value in bold indicate a significant shift in daily temporal activity. Shaded grey blocks indicate species where detection was too low to calculate delta.

Species	**Core**		**Edge**		**Control**	
	A - B	***A - C***	***A - B***	***A - C***	***A - B***	***A - C***
	Δ (Boot CI)	*Δ (Boot CI)*	*Δ (Boot CI)*	*Δ (Boot CI)*	*Δ (Boot CI)*	*Δ (Boot CI)*
Hare spp.	0.94 (0.92 – 1.00)	0.91 (0.87 – 1.00)	0.92 (0.90 – 1.00)	0.83 (0.75 – 0.89)	0.88 (0.82 – 0.96)	0.93 (0.91 – 1.01)
Rock Rabbit	0.83 (0.73 – 1.01)	0.85 (0.78 – 1.03)	▨	**0.12** (-0.10 – 0.37)	**0.67** (0.45 – 1.07)	**0.67** (0.46 – 1.05)
Steenbok	0.80 (0.73 – 0.94)	0.71 (0.58 – 0.79)	0.74 (0.64 – 0.94)	0.71 (0.59 – 0.91)	0.86 (0.80 – 1.02)	**0.69** (0.55 – 0.85)
Springbok	0.76 (0.66 – 0.98)	**0.66** (0.49 – 0.82)	0.86 (0.82 – 0.98)	0.85 (0.80 – 0.95)	**0.69** (0.54 – 0.82)	0.76 (0.70 – 1.26)
Rock Hyrax	0.88 (0.85 – 1.05)	**0.31** (0.02 – 0.53)	0.85 (0.79 – 0.95)	▨	0.87 (0.82 – 1.07)	0.87 (0.83 – 1.10)
Bat-eared Fox	0.87 (0.81 – 1.05)	0.86 (0.79 – 1.05)	0.78 (0.67 – 0.89)	0.86 (0.80 – 0.98)	0.87 (0.79 – 1.02)	0.92 (0.89 – 1.06)
Cape Fox	0.84 (0.75 – 1.05)	**0.65** (0.46 – 0.89)	**0.63** (0.42 – 0.89)	0.73 (0.58 – 1.04)	0.87 (0.81 – 1.01)	0.87 (0.80 – 0.98)
Aardwolf	0.91 (0.88 – 1.16)	0.82 (0.73 – 1.07)	0.74 (0.58 – 0.95)	**0.57** (0.32 – 0.84)	0.85 (0.76 – 0.96)	0.85 (0.76 – 0.98)
Yellow Mongoose	0.74 (0.67 – 1.05)	**0.64** (0.53 – 0.95)	0.73 (0.61 – 0.92)	**0.65** (0.48 – 0.92)	0.77 (0.67 – 1.03)	0.79 (0.71 – 1.02)
Cape Porcupine	0.71 (0.53 – 0.91)	0.80 (0.69 – 1.02)	0.82 (0.71 – 1.15)	0.85 (0.74 – 1.48)	0.77 (0.61 – 1.24)	0.84 (0.75 – 1.22)

Within edge sites three species exhibited a significant shift in daily activity patterns between survey A and survey C, namely: rock rabbit (Δ = 0.12), aardwolf (Δ = 0.57) and yellow mongoose (Δ = 0.65) (Table 4.15). Activity patterns for rock rabbits shifted significantly from a single peak at 01:00 in survey A to two peaks (06:00 and 12:00) in survey C (Figure 4.12). Activity patterns for aardwolf are fairly similar between survey A and survey C however delta indicates a significantly shift from early morning in survey A toward late evening in survey C (Figure 4.12). Similar shifts are seen for yellow mongoose where activity is bound between the same timeframe (peaks between 06:00 and 18:00) in both surveys, however there is a more defined peak at 10:00 in survey C compared to survey A (Figure 4.12).

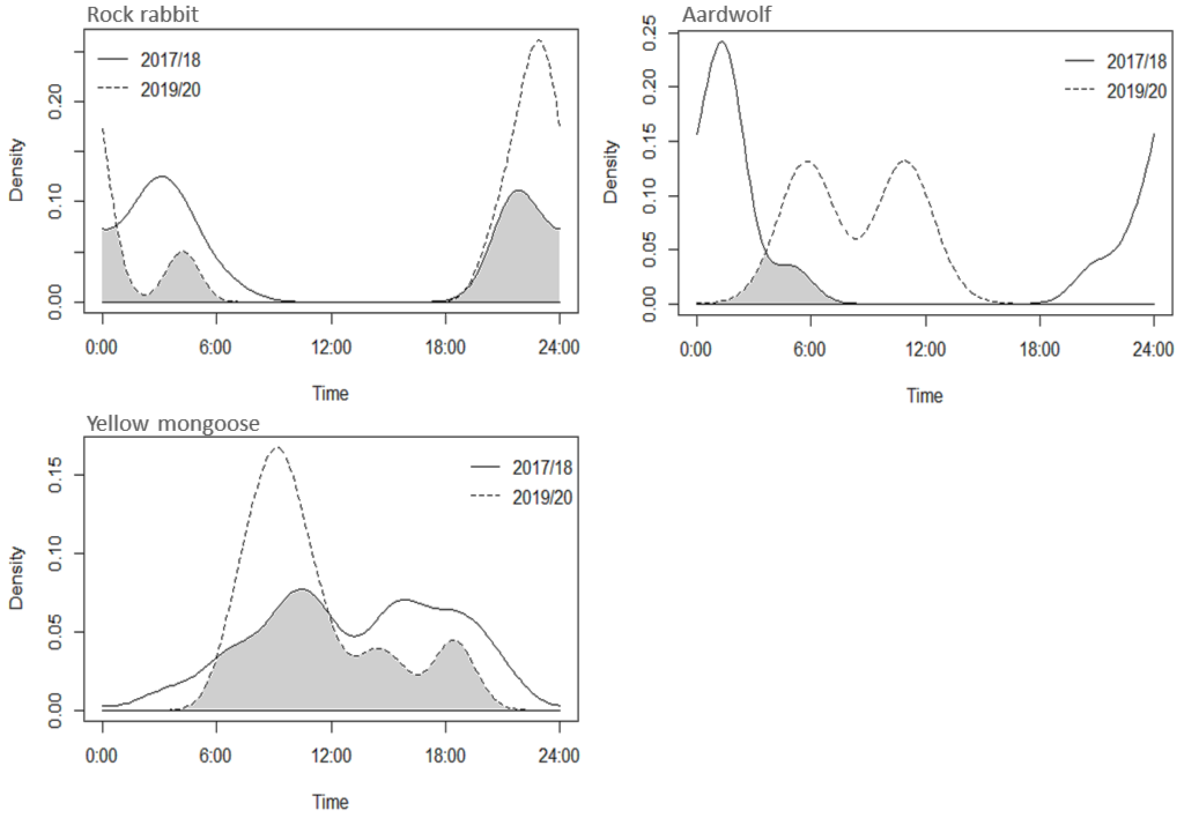


Figure 4.12: Changes in the density of time stamps for three mammal species on edge sites during survey A (2017/18, solid line) and survey C (2019/20, dotted line). Grey shaded area indicates the overlap between activity between the two years (also known as delta).

Within control sites only two species had a significant shift in daily activity patterns between survey A and survey C, namely: rock rabbit (Δ = 0.67) and steenbok (Δ = 0.69) (Table 4.15). The shift in activity for rock rabbit showed a more defined peak in activity (around 05:30) in survey C compared to survey A, however survey A followed the same activity pattern as survey

C (Figure 4.13). Steenbok activity patterns during survey A had two defined peaks (06:00 and 19:00), while during survey C the focus was more in the morning with the peak shifting closer to the middle of the day and becoming less defined (Figure 4.13).

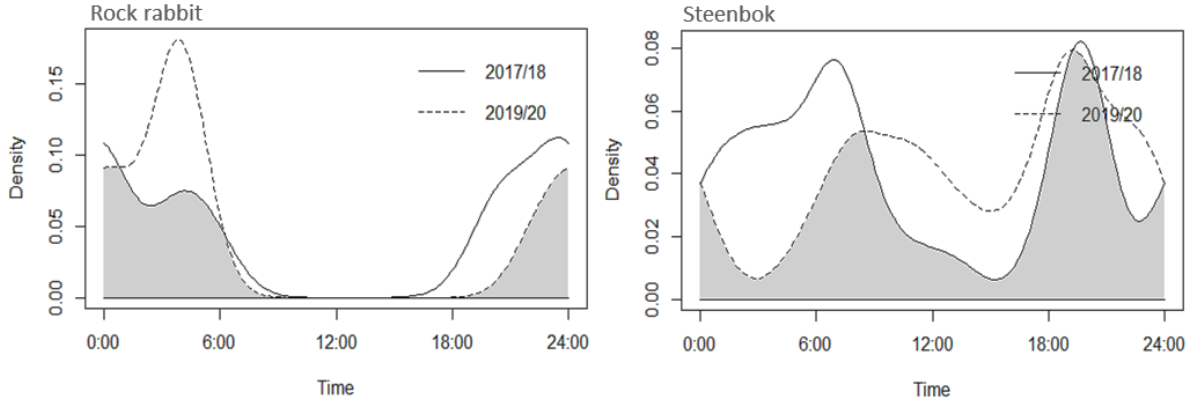


Figure 4.13: Changes in the density of time stamps for two mammal species on control sites during survey A (2017/18, solid line) and survey C (2019/20, dotted line). Grey shaded area indicates the overlap between activity between the two years (also known as delta).

Discussion

Camera trap surveys identified 27 medium and large mammal species within the greater SKA region, which when combined with the eight small mammal species (including cryptic species, see Chapter 3), equals 35 mammal species (excluding bats). This exceeds the 25 mammal species identified through the MammalMap database (Todd & Henschel 2016) but is less than the 40 mammal species predicted by Todd & Henschel (2016) during SEAs for the area (in both cases estimates excluded bats). Expected species that were not recorded during this study include brown hyena (*Hyaena brunnea*), leopard (*Panthera pardus*), honey badger (*Mellivora capensis*), eland (*Taurotragus oryx*), common duiker (*Sylvicapra grimmia*) and riverine rabbit (*Bunolagus monticularis*).

As predicted (P1) species richness, diversity, community structure and composition were similar for all three farm types during survey A (when all three farm types were actively farming small livestock). This confirmed that for this study all three farm types had a similar baseline mammal population structure, suggesting that any shifts in species richness, diversity or composition as a result of a cessation in livestock farming could be detected. Species richness during survey A was similar to other studies carried out in small livestock areas within the Karoo (Mann 2014, Drouilly *et al.* 2018, Woodgate *et al.* 2018, Drouilly & O'Riain 2019), and accumulation curves support the general trend that these semi-arid regions have a relatively low species detectability and richness compared to more productive landscapes (Dean & Milton 1999, Joubert & Ryan 1999).

Species diversity and photographic rate (RAIs) during survey A were also typical of Karoo systems, and high photographic rates for several species supports the hypothesis that medium-intensity grazing by livestock may favour select cosmopolitan species (Yeo *et al.* 1993, Blaum *et al.* 2009, Georgiadis *et al*. 2007, Kiffner *et al.* 2015, Schieltz & Rubenstein 2016, Woodgate *et al*. 2018), which in this study included cape fox, bat-eared fox, steenbok and hare spp.. Drouilly & O'Riain (2019) provided a similar result with bat-eared fox, steenbok and hare spp. all having high relative abundance on farmland in the central Karoo. Overall species accumulation curves (farm types pooled per year) suggested that while sampling effort during survey B was sufficient (curve reaching an asymptote during the survey period), that more effort was required during survey A and C as asymptotes were not reached. Likely reasons for the difference in curves despite similar sampling effort on the same land is that survey B had the lowest number of species detected overall and rare species were captured more often during survey B compared to survey A and C.

The changes in the general patterns of species detection over the three survey years might be linked to the changing drought conditions over the course of the study period. The Karoo is in the grip of an extended drought with rainfall the lowest during survey year B (see rainfall data in Chapter 2). In arid landscapes drought can influence activity patterns of several species, increasing distance travelled in the search for food and water as well as shifting daily activity to avoid hotter periods of the day (Davimes *et al*. 2017, Levy *et al.* 2018, Abraham *et al.* 2019, Gedir *et al.* 2020). The greater detection of rarer species may be linked to their increased activity in survey B where drought conditions were the most severe and hence animals forced to travel further to obtain resources. Prugh *et al.* (2018) suggested that rare species may also become more abundant in a response to drought, while abundant species were likely to decline. The lower number of species detected in survey B, compare to survey A and C, further supports the idea that severe drought during this year had a more profound impact on mammal populations than during survey A and C (Woodward *et al.* 2012, Abraham *et al.* 2019).

Spatial and temporal changes in diversity measures and community composition

Similar to other studies species richness did not change despite the shift in land use on the core which supported my prediction (P2) (Rannestad *et al.* 2006, Kinnaird & O'Brien 2012, Msuha *et al.* 2012, Mann 2014, Kiffner *et al.* 2015, Drouilly *et al.* 2018a). Mammal species richness is often not significantly different between farmlands and protected areas within semi-arid landscapes possibly due to the intermediate disturbance hypothesis (i.e., richness can be higher than expected on disturbed land when the disturbance is intermediate in frequency and intensity) (Msuha *et al.* 2012, Kiffner *et al.* 2015, Drouilly 2019). The historic relationship between large herds of indigenous herbivores and Karoo ecosystems may explain the resilience of these ecosystems to extensive small-livestock grazing, and may indicate why species richness in the Karoo is often similar between farmland and protected areas (Dean & Milton 1999, Todd 2006). Furthermore one would not expect species richness to increase on the core after the cessation of farming activities simply due to the lack of a suitable species pool within reasonable recolonisation distance (Schweiger *et al.* 2018, Simms *et al.* 2018). Protected area richness would reflect that of the surrounding farmland as this surrounding farmland would form the basis on the potential species pool (Simms *et al.* 2018). Unless mammal reintroductions within the core take place (which is not expected) species richness is unlikely to differ from the surrounding farmland (Schweiger *et al.* 2018), which was reflected in my data.

My prediction that species diversity would increase on core farms over the years (P3) was not supported however, my data did align with my prediction that diversity measures would remain constant on edge farms (P7). Between the three survey years diversity and evenness for all three farm types showed a negative trend but differences from baseline diversity measures were not significant. The parallel decreases in diversity measures on core, edge and control farms during survey C suggests decreases in diversity measures were a result of landscape level environmental processes, as opposed to local scale cessation of farming activity effects. This was supported by the significant changes in effective number of species (ENS). ENS is considered a more robust measure of diversity compared to Shannon-Wiener diversity indices, and accounts for issues with linear scaling with increasing richness (Jost 2006, Chao *et al.* 2014). Generalised linear models illustrated that survey year had a greater impact on ENS across all farm types, compared to farm types. While during each survey year there were significant changes between control farms and core and edge farms, this was mostly the result of the significant decrease in ENS on control farms between survey A and survey B, and the subsequent increase in ENS between survey B and C. This may be further evidence that overall drought conditions had a greater impact on richness and diversity across all farm types over time and effectively suppressed any changes linked to the intervention. Drought conditions are expected to have a negative impact on species richness and diversity across the globe. When exploring the potential impact of climate change on mammal richness in Europe, areas where temperatures are likely to increase, and rainfall decrease (typical drought conditions) are predicted to exhibit declines in mammal species richness (Levinsky *et al.* 2007).

Within southern Africa drought has been shown to impact herbivore richness and diversity negatively, with small herbivore species being more vulnerable to drought conditions (Owen-Smith & Ogutu 2012). This is likely a result of reduced plant productivity and overall habitat desiccation that has been shown to occur with reduced rainfall (Owen-Smith & Ogutu 2012). The impact of drought can be particularly noticeable where competition for food and water with livestock is evident (Owen-Smith & Ogutu 2012). In the Karoo drought conditions can be particularly detrimental as extensive fencing restricts movement of species (migration being a common natural response to drought), amplifying competition between livestock and wild herbivores for scarce resources (Owen-Smith & Ogutu 2012, Dean *et al*. 2018). It is interesting to note that there seemed to be a lag effect on core farms where ENS and diversity only started decreasing significantly during survey C, while edge and control farms saw a similar decrease during survey B and C. This was confirmed when looking at species loss turnover, for which core sites had the lowest proportion of species lost over the years compared to edge and control sites. This lag effect may be the result of the removal of sheep on core farms, where immediately after sheep removal herbivore populations may have benefitted from less resource competition providing a buffer from drought conditions (Owen-Smith & Ogutu 2012). This competitive release was not seen on edge and control farms which may explain the initial decrease in richness during the survey year which saw more severe drought conditions (survey B). Competitive exclusion of wild herbivores by livestock is poorly researched and hence a causal link remains tentative (Prins 2000, Madhusudan 2004, Mishra *et al.* 2006). However, it is widely assumed that wildlife and livestock share similar resources, and that livestock may have a competitive advantage over wild herbivores given they benefit from supplemental feeding and care (Prins 2000, Madhusudan 2004, Mishra *et al.* 2006). Where livestock have been removed, wild herbivore abundance has been observed to increase within a number of systems on the Indian subcontinent (Madhusudan 2004, Mishra *et al.* 2006).

Changes in rank abundance for all three farm types between baseline (survey A) and 18 months following the cessation of farming (survey C) was minimal, with edge farms showing the greatest degree of rank change. However, when comparing rank change measures between the three farm types in survey C there was no significant difference. Core sites were more likely to have a higher similarity to other core sites over the years, rather than to edge and control sites within the same year. This suggests that core sites had a significantly different community composition and structure throughout the surveys compared to edge and control sites. Despite the drought potentially shifting community composition in edge and control sites from baseline communities, core sites were more likely to remain similar to baseline communities. The potential competitive release and cessation of predator persecution experienced on core sites, may have acted as a buffer to these communities, resulting in a lagged response to drought effects which were seen due to shifting communities in edge and control sites (where farming practices were still active). This did not align with my predictions (P4 and P7) because drought was predicted to impact all communities concurrently. Prugh *et al.* (2018) suggested that drought may have a greater negative effect on higher trophic level mammal species (i.e., insectivores and carnivores) and plants compared to middle trophic levels (i.e., herbivores and omnivores). This supports the theory that drought may have a negative impact on overall community composition (Prugh *et al.* 2018). My study showed that while relative abundance did not shift significantly between survey year for carnivores (Table 4.14), edge and control sites did see a marked decrease in carnivore RAI between survey A and survey C, while core sites remained constant. These shifts in RAI may explain why edge and control sites saw a difference in community composition while core sites did not. If drought is more likely to impact carnivore guilds and primary productivity, one can assume core sites were less impacted by drought, which was reflected in the lack of community composition change between years. Reduced persecution of predators and reduced competition for limited vegetation of wild herbivores (sheep removed) may have helped buffer core carnivores from the adverse impacts of drought delaying community composition shift by an extra year, compared to edge and control sites (Prugh *et al*. 2018). These results partially supported my hypothesis (H1) as the cessation in farming did have an indirect impact on community composition over time, but this was not evident in any diversity measures. The results did however support my sixth prediction

(P7) as diversity measures and community composition on edge sites remained unchanged. Any changes seen on edge farms where often mirrored on control farms suggesting that changes in communities were likely a response to abiotic landscape level factors rather than edge effects resulting from the cessation of farming activities on adjacent core farms.

Spatial and temporal changes in species abundance and functional diversity

Prediction P5 was not supported by the data as overall relative abundance of mammals did not increase between surveys on core sites, rather overall relative abundance remained constant on all three farm types across all surveys supporting prediction 6. However, I also predicted that relative abundance on core sites would increase over time after the cessation of farming which was not apparent. There was no significant difference in the photographic rates (RAIs) of different trophic groups between survey A and survey C for any farm type. Furthermore, the RAIs for each trophic group was not significantly different between farm types in either survey A or survey C. This suggested that while community composition may be impacted by the intervention on core farms, the overall abundance of species was not significantly affected.

Several studies have provided evidence supporting the theory that the Karoo predominantly functions through bottom-up processes (Todd & Hoffman 1999, Kraaij & Milton 2006, Hoffman *et al.* 2009, du Toit *et al.* 2018). Therefore, shifts in animal diversity or community composition are likely a response to significant changes in rainfall and hence vegetation. However, the Karoo is characterised by extremely slow vegetation recovery (see Chapter 3) (Boardman *et al.* 2010, Rahlao *et al.* 2008, van Rooyen *et al.* 2015, McManus *et al.* 2018), therefore herbivores are likely to compete intensely for limited vegetation, especially during drought. When grazing pressure is reduced on vegetation, remaining wild herbivores are likely to benefit however, overall vegetation biomass is unlikely to improve substantially within a short-time period (Boardman *et al.* 2010, Rahlao *et al.* 2008, van Rooyen *et al.* 2015, McManus *et al.* 2018). Therefore, as this study only spanned three years and a drought persisted throughout, vegetation would have had only a limited recovery window. This is supported by the vegetation surveys conducted in Chapter 3 of this study which revealed no change in cover, richness or diversity between the first survey and the last (18 months after the intervention).

Functional diversity was also not significantly different between years or farm types. This finding aligns with other recent results by Drouilly & O’Riain (2019) which suggested that only large mammal occupancy is adversely affected by small livestock farming and that livestock does not always negatively affect the abundance of medium sized mammals (Yeo *et al.* 1993, Blaum *et al.* 2009, Georgiadis *et al*. 2007, Kiffner *et al.* 2015, Schieltz & Rubenstein 2016). Most species within my study were in the medium body size range compared to Drouilly & O'Riain (2019) who through the inclusion of a protected area reported more larger species. This suggests that differences in abundance of species of different body sizes were unlikely to be detected given the limited range in my study area.

Temporal shifts in daily activity patterns

When investigating species daily activity patterns, I looked at the top ten most abundant mammal species across the three farm types for each year so as to standardise comparisons. I did however, exclude black-backed jackal and caracal as, while these species are of particular interest to both farmers and the SKA managers, I focus on them specifically in Chapter 5. My results supported my prediction (P8) that daily activity patterns for common species on core sites would tend towards more even activity patterns throughout the day. While only four species exhibited a significant shift in activity these species showed a shift towards more diurnal activity patterns. In particular, cape fox which are typically a nocturnal species (Kamler & Macdonald 2014) saw a peak in activity at midday during survey C on core farms, which was not evident during survey A (when farming was still active). This pattern of increased activity during the middle of the day was consistent for the three other species where a significant shift was observed (springbok, rock hyrax and yellow mongoose). A likely reason for this shift is due to the decrease in human disturbance on these farms evident by the significant decline in the RAI of people and cars detected on core farms (survey A = 0.04 and survey C = 0.001). Predator species are particularly sensitive to human disturbances which could explain why cape fox had such a clearly visible shift in activity once humans were less activity within core sites.

Human activity has been linked to changes in activity patterns for various species, mostly because of hunting, direct interference (chasing) or indirect interference (human presence impacting shy species) (Frid & Dill 2002, Barrueto *et al.* 2014, Frey *et al.* 2017, Gaynor *et al.* 2018). In Japan, both direct and indirect human activity had significant impact on wild boar activity, causing a complete shift to nocturnal activity (Ohashi *et al.* 2013). A similar pattern was seen in various protected areas in France, where hunting resulted in more species choosing to be active at night despite preferred crepuscular and diurnal activity times (Marchand *et al.* 2014). Human disturbances, including active hunting, are common within the Karoo resulting in many species shifting to nocturnal activity peaks as seen in various other systems where animals tend more towards nocturnality with increasing human disturbance (Gaynor *et al.* 2018). These results support my prediction that decreased human disturbance allows select species to be more active during daylight hours (P8).

Visual inspection of daily activity patterns (Figure 4.11, 4.12 and 4.13) reveals that while edge and control sites may have several species whose overlap coefficient (Δ) showed a significant shift between survey A and survey C, the overall pattern of activity did not shift. For example, rock rabbit activity followed the same pattern between different years despite a low delta value which was explained more by changes in density than changes in active hours (Figure 4.12). The only exception to this was for aardwolf on edge farms, where activity seems to shift completely from nocturnal patterns, to more diurnal patterns (Figure 4.12). As a result, I would argue that activity patterns on edge and control sites did not significantly change between survey A and C for the majority of common species supporting my initial prediction (P9). This further supports the idea that the cessation of farming activities on core farms would not affect the activity pattern of common species on edge and control sites, as human disturbance persists.

Conclusions

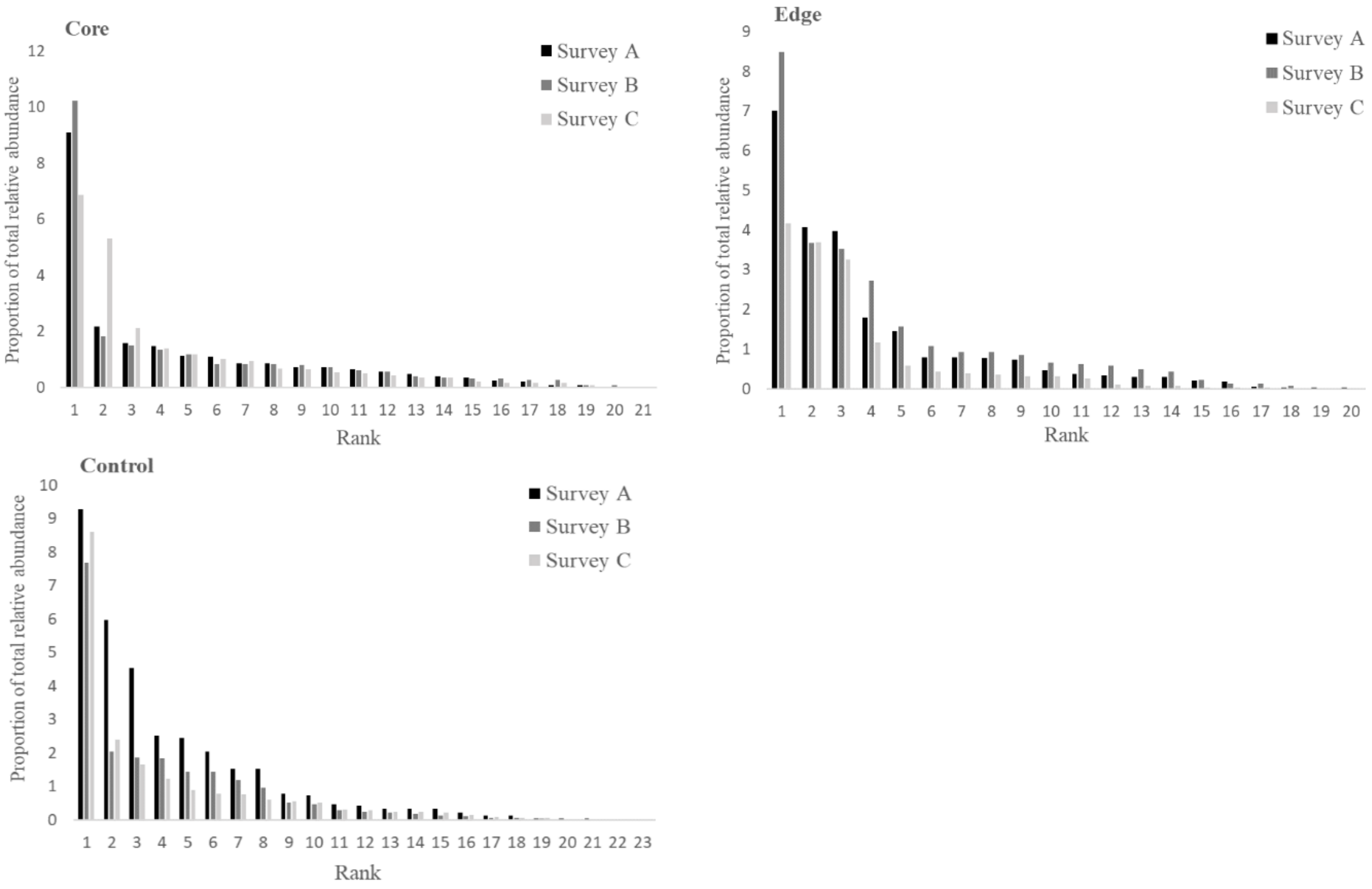
My results highlight that the recovery of mammal communities following the cessation of farming activities within the semi-arid Karoo is a slow process (Prins 2000, Mishra *et al.* 2002) that has likely been dampened by the extreme drought conditions that prevailed during the study. Despite this, sheep removal on the core may have buffered the impacts of drought for many wild herbivores through decreased competition. This was highlighted by the fact that during drought years core farms were more likely to have mammal community structures closer to years with less severe drought than edge and control farms (where sheep were still present and competing for resources) which shifted significantly to communities seen in years with less severe drought. Decreased human disturbance associated with a cessation of farming activities resulted in several mammal species becoming more active during what were historically "peak human activity" periods. I recommend that a subset of camera stations are monitored over the next 10 years (see chapter 7, synthesis) to understand how medium and large mammals will continue to respond to the change in land use from small livestock farming to that of protected area. I predict that with an end to the drought a surge in primary productivity will improve overall vegetation condition and with that an increase in the abundance of both wild prey and predator species on all farm types but significantly so on core farms. It is however unlikely that species richness will recover given the SKA core is isolated by extensive small livestock farming activities which will continue to adversely impact species which are rare because of anthropogenic impacts (e.g., leopard, brown hyaena, honey badger, eland, duiker and riverine rabbits). The results of Drouilly *et al.* (2018a) reveal that following more than 30 years since farming activities ended, the protected area of Anysberg had experienced a shift in community structure where larger mammals (specifically larger herbivore species and large carnivores such as leopards) had a higher probability of occurrence within the protected area compared to the surrounding farmland. However, despite the shift in functional diversity, neither species richness nor mean occupancy differed significantly between the two types of land use (protected area versus farmland). Similar patterns were observed in the Tarangire-Manyara Tanzanian ecosystem (Kiffner *et al.* 2015) and Namibian farmlands (Kauffman *et al.* 2007), both of which have a patchwork of well-established PAs and unprotected farmland. The lack of species richness recovery in these well-established protected areas highlights the likely trend expected for the SKA protected area. Abundance of species may ultimately be positively affected by the cessation of farming activities as well as the potential recovery of large mammal species (e.g., kudu and leopard) however, without reintroduction species richness will remain similar to surrounding farmland.

Reintroductions are an important conservation tool when dealing with areas with locally extinct species (i.e., mountain zebra, *Equus zebra* and black rhinoceros, *Diceros bicornis* in Namaqua National Park), species with a critically endangered status (i.e., riverine rabbit *Bunolagus monticularis*) or species with populations in great decline (i.e., lions, *Panthera leo*, in southern Africa) (Landman *et al.* 2006, Fourie *et al.* 2015, Collins & du Toit 2016, Hale & Koprowski 2018, Pedler *et al.* 2018). However, these programs can be costly and, particularly in the case of predator reintroduction, often dependent on public acceptance (Pedler *et al.* 2018, Hiroyasu *et al.* 2019). The benefits of reintroduction of particular species would need to be weighed against the specific conservation goals of the SKA protected areas and the degree of buy in from surrounding landowners. Large herbivore species like black rhinoceros for example may be suited for the SKA habitat (Landman *et al.* 2006), however the scientific goals of the SKA may not be aligned with large and potentially dangerous species. Lion reintroductions in the Karoo National Park have been relatively successful (Fourie *et al.* 2015), although recent breakouts onto neighbouring farmland have raised conflict levels with neighbouring farmers significantly. The benefits of reintroductions of extant apex predators on ecosystem level functioning is evident from case studies in Yellowstone National Park with wolf reintroductions (Ripple & Beschta 2012). However, the extreme negative perception towards mesopredators within the SKA region suggests reintroduction of predators will be met with increased farmer hostility. Furthermore, the issue of conflicting conservation and scientific goals of the SKA suggests larger predators in the PA may pose a threat to researchers working on the telescopes and would require additional infrastructure to mitigate this threat. While the area may be suitable for reintroduction of charismatic large mammal species the context of the protected area (mostly for scientific research with little public access) suggests the PA would be most suited to smaller endangered herbivore species such as the riverine rabbit. The riverine rabbit is a critically endangered species with historic distribution records suggesting this species was present in areas near Carnarvon (approx. 90 km from Losberg) (Hughes *et al.* 2008, Collins & du Toit 2016). This may indicate that the SKA PA would be a suitable area for reintroduction of this species. Ultimately the benefits of the SKA becoming a protected area should focus more on the recovery of existing ecologically, important fauna and flora species (e.g., aardvark and porcupine) as well as vulnerable species (i.e., small-spotted cat) with the potential for reintroduction of smaller non-threatening endangered species.

Appendix 4: Medium and large mammal appendices

App 4.1: AIC values for negative binomial GLMER (response variable ENS and J') and LMER (response variable H') and corresponding null models. Where null AIC is less than model AIC variance in data is a result of random variation rather than response variable.

Response variable	Model	AIC
Effective number of species (ENS)	ENS ~ 1 + (1|Type)	1454.01
	ENS ~ Survey + (1|Type)	1450.86
	ENS ~ 1 + (1|Survey)	1452.44
	ENS ~ Type + (1|Survey)	1452.88
Pielou's evenness (J')	J' ~ 1 + (1|Type)	161.10
	J' ~ Survey + (1|Type)	165.03
	J' ~ 1 + (1|Survey)	161.10
	J' ~ Type + (1|Survey)	162.26
Shannon-Wiener diversity (H')	H' ~ 1 + (1|Type)	715.35
	H' ~ Survey + (1|Type)	718.95
	H' ~ 1 + (1|Survey)	713.76
	H' ~ Type + (1|Survey)	719.55



App 4.2: Rank abundance distributions for three farm types (core, edge and control) over three survey years (A = 2017/18 before sheep were removed on core farms, B = 2018/19 six months after sheep were removed on core farms and C = 2019/20 eighteen months after sheep removal). Species are ranked along the x-axis according to decreasing proportion of abundance based on farm type level RAIs.

App 4.3: Deviance criteria for five types of models (null, pre-emption, lognormal, Zipf and Zipf-Mandelbrot) fitted to rank abundance distributions of species seen within three farm types (core, edge and control) across three survey years (A = 2017/18, B = 2018/19 and C = 2019/20).

Survey	**Farm Type**	**Null**		**Pre-emption**		**Lognormal**		**Zipf**		**Mandelbrot**	
		Dev	*AIC*	*Dev*	*AIC*	*Dev*	*AIC*	*Dev*	*AIC*	*Dev*	*AIC*
A	Core	204.06	300.68	198.60	297.22	58.90	159.52	62.25	162.87	62.25	164.87
	Edge	197.52	289.63	49.01	143.12	41.06	137.17	97.95	194.06	29.50	127.60
	Control	137.61	230.22	19.45	114.05	27.74	124.34	91.15	187.76	12.77	111.38
B	Core	275.33	371.80	287.77	386.24	111.36	211.83	72.49	172.96	72.49	174.96
	Edge	98.75	188.27	65.45	156.97	17.66	111.18	49.28	142.80	29.33	124.86
	Control	131.92	215.38	80.42	165.89	34.76	122.22	68.24	155.71	61.99	151.45
C	Core	114.28	201.95	62.69	152.36	23.56	155.24	36.48	128.16	19.79	113.47
	Edge	137.25	205.42	37.30	107.46	67.86	140.03	102.08	174.25	34.23	108.40
	Control	286.86	380.77	152.06	247.98	23.13	121.04	31.66	129.57	31.66	131.57

App 4.4: ANOVA results comparing FDis measures for three different farm types (core, edge and control) during three different survey years (A = 2017/18, B = 2018/19 and C = 2019/20).

Comparison	**diff**	**p. adjust**
Core A – Edge A	0.04	0.99
Core A – Control A	0.02	1.00
Edge A – Control A	-0.02	1.00
Core B – Edge B	0.06	0.99
Core B – Control B	0.05	0.99
Edge B – Control B	-0.01	1.00
Core C – Edge C	-0.09	0.99
Core C – Control C	-0.05	0.99
Edge C – Control C	0.04	0.99
Core A – Core B	0.01	1.00
Core A – Core C	0.09	0.99
Edge A – Edge B	0.03	0.99
Edge A – Edge C	-0.05	0.99
Control A – Control B	0.04	0.99
Control A – Control C	0.02	1.00

CHAPTER 5

EVALUATING CHANGES IN PREDATOR ABUNDANCE, ACTIVITY PATTERNS AND LIVESTOCK LOSSES FOLLOWING THE REMOVAL OF SHEEP FROM THE SKA CORE

Camera trap image of a black-backed jackal (*Canis mesomelas*) captured on control farm 2 (top) and caracal (*Caracal caracal*) captured on edge farm 3 (bottom) taken during a 70-day camera trap survey in 2019/2020, Northern Cape, South Africa (© Michelle Blanckenberg).

Abstract

Mesopredator conflict in the Karoo centres around the many costs associated with livestock depredation and the resultant persecution of predators. With the cessation of farming activities in the SKA core, concerns around increasing predator abundance and subsequent livestock losses on surrounding farms have intensified. I used camera trap data for four target predator species (black-backed jackal *Canis mesomelas*, caracal *Caracal caracal*, cape fox *Vulpes chama* and baboon *Papio ursinus*) to investigate the impact of a land use change from small livestock farming to protected area on predator abundance over three years. Predator abundance was measured on three farms within the core/protected area, three farms immediately outside the core/protected area and three farms at least 50 km from the core boundary as control farms. I further conducted face-to-face interviews with famers on each of the nine study farms during each survey year to assess changing perceptions towards predators, predators killed and estimated livestock losses. Cape fox was the most abundant predator on all farm types (core, edge and control) across survey years, followed by black-backed jackal, caracal and baboon. Predators were detected on more camera stations during survey C compared to survey A, however there was no significant change in predator abundance between farm types within survey A (before farming activity ended) and survey C (eighteen months after farming activity ended), or between survey years within a specific farm type. Predator activity was more diurnal on core farms after farming stopped, shifting from the primarily nocturnal activity patterns evident on edge and control farms. This suggested that while predator abundance did not respond to a change in land use, predator behaviour, which is more labile, did. Famer perceptions towards predators remained negative over successive surveys and with increasing economic pressures and livestock losses resulting from persistent drought conditions, hunting of predators on edge and control farms increased. These findings suggest that predator management in the future will depend heavily on the socio-political and economic pressures within the area rather than statistically significant changes in predator populations.

Introduction

Human-wildlife conflict is a widespread and complex issue within many ecosystems around the world (Dickman 2010). Increasing human population growth has resulted in increasing transformation of natural habitats for agricultural and urban land use (Lamarque *et al*. 2009). As humans expand into natural environments the likelihood of animal species and humans competing over limited resources increases (Dickman 2010, Pooley *et al.* 2016). The result is a complex network of costs and benefits for both humans and wildlife (Redpath *et al.* 2015, Pooley *et al.* 2016). For wildlife the increased encroachment of humans on natural areas can have either positive or negative impacts on food sources, habitats and population dynamics, therefore wildlife responses to human activities can be highly varied (Fehlmann *et al.* 2020). Several studies have shown that in some cases generalist bird and small mammal species have benefitted from increased agriculture within a landscape (Gentili *et al.* 2014, Carrara *et al.* 2015), however there are numerous examples of larger species with wide ranging patterns (Blowes *et al.* 2019, Bogoni *et al.* 2020, Chase *et al*. 2020) and forest species declining to the point of possible extinction due to increased habitat loss and fragmentation (Nakagawa *et al.* 2006, Broadbent *et al.* 2008, Schwitzer *et al.* 2011).

For humans the impacts of increased interaction with wildlife are almost exclusively perceived as negative. Crop damage is a major catalyst for negative human-wildlife interactions globally with particularly severe impacts for small scale subsistence farmers (O'Connell-Rodwell *et al*. 2000, Gross *et al*. 2018, Torres *et al.* 2018). Often these conflicts occur where human communities are in proximity to both fenced and unfenced nature reserves (Naughton-Treves 1997, Woodroffe *et al.* 2005, Kaplan 2013, Redpath *et al*. 2013). In Africa, elephant (*Loxodonta africana*), baboons (*Papio anubis*) and bushpigs (*Potamochoerus sp.*) are all examples of pervasive damage causing animals (Hoffman & O'Riain 2012, Fehlmann *et al.* 2020, Perry *et al.* 2020). Wild animals can also have detrimental impacts on infrastructure (Soulsbury *et al.* 2016), pose a direct threat to human safety (Packer *et al.* 2018), and increase the risk of zoonoses (Bengis *et al.* 2004, Hassell *et al.* 2017). There is also the added pressure of resource competition in pastoral lands where wild herbivores directly compete with livestock for often limited resources (Young *et al*. 2005, Odadi *et al.* 2011). The financial and social costs of wildlife within agricultural landscapes have resulted in humans having a negative perception towards such wildlife that are often referred to as "pest species", and subject to indiscriminate lethal management techniques (Romañach *et al.* 2007, van Eeden *et al.* 2017, Perry *et al.* 2020).

Within pastoral systems, livestock losses to predators are arguably the main cause of conflict between humans and wildlife (Zimmermann *et al.* 2005, Holmern *et al.* 2007, Gusset *et al.* 2009, Kinnaird & O'Brien 2012, Perry *et al.* 2020). The loss of livestock puts economic, psychological and social pressure on individuals and communities relying on livestock production as their main source of income (Dickman 2010, Karanth *et al.* 2012, Drouilly *et al*. 2018b). Conflict between predators and people can be a complex issue, which is highly context specific, with different predator species having different impacts on different livestock. For example, in Zimbabwe baboon and lion account for 52% and 34% of livestock loss to predators respectively, however baboons typically attacked during the day focusing on small livestock species (sheep and goats), while lions killed at night and would attack both small and large livestock species (sheep, cattle and donkeys) (Butler 2000).

Given the diversity of predators and prey and the marked variation in the legal and socio-economic framework in which predators and livestock interact, it is no surprise that predator management approaches are highly variable both locally and globally (Treves & Kananth 2003, Graham et al. 2005, du Plessis *et al.* 2018). Fencing, building kraals or bomas, visual deterrents and adaptive herding techniques can all be effective non-lethal predator management techniques (Shivik 2004, du Plessis *et al.* 2018, Smith *et al.* 2020c). However, the perceived costs and effort required to establish and maintain these techniques has resulted in many livestock owners opting for lethal management (Treves & Kananth 2003, Bangs *et al.* 2006, McManus *et al*. 2015). Retaliatory or pre-emptive killing of predators is often the most time and cost-effective management technique available to land or livestock owners (Graham *et al.* 2005, Dickman 2010, McManus *et al.* 2015, Drouilly *et al.* 2018b). However, the removal of predators from a system can have profound effects on ecological processes (Ritchie & Johnson 2009, Gordon *et al*. 2016, Morris & Letnic 2017). Specifically, predators influence ecosystems by controlling the abundance and distribution of prey species through top-down effects (Thaker *et al*. 2011, Kuijper *et al*. 2013, Laundré *et al.* 2014).

In the Karoo, larger apex predators such as lion (*Panthera leo*), spotted hyena (*Crocuta crocuta*) and wild dog (*Lycaon pictus*) are all locally extinct with leopards being the only remaining large predator largely confined to mountain refuges (Mann *et al.* 2020). The absence of apex predators coupled with the introduction of abundant and easy to catch and kill livestock has created favourable conditions for mesopredators (e.g., black-backed jackal and caracal) to thrive. Despite the well documented importance of predators as regulators of the abundance of smaller wildlife species in pastoral landscapes, many of which complete with livestock for grazing, lethal management of predators remains pervasive and is often indiscriminate, illegal (e.g., poisoned carcasses) and causes significant welfare harms (e.g., foot hold traps) (du Plessis *et al.* 2015, Nattrass & Conradie 2015, du Plessis *et al.* 2018).

The Karoo is known as an important pastoral region for sheep production, with most landowners managing large herds of sheep (typically dorper *Ovis aries*) within fenced properties (Figure 5.1). There are several key species which are widely reported as the primary predators of small livestock within the Karoo, namely black-backed jackal (*Canis mesomelas*), caracal (*Caracal caracal*), leopard (*Panthera pardus*), cape fox (*Vulpes chama*) and baboon (*Papio ursinus*) (Nattrass & Conradie 2015, Conradie & Nattrass 2017, Drouilly *et al*. 2018b, Minnie *et al.* 2018, Nattrass *et al.* 2020). Small livestock, especially young animals, are relatively easy prey for these species and where natural resources are typically limited, small livestock act as a relatively low energy output prey species (Figure 5.1) (du Plessis *et al.* 2015, McManus et al. 2015, Drouilly *et al.* 2018b). Negative interactions between predators and farmers within the Karoo region of South Africa has been the subject of much recent research (du Plessis 2013, Kamler *et al.* 2013, du Plessis *et al.* 2015, Minnie 2016, du Plessis et al. 2018, Drouilly *et al.* 2018b, Minnie *et al.* 2018, Nattrass *et al.* 2020) and includes discussion on the escalating conflict between stakeholders on how best to reduce such interactions (Nattrass & Conradie 2015, McManus *et al*. 2015, Nattrass & Conradie 2018).

The extent to which predators contribute to livestock losses in the Karoo, however, is uncertain (du Plessis *et al.* 2015, Nattrass & Conradie 2015, Drouilly *et al.* 2018b, Nattrass & Conradie 2018, Nattrass *et al.* 2020). Predator abundance is perceived by farmers to have fluctuated considerably over time (see Chapter 1), but a recent study by Drouilly *et al.* (2018) suggested that predator abundance (particularly black-backed jackals) in the central Karoo has steadily increased within farmlands since 2000. This increase is thought to have coincided with a decrease in the number of active livestock farmers and farm workers within the Karoo, as well as increased mean farm size (Nattrass & Conradie 2015). With fewer people managing farm infrastructure and actively herding sheep, livestock losses have unsurprisingly increased. The lack of resources (time, employees and money) has resulted in many farmers opting for lethal management (usually call and shoot methods but poisoning too) with contiguous groups of landowners pooling resources to engage in organised block hunts (Bailey & Conradie 2013).

Figure 5.1: The dominant small livestock species that is farmed in the Karoo, a dorper sheep with her weaned offspring (left). Lambs are often targeted by predator species (right) driving retaliatory measures by farmers and fuelling conflict between stakeholders on how best to reduce predation. Images captured during extensive camera trap surveys in SKA region of the Karoo, South Africa (© Michelle Blanckenberg).

The effectiveness of lethal management on reducing predator populations and hence livestock losses is however, increasingly debated (Treves & Karanth 2003). Many researchers suggest that lethal management is not an effective method for long term predator management (McManus *et al.* 2015, Lennox *et al*. 2018, Nattrass *et al.* 2020), while landowners feel that lethal measures are the only long-term viable options that they can afford given their financial and time constraints (du Plessis *et al.* 2015, McManus *et al.* 2015). Nattrass *et al.* (2020) showed that where lethal management was used livestock losses to predators increased in subsequent years, suggesting lethal management was counterproductive. This led to their suggestion that non-lethal predator management techniques (e.g., improving fencing, active herd management and housing livestock in kraals or bomas at night) would be more effective at reducing livestock losses to predators within farmlands than lethal management.

Another aspect of the predator conflict debate focuses on the conflict between protected areas and farmland and how predators move between the two. Proximity to the boundaries of protected areas is a well-documented risk for livestock owners as often there are increases in livestock losses in neighbouring farms. Reported cases of predator related livestock loss within communities in Zimbabwe (along the boundary of Sengwa Wildlife Research Area) and Kenya (adjacent to the boundary of Tsavo East National Park) illustrate the potential risk of having farmland bordering protected areas (Butler 2000, Patterson *et al.* 2004). However, there has been limited experimental research into how protected areas may influence predator abundance in surrounding farmland within South Africa (Minnie 2016, Minnie *et al.* 2018).

Several studies have investigated predator abundance within protected areas versus small livestock farming areas in the Karoo (Woodgate *et al.* 2018, Drouilly *et al.* 2018a, Drouilly & O'Riain 2019). Evidence from these studies suggests that predator abundance between the two different land uses is not significantly different, indicating that predators are not favouring farming areas over protected areas as predicted by landowners. Unfortunately, these studies typically only compare predator ecology within already established protected areas versus established farming areas. To my knowledge there has been no study in the Karoo that tracks the potential changes in predator abundance and behaviour following the change in land use from farming to protected area. The lack of such baseline data makes it difficult to predict how predators would respond to the absence of sheep outside of protected areas and therefore whether livestock farming does promote mesopredator abundance.

As discussed in chapters 3 and 4, the removal of sheep is predicted to have positive impacts on vegetation, small mammal abundance and medium and large wild herbivore abundance (see Chapter 3 and 4) (Prins 2000, Bosing *et al.* 2014, Hempson *et al.* 2017, Hoffman *et al.* 2018). However, the predictions for how a cessation of farming activities including actively hunting predators and the removal of sheep may impact mesopredator abundance are less clear. Small livestock farmers predict that with the removal of sheep in one area, surrounding small livestock farms which are still active will experience an immigration of predators and hence suffer from increased livestock losses. This argument is derived from the experiences of farmers adjacent to protected areas who have experienced increases in predator abundance and livestock losses as a result of immigration from a protected area (Minnie *et al.* 2018). As predators may prefer small livestock as prey (Drouilly *et al.* 2018c), farmers predict that predators will actively hunt on livestock farms but will den and socialise in the newly formed protected area to avoid persecution. The implication here is that predator abundance will increase on both core and edge farms with predators having improved survival (reduced persecution) while still accessing locally abundant and easy to catch livestock prey. Drouilly *et al*. (2018c) assessed the diet of small livestock predators (jackal and caracal) in a protected area and a similar sized region of livestock farms to test this prediction. The study showed that while jackal and caracal do target sheep when in a farming area (jackal more so than caracal), predator scat within the protected area showed almost no evidence of livestock and a preponderance of plant material and small mammals (Drouilly *et al.* 2018c). This suggest that predators within protected areas are rarely hunting on neighbouring active livestock farms and favour wild prey species when they are available (Drouilly *et al*. 2018c).

Within the SKA region of the Karoo four species have been identified as major predators of sheep and small livestock (Terblanche 2020) (Figure 5.2). Black-backed jackal (hereafter referred to as jackal) and caracal have been reported by farmers as extremely problematic predator species with some studies suggesting landowners attribute up to 12% of livestock losses per year to these species (Nattrass & Conradie 2015). Chacma baboon (hereafter referred to as baboon) in the Northern Cape and cape fox are not considered extremely problematic due to low population sizes (baboon) and infrequent attacks (cape fox) however, both can cause severe damage to young lambs on occasion, resulting in some farmers considering them as threating and potentially damage causing species (Figure 5.2, du Plessis *et al.* 2018). The ecology of each predator species within the Karoo is highly variable making conflict management increasingly complex.

Jackal are highly adaptive predators often referred to as opportunistic hunters and scavengers (Humphries *et al.* 2016a, Bergman *et al*. 2013). They are medium sized mammals weighing between 6 and 11 kgs (males typically larger than females) (Sheldon 1992, Humphries *et al.* 2016a, Bergman *et al*. 2013). As generalist omnivores their diet can be highly variable including invertebrates, berries, reptiles, small mammals, birds and medium sized wild (e.g., steenbok) and domestic (e.g., sheep) mammals (Sheldon 1992, Humphries *et al.* 2016a, Bergman *et al*. 2013, Nattrass *et al.* 2020). Jackal are typically crepuscular species however, due to their adaptability and sustained levels of persecution within the Karoo, jackal have been shown to shift towards a more nocturnal activity pattern to avoid detection (Sheldon 1992, Humphries *et al.* 2016a, Bergman *et al*. 2013). Jackal prefer more open, flat shrubby or grassy habitats however, they have been recorded in a wide variety of habitats and elevations (Loveridge & Macdonald 2002, Humphries *et al.* 2016a, Bergman *et al*. 2013, Drouilly *et al.* 2018a). The generalist, adaptable nature of this species makes them highly successful in the

Karoo where resources can be equally variable depending on rainfall (Humphries *et al.* 2016a, Bergman *et al*. 2013).

Caracal are solitary generalist species with excellent camouflage and a more cryptic nature (Braczkowski *et al.* 2012, Stuart & Stuart 2013, Avenant *et al.* 2016). They are robust medium sized predators ranging between 7 and 19 kgs (males typically larger than females) (Braczkowski *et al.* 2012, Stuart & Stuart 2013, Avenant *et al.* 2016). Caracal prey on a range of mammal species (e.g., small mammals, rock hyrax and hares), as well as birds and larger herbivore species (Braczkowski *et al.* 2012, Stuart & Stuart 2013, Avenant *et al.* 2016). Caracal can target small livestock (i.e., sheep and goats) but consume less livestock than jackal on farmlands (Braczkowski *et al.* 2012, Stuart & Stuart 2013, Avenant *et al.* 2016). Predator diet analysis within Anysberg protected area and surrounding farmland showed that caracal would typically select wild prey over livestock (Drouilly *et al.* 2018c). This indicated that where livestock predation by caracal was observed, wild prey populations (e.g., small mammals, which contributed ~80% to caracal diet in protected areas) were likely limited by the impacts of livestock on the landscape and/or climate (Hoffman *et al.* 2005, Muck & Zeller 2006, Torre *et al*. 2007, Drouilly *et al.* 2018c). In the Karoo, caracal prefer rockier habitat with slight elevation and taller shrubs in order to remain hidden (Stuart & Stuart 2013, Avenant *et al.* 2016, Drouilly *et al.* 2018c). Unlike jackal, caracals are predominantly nocturnal (Braczkowski *et al.* 2012, Stuart & Stuart 2013, Avenant *et al.* 2016).

Cape foxes are ecological similar to jackal although being much smaller with weights ranging from 2.5 to 4 kgs (Kamler 2012) they typically consume smaller prey. Cape fox are also seen as generalist, opportunistic predators, with diets ranging from insects to small reptiles and rodents (Kamler 2012, Kamler *et al.* 2013). In the Karoo, cape fox has been known to hunt newly born lambs. Like jackal, cape foxes prefer open grassy or shrubby areas but are typically more nocturnal than jackal (Kamler 2012, Kamler *et al.* 2013). Cape fox have also been shown to respond inversely to changes in black-backed jackal densities (i.e., when jackal densities decrease, cape fox densities increase) (Kamler *et al.* 2013). This may be the result of meso-predator release interactions where jackal have nonlethal effects on cape fox populations where these two species interact (Kamler *et al.* 2013). Changes in cape fox densities may highlight and reflect changes in black-backed jackal densities as a result of this interaction (Kamler *et al.* 2012a, Kamler *et al.* 2013).

Within the SKA region of Karoo, chacma baboon are rare with troops being small compared to the central Karoo regions (Drouilly *et al.* 2018a, Tew *et al.* 2018). Baboons are diurnal species unlike the other predator species in this area and are typically larger than the other predator species ranging from 16 to 35 kg (Barrett & Henzi 2008). Baboons are highly adaptable and can thrive in a variety of habitats, however they are highly dependent on water and their presence throughout much of the farming areas of the Karoo is almost certainly linked to water provisioning for sheep (Tafani & O'Riain 2017, Tew *et al.* 2018). Similar to jackal, baboons are generalist omnivores with diets ranging from roots and bulbs to insects, rodents, hares and birds (Tafani & O'Riain 2017, Tew *et al.* 2018). Within the Karoo, baboons have been reported to prey on lambs especially during drought conditions when farmers often provision their livestock and in so doing attract baboons into close physical contact with livestock at feeding sites (Tafani & O'Riain 2017).

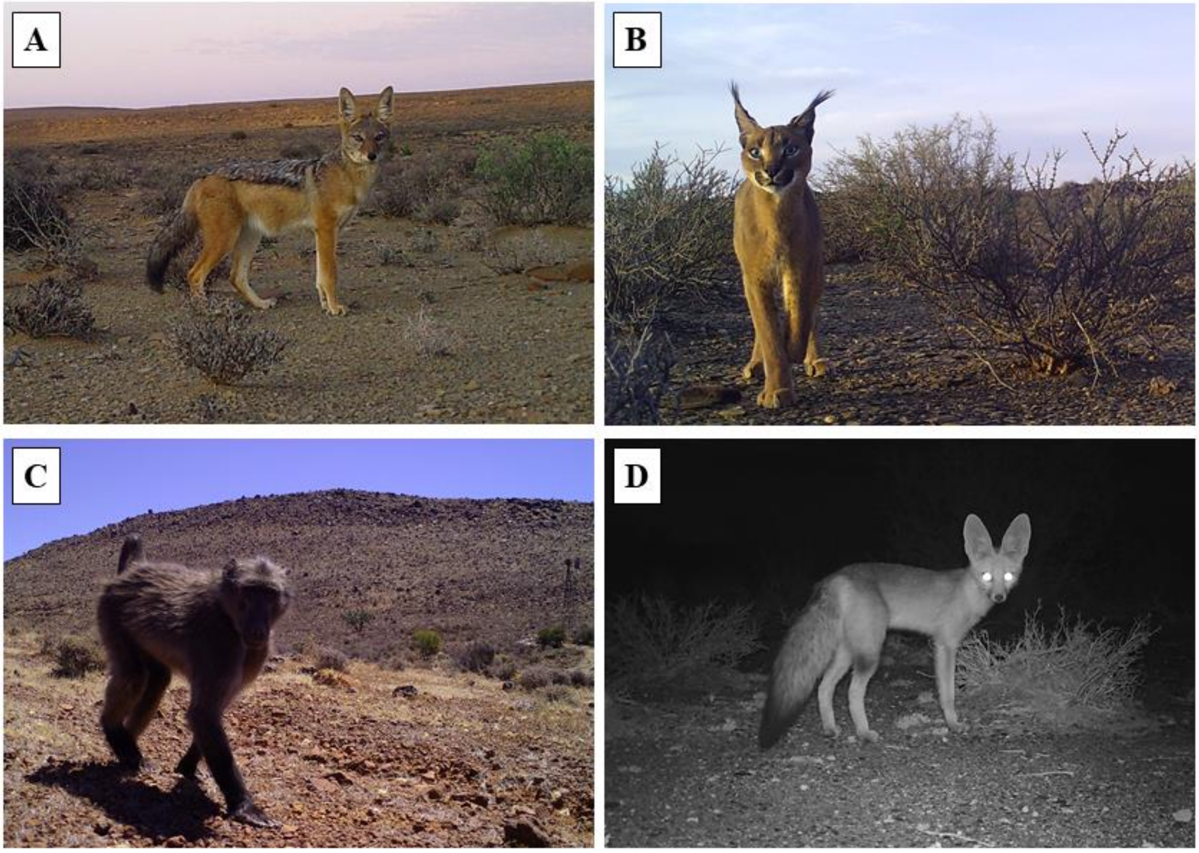


Figure 5.2: The four main predator species that are considered to pose a threat to livestock in SKA region of Karoo. Black-backed jackal (A) and caracal (B) are considered extremely problematic, while chacma baboon (C) and cape fox (D) are considered moderately problematic. Images captured through extensive camera trap surveys in SKA region of the Karoo, South Africa (© Michelle Blanckenberg).

This chapter aims to understand how the cessation of farming activities on core farms will influence the relative abundance and activity patterns of select predator species known to predate on livestock. I hypothesised a change in land use from small livestock farming to protected area would be associated with a change in the relative abundance of mesopredator species (hypothesis 1, H1), species composition (H2) and their activity (H3). I predicted that in the absence of people and the active persecution of predators, all predator species abundance would increase on core farms (prediction 1, P1). I also predicted that jackal and caracal abundance on edge farms would increase after sheep are removed on the core as these species would immigrate onto edge farms in search of domestic prey species (i.e., sheep) which are more abundant because of being provisioned and easier to catch than wild prey (P2), while baboon and cape fox abundance would remain constant (P3). I predicted that removal of sheep on core farms would result in a shift in functional diversity of predator-prey communities on core farms (with wild prey abundance decreasing due to increased predation as predators shift from domestic to wild prey) but remaining unchanged on edge and control farms (P4). I also predicted that farmers perceptions of predators would remain constant (and negative) (throughout the survey period (P5).

Methods

Camera trap placement and data collection

I used the data from the extensive camera trap surveys on the nine study farms detailed in chapter 4. Survey A (2017/18) focused on the period before farming ceased on core farms and acted as baseline data for comparisons with survey B (2018/19) and survey C (2019/20), which were six months and eighteen months after the termination of farming activity on core farms, respectively. In this chapter I focus on the distribution of detections, relative abundance and activity patterns of four predator species that farmers in the region had identified (through various interviews during the study period) as posing a risk to their livestock. Two species, jackal and caracal were considered extremely problematic animals by farmers, while the other two species baboon and cape fox were considered moderately problematic animals. I extracted data for select (i.e., most consumed) wild prey species of these four predators to explore changes in the predator-prey communities in response to a change in land use from small livestock farming to protected area.

Data analyses

Independent captures, naïve occupancy and photographic rates (RAI) for predators

As detailed in Chapter 4 (see methods sections) data from camera trap surveys within the study site were over-dispersed (high prevalence of zeros) resulting in occupancy models failing to converge/distinguish between true absence and low detection (MacKenzie *et al*. 2002, MacKenzie and Bailey 2004, MacKenzie *et al.* 2004). Consequently and similar to Chapter 4, I opted to not use occupancy models and rather explore the relative abundance of target species across survey years and farm types, making sure to standardised survey effort. All statistical analyses were conducted using RStudio version v3.5.3 (RStudio Team 2019).

Therefore, for each target predator species, I calculated the number of independent captures (photographic events at least 30 minutes apart) per farm type for each survey year, as well as naïve occupancy (proportion of sampled trap stations where a species was present, does not take detectability into account). I mapped the distribution of problematic predators as detected/not detected at each camera station within each farm type both before (survey A) and after sheep removal and the cessation of farming activities on core farms (survey B and C). I calculated photographic rate (also known as relative abundance index, RAI) for each species per farm type and survey year. I compared the difference in photographic rate for each predator species between survey years within a specific farm type using paired Wilcox signed-rank tests. I further compared photographic rate for these species between farm types within a specific survey year using a non-parametric Kruskal-Wallis test with a post-hoc pairwise Wilcox test. Due to low detection rates for baboon across the survey period, I combined baboons and cape fox data together into one category of “moderately problematic species” and used the combination of Wilcox signed-rank tests and Kruskal-Wallis tests to investigate differences in photographic rates of this category between years and between farm types.

Functional diversity

I explored the functional diversity within the different farm types across the three survey years by estimating species level RAI’s for different functional groups and body masses (see Chapter 4; Drouilly & O’Riain 2019) (Table 5.1). Here functional group was assigned according to whether a species was either predator or prey. Prey was divided into two categories, domestic (sheep), and wild (i.e., hare spp., rock hyrax, rock rabbit spp., steenbok and small mammal spp.). Wild prey were derived from a recent dietary study by Drouilly *et al.* (2018) using scat analysis for jackal and caracal within the central Karoo.

Table 5.1: Functional group, persecution level and mean body mass (grams) of select predators and their main prey species recorded in three farm types (core, edge and control) over three survey years in the SKA region of the Karoo, South Africa.

Species	Functional group	Persecution level	Body mass (grams)
Black-backed jackal *Canis mesomelas*	Predator	High	8000
Cape fox *Vulpes chama*	Predator	Medium	3250
Caracal *Caracal caracal*	Predator	High	13000
Chacma baboon *Papio ursinus*	Predator	Medium	16000
Dorper *Ovis aries*	Domestic prey	None	90000
Hare spp. *Lepus* spp.	Wild prey	None	2950
Rock hyrax *Procavia capensis*	Wild prey	Low	3500
Rock rabbit spp. *Pronolagus* spp.	Wild prey	None	1750
Steenbok *Raphicerus campestris*	Wild prey	Low	11000
Small mammal spp.	Wild prey	None	50

Small mammals (shrews, rodents and gerbils) were captured frequently during my camera trap surveys however species level identification was often difficult. Camera trapping is considered an unreliable method for surveying small mammals especially when cameras are not specifically optimised for this group (Glen *et al.* 2013, Loggins *et al.* 2019). I therefore opted to use abundance measures from Sherman live trapping on each farm to derive a proxy for small mammal abundance (see Chapter 3). Due to limited information on which small mammal species are preferred prey of predators I averaged the body mass of the five taxa captured (see Chapter 3) to derive a single mean small mammal mass as a presentative of the overall small mammal prey group (body mass ranged from 21 g – 100 g based off measurement taken in the field during small mammal trapping). As small mammal abundance was only recorded during survey A and survey C, small mammals were excluded from functional diversity measures. However, they were included in the generalised linear models described below. Domestic prey RAIs (i.e., sheep) were calculated through camera trapping events as opposed to reported stocking number to ensure consistency in comparisons between both predators and wild prey on each farm type in each survey. Body mass was again presented as the log-transformed mean body mass in grams of each species (see Chapter 4). I also calculated the functional dispersion index (FDis) for each farm type in a specific year following the same methods as described in Chapter 4 and comparing differences using an ANOVA with a post-hoc Tukey test.

I used General Linear Models (GLMs) to model predator RAI (response variable) as a function of year (survey A or C), farm type (core, edge or control), farm management style (active or passive), sheep RAI, medium and large wild prey RAI and small mammal abundance. The model only included survey's A and C as these were the two years for which I had small mammal abundance estimates for each farm. Farm management style was binary with farms being either actively or passively managed (see Chapter 4). Active management referred to farms where either the landowner or permanent employees lived on the farm and therefore would actively manage sheep daily. A passive management style referred to farms where landowners or employee did not live or work full time on the farm and therefore would typically only attend to sheep on a weekly, or bi-weekly basis. Thus, human presence and activity was lower on passive farms.

I used the *glm* function from the 'stats' package (R Core Team 2020) to test if either jackal or caracal RAI were significantly affected by any of the covariates. I determined the most parsimonious model using the *drop1* function from the 'stats' package (R Core Team 2020) and where the Akaike Information Criterion (AIC) for a covariate is lower than the AIC for the global model then that covariate was dropped from the final model (see App 5.1, 5.2 and 5.3). I also combined jackal and caracal RAIs to produce a 'general predator RAI' which I then used as a response variable within a GLM with the same covariates. The *anova* function from the 'stats' package was used to determine p-values for each predictor covariate, and both the multivariate and univariate results were reported for each model. GLMs were fitted with a Poisson distribution which is typical for data which is not normally distributed including data where abundance values for a specific species are low (Wang *et al.* 2012).

Daily activity patterns

I followed a similar method to that outlined in Chapter 4, where the 'overlap' package (Ridout & Linkie 2009) was used to determine the temporal overlap coefficient for specific species between different survey years. Low detections of baboons and caracal precluded an estimate of overlap coefficients, for both species. I thus focussed on jackal (arguably the most problematic predator species) and then combined jackal, caracal and cape fox into a "predator" category to explore temporal changes in activity across surveys. I excluded baboon from this combined predator category as this species is strictly diurnal which would confound results.

The Δ is bound between 0 and 1, with 0 being no overlap and 1 being complete overlap (Noor *et al.* 2017). I further derived 95% confidence intervals using 1000 bootstrap resampling technique (Noor *et al.* 2017). Once again, a Δ coefficient below 0.70 was considered a significant shift in daily activity patterns (Linkie & Ridout 2011, Noor *et al.* 2017, Dias *et al.* 2019).

Longitudinal surveys and landowner questionnaires

During each survey the landowners of key study farms (total of 8 farms, as one core landowner was not available) were interviewed to gather information on livestock losses, predators killed, as well as the landowner's perceptions towards predators. Several key questions were repeated over the three survey years and helped form the basis for several covariates when determining patterns in predator abundance and distribution (Table 5.2). Low sample sizes precluded quantitative analyses and these data were mostly used to understand farmer perceptions on the nine study farms.

Table 5.2: Key questions discussed with eight landowners during three different wildlife surveys across three different farm types in the SKA region of the Karoo, South Africa.

Question category	Key questions
Landowner information and management style	Q1: Size of property? Q2: Number of years farming experience? Q3: Type and number of livestock? Q4: Number of permanent employees and number of employees living full time on property, if any?
Livestock losses	Q5: Percentage, if any, of sheep lost within a specific year? Q6: Perceived causes of livestock losses?
Predator management and perceptions around predators	Q7: Which wild animals require active management? Q8: What is the first thing you think about when I say "jackal" or "caracal"? Q9: Which method is preferred to manage predator populations
Perceptions around protected areas	Q10: How will the creation of a protected areas impact wildlife on core and edge farms respectively? Q11: How will the creation of a protected areas impact predators on core and edge farms respectively? Q12: Do you feel a nearby protected area will negatively or positively impact your property?

I collated data on the number of predators killed on each farm in a specific survey year and correlated this with the observed predator RAIs for each farm (determined through extensive camera trapping). Furthermore, livestock losses attributed to predators were often used by landowners as a proxy for increases or decreases in predator abundance. I therefore compared observed predator RAI (jackal and caracal combined) with livestock losses and number of predators killed through hunting using the *ggpairs* function from the “GGally” package (Schloerke *et al.* 2020). I then used combined observed predator RAIs for jackal and caracal and regressed these against reported livestock losses and the number of predators killed through hunting, respectively for both survey A (baseline) and survey C (two years post baseline) using the *cor.test* function from the ‘ggpubr’ package (Kassambara 2020).

Results

Independent captures, naïve occupancy and photographic rates (RAI) for predators

Overall cape fox had the highest capture rate and naïve occupancy across farm types and surveys of the four predator species (Table 5.3). Captures were highest for cape fox on control farms during survey A and lowest on edge farms during survey A (Table 5.3). Captures of cape fox showed a downward trend on all three farm types across survey years (Table 5.3). Baboon had the lowest capture rate and naïve occupancy of all predators throughout the survey period (Table 5.3). Baboons were only captured on core and control farms during survey A and only captured on core farms during survey B and C (Table 5.3). Jackal were captured more often than caracal on all three farm types in all three surveys (Table 5.3). Core farms had the highest captures and naïve occupancy for both jackal and caracal (Table 5.3).

Survey C had the highest jackal captures on core farms while survey B saw the highest captures for caracal on core farms (Table 5.3). Caracal capture remained fairly constant between surveys on edge and control farms with slightly higher captures on control farms compared to edge (Table 5.3). Captures for jackal were higher on edge farms compared to control farms with survey B having the highest captures on edge farms and survey C showing the highest for control farms (Table 5.3).

A similar pattern is seen with photographic rate (also referred to as relative abundance index, RAI) for target predator species as with number of captures and naïve occupancy (Table 5.3). Cape fox has the highest photographic rate across the survey period and area, while baboon has the lowest (Table 5.3). Jackal and caracal showed a trend of increasing photographic rates over the three surveys for all farm types, however survey B had slightly higher photographic rates on edge farms compared to survey C (Table 5.3).

Table 5.3: The number of independent photographic captures for four predator species on nine different farms in three surveys A, B and C (A = 2017/18, B = 2018/19 and C = 2019/20). Farms were categorised according to their geographical location as either within the SKA protected area (core), on the edge of the protected area (edge) or at least 50km from the edge of the protected area (control). Data extracted from Chapter 4 - Table 4.4, 4.5 and 4.6.

Species	**Core**			**Edge**			**Control**		
	A	*B*	*C*	*A*	*B*	*C*	*A*	*B*	*C*
	Number of independent captures								
Black-backed jackal *Canis mesomelas*	20	18	28	6	20	11	3	8	16
Caracal *Caracal caracal*	1	9	5	1	0	2	3	2	2
Cape fox *Vulpes chama*	27	27	16	15	19	12	129	51	50
Chacma baboon *Papio ursinus*	1	3	1	0	0	0	0	0	1

Mean relative abundance (RAI) for cape fox was significantly higher ($H_{(2)}$ = 5.68, p.adjust = 0.05) on control farms during survey A (p = 0.05) but not during survey B (p = 0.06) and C (p = 0.06) (Figure 5.3). There was no significant difference in RAI between farm types or survey years for caracal (Figure 5.3, Table 5.4 and Table 5.5). Jackal RAI was significantly higher on core farms compared to edge and control farms during survey A, however there was no significant difference between farm types in survey C (Table 5.5 and Figure 5.3). Similarly, within each farm type there was no significant change in jackal RAI between survey years (Table 5.4 and Figure 5.3). Combined predator RAI was significantly higher on control farms during survey A ($H_{(2)}$ = 5.95, p.adjust = 0.05) (Table 5.4 and Figure 5.4). During survey C combined predator RAI was not significantly different between core, edge or control farms (Table 5.5 and Figure 5.4). There was no significant difference between farm types for combined predator RAI during survey B (Figure 5.3). Overall, combined predator RAI did not change significantly between survey years within specific farm types (Table 5.4 and Figure 5.3).

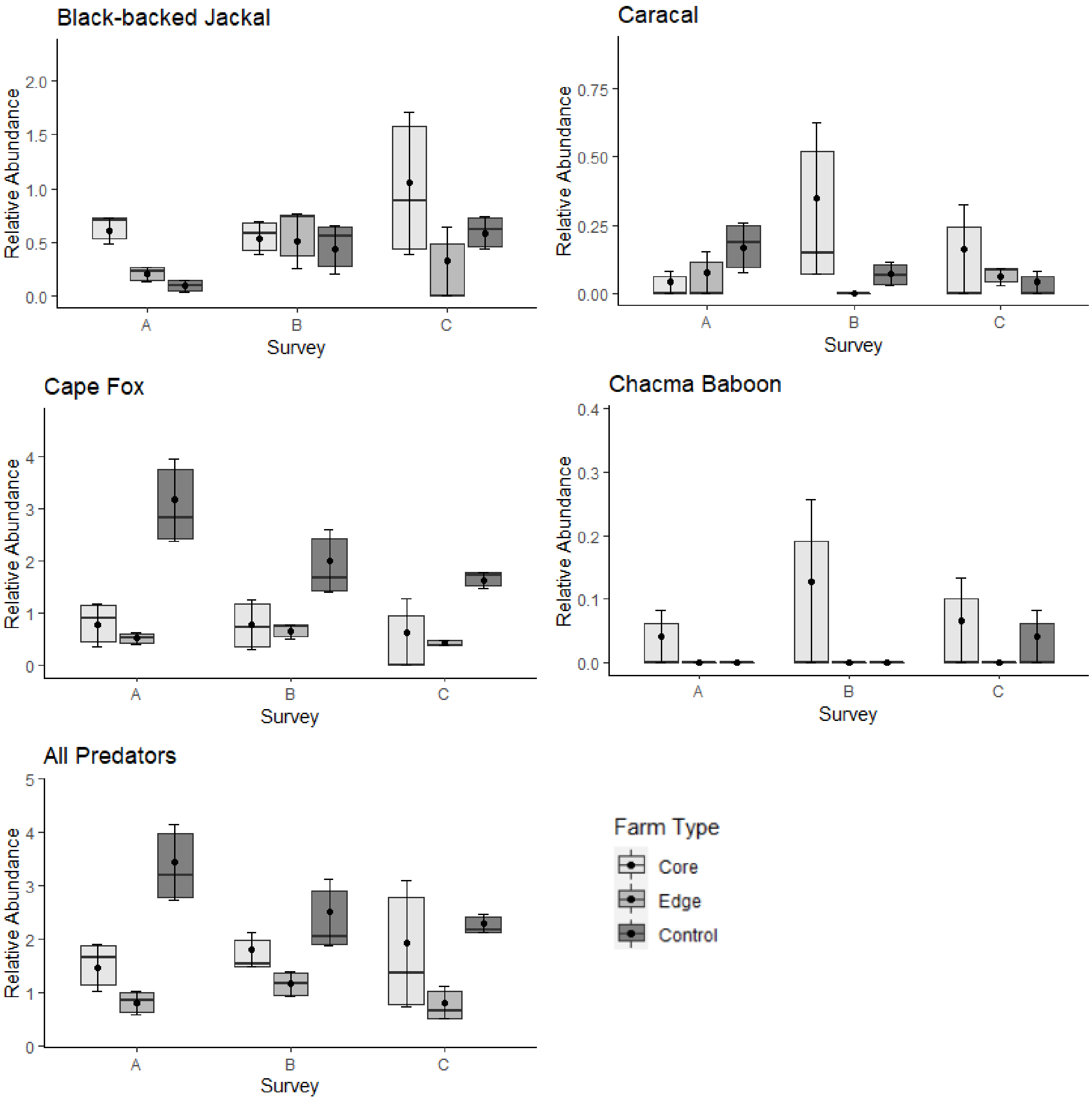


Figure 5.3: Boxplots representing photographic rates (RAIs) for four predator species as well as combined predator RAI on three farm types (core, edge and control) over three survey years (A = 2017/18, B = 2018/19 and C = 2019/20). Shaded boxes indicate lower quartile, median (thick black line) and upper quartile for RAIs, while black dot indicates mean RAI with error bars representing standard error.

Table 5.4: Results from both paired and unpaired Wilcox tests comparing RAIs for black-backed jackal, caracal and combined predators found within core, edge and control farms between survey A (2017/18) and survey C (2019/20). Comparisons are considered significantly different when p.adjust < 0.05 and are indicated with an asterisk.

Farm Type	**Comparison**	**Black-backed jackal**			**Caracal**			**Combined predators**		
		statistic	*n*	*p.adjust*	*statistic*	*n*	*p.adjust*	*statistic*	*n*	*p.adjust*
Core	A – C	2	3	1.00	1	3	1.00	3	3	1.00
Edge	A – C	3	3	1.00	3	3	1.00	3	3	1.00
Control	A – C	3	3	0.75	5	3	1.00	6	3	0.75

Table 5.5: Results for Kruskal-Wallis test with post-hoc pairwise Wilcox test comparing RAIs for different predators found within survey A (2017/18) and survey B (2019/20) communities between three farm types (core, edge and control). Comparisons are considered significantly different when p < 0.05*.

Year	Trophic level	Chi-squared	df	p	Comparison	Wilcox post hoc p value
A	Black-backed jackal	5.95	2	0.05*	Core – Control	0.05*
					Edge – Control	0.40
					Edge - Core	0.05*
	Caracal	1.38	2	0.49	Core – Control	0.96
					Edge – Control	0.96
					Edge - Core	1.00
	Combined predators	5.95	2	0.05*	Core – Control	0.05*
					Edge – Control	0.05*
					Edge - Core	0.40
C	Black-backed jackal	0.82	2	0.66	Core – Control	0.70
					Edge – Control	0.70
					Edge - Core	0.70
	Caracal	0.10	2	0.94	Core – Control	1.00
					Edge – Control	1.00
					Edge - Core	1.00
	Combined predators	2.75	2	0.25	Core – Control	1.00
					Edge – Control	0.30
					Edge - Core	1.00

The percentage of cameras that detected either a jackal or a caracal on core farms varied minimally from survey A (22.7%) to survey B (29.5%) and C (25%). On edge farms survey A had the had the lowest number of cameras detecting predators (13.9%) compared to survey B (18.6%) and C (20.9%), similar to control farms (A = 9.6%, B = 15% and C = 21.1%). Overall, there were more captures at camera stations closer to fence lines (Figure 5.4). During survey A 80% of cameras detecting a predator on core and control farms were outer edge cameras, while 100% of cameras detecting predators on edge farms were outer edge cameras (Figure 5.4). During survey B for all farm types only 60% of cameras detecting predators were outer edge cameras, and in survey C this decreased to 45 – 54% (Figure 5.4).

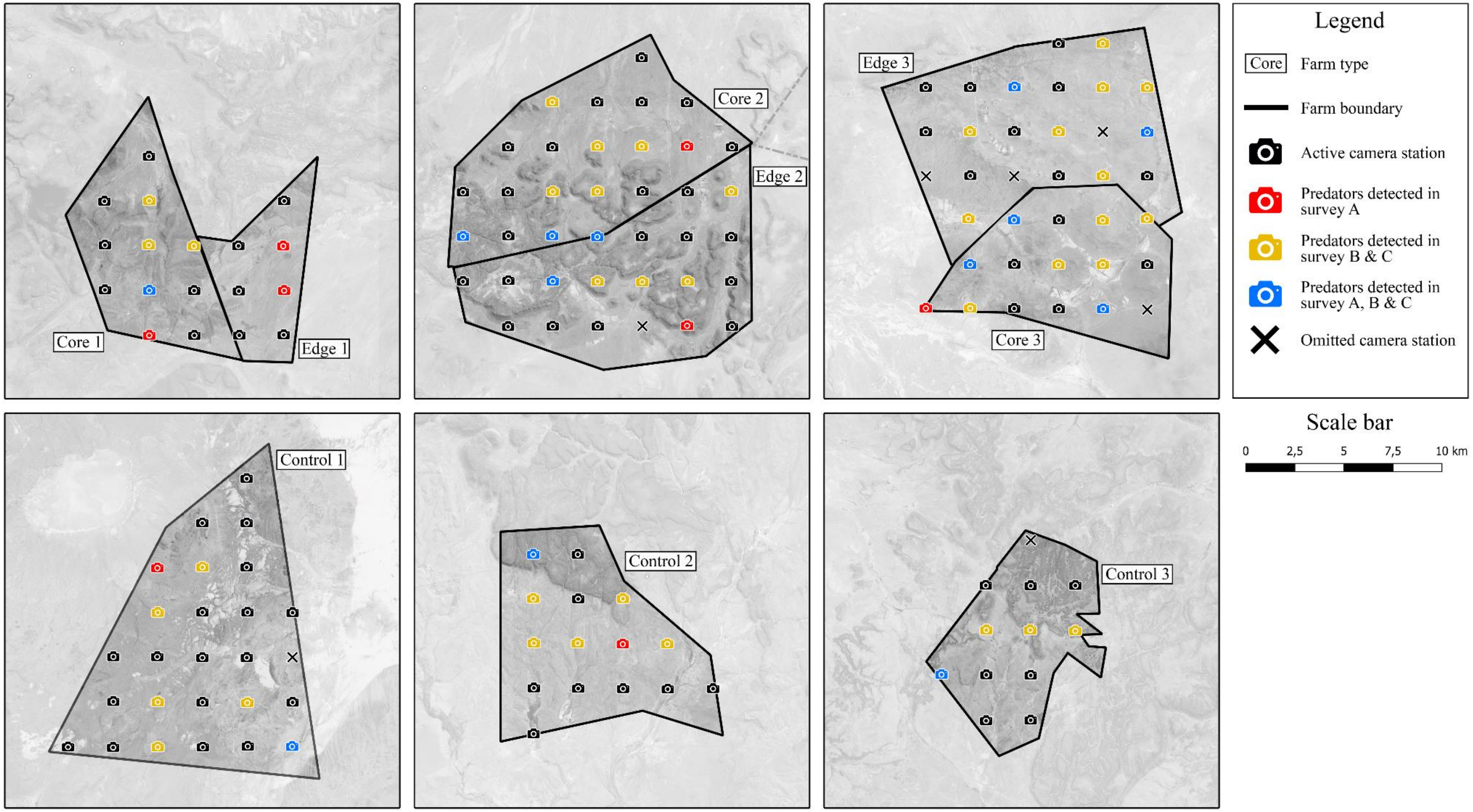


Figure 5.4: Camera trap (camera icons) survey design across the nine small livestock farms showing camera station were either black-backed jackal or caracal were captured over the three survey years (red camera icons = survey A only, yellow camera icons = survey B and C collectively, blue camera icons = where survey A, B and C overlap). Map includes core (n=3 with 44 cameras), edge (n=3 with 43 cameras) and control farms (n=3 with 52 cameras) with cameras placed at regular intervals on a randomly situated 2 x 2 km grid. Core 1 = Janseboom, Core 2 = Jas Kloof, Core 3 = Lovedale, Edge 1 = Hondeblaf, Edge 2 = Rietpoort, Edge 3 = Gannabos Leegte, Control 1 = Hoezar-Wes, Control 2 = Leeuwkrans and Control 3 = Skurwekloof.

Daily activity patterns

Coefficients of overlap (Δ) were not significantly different for jackals on core farms between survey A and B, or between survey A and C (Table 5.6). The shift in activity was significant for edge and control farms between survey A and B and between survey A and C (Δ below 0.70 therefore considered significant) (Table 5.6). During survey A there were significant shifts in activity patterns for jackal between all three farm types with comparisons between edge and control farms having the lowest overlapping coefficient (Δ = 0.39) and therefore the most significant shift (Table 5.6). During survey B, only core and control farms, and edge and control farms had significant shifts in daily activity (Table 5.6). Only comparisons between daily activity of jackal between core and control farms during survey C saw significant shifts in daily activity patterns (Table 5.6).

Table 5.6: Overlapping coefficients (Δ) with 95% bootstrap confidence intervals for black-backed jackal across three farm types (core, edge and control) over three survey years (A = 2017/18, B = 2018/19 and C = 2019/20). Values in bold indicate a significant shift in daily temporal activity.

Farm Type	Comparison	Overlapping coefficient Δ	Bootstrap CI
Between years in each farm type			
Core	A – B	0.90	0.89 – 1.25
	A – C	0.82	0.75 – 1.08
Edge	A – B	**0.53**	0.27 – 0.83
	A – C	**0.49**	0.22 – 0.80
Control	A – B	**0.60**	0.38 – 1.17
	A – C	**0.58**	0.34 – 1.11
Between farm type in each year			
A	Core - Edge	**0.55**	0.34 – 0.88
	Core - Control	**0.68**	0.61 – 1.28
	Edge - Control	**0.39**	0.08 – 0.84
B	Core - Edge	0.76	0.64 – 1.01
	Core - Control	**0.51**	0.25 – 0.73
	Edge - Control	**0.60**	0.40 – 0.84
C	Core - Edge	0.75	0.64 – 1.04
	Core - Control	**0.55**	0.37 – 0.74
	Edge - Control	0.70	0.54 – 0.99

Between survey A and C activity patterns on core farms for jackal remained relatively constant with peaks at 06:00 and 19:00 (Figure 5.5A). While activity on control farms shifted significantly between survey A and C with the peak activity during survey A occurring at 04:00 and at 18:00, and at 00:00 and at 06:00 in survey C (Figure 5.5C). Activity on edge farms peaked at 00:00 and 06:00 during survey A, with similar patterns in survey C however peaks were much less defined (Figure 5.5B). During survey C peak activity on all three farm types for jackal was roughly between 01:00 and 06:00, as well as 18:00 and 00:00 (Figure 5.6). Core farms had a more even activity pattern, with jackal activity shifting towards daytime compared to the defined night time peaks on control farms (Figure 5.6A).

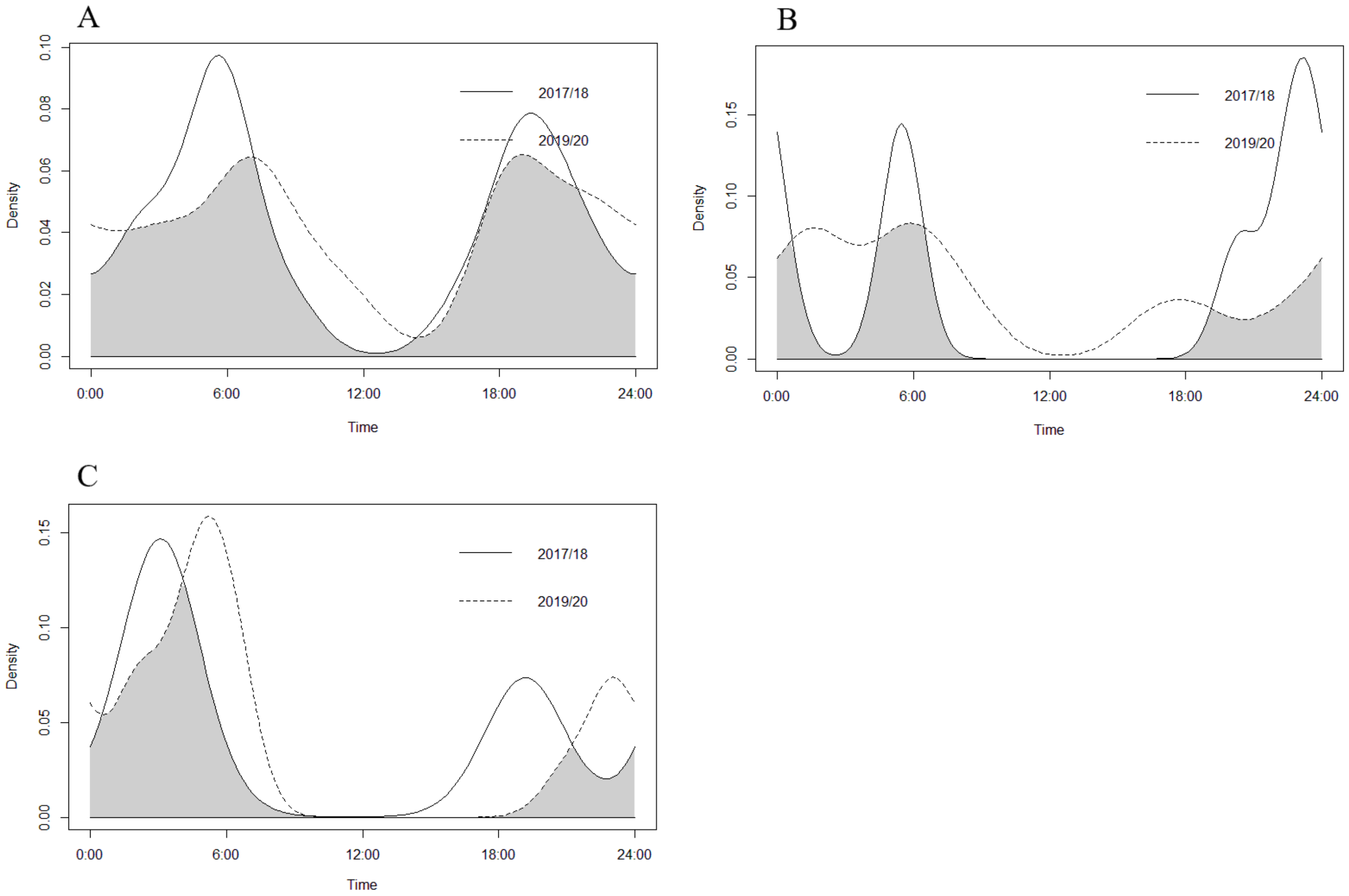


Figure 5.5: Daily activity patterns of black-backed jackal on core (A), edge (B) and control (C) sites during survey A (2017/18, solid line) and survey C (2019/20, dotted line). Grey shaded area indicates the overlap in activity between the two survey years (also known as delta).

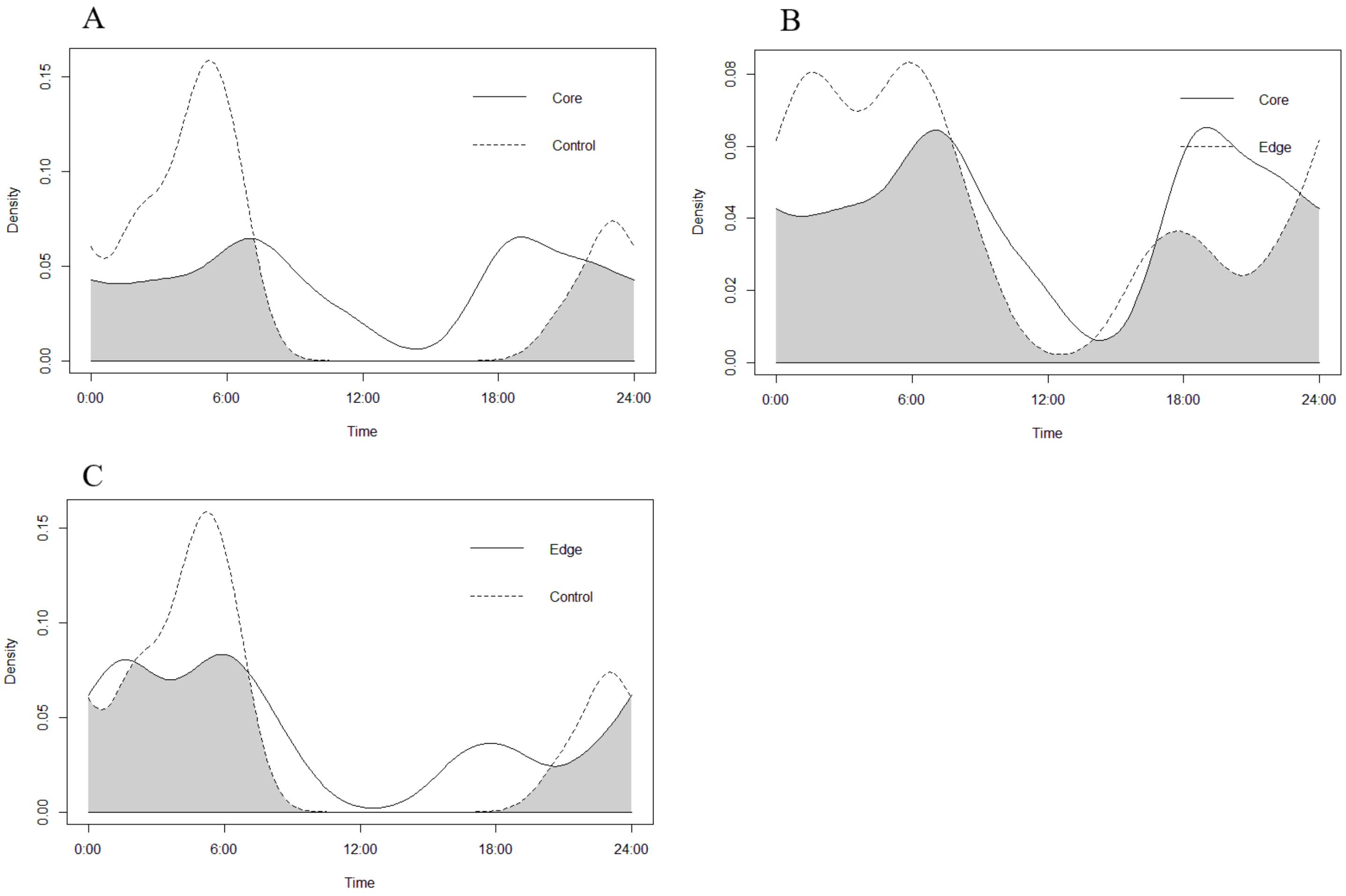


Figure 5.6: Daily activity patterns of black-backed jackal during survey C on three different farm types. A indicates comparisons between core (solid line) and control farms (dotted line), B indicate comparisons between core (solid line) and edge (dotted line) sites and C indicates comparisons between edge (solid line) and control (dotted line) sites. Grey shaded area indicates the overlap between activity between the two years (also known as delta).

When comparing activity patterns for combined predators (excluding baboon) between years, only edge farms revealed a significant shift in activity patterns between survey A and B (Δ = 0.64), and between survey A and C (Δ = 0.63) (Table 5.7). During survey A activity patterns for combined predators were significantly different between core and edge farms (Δ = 0.65), while during survey C only core and control farms saw a significant shift between activity patterns of predators (Δ = 0.69) (Table 5.7).

Table 5.7: Overlapping coefficients (Δ) with 95% bootstrap confidence intervals for combined target predator species (excluding baboon) across three farm types (core, edge and control) over three survey years (A = 2017/18, B = 2018/19 and C = 2019/20). Values in bold indicate a significant shift in daily temporal activity.

Farm Type	Comparison	Overlapping coefficient Δ	Bootstrap CI
	Between years in each farm type		
Core	A - B	0.87	0.81 – 1.02
	A - C	0.80	0.71 – 0.96
Edge	A - B	**0.64**	0.46 – 0.82
	A - C	**0.63**	0.44 – 0.84
Control	A - B	0.89	0.84 – 1.01
	A - C	0.86	0.80 – 0.96
	Between farm type in each year		
A	Core - Edge	**0.65**	0.46 – 0.82
	Core - Control	0.82	0.74 – 0.94
	Edge - Control	0.73	0.58 – 0.91
B	Core - Edge	0.92	0.91 – 1.12
	Core - Control	0.77	0.67 – 0.89
	Edge - Control	0.80	0.70 – 0.93
C	Core - Edge	0.81	0.72 – 1.00
	Core - Control	**0.69**	0.56 – 0.81
	Edge - Control	0.79	0.69 – 0.97

During survey A there were two distinct predator activity peaks on core farms, namely 02:00 and 18:00, while during survey C activity was more evenly spread throughout the day, with an additional activity peak around noon (Figure 5.7A). On edge farms activity followed similar patterns between survey A and C, however density shifted with more predators active in the early morning during survey C while more predators were active in the evening during survey A (Figure 5.7B). A similar pattern was observed when comparing activity patterns within survey C for combined predators. Core and edge farms as well as edge and control farms had very similar peak activity times between 01:00 and 06:00, and 18:00 and 00:00 (Figure 5.8). However, activity on core farms was more evenly spread throughout the day compared to control farms specifically (Figure 5.8A). There is a slight increase in predator activity around noon on core farms during survey C (Figure 5.8A).

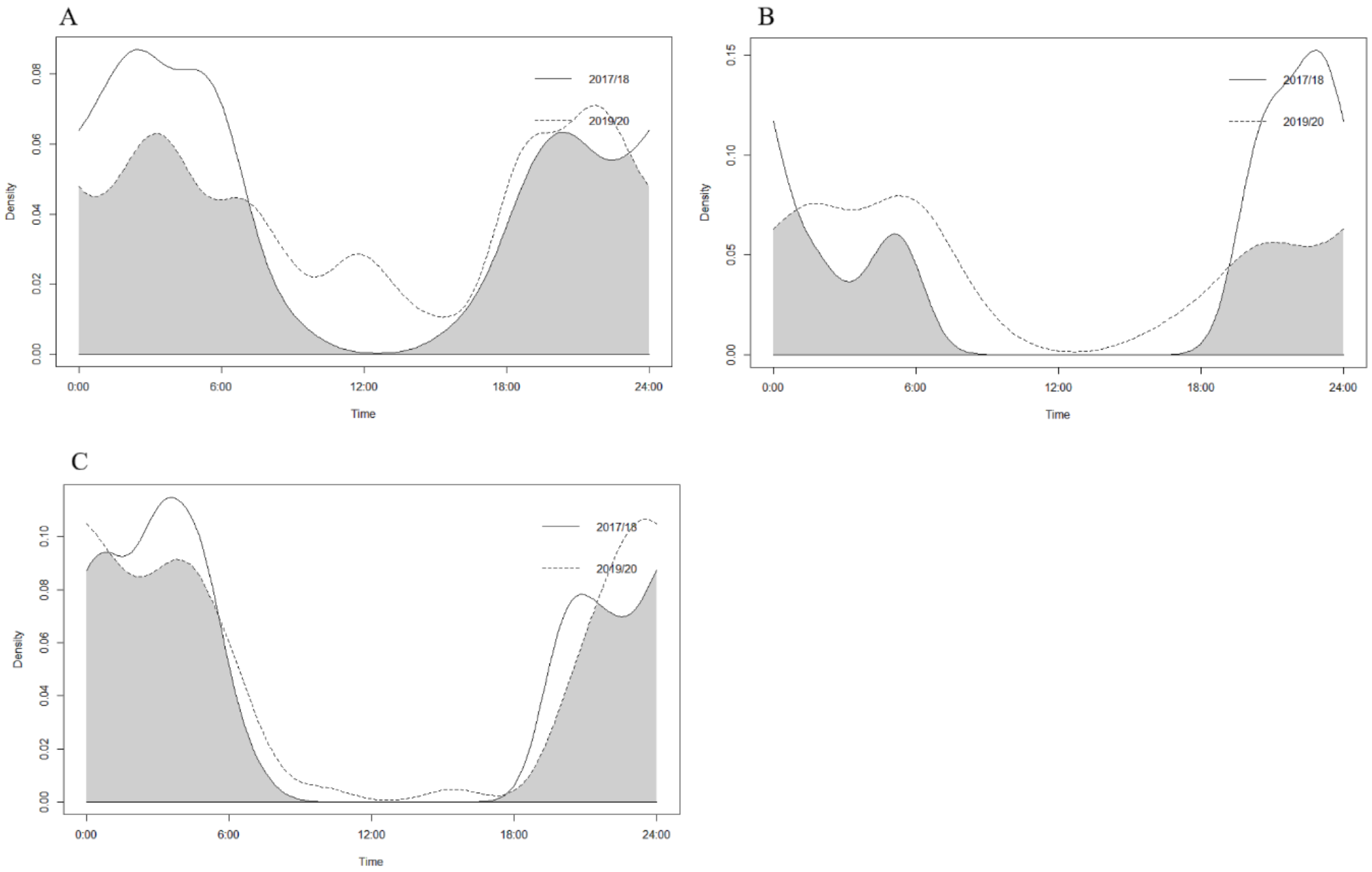


Figure 5.7: Daily activity patterns of combined predators (excluding baboon) on core (A), edge (B) and control (C) sites during survey A (2017/18, solid line) and survey C (2019/20, dotted line). Grey shaded area indicates the overlap between activity between the two years (also known as delta).

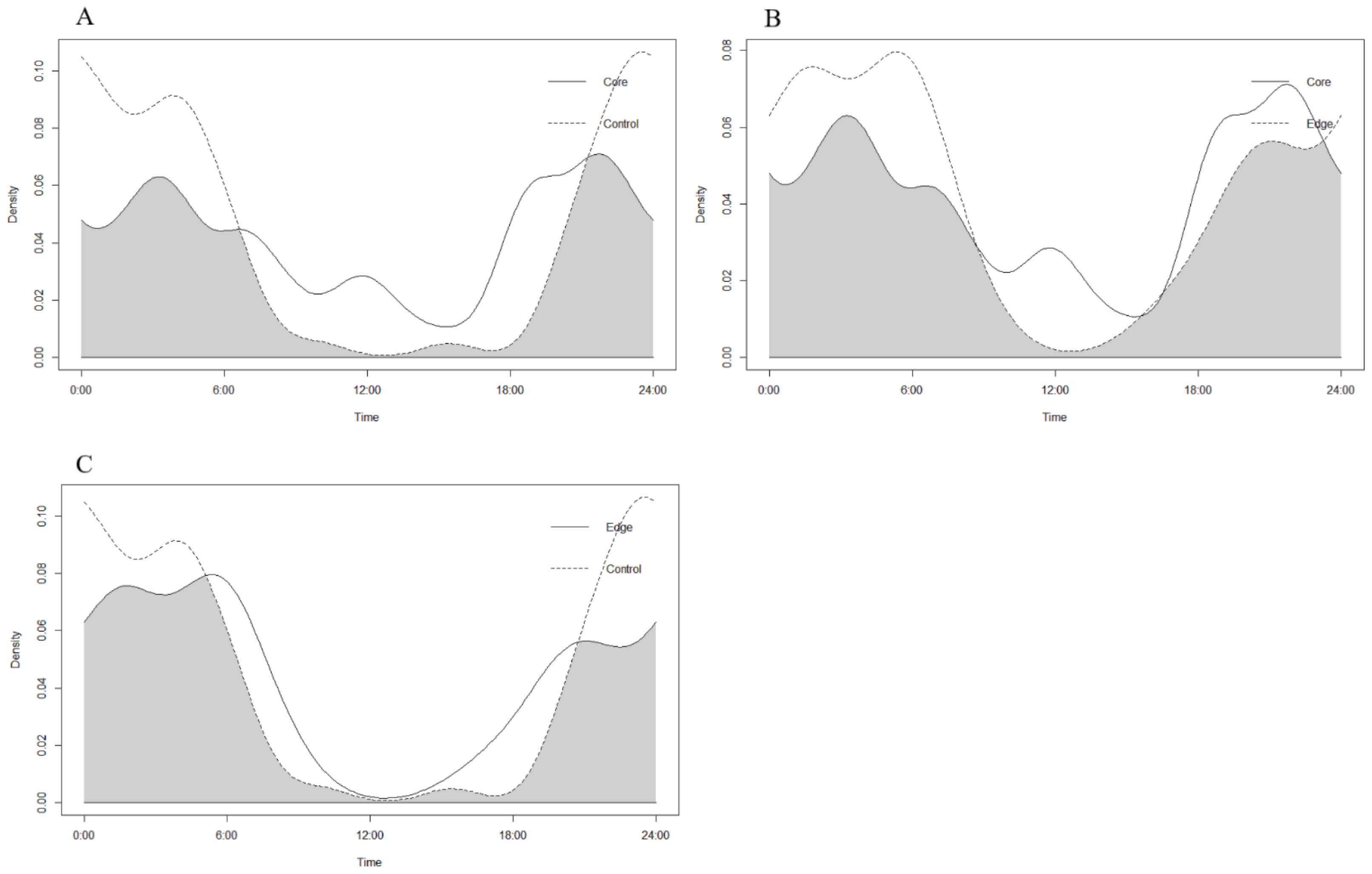


Figure 5.8: Daily activity patterns of combined predators (excluding baboon) during survey C on three different farm types. A indicates comparisons between core (solid line) and control farms (dotted line), B indicate comparisons between core (solid line) and edge (dotted line) sites and C indicates comparisons between edge (solid line) and control (dotted line) sites. Grey shaded area indicates the overlap in activity between the two years (also known as delta).

Functional diversity

During survey A there was no significant difference between functional diversity measures (FDis) on core (0.44), edge (0.41) and control farms (0.43). A significant decrease in FDis was evident between core (0.12) and control farms (0.46) during survey B (ANOVA diff = -0.70, p.adjust = 0.05). However, there was no significant difference between edge farms (FDis = 0.35) and core and control farms. During survey C there was no difference in FDis between edge and control farms (0.45 and 0.46 respectively), while core farms had a significantly lower FDis (0.17) (ANOVA diff = -0.60, p.adjust = 0.05). Between survey years, edge and control site functional diversity did not change. While core farms saw a decrease in FDis between survey A and survey B and C, however FDis values were not significantly different between survey B and C.

There was no observed change in predator RAI between years within any of the farm types (Figure 5.9). Wild prey ranged from small to medium body size and similar to predators there was no observed shift in RAI between survey years or farm types (Figure 5.9). Wild prey species did not change between years for core and control farms (Figure 5.9). On edge farms hare spp. and rock rabbit spp. were no detected during survey B but were detected during survey A and C (Figure 5.9). Rock hyrax were not detected on edge farms during survey C (Figure 5.9). Domestic prey remained relatively constant on edge and control farms between the survey years. However, on core farms domestic prey completely disappeared during survey B, while during survey C domestic prey populations returned albeit in small numbers compared to survey A (Figure 5.9). Multivariate GLMs suggest that the relative abundance for jackal and, caracal and combined predator species were not significantly influenced by any covariates (Table 5.8).

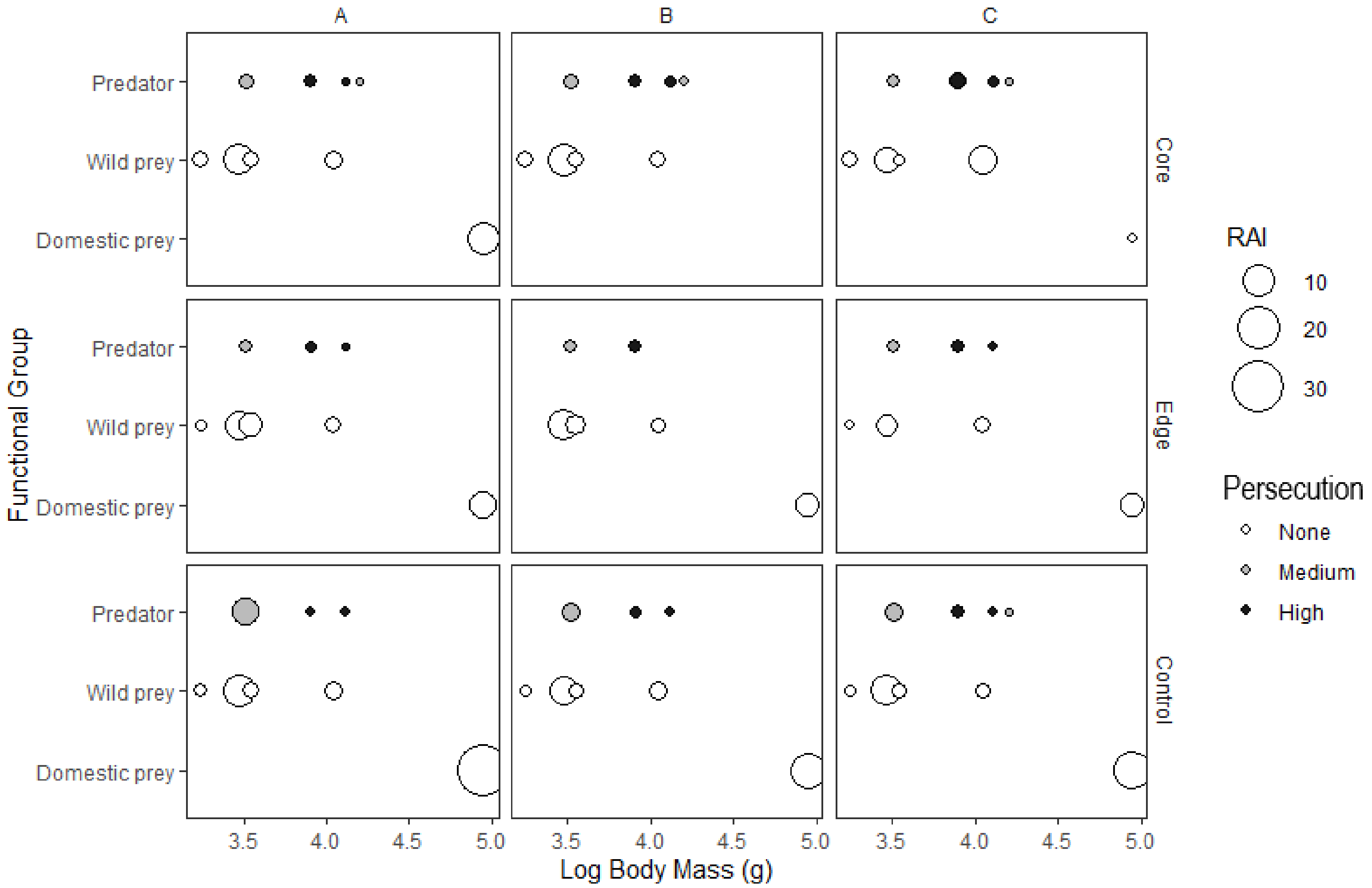


Figure 5.9: The functional diversity of four predator species, five wild mammal prey species and one domestic mammal prey species on three farm types (core, edge and control) across three survey years (A = 2017/18, B = 2018/19 and C = 2019/20), grouped according to functional group and log body mass (g). Each circle represents a specific species within a community, circle size reflects photographic rate (RAI). Circle colour indicates level of persecution within a specific farm type and survey year.

Table 5.8: ANOVA table summarising statistical significance of the most parsimonious multivariate GLMs for black-backed jackal RAI, caracal RAI and combined predator (jackal and caracal) RAIs. *p* values were calculated using 999 resampling. Significant p values ($p \leq 0.05$) marked with an asterisk.

Response variable	Covariate	Estimate	Std.Error	z value	p value
Black-backed jackal RAI	Year A ~ C	0.56	0.90	0.63	0.52
	Control ~ Core	0.81	1.46	0.55	0.57
	Control ~ Edge	-0.34	1.48	-0.23	0.81
	Sheep RAI	0.02	0.09	0.23	0.81
	Management style	1.07	1.557	0.67	0.49
	Wild prey RAI	-0.01	0.07	-0.27	0.78
	Small mammal abundance	-0.11	0.32	-0.36	0.71
Caracal RAI	Year A ~ C	-0.02	1.76	-0.01	0.98
	Control ~ Core	-0.70	3.25	-0.21	0.82
	Control ~ Edge	-0.58	2.67	-0.21	0.82
	Sheep RAI	0.09	0.20	0.43	0.66
	Management style	1.67	3.76	0.44	0.65
	Wild prey RAI	-0.10	0.18	-0.55	0.58
	Small mammal abundance	0.35	0.78	0.45	0.65
Combined predator RAI	Year A ~ C	0.47	0.79	0.60	0.54
	Control ~ Core	0.58	1.30	0.44	0.65
	Control ~ Edge	-0.34	1.28	-0.27	0.78
	Sheep RAI	0.03	0.08	0.37	0.70
	Management style	1.13	1.42	0.79	0.42
	Wild prey RAI	-0.03	0.06	-0.49	0.61
	Small mammal abundance	-0.04	0.29	-0.14	0.88

Farmer perceptions of livestock losses and attitudes to predators

During survey A farmers consistently identified jackal and caracal as the main threats to livestock (see App 5.4). Language around these predators was generally negative, with words like “loss”, “reduce” and “dead” being frequently associated with the two species (see App 5.4). “Fencing” was mentioned often when asked how predators were most effectively managed (see App 5.4). During survey C, jackal and caracal were again the most commonly identified predator species, with some farmers highlighting baboon as well (see App 5.5). Language was mostly negative with “bad”, “losses”, and “problem” all highlighted as common language associated with predators. “Drought” was a recurring theme during interviews in survey C, as well as the idea of predators “increasing” within the landscape (see App 5.5).

During survey A there was no correlation between jackal RAI and livestock losses attributed to predators (r = -0.16, p = 0.67) (Figure 5.10). There was also no correlation between jackal RAI and number of predators killed (r = -0.37, p = 0.32) (Figure 5.11). A similar trend was seen for caracal RAI where there was no correlation between livestock losses (r = -0.18, p = 0.64) (Figure 5.10) or predators killed through hunting (r = -0.42, p = 0.25) (Figure 5.11). Furthermore, there was no correlation between number of livestock losses due to depredation and number of all predators killed through hunting (r = 0.30, p = 0.42).

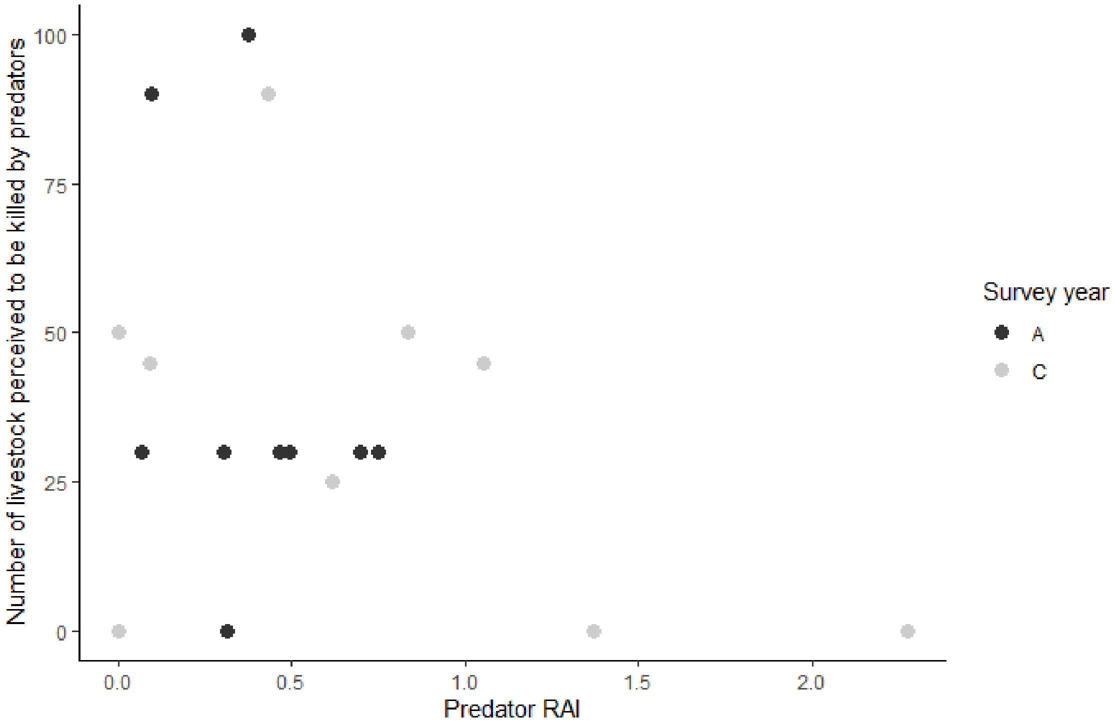


Figure 5.10: Correlation plots of the number of livestock farmers perceived to have been killed by predators and the relative abundance of predators (jackal and caracal combined) for the baseline period: A (2017/18) and two years following the termination of farming activity: C (2019/20). All nine farms are represented.

During survey C there was no correlation between jackal RAI and livestock losses (r = -0.40, p = 0.28) (Figure 5.10) and no correlation between jackal RAI and number of predators killed through hunting (r = -0.50, p = 0.16) (Figure 5.11). Correlation coefficients were higher in survey C compared to survey A. Similar trends were seen for caracal RAI where there was no correlation between livestock losses (r = -0.19, p = 0.61) (Figure 5.10) or predators killed through hunting (r = -0.06, p = 0.87) (Figure 5.11). However, there was a strong positive correlation between livestock losses attributed to combined predators and the number of combined predators killed through hunting during survey C (r = 0.71, p = 0.03).

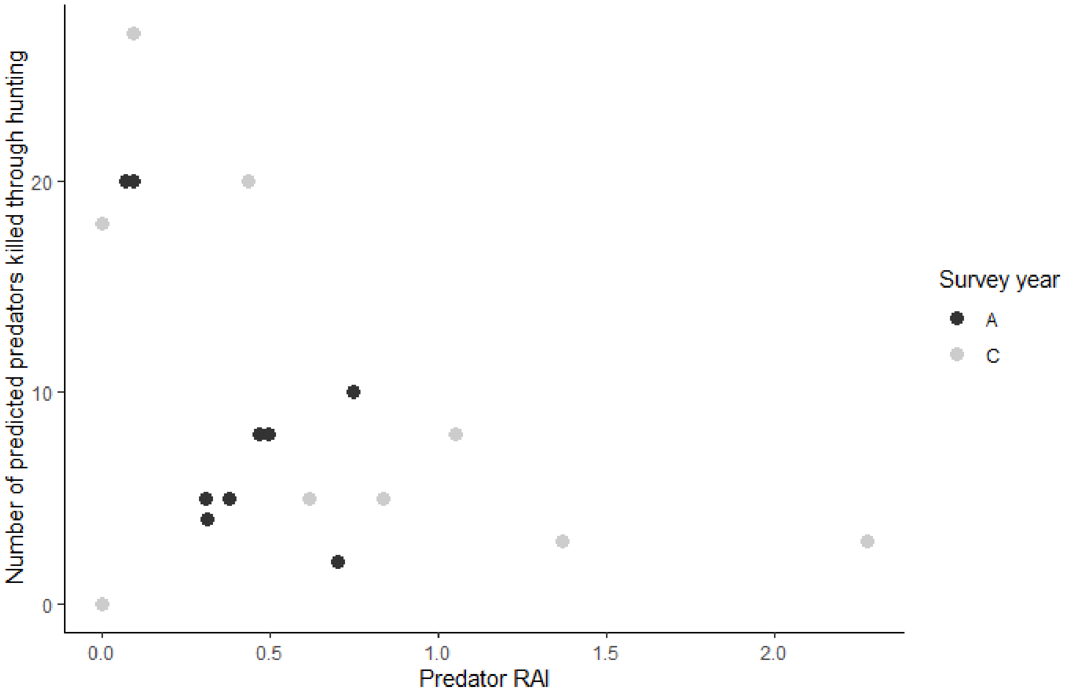


Figure 5.11: Correlation plots between combined black-back jackal and caracal RAI and number of predicted predators killed from hunting during two survey years (A = 2017/18 and C = 2019/20). All nine farms are represented.

Discussion

Extensive camera trap surveys showed that of the four predator species, that farmers perceive as a threat to livestock, the cape fox was the most abundant and widespread throughout the study farms and in all surveys. This finding is similar to other studies carried out in the Karoo which show cape fox to be an abundant carnivore compared to species like black-backed jackal and caracal (Drouilly *et al*. 2018a, Woodgate *et al.* 2018). In contrast to recent wildlife surveys in the karoo (Woodgate *et al.* 2018, Drouilly *et al.* 2018a) chacma baboons were rarely detected. The low abundance of baboons cannot be linked to a lack of water with borehole water present throughout the study area. Rather baboon absence from most farms likely reflects the absence of suitable roosting sites (steep cliffs) with baboons only routinely detected on one farm (Core 1 - Janseboom) which had suitably rugged terrain including steep cliffs typical of those that would be used by baboons in other parts of the Karoo (O'Riain 2019 pers. obs.). Generally, rainfall in the Karoo is highly variable with the northern region typically the driest (see Chapter 2). This may explain the generally lower RAI of wildlife species in the SKA region compared to other studies within similar Karoo landscapes (Drouilly *et al.* 2018a, Woodgate *et al.* 2018). Farmers confirmed that during drought conditions they were more likely to see baboons which may be linked to their provisioning of livestock which is likely to attract an adaptable, generalist species like baboons. Increased overlap between sheep and baboons at provisioning sites may explain why baboons were identified by farmers as causing more damage to livestock during survey C compared to survey A (Figure 5.11).

Of the two predator species identified by farmers as problematic black-backed jackal was more frequently detected compared to caracal (App 5.6). A similar pattern is seen in other studies on livestock farms which frequently report higher detection of black-backed jackal compared to caracal (Kamler 2012, Drouilly *et al.* 2018a, Woodgate *et al.* 2018). This is likely the result of the generally smaller home ranges and lower abundance of caracal compared to jackal resulting in low detectability compared to jackal (Avenant *et al.* 2016). Additionally, farmers consistently state that it is easier to catch and kill caracal relative to jackal and hence it is easier to reduce their numbers through active hunting relative to the 'cleverer' jackal (Terblanche 2020).

Spatial and temporal changes in predator abundance and distribution

Mean predator abundance was most variable between farm types during survey A when all landowners were actively farming sheep. However, overall predator abundance did not change significantly once farming activity, including sheep presence, ended on core farms. The slight decreases in abundance of cape fox on control farms reflected the general pattern of decreasing mammal abundance with successive surveys as the drought conditions worsened in the region (see Chapter 4). I thus rejected the hypothesis that a change in land use from active farming of small livestock would impact predator abundance on core farms (H1) and the prediction of an increase in predator abundance over time (P1) on core farms was not supported. Jackal in particular are highly adaptive species and several studies have suggested that jackal can respond quickly to changes in human disturbance (Ferguson *et al.* 1988, Drouilly & O'Riain 2019, Kamler *et al.* 2020). Increased activity of jackal on farms in the absence of humans further suggests that human disturbance may impact the activity of jackal within an area (Kamler *et al*. 2020). It is possible that the lack of a change in predator abundance following the cessation of farming activity on core farms is a consequence of both negative and positive impacts effectively cancelling one another out. Thus, sheep removal would have greatly reduced the standing biomass of prey on core farms and in the absence of a rapid recovery of vegetation and hence wild prey biomass, is predicted to have negatively impacted predator abundance. By contrast, the absence of farmers and farm labour would have greatly reduced active persecution of predators on core farms which is predicted to have a positive impact on predator abundance. The net effect may be little to no detectable change in the relative abundance of predators on core farms following their change from active livestock farms to protected areas.

Wildlife in the Karoo is strongly influenced by bottom-up processes that are in turn linked to the extreme variability in rainfall and low mean averages (Boardman *et al.* 2010, Hoffman *et al*. 2018). In Chapter 3 I show the slow recovery of both vegetation and small mammals within the study area (see Chapter 3), results which are consistent with several studies exploring long term shifts in vegetation within the Karoo (Rahlao *et al*. 2008, Boardman *et al.* 2010, Hoffman *et al*. 2018, Nenzhelele *et al.* 2018). As discussed in Chapter 4, wild herbivore abundance did not change significantly over the study period while domestic herbivores declined sharply on core farms and more generally on both edge and control farms as farmers reduced their stocking rates in response to the drought. It is well established that predator abundance and predation rates are closely linked to changes in prey abundance (Sih 1987, Abrams & Ginzburg 2000, Vucetich *et al*. 2002, Shultz *et al.* 2004). Meso-predators in protected areas of the Karoo have been shown to rely almost exclusively on wild prey despite the presence of neighbouring livestock farms (Drouilly *et al.* 2018c). However, this result was from a PA that had been proclaimed more than 30 years prior to the study allowing sufficient time for the recovery of both vegetation and prey species biomass (Drouilly *et al.* 2018c). Diet analysis of predators between protected areas and farmland provides valuable evidence on the prey preference of various predators on different land uses, helping to support predictions established from abundance analyses (Drouilly 2019). Scat samples were collected during this study for both black-backed jackal and caracal during all three surveys however scarcity of scat meant I did not have enough samples for robust analysis and trends in diet would be anecdotal at best. I therefore opted to focus more on abundance analysis, linking predictions over prey preference to the extensive diet analysis presented by Drouilly *et al.* (2018c).

My findings contradicted the prediction that jackal and caracal abundance would increase on edge farms (P2) as predators would seek out sheep which are more abundant and easier to catch than wild prey. In addition, semi-permeable fences would allow easy passage of predators from core to edge farms (see Chapter 6). Jackal and caracal abundance did not however vary on edge farms between the survey years. Furthermore, jackal and caracal abundance on edge farms was not significantly different from core farms for any of the survey years, suggesting there was no significant movement from core farms to edge farms as sheep abundances changed (see also Chapter 6). These results aligned with those from multiple other studies that suggest mesopredator abundance varies little between protected areas and farmland (Ramesh & Downs 2015, Woodgate *et al.* 2018, Drouilly *et al.* 2018a, Drouilly & O'Riain 2019). These findings do however contradict the farmers' predictions that predators would move from the core area to edge farms where sheep, their preferred prey, were still present. While camera traps may not be able to determine where predators sleep versus where they hunt, if predators where hunting more on edge farms (targeting sheep) there would an increase in detection of predators on edge farms compared to core farm. As there was no difference between predator abundance on edge farms before or after sheep were present on the core, one can assume jackal and caracal were not more drawn to areas with sheep compared to areas without.

My results did, however, support the prediction that cape fox and baboon abundance would remain constant on core and edge farms (P3). Originally it was predicted that decreased persecution on core farms would increase cape fox and baboon abundance (P1), however there was no change in these species RAI between years despite removal of sheep on the core. A likely reason for this is farmers deprioritising hunting these species due to low sheep predation risk (from cape fox) or low abundance (baboon). This suggests the removal of sheep would have little immediate impact on cape fox and baboon, however in the long-term changes in other predator abundances may influence cape fox and baboon populations which may be influenced by large predators within the region (jackal and caracal) (Bettridge & Dunbar 2012, Kamler *et al.* 2012a). Additionally the lack of significant changes in cape fox abundance may have provided further evidence that jackal abundance did not change in the core despite contrary predictions by various stakeholders (Kamler *et al.* 2012a, Kamler *et al.* 2013). Kamler *et al.* (2013) suggested that a decrease in black-backed jackal density positively influence cape fox density as a result of the nonlethal effects of jackal on cape fox (which have similar diet and habitat use to jackal). Although this interaction is not always significant (Bagniewska & Kamler 2014), it does suggest that when jackal abundance changes within a system there should be some reflection of this change in cape fox abundance (Kamler *et al.* 2012a, Kamler *et al.* 2013). Cape fox detection within the study area was much greater than jackal, suggesting fluctuation in abundance would be more obvious within this species and if any changes in jackal abundance did occur it should be reflected in cape fox abundances. This suggests that future study of cap fox populations would provide helpful insights into larger predators' densities (mostly black-backed jackal), even where detection of this species is low (Kamler *et al.* 2012a, Kamler *et al.* 2013).

It should be noted that during January 2020 there were reports that a block hunt event took place on roughly 10 farm properties between Williston and the south west boundary of the SKA core area. Block hunts are described as large-scale collective hunting events where many landowners and often professional hunters "sweep" an area and shoot predators (mostly jackal and caracal) on multiple farms over several days. This block hunt included one of the edge farms in this study and it is suspected that there may have been some spill over hunting on one of the core farms too. It is unclear if this hunting event skewed data for these two farms during survey C, however predator abundance trends seen within this edge/core pair where similar to trends seen on the other two edge/core pairs suggesting the impact was negligible. This event highlights the challenges of the working at a landscape level on private properties and it is important to note that I could not ascertain whether edge farmers were hunting on neighbouring core farms either although farmers did suggest this was likely.

Temporal shifts in predator daily activity pattern

Changes in daily activity patterns of predators supported my hypothesis that a change in land use would influence predator activity patterns on core farms (H3). Both jackal daily activity and combined predator daily activity shifted significantly on core farms compared to both control and edge farms with increased diurnal activity around noon compared to the nocturnal or crepuscular activity patterns as seen on edge and control farms. These trends became more marked over time (from survey B to C) on core farms for both jackal and combined predator species (Figure 5.8 and 5.10).

Reduced human presence and hunting within the core may have released predators from persecution and allowed them to be more active during the day. Predators have been shown to shift their activity patterns depending on the amount and type of human activity within an area (Lawrance & Higginbottom 2003, Weckel 2006, Oriol-Cotterill *et al.* 2015, Smith *et al.* 2017, Gaynor *et al.* 2018). Where persecution of jackal for example is high, this typically crepuscular species has been shown to shift its activity peak to nocturnal hours to avoid detection by humans (Ferguson *et al.* 1988, Clinchy *et al.* 2017, Shamoon *et al.* 2018). Similarly, brown bears (*Ursus arctos*), and coyotes (*Canis latrans*) all shifted key foraging times to avoid periods of the day when risk of being hunted or disturbed by humans was higher (McClennen *et al.* 2001, Way 2004, Hertel *et al.* 2016). There is further evidence that jackal and fox species within agricultural landscapes in Israel have shortened total activity during the day in response to increased human activity which compresses foraging opportunity (Shamoon *et al.* 2018).

In Chapter 4 I reported that only a few wild prey species (i.e., steenbok, rock hyrax, cape fox and yellow mongoose) exhibited significant shifts in daily activity patterns following the cessation of active farming on core farms. Similar to predators these shifts included increased activity around noon and it is possible that predators have shifted their activity to overlap more with prey species (e.g., steenbok and rock hyrax), which in turn have adjusted their activity to the absence of people (Beest *et al.* 2013, Tambling *et al.* 2015). These findings are similar to other studies showing a prey response to avoid temporal overlap with predators (Cresswell *et al.* 2010, Beest *et al.* 2013, Monterroso *et al.* 2013). Research in Addo Elephant National Park, South Africa showed that prey species exposed to reintroduced nocturnal predators were more likely to be active during the day (Tambling *et al.* 2015).

Spatial and temporal changes in predator-prey functional diversity

While FDis measures saw significant changes in functional diversity on core farms between survey years and in some case between other farm types this was reflective of the removal of domestic livestock only which shifted the prey composition on these farms. With the exception of a sharp decline in domestic prey on core farms during survey B and C there were no significant shifts in the functional diversity of predators and prey for any farm type in different survey years (Figure 5.9). This further supported the idea that despite the cessation of farming activity and the removal of domestic prey species within one area, the relationship between predator abundance and prey abundance was not significantly impacted. Dietary studies in the Karoo suggest that both jackal and caracal in well-established protected areas surrounded by livestock farms do not rely on sheep as a source of prey (Drouilly *et al.* 2018c). Core farms may thus require more time to recover from sustained livestock grazing (see Chapter 4) and predator persecution. These findings contradicted my original hypothesis about predator-prey dynamics on core farms (H2, P4). However, it is important to note that my hypotheses and predictions did not factor in the effects of a prolonged drought throughout the region. The pervasive effects of the drought may explain the finding that predator abundances were not significant influenced by any covariates (Table 5.8). In semi-arid systems like the Karoo there is evidence that fauna and flora are heavily influenced by rainfall which may overshadow the potential impacts of biotic influences such as human impacts and prey availability (Kraaji & Milton 2006).

When comparing jackal versus caracal, changes in jackal RAI were slightly more influenced by time, sheep abundance and management style (jackal abundance being slightly higher on passive management farms) compared to caracal RAI (Table 5.6). This suggests that over time jackal abundance may increase in areas with more passive management styles while caracal abundance will remain unchanged, a finding supported by the recent study of Conradie *et al.* (2020) which revealed a dramatic increase in livestock losses associated with a transition from active farming to lifestyle farms in the central Karoo.

Patterns of livestock losses, hunting and farmer perceptions towards predators

Farmer reports of livestock losses to predators increased between survey A and C as did the number of predators recorded as killed by farmers (App 5.7). Retaliatory or pre-emptive killing of predators is a pervasive form of predation management by farmers in the Karoo (Graham *et al.* 2005, Nattrass & Conradie 2015, McManus *et al.* 2015, Nattrass *et al.* 2020). Several farmers reported that between survey A and survey C predator populations (specifically jackal and in some cases baboon) had increased. This was contradictory to my findings which showed no significant changes in predator RAI between survey A and survey C for any farm type. While livestock losses and number of predators killed through hunting were positively correlated, neither value was significantly correlated with predator RAI for survey A or C (Figure 5.5 and 5.6). While the number of livestock losses to predators were derived from farmer estimates, Conradie & Nattrass (2017) as well as Nattrass *et al.* (2020) provided evidence that estimates of livestock losses due to predators in the Karoo were fairly consistent across different survey methods and survey periods. It was, however, interesting to note that these correlations were negative (albeit not significant), suggesting livestock losses and number of predators killed was highest when predator abundance was lowest.

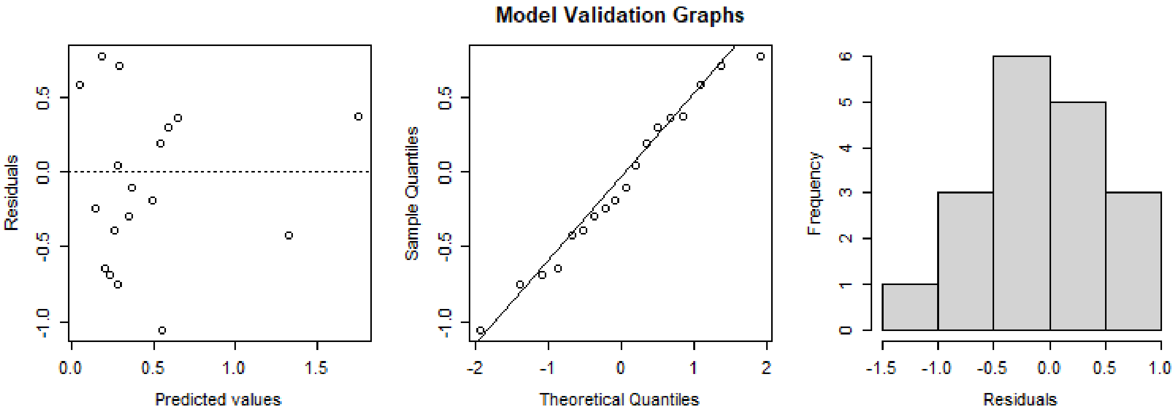
The mismatch between the perceived increase in predators and observed predator abundance may be the result of sustained hunting of predators in the region which included a block hunt in January 2020 in the Williston area. By combining predator RAI and the number of predators killed on each farm type it is apparent that predators have increased on edge and control farms, but their numbers have been suppressed in the short term through active hunting. Additionally, the persistent drought conditions resulted in increased socio-economic pressures across survey years with farms highlighting this as major concern during annual interviews. Almost all farmers had moved their pregnant ewes and young lambs close to farmhouses where provisioning and protection from predators is easier. It is possible that the concentration of livestock in close proximity to people increased the likelihood of predator detection by farmers as predators would have been attracted to the high concentration of livestock. This, however, does not necessarily mean predators increased on the farm, rather that the spatial overlap between predators and humans increased.

Perceptions towards predators did not shift between survey A and C supporting my prediction that time and predator abundance would not impact negative perceptions towards predators (P5). Almost all farmers expressed consistent negative associations with jackal and caracal over the years. Interviewed farmers associated the words “jackal” and “caracal’ with phrases like “financial loss”, “they must all die” and “big problem” (App 5.4 and 5.5). During survey C these negative perceptions seemed exacerbated by added pressure from the drought. During 2018 and 2019 this area of the Karoo was particularly hard hit by extreme drought conditions. Many landowners suffered financially as sheep required supplemental food which includes high transport costs. While observed predator abundance may not have changed over the survey period, the perceived threat of these predators may have increased with the ongoing worsening of the drought conditions. Increases in predator detection during survey C as well as increased overall activity patterns compared to survey A may indicate increased predator movement in search of scarce resources including water. However, again it should be noted that predator abundance may have increased during later surveys, but this increase was not detected in RAI estimates from camera trapping because hunting by edge and control farmers suppressed predator numbers.

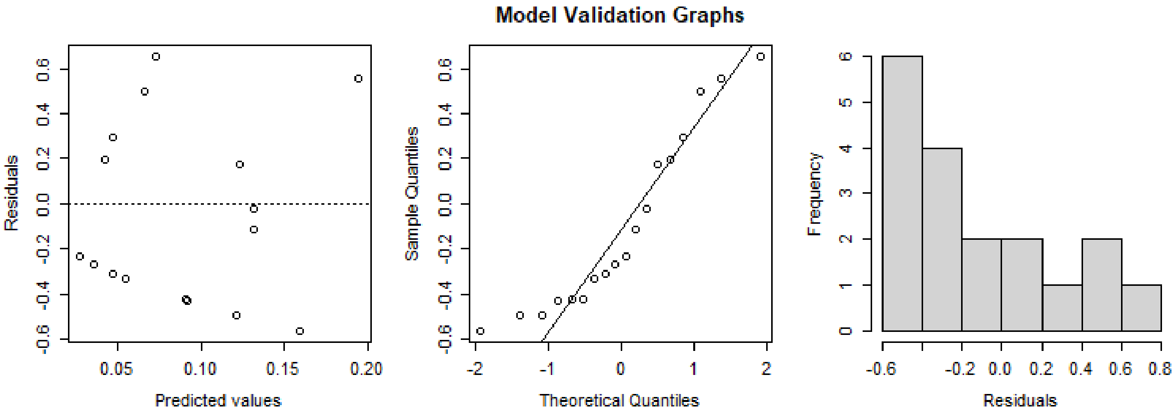
Conclusions

My results contradict the farmers' prediction that predators would move onto edge farms increasing in abundance following the cessation of farming activities in the core. This because farmers actively suppress predator numbers largely through lethal management and their absence will release predators from this top-down control. Predator abundance remained similar across farm types and surveys aligning with other recent studies in the Karoo showing a negligible impact of land use on predator abundance (Drouilly *et al.* 2018a, Woodgate *et al.* 2018). Given both caracal and jackal are actively hunted throughout the region my experimental design did not succeed in controlling for farmer behaviour including a possible increase in hunting effort on edge and control farms. Thus, data for the less persecuted cape fox which seldom consumes adult sheep are perhaps more illuminating and showed a marked decrease in RAI from the baseline period to the final survey (survey C) (Figure 5.4) on control farms. The latter result is consistent with predictions for a dietary generalist in a prolonged and severe drought that characterised the entire study area and was mirrored in declines for a variety of other mammal species during the study period (e.g., springbok, steenbok, rock hyrax, small grey mongoose, yellow mongoose, hare spp., small-spotted genet and aardwolf – see Chapter 4). During severe drought conditions predators are more likely to increase distance travelled to find limited resources (e.g., prey and water) (Tuqa *et al.* 2014) which was reflected in the higher percentage of cameras detecting predators on a specific farm type in survey B and C (more severe drought conditions) compared to A. This increased activity coupled with sheep being moved closer to farmhouses may have resulted in the perceived increase in predator abundance by farmers. The change in land use did correspond with a change in daily activity patterns of predators which all became more active during the day on core farms relative to edge and control. Behavioural responses to an intervention are more rapid than population level effects (e.g., a change in abundance) and were thus more likely to be detected in this fairly short duration study. Predators are typically nocturnal in agricultural landscapes with high levels of persecution (Clinchy *et al.* 2017, Shamoon *et al.* 2018) and thus the shifts to more diurnal activity patterns were predicted and have implications for prey species within the core as the landscape of fear shifts temporally (Tambling *et al.* 2015).

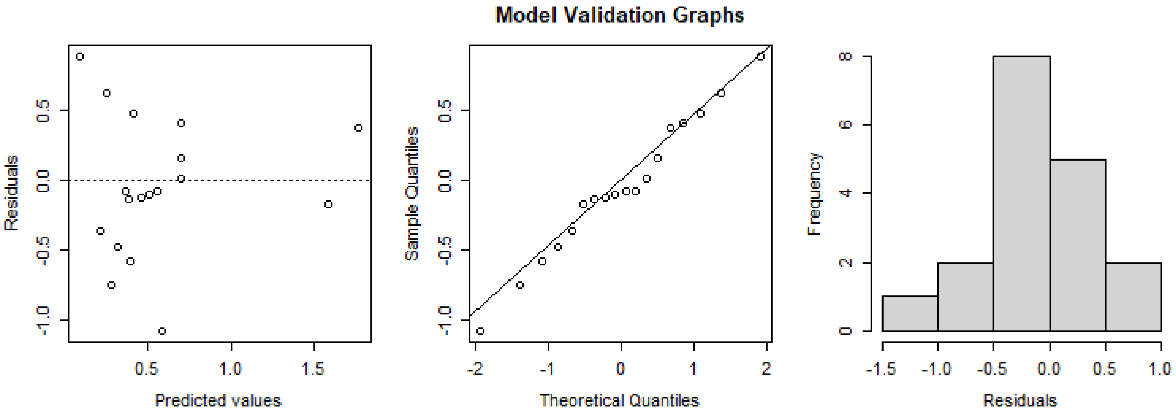
Appendix 5: Predator population appendices



App 5.1: Model validation graph for top predator (black-backed jackal only) model showing residual versus predicted values spread (left), sample versus theoretical quantile spread (middle) and distribution of data (right).

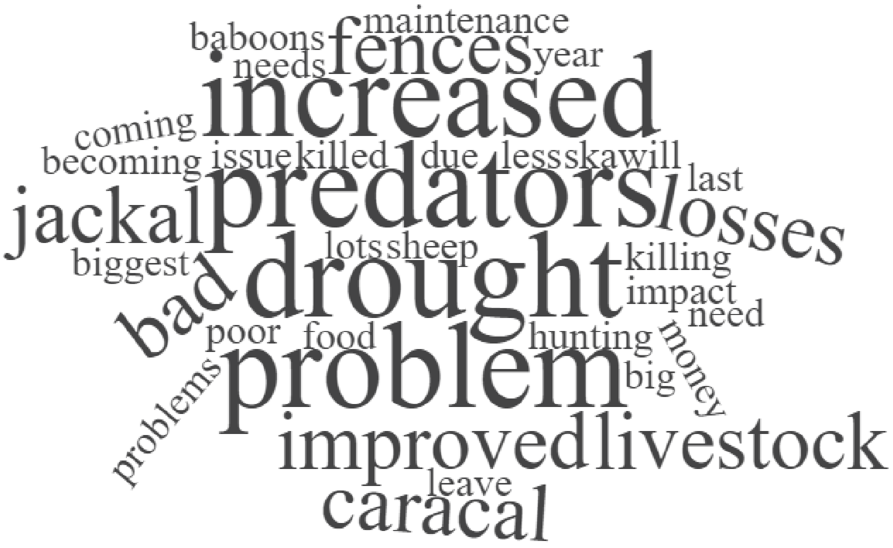


App 5.2: Model validation graph for top predator (caracal only) model showing residual versus predicted values spread (left), sample versus theoretical quantile spread (middle) and distribution of data (right).



App 5.3: Model validation graph for top predator (all species combined) model showing residual versus predicted values spread (left), sample versus theoretical quantile spread (middle) and distribution of data (right).

App 5.4: Word cloud illustrating farmer perceptions toward predator species within the SKA region of the Karoo, South Africa. Images were derived from interviews with eight of the nine landowners within the study site that were still actively farming core, edge and control farms during survey A (before sheep were removed on the core farms and a protected area was established). Size of words indicates the frequency the word was used when landowners were asked specific questions.



App 5.5: Word cloud illustrating farmer perceptions toward predator species within the SKA region of the Karoo, South Africa. Images were derived from interviews with eight of the nine landowners within the study site that were still actively farming core, edge and control farms during survey C (eighteen months after sheep were removed on the core farms and a protected area was established). Size of words indicates the frequency the word was used when landowners were asked specific questions.

App 5.6: Naïve occupancy and photographic rate of four predator species on nine different farms in three surveys A, B and C (A = 2017/18, B = 2018/19 and C = 2019/20). Farms were categorised according to their geographical location as either within the SKA protected area (core), on the edge of the protected area (edge) or at least 50km from the edge of the protected area (control). Naïve occupancy indicates the proportion of camera stations where a species was detected. Data extracted from Chapter 4 - Table 4.4, 4.5 and 4.6.

Species	**Core**			**Edge**			**Control**		
	A	*B*	*C*	*A*	*B*	*C*	*A*	*B*	*C*
				Naïve occupancy					
Black-backed jackal *Canis mesomelas*	0.286	0.237	0.281	0.128	0.250	0.222	0.071	0.171	0.227
Caracal *Caracal caracal*	0.029	0.132	0.156	0.026	0.000	0.056	0.048	0.057	0.023
Cape fox *Vulpes chama*	0.400	0.316	0.156	0.179	0.278	0.222	0.738	0.571	0.545
Chacma baboon *Papio ursinus*	0.029	0.079	0.031	0.000	0.000	0.000	0.000	0.000	0.023
				Photographic rate					
Black-backed jackal *Canis mesomelas*	0.633	0.564	1.188	0.185	0.657	0.402	0.139	0.288	0.508
Caracal *Caracal caracal*	0.032	0.282	0.212	0.031	0	0.073	0.139	0.072	0.063
Cape fox *Vulpes chama*	0.855	0.846	0.679	0.463	0.625	0.438	5.983	1.837	1.650
Chacma baboon *Papio ursinus*	0.032	0.094	0.042	0	0	0	0	0	0.032

App 5.7: Estimated number of livestock lost to predators (per year) and estimate number of predators (jackal and jackal) killed by farmers (per year) for nine different farms within the SKA region during two different survey years.

Survey	**Farm**	**Estimated livestock loss (per year)**	**Estimated predators killed (per year)**
2017	Core 1 – Janseboom	30	8
	Core 2 – Jas Kloof	30	10
	Core 3 – Lovedale	30	2
	Edge 1 – Hondeblaf	30	8
	Edge 2 – Rietpoort	30	20
	Edge 3 – Gannabos Leegte	30	5
	Control 1 – Hoezar-Wes	90	20
	Control 2 – Leeuwkrans	0	4
	Control 3 - Skurwekloof	100	5
2019	Core 1 – Janseboom	0	0
	Core 2 – Jas Kloof	0	3
	Core 3 – Lovedale	0	3
	Edge 1 – Hondeblaf	50	18
	Edge 2 – Rietpoort	45	27
	Edge 3 – Gannabos Leegte	45	8
	Control 1 – Hoezar-Wes	90	20
	Control 2 – Leeuwkrans	25	5
	Control 3 - Skurwekloof	50	5

CHAPTER 6

EVALUATING FENCE QUALITY, MAINTENANCE AND THE USE OF HOLES BY WILDLIFE ON CORE AND EDGE FARMS

Camera trap images of mammal species using fence holes taken during a 30-day camera trap fence survey in 2019, Northern Cape, South Africa. Animals include bat-eared fox (*Otocyon megalotis*) (top left), steenbok (*Raphicerus campestris*) (top right), black-backed jackal (*Canis mesomelas*) (bottom left) and caracal (*Caracal caracal*) (bottom right). Images were captured along fence section 3, except for the caracal which was captured along fence section 2 (© Michelle Blanckenberg).

Abstract

Fences are a common tool for separating human activity from wildlife and to control the movement of free ranging livestock. Fencing between protected areas (PA) that host predators and agricultural land with livestock is particularly important not only to prevent predators leaving the PA and consuming livestock but to prevent livestock from foraging within the PA. Despite extensive fencing across the Karoo, there has been very little research on how successful it is at restricting the movement of both domestic and wild mammals. The establishment of a protected area within an established farming region in the Karoo has generated considerable conflict between the managers of the PA and the farmers on its periphery. Farmers perceive the quality and maintenance of the fence to be essential to curbing the influx of predators that will now have protected status within the PA and hence, in their opinion will proliferate. In this chapter I surveyed the quality and level of maintenance of the PA/farm boundary fence and asked how these variables influenced the species richness of mammals detected along fences and using holes in fences and how this changed following the cessation of farming on the one side of the fence. Approximately 60% of mammals detected on farms were detected along fences, while between 40% and 55% of all mammals used holes along fences. Fence quality significantly influenced mammal relative abundance along fences and hole use (specifically during the 2019 survey). There was no preference in the direction of movement through holes (i.e., core to edge or edge to core). Results suggest that regular fence maintenance will reduce movement of mammals between the PA and farmland. Fences within this area are shown to be an important part of managing livestock depredation as results did show a decrease in predator fence utilisation where fence quality was high. Increased monitoring and fence hole repair still allows some species to move between land types (benefitting migration and gene flow) but impedes predator hole utilisation. This suggests that with adequate buy in from both PA management and farm landowners, fencing can provide a win-win scenario for mammal populations within the area.

Introduction

Fences are considered free-standing structures that aim to restrict or stop movement across a certain boundary (Hayward & Kerley 2009). This definition includes a variety of fencing methods not limited to standard post and wire fences, electric fencing, virtual fences and live fences (i.e., hedges) (Hayward & Kerley 2009). Fencing is a worldwide phenomenon with a wide variety of stakeholders erecting fencing for diverse reasons (Lindsey *et al*. 2012, Jakes *et al.* 2018). One of the more common reasons for fencing is the need to separate human activity from wildlife (Jakes *et al*. 2018, Weldemichel & Lein 2019). This can take the form of fencing around protected areas (PA) to limit movement of wild animals out of a PA and both humans and domestic animals into the PA. In agricultural landscapes fencing is used to protect livestock or crops from both wildlife and other people and to curtail the movement of livestock (Hayward & Kerley 2009, Lindsey *et al.* 2012). In short, fencing is a relatively easy method of "protecting" one's assets from outside factors, but extensive fencing has been linked to both the fragmentation and isolation of habitats and wildlife populations (Hayward & Kerley 2009, Jakes *et al.* 2018). The impacts of fences is currently less well understood (Jakes *et al.* 2018) than for other man-made linear structures (e.g., roads and powerlines), that also impact negatively on natural ecosystems (Taylor & Knight 2003, Berger 2004, Benítez-López *et al.* 2010).

There have however, been a few key reviews investigating the large-scale negative impact of fencing on wildlife populations (Caughley *et al.* 1987, Hayward & Kerley 2009, Dickman 2012, Pirie *et al.* 2017, Smith *et al.* 2020a). A common theme emerging from these studies is the restriction of the movement of wildlife and exclusion from critical resources. Several studies have investigated how exclusion fences (either from agricultural areas or around protected areas) have led to increased mortality (Caughley *et al.* 1987, Hayward & Kerley 2009), decreases in migration (Mbaiwa & Mbaiwa 2006, Williamson & Williamson 2009), disrupted gene flow within a population (Boone & Hobbs 2004, Hayward & Kerley 2009) and direct fatalities through electrocution (e.g., tortoises) (Beck 2010). By constricting the movement of species, resources within an area can be over-exploited (Pirie *et al.* 2007, Smith *et al.* 2020a). For example, in the Okavango Delta and Makgadikgadi (Nxai Pan National Parks) and northern Kalahari (Moremi Game Reserve) in Botswana survival of migrating ungulate species has been strongly linked to the availability of high-quality forage (as opposed to abundance), and the ability of animals to actively track this resource (Bartlam-Brooks *et al.* 2011). With increasing fragmentation from fences (e.g., veterinary cordon fences) the ability for herbivore species to migrate has declined causing decreases in populations as well as increased grazing pressure within fenced areas (Bartlam-Brooks *et al.* 2011). A similar result is seen for elephants (*Loxodonta africana*) in the Kilombero Valley, Tanzania where connectivity is severely hindered by agricultural fencing disrupting important social and ecological processes (Bonnington *et al.* 2010). The recent mass mortality of elephants in northern Botswana has been linked to fencing that forced elephants to drink from contaminated ephemeral pans (Azeem *et al.* 2020).

Despite the various negative impacts of fencing on wildlife, studies have also highlighted the ecological and conservation benefits. Lindsey *et al.* (2012) suggested fences benefit wildlife restricted to small natural habitats by reducing edge effects where wildlife and human activity may overlap. Fencing provides a valuable conservation tool by reducing the likelihood of hunting, poaching, as well as human-wildlife conflict, therefore protecting endangered species or habitats (Grant *et al.* 2007) and allowing species with declining populations (e.g., lions *Panthera leo*) to reach carrying capacity inside protected areas (Packer *et al.* 2013, Bauer *et al.* 2015). Similarly, in Australia, fences have been successfully used to protect high-value native species from predation by introduced red foxes (*Vulpes vulpes*) and feral house cats (*Felis catus*) (Moseby & Read 2006, Dickman 2012, Paul & Marlow 2012, Smith *et al.* 2020b). Furthermore, fences help reduce the spread of disease between domestic and wild animal populations as there is a physical barrier preventing the two populations from interacting (Thomson *et al.* 2004, Pirie *et al.* 2017, Jakes *et al.* 2018). Fencing is a complex topic as impacts can be considered positive or negative depending on the purpose of the fence and effects of fencing on target versus non-target species (Lindsey *et al.* 2012, Smith *et al*. 2020a).

One of the most common reasons given for fencing is to reduce negative interactions between wildlife and communities or landowners utilising a particular landscape for livestock production. Conflict between livestock owners and predators is a widely researched topic (Naughton-Treves 1997, O'Connell-Rodwell *et al*. 2000, Dickman 2010, Drouilly *et al*. 2018b, Perry *et al.* 2020). Fencing can act as an efficient exclusion barrier for livestock farmers coexisting with predators. Australian research for example, showed extensive evidence that predator proof fencing around sheep farming zones helped exclude dingo (*Canis lupus dingo*), which at the time had rapidly increased through access to livestock as a food source (Yelland 2001, Allen & Fleming 2004, Clark *et al.* 2018). Hayward *et al.* (2009) investigated the impact of fencing around a relatively small reserve in South Africa (Addo Elephant National Park) on the populations of reintroduced predators (namely lion, leopard *Panthera pardus* and spotted hyaena *Crocuta crocuta*). Here it was suggested that fencing as a conservation tool did not impact the natural behaviour of predators on an evolutionary scale and that predators were rather regulated by prey abundance (Hayward *et al*. 2009). Alternatively, fences have been shown to negatively impact predator populations by limiting gene flow within an area necessitating the implementation of metapopulation management of known pedigrees to improve the genetic health of small and isolated predator populations (Boast *et al*. 2018, van der Merwe *et al.* 2019).

Fences have clear benefits to small livestock owners, confining stock to designated camps within a farm and thus allowing for improved management of the veld in addition to preventing the movement of potential predators onto the farm (du Plessis *et al.* 2018). However, several studies have noted that the benefits of fencing in terms of predator management are only effective with regular monitoring and maintenance of fences (Nattrass & Conradie 2015, Clark *et al.* 2018, Du Plessis *et al*. 2018). Mesopredators are particularly efficient at exploiting weaknesses in fences, using holes to move between natural and agricultural areas (Coates 2013). While predators may not directly damage fences in order to move areas across them, they may use holes made by several other species (Hoare 1992, van Rooyen *et al.* 2002, Pirie *et al*. 2017). Warthog (*Phacochoerus africanus*), aardvark (*Orycteropus afer*) and porcupine (*Hystrix africaeaustralis*) have all been reported as major fence damaging species (Weise *et al.* 2014), suggesting that understanding how all animal species interact with fences will benefit long term fence management and therefore predator/livestock management (Reidy *et al.* 2010, Karanth & Kudalkar 2017).

Predator proof fencing is widespread across South Africa, particularly in the Karoo, and is the preferred non-lethal method for managing predation of livestock (Du Plessis *et al.* 2018). Fences are only successful at excluding predators if the type of fence matches the target species (Du Plessis *et al.* 2018, Smith *et al.* 2020a, Smith *et al.* 2020b). Historically black-backed jackal (*Canis mesomelas*) (henceforth referred to as jackal) has been the most prominent predator for small livestock within the Karoo which has resulted in most boundary fencing being wire mesh ‘jackal-proof’ fencing (Nattrass & Conradie 2015, Du Plessis *et al.* 2018). Jackal-proof fencing became popular across commercial livestock farms in the Karoo in the early 1900s largely due to technological advances that allowed for mass production of mesh and government financial support to be able to procure and install such fencing (Nattrass & Conradie 2015). The combination of fencing and hunting efforts within enclosed areas greatly reduced jackal presence and hence livestock predation within the Karoo (Nattrass & Conradie 2015). Many regions reported a complete absence of jackal for many decades but by the early 1990s the tide of support for farmers was changing and with that the return of the jackal was apparent (Drouilly *et al.* 2019). Hunting and fencing subsidies to farmers from the government were phased out making the management of predation the sole responsibility of private landowners (Nattrass & Conradie 2015). Rising minimum wages coupled with land claims by farm workers served to reduce the available labour for both small livestock husbandry and predation management (Nattrass *et al.* 2020). Together these factors are thought to have contributed to both less fence maintenance and the reduced construction of new fences increasing the permeability of farm boundaries to predators and limiting the effectiveness of predation management within farms (Nattrass & Conradie 2015, Du Plessis *et al.* 2018). A final contributing factor to the perceived increase in jackal, caracal and baboon depredation of livestock throughout much of the Karoo has been the change in land use from commercial to so-called ‘weekend farming’ and ‘lifestyle and farming’ operations (Drouilly *et al.* 2019). Both land uses are associated with reduced human presence on farms providing a reprieve for predators and reducing routine maintenance of fences (Conradie *et al.* 2019).

With the creation of a protected area (PA) within the SKA core, plans have been put into place to improve the boundary fence between core and edge farms. Stakeholder meetings between the SKA and farmers revealed the perceived importance of this barrier to reducing the immigration of predators from the core onto neighbouring livestock farms (Terblanche 2020). Following the appointment of South African National Parks to manage the SKA it has been suggested that game proof fencing be used as an exclusion barrier to avoid both wildlife escaping the park and humans entering. Game proof fences are typically wire mesh fencing that can range between 2.4 and 2.7 m in height (depending on the wildlife within the PA) and can be both electrified or non-electrified (Kesch *et al.* 2015). Electrification is unlikely given the potential for radio interference with the SKA research, but the construction of a more substantive fence than currently exists has been proposed with routine maintenance of the existing jackal-proof fence a stated deliverable by the SKA once the core area is established in July 2018.

Private landowners bordering the SKA core have repeatedly stressed the importance of a well-constructed and maintained boundary fence as the first step to improved relations between them and the managers of the SKA. Most landowners believe jackals in particular will use the PA as a refuge where they will den and raise pups, briefly moving onto their farms to hunt their livestock. These perceptions hold despite data provided by Drouilly *et al.* (2018c) that predators in Anysberg Nature Reserve consumed almost exclusively wild prey and despite regularly leaving the reserve seldom included livestock in their diet.

Camera trapping is a reliable, cost effective method for investigation multi-species mammal communities within a landscape (Steenhuisen *et al.* 2015, Wang *et al.* 2015, Dupuis-Desormeaux *et al.* 2016, Adila *et al.* 2017) and has also been proven to be effective in targeted investigations (i.e., fence surveys) (Dupuis-Desormeaux *et al.* 2018, Jakes *et al.* 2018, Butler *et al.* 2019). Investigating how predators move along fence lines and through holes in fences can provide valuable information on how fence quality and maintenance influences fence porosity and hence predation management on farms (Dupuis-Desormeaux *et al.* 2016, Butler *et al.* 2019, Segar & Keane 2020). This chapter aims to investigate the current effectiveness of the SKA boundary fence and how the cessation of farming within the SKA core may impact the quality and maintenance levels of fences and the subsequent movement of mammals, and predators in particular. I hypothesised that fence quality and maintenance would influence wildlife movement across the fence (hypothesis 1, H1). I predicted that poor quality fences (i.e., poor maintenance) on both edge and core farms would have both a higher species richness (P1) and a higher RAI (P2) of mammals both moving along them and utilising holes in them. I also predicted that the cessation of farming activities on core farms would result in increased movement of non-predator mammals through holes towards core farms (P3) to avoid competition with domestic livestock and persecution by farmers. I predicted that predators would increase their use of holes in the direction of edge farms (P4) after the removal of sheep on core farms.

Methods

Survey design and data collection

I used fence line surveys along the SKA boundary to assess the movement of mammals, particularly predators, both along fence lines and between core and edge farms (Figure 6.1). Surveys entailed the measurement of fence attributes and the monitoring and measuring of open and repaired holes along fences, and camera placement at open holes to provide information on mammal species using the holes and their direction of movement (towards or away from core farms). A total of 21 km of SKA boundary fence was surveyed across two years both before and after farming activities were terminated on the core farms. This represented a comparative subsample of each core/edge pair of which the total length of the boundary fence equated to ~ 30% of the total SKA boundary fence length. Sampled sections of the fence between the three core/edge pairs all had similar soil types (predominantly sandy) so as to ensure consistency in the substrate between fence comparisons.

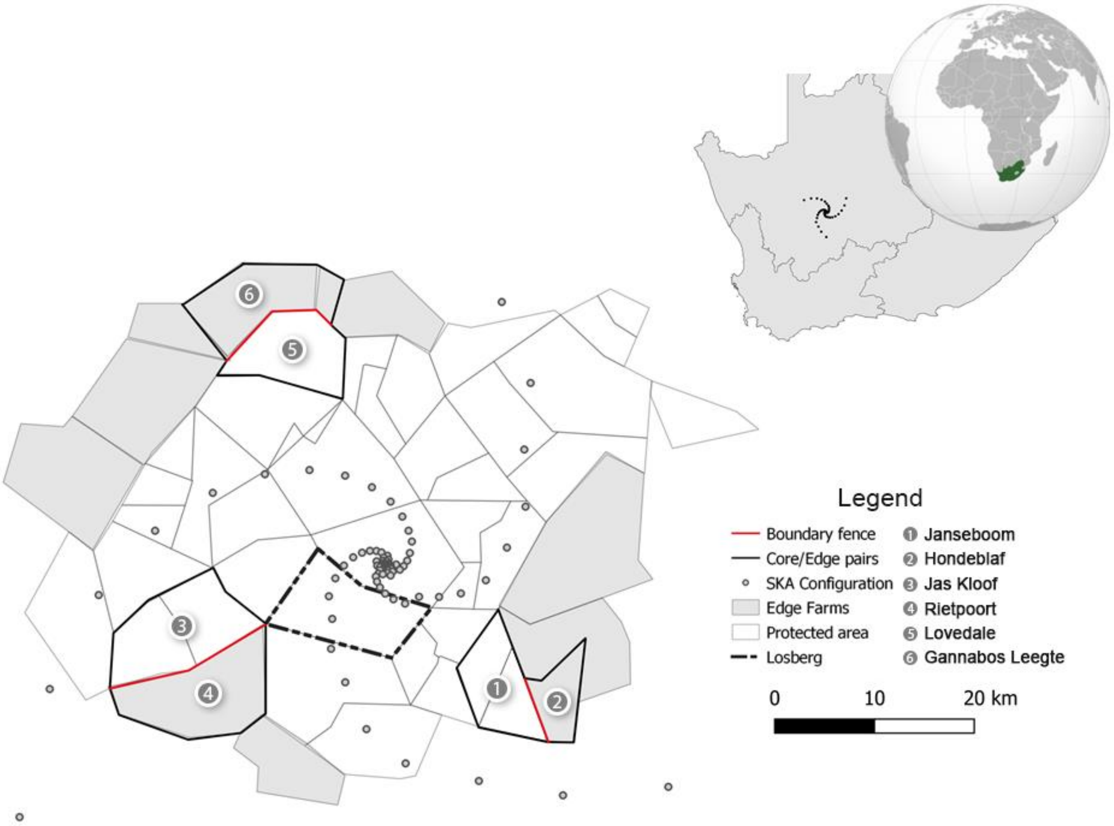


Figure 6.1: Location of three surveyed fence sections (red line) along the SKA boundary that separates core and edge farms (black line) included in the study. Grey circles indicate the proposed position of SKA dishes within the core (white polygons) and edge (grey polygons) farms.

The first survey was in May 2018 and the second during June 2019 (12 months after farm activities were terminated on core farms). The sections of fence surveyed were on the three paired core and edge farms included in Chapters 2 - 4 which encompasses the broad geographic variation across the SKA (Figure 6.1). Surveys were carried out during winter months when camera traps and personnel were available following the completion of the summer biodiversity surveys (see Chapters 2 - 4). Fence surveys were carried out within the same two-month period in successive years effectively controlling for season but exploring the effects of a change in land use from commercial livestock farming to protected area.

Fence quality and maintenance

Understanding the quality and maintenance of a fence helps determine its permeability to animals within the landscape (Pirie *et al.* 2017). Fences with broken wire or mesh, poorly maintained posts, and those constructed on soft substrate that make digging under the fence easy (usually reduced by placing rocks along the bottom of the fence) are more easily damaged and circumvented by animals (Pirie *et al.* 2017).

To determine the quality of fence I randomly selected five standardised lengths (i.e., the distance between two major fence posts) for each of the three fence sections. This resulted in 15 samples per fence section which were repeat sampled in the two survey years. Each sample included the distance (m) between the two major fence posts, the maximum height (m) of the mesh fence excluding any single string top wires (measured at the midpoint between two fence posts), the total number of rocks placed at the base of the sampled fence subsection and the average distance (m) between these subsampled rocks.

I recorded the total number of open and repaired holes along the entire fence section sampled for each paired core/edge farm (Figure 6.2). Repaired holes were identified as any area in the fence where the fence was damaged or an old hole visible, but the opening was physically blocked by either multiple well-placed branches, rocks or a new section of wire mesh (Figure 6.3). Open hole size was measured as the maximum height and width of the hole (Figure 6.4) and I excluded holes with a height of <5 cm which would be unlikely to allow the passage of target mammal species within the area. While these holes are still considered damage to fences, such small holes may be attributed to natural weathering of the fence and not regular animal use which is the focus of this chapter.

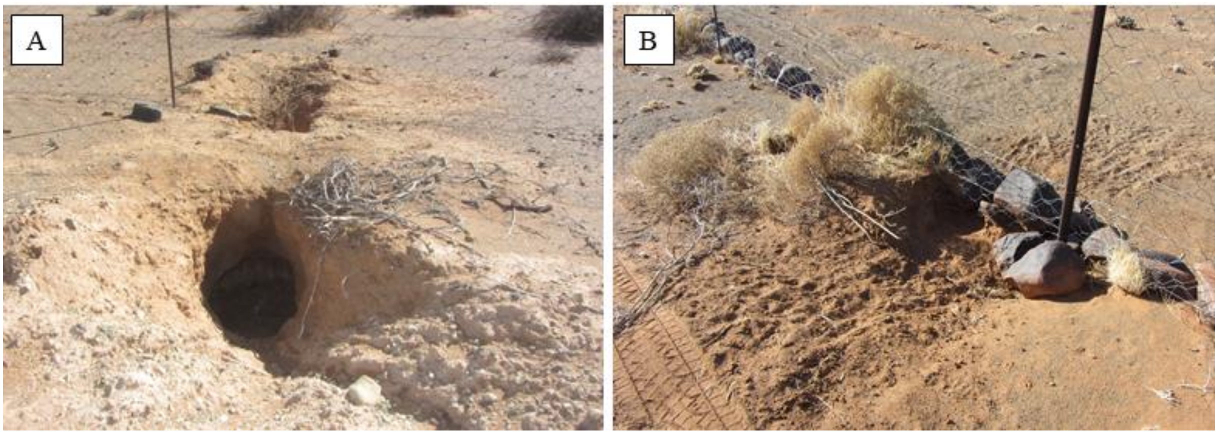


Figure 6.2: Example of an open active hole dug below the fence with no repairs effected (A) and a scraped hole dug underneath both the fence and the rocks which were placed at the base of the fence to discourage digging (B).

Figure 6.3: Example of holes repaired with rocks (A and C), or branches and poles (B and C).

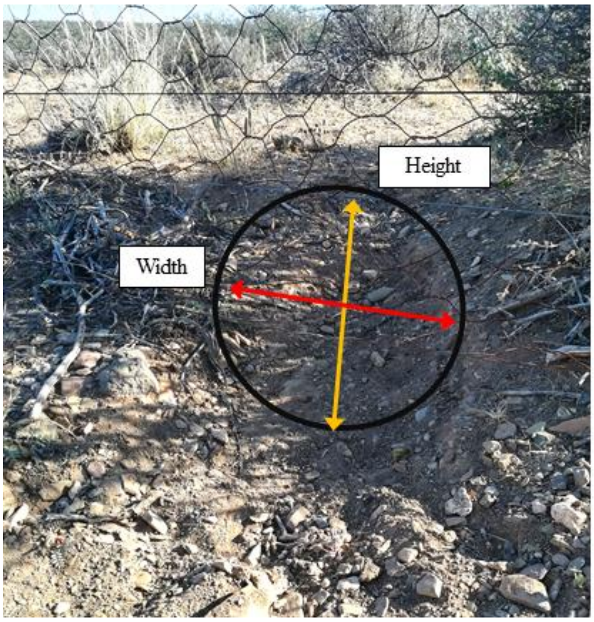


Figure 6.4: Example of how holes were measured. Height (orange line) represents the distance from the lowest point in the ground below the fence to the wire, while width (red line) represents largest side to side diameter of the hole.

Camera trap placement

To analyse hole utilisation of mammal species between core and edge farms I paired Bushnell Trophy CAM HD cameras (see Chapter 4 for specifications) and placed one camera on either side of the fence at a random subsample of holes with high levels of animal activity evident (e.g., digging, trails, spoor and hair present at or near hole) along fences separating core and edge farms (Table 6.1 and Figure 6.5). The two cameras were placed on either side of the hole (core and edge side) facing each other so that camera 2 can be used to confirm species identity, count and direction of ambiguous crossing events camera 1 has captured and *vice versa*. I limited each fence section to a maximum of ten paired cameras (an average of at least one camera per km) with a minimum distance of at least 500 m between camera sites where possible. Each camera was set up at least 1.5 m from the hole so as reduce disturbing animals using the hole while still having a good view of the hole (Figure 6.5). Cameras were programmed to take three photographs when triggered (in order to include pairs of animals) with a one-minute delay between triggers to avoid multiple photos of gregarious species (e.g., bat-eared foxes). The sensitivity of the infrared sensor was set on high and image size was set at 8M pixel, while LED control was set at medium and field scan was off. Cameras were attached to 10mm thick metal stakes at a height of 30 cm off the ground and typically facing outward from a bush so that they were less conspicuous. Cameras were active for 30 consecutive days during which the cameras were not disturbed by me. When placing cameras at biased locations (i.e., at a well-used hole) a 30-day survey is considered to be sufficient time to capture the full range of species using a specific site (Cusack *et al.* 2015).

Table 6.1: Length of each SKA boundary fence section surveyed as well as number of paired cameras set up along each section per survey year. The number of paired cameras varied with the size, number and use of holes.

Fence Section	**Length (km)**	**Number of paired cameras**	
		May 2018	*June 2019*
1	5	6	3
2	6	4	4
3	10	10	7

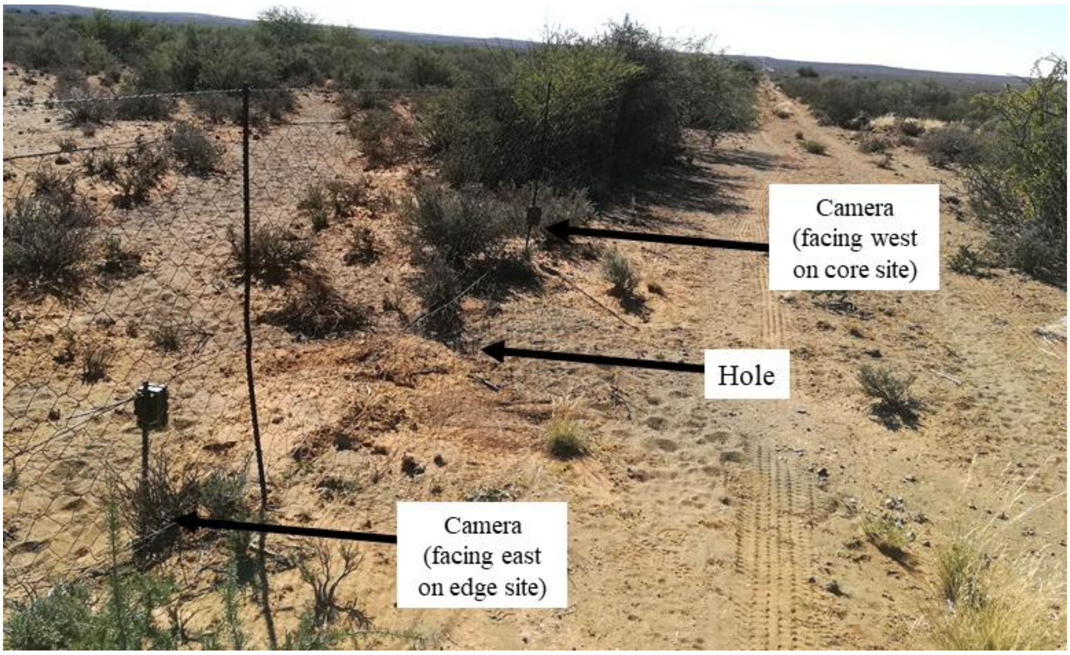


Figure 6.5: Example of how cameras were set up to determine which mammal species utilise a specific hole in the SKA boundary fence between the core and edge farms. Cameras were placed on either side of the fence facing each other, at least 1.5 m away from the hole.

Camera trap data were cleaned by removing false captures (any image that did not contain an animal) (see Chapter 4). I defined an independent capture if more than one image was captured 30 minutes apart. Any consecutive images of the same species within the 30 min limit were grouped and considered a single independent event. Images that contained individuals that were difficult to identify (e.g., night images that were over-exposed) were discarded. Images of domestic animals were used to estimate sheep abundance between farm types and years. Images were categorised into hole use versus no hole use. Within the “hole use” category the identity of the species, the total number of times a hole was used, and the direction of movement was recorded (to or from core sites).

Data analyses

For each fence section in each year, I calculated the mean (± standard error, SE) distance between major fence posts, mean number of ground rocks between major posts, mean gap between ground rocks (m), mean height of fence (cm) and where applicable the mean width of the apron fence running along the ground (cm). I compared fence characteristics between the three fence sections within specific years using a non-parametric Kruskal-Wallis test with a post-hoc pairwise Wilcox test. I further compared the density of rock along the bottom of fences between fence sections as well as between years for a given section using a paired Wilcox signed-rank test. I also calculated the total number of repaired and open holes per fence section per year, and the mean (± SE) number of repaired and open holes per year. I compared mean number of repaired and open holes between years using a paired Wilcox signed-rank test (due to a small sample size of three fence sections per year). All data analysis was calculated in RStudio Version 3.5.3 (RStudio Team 2019).

Species richness along fences

Using camera trap data from fence surveys I calculated the observed species richness (S_{obs}) (excluding small mammals) for each fence section on each farm type (e.g., section 1 on the core and edge side) specifically calculating species richness for mammals actively using holes as well as the overall richness of mammals detected along fences. I further calculated the overall S_{obs} for each survey (May 2018 and June 2019) on both sides of the fence (core and edge side) for both species using the holes and overall fence richness. Chao 1 estimates were used as a non-parametric species richness estimator for each fence section and for each fence survey in a particular year. These estimates are used to account for potential undetected species. Using the 'iNEXT' package (Hsieh *et al.* 2020) I determined overall rarefaction curves (all fence sections combined) based off Chao 1 estimates for species found along fences on both core and edge sides of the fence during 2018 and 2019 (see Chapter 4 for details). I further calculated the percentage S_{obs} of all species detected on each farm that were detected at the fence section of that specific farm type (e.g., section 1 on the core side).

$$\% \, S_{obs} = \frac{fence\ section\ S_{obs}}{overall\ farm\ S_{obs}} \times 100$$

Species abundance along fences

Species abundance along fences included all types of interactions with the boundary fence (i.e., using holes, moving along fence but no hole use). Movement of individuals across the fence meant that abundance estimates on either side of the fence (core and edge) were not independent. I only included individuals in abundance estimates for a farm type if they originated on that farm and then moved through a hole to the other side. These data were then added to data of individuals who were not using fence holes but detected moving along fences to derive an abundance estimate for each farm type. While this may skew abundance estimates, methods were standardised for farms and between survey years allowing me to identify trends of species abundance at "origin" farms.

For each survey (2018 and 2019) and fence section (section 1, 2 and 3) I calculated the number of independent capture events (standardised per 14 cameras, i.e., the lowest number of active cameras during a survey) and the photographic rate (also known as relative abundance index, RAI) for each species (excluding small mammals) found on either side of the fence (core and edge side). Photographic rate or RAI is calculated by dividing the total number of independent captures per farm type by the total number of trap nights all cameras were active per farm, multiplied by 30, creating a standardised species abundance per 30 trap nights for all surveys (O'Brien *et al*. 2003, Sollmann 2018) (see Chapter 4 methods). I also specifically calculated number of independent captures and photographic rate for predators (black-backed jackal and caracal combined because of low overall detections particularly of caracal).

For both total species recorded and predators specifically I compared RAI along fences using a Generalised Linear Model (GLM) from the 'stats' package (R Core Team 2020) in RStudio Version 3.5.3 (RStudio Team 2019). Covariates included year (2018 versus 2019 – before and after the change in land use), fence section (which acted as a proxy for maintenance level), domestic livestock presence and farm type (core or edge side of the fence). I used a Poisson distribution (link = "log") for total species abundance models. Predator captures were very low therefore I converted these into presence and absence data and used a negative binomial distribution for predator specific models.

Species utilisation of holes and direction of movement

To investigate hole utilisation by species as well as direction of movement between edge and core farms I again calculated number of independent capture events (standardised per 14 cameras, i.e., the lowest number of active cameras during a survey) and photographic rate (also known as relative abundance index, RAI) for each species (excluding small mammals). Independent captures and RAI were categorised by direction of movement (core = movement from core to edge farms while, edge = movement from edge to core farms). Photographic rate or RAI was calculated by dividing the total number of independent captures per farm type by the total number of trap nights all cameras were active per farm, multiplied by 30, creating a standardised species abundance per 30 trap nights for all surveys (O'Brien *et al*. 2003, Sollmann 2018) (see Chapter 4 methods). I also specifically calculated number of independent captures and photographic rate for predators of interest viz., black-backed jackal and caracal.

I used General Linear Models (GLMs) to explore the RAI of mammals in general and predators in particular, using holes in each section (acting as a proxy for the quality of fence), year (2018 versus 2019 – before and after the change in land use), and the direction of movement (core to edge versus edge to core) (Table 6.2).

Table 6.2: Description of categorical covariates used to assess differences in overall mammal abundance and predator abundance using fences along the SKA boundary fence within the SKA region of the Karoo. The predicted response describes for each covariate is described as increasing (+), decreasing (-) or remaining constant (+/-).

Covariates	**Predicted response**	
	Total species RAI	*Predator RAI*
Year	+	+
Fence section		
Section 1	+/-	+/-
Section 2	-	-
Section 3	+	+
Direction of movement		
Core to edge	-	-
Edge to core	+	+
Domestic livestock presence	+/-	+

I used the *glm* function from the 'stats' package (R Core Team 2020) to test if either total species relative abundance or predator (jackal and caracal) RAI were significantly affected by any of the covariates. I determined the most parsimonious model using the *drop1* function from the 'stats' package (R Core Team 2020), and where the Akaike Information Criterion (AIC) for a covariate is lower than the AIC for the global model then that covariate was dropped from the final model (see Chapter 3 methods). No covariates were dropped from any of the GLMs run. The *anova* function from the 'stats' package (R Core Team 2020) was used to determine p-values for each predictor covariate, and both the multivariate and univariate results were reported for each model. GLMs for total species relative abundance were fitted with a Poisson distribution (link = "log") while GLMs for predator presence were fitted with a negative binomial distribution which is typical for presence or absence data.

Paired Wilcox signed-rank tests were used to compare changes in the abundance of species moving from core to edge farms between 2018 and 2019, and *vice versa*. Unpaired Wilcox rank-sum tests were used to determine if there was a change in abundance of species moving from core to edge farms or moving from edge to core farms within a specific survey year. Movement between farms across the boundary fence meant species abundance was not independent between farm types, therefore comparison could only focus on changes in the number of species and species moving in specific directions.

I used generalised linear models (GLMs) to explore variables influencing the frequency of hole use (number of times a given camera trapped hole was used during a survey). Covariates included: fence sections (1-3), level of fence maintenance (number of repaired holes) and survey year (2018 and 2019). Number of repaired holes per km for each fence section was used as a proxy for the level of fence maintenance, where repaired holes equalled or exceeded two thirds of overall holes (high number of repaired holes) this indicated good fence maintenance. GLMs were carried out using the *manyglm* function within the 'mvabund' package (Wang *et al.* 2020) in RStudio version v3.5.3 (RStudio Team 2019). The 'mvabund' package is a relatively new method of modelling and visualising multivariate abundance data. Unlike previous methods (i.e., ANOSIM and PERMANOVA) the 'mvabund' package is more powerful and better at dealing with a range of abundance data types (count, presence/absence, etc.) (Wang *et al.* 2012, Warton *et al.* 2012). The *manyglm* function fits separate GLM models to each species within a data set using a common set of environmental or predictor variables

(Wang *et al.* 2012, Warton *et al.* 2012). Therefore, summary statistics for the model (using the *anova* function) provide information for both multivariate variables (i.e., the effect of environmental variable on the entire dataset) as well as univariate variables (looking at the effect of predictor variables on individual species) (Wang *et al.* 2012, Warton *et al.* 2012) (see Chapter 3 methods).

GLMs were fitted with a negative binomial distribution which is typical for count data where mean-variance is quadratic rather than linear (Wang *et al.* 2012). Full diagnostic plots were further run on each model and showed signs of non-constant variance suggesting appropriate model fit for the data sets (see appendix). The *anova.manyglm* function was used to determine p-values for each predictor covariate, and both the multivariate and univariate results were reported for each model specifically for predator species. This showed both the general effect of covariates on the response variable but also the effects of each covariate on black-backed jackal and caracal combined. To visualise the patterns in mammal hole utilisation along fence sections a non-metric multidimensional scaling (nMDS) ordination plot was constructed using the 'vegan' package (Woese *et al.* 1990, Oksanen *et al.* 2019). I used a Jaccard (presence/absence) similarity index to determine groupings within mammal hole utilisation. Contour environmental variables were determined using the *ordisurf* function from the 'vegan' package (Oksanen *et al.* 2019) to show how number of repaired holes per km may affect the hole utilisation patterns. The *ordisurf* function uses generalised additive models (GAM) to fit smooth surfaces or contours to the ordination space (Oksanen *et al.* 2018).

Results

Fence characteristics and quality

The length of fence between major posts was significantly different between the three fence sections ($H_{(2)} = 15.91$, $p = 0.0003$; Table 6.3). Post-hoc pairwise Wilcox comparisons showed that section 3 was significantly shorter than both section 1 ($p = 0.003$) and section 2 ($p = 0.0004$). The height of fences was significantly different between fence sections ($H_{(2)} = 10.37$, $p = 0.005$), with section 1 and 3 significantly higher than section 2 ($p = 0.05$ and $p = 0.01$ respectively).

The mean number of rocks found along the base of the fence was highly variable between fence sections and years (Table 6.3). During 2018 the number of rocks found along fences (Table 6.3) was significantly different between fence sections ($H_{(2)} = 7.54$, $p = 0.02$), with fewer rocks along section 3 compared to section 1 ($p = 0.02$) and sections 2 ($p = 0.05$). During 2019 there was no overall difference in rock density between sections ($H_{(2)} = 5.52$, $p = 0.06$). Rock density did not change significantly between survey years (2018 vs. 2019) for each specific fence section (section 1: H = 5, p.adjust = 0.62, section 2: H = 8, p.adjust = 0.36, section 3: H = 1, p.adjust = 1.00) (Table 6.3). Where rocks were present, the gap between rocks was relatively small for all fence sections in 2018 with no significant difference in gap distance between fence sections ($H_{(2)} = 4.02$, $p = 0.13$). During 2019 rocks were consistently placed with no gap between rocks for all three fence sections (Table 6.3).

Table 6.3: Summary characteristics of three sections of the SKA boundary fence (between core and edge farms) during two fence surveys before (2018) and after (2019) the cessation of farming activity on core farms. Bold values indicate mean (± standard error, SE) measurements between the three sections for each year.

Year	Fence Section	Mean dist. between major posts (m)	Mean height of fence (cm)	Mean # of rocks between major posts	Mean gap between rocks (m)
2018	Section 1	16.54 (± 1.22)	127 (± 2.88)	76.8 (± 25.5)	2.87 (± 1.53)
	Section 2	17.64 (± 0.45)	125.2 (± 0.48)	41.97 (± 18.77)	0.5 (± 0)
	Section 3	13.5 (± 0.27)	127.4 (± 1.46)	1.4 (± 1.4)	0 (± 0)
	Mean (± SE)	**15.89 (± 1.07)**	**126.53 (± 1.80)**	**49.93 (± 23.25)**	**1.78 (± 1.24)**
2019	Section 1	16.54 (± 1.22)	127 (± 2.88)	95.2 (± 16.24)	0 (± 0)
	Section 2	17.64 (± 0.45)	125.2 (± 0.48)	50.6 (± 22.16)	0 (± 0)
	Section 3	13.5 (± 0.27)	127.4 (± 1.46)	13 (± 13)	0 (± 0)
	Mean (± SE)	**15.89 (± 1.07)**	**126.53 (± 1.80)**	**52.93 (± 22.49)**	**0 (± 0)**

There was no significant difference in the mean (of all the sections) number of repaired holes (H = 1, p.adjust = 0.50) and the mean (of all the sections) number of open holes (H = 0, p.adjust = 0.37) between 2018 and 2019 (Table 6.4). Fence section 3 had the most open holes along surveyed fences during both 2018 and 2019 while, section 2 had the fewest open holes for both years (Table 6.4). Section 1 and section 2 had a similar number of open holes between survey years, while section 3 saw a slight increase in open holes (Table 6.4).

The number of repaired versus open holes per km of fence for each fence remains fairly consistent between years for each fence section (Figure 6.6). Section 3 has the most open holes in both years while section 2 has the most repaired holes with section 1 having the least repaired and open holes in both survey years (Figure 6.6). Total number of holes (repaired and open) per km increased between 2018 and 2019 for all three fence sections (Figure 6.6).

Table 6.4: Number of repaired and open holes found along three SKA boundary fence sections (between core and edge farms) during two fence surveys before (2018) and after (2019) sheep were removed from core farms. Bold values indicate the mean (± standard error) measurements for all three sections for each year.

Year	Fence Section	Total length of section (km)	Total # of repaired holes/km	Total # of open holes/km
2018	Section 1	5	2.20	2
	Section 2	6	7.50	1
	Section 3	10	4.70	3
	Mean (± SE)	**7 (± 1.52)**	**4.80 (± 1.53)**	**2 (± 0.57)**
2019	Section 1	5	5.40	2
	Section 2	6	8.80	1.33
	Section 3	10	4	4.60
	Mean (± SE)	**6.33 (± 0.88)**	**6.07 (± 1.43)**	**2.65 (± 1.00)**

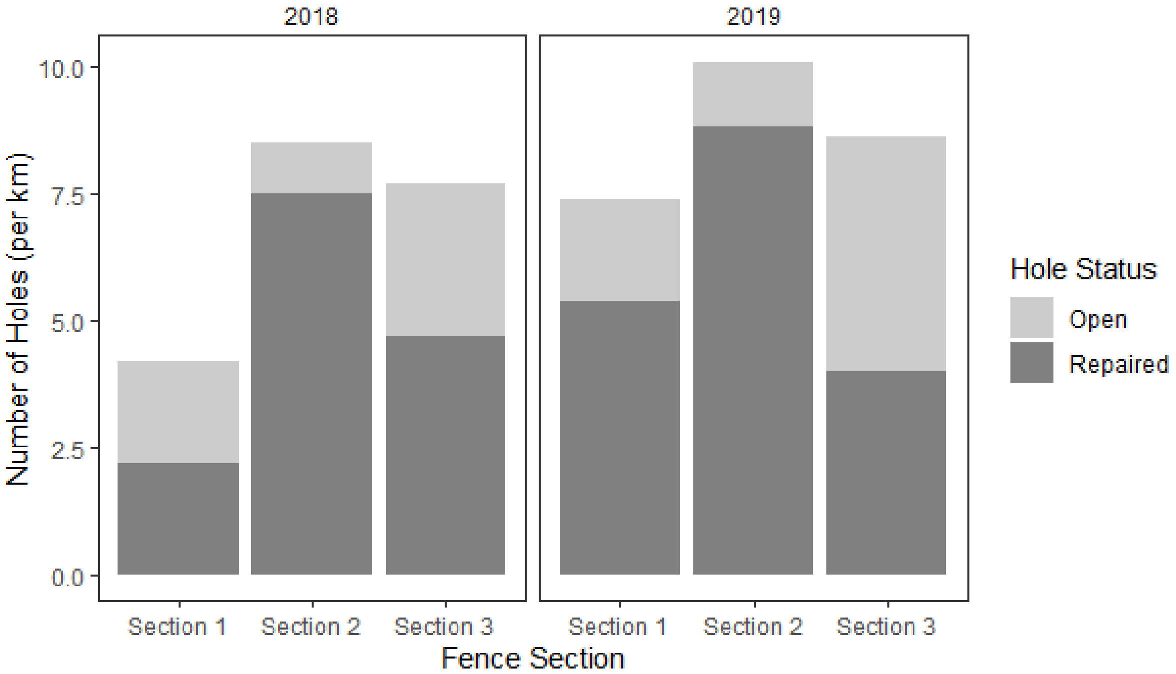


Figure 6.6: Number of repaired and open holes found along three different sections of SKA boundary fence separating core and edge farms, during two survey years. 2018 represents the period before farming activities were terminated on core farms, while 2019 represent 12 months after farming activities were terminated on core farms.

Average size of open holes was not significantly different between 2018 and 2019 for both fence section 2 (Z = 22, p = 0.53) and 3 (Z = 530, p = 0.13) however, for fence section 1 hole size was significantly larger in 2018 compared to 2019 (Z = 108, p = 0.008) (Figure 6.7).

During 2018 hole size was significantly different between fence section ($H_{(2)} = 9.88$, $p = 0.007$). Post-hoc pairwise Wilcox tests showed that hole size was not significantly different between section 2 and 3 ($p = 0.17$), while section 1 had significantly larger holes compared to section 2 ($p = 0.03$) and section 3 ($p = 0.01$). During 2019 hole size was not significantly different between any fence section ($H_{(2)} = 3.51$, $p = 0.17$) (Figure 6.7).

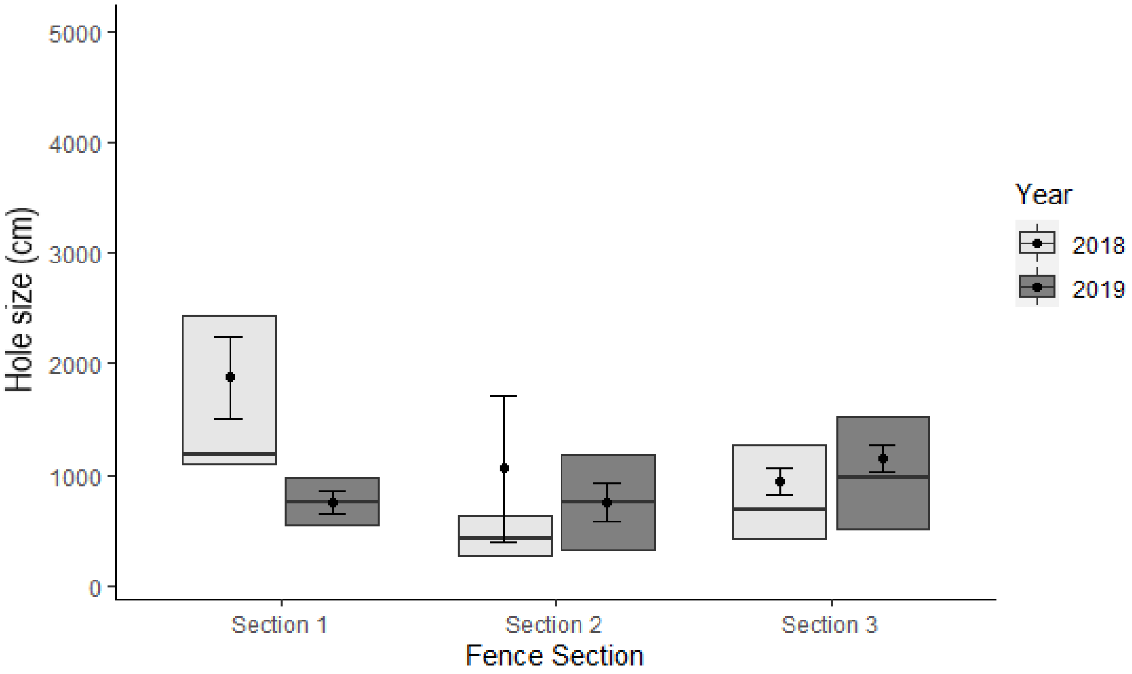


Figure 6.7: Boxplots representing the size (height x width) of open holes found along three SKA boundary fence sections (section 1, 2 and 3) over two survey years (2018 and 2019). Shaded boxes indicate lower quartile, median (thick black line) and upper quartile for height x width, while black dots indicate the mean and error bars representing standard error.

Species richness along fences

During both fence surveys (2018 and 2019) over 60% of overall farm mammal richness was detected along fences (both using and not using holes) (Table 6.5). During the 2018 survey 15 mammal species (55.56%) were seen using fence holes from both core and edge sites (Table 6.5) with only one more mammal species detected on core ($n = 15$) compared to edge sides ($n = 14$) of the fence (Table 6.5). Chao 1 estimates of species richness were higher than S_{obs} for both hole users and animals moving adjacent to the fence on core and edge sides of the fence (Table 6.5). Fence section 3 had the highest number of species using holes, as well as the highest overall species richness for animals detected moving along the fence on both core and edge farms (Table 6.5). Less than 40% of the total species richness detected on farms 1 and 2 were detected using holes while more than 40% of total species richness was detected moving along these fences (Table 6.5). Fence section 2 had the lowest overall mammal richness as well as the lowest mammal richness seen using fence holes (Table 6.5). For species using holes Chao 1 estimates were highest (further from S_{obs}) for section 1 on the edge side (31.41 ± 25.98) (Table 6.5). Chao 1 estimates were lowest (closest to S_{obs}) for section 3 on the core side (14.35 ± 2.09) (Table 6.5).

During 2019 overall fence spp. richness was similar to 2018 on both sides of the fence (core and edge side) (Table 6.5). The total number of cameras along fences in 2019 was less than during the 2018 survey however, during 2019 a higher number of mammal species were recorded using holes compared to 2018 (Table 6.5). Chao 1 estimated higher richness for species using holes, as well as overall fence richness (Table 6.5). Overall Chao 1 estimates were higher during 2019 compared to 2018 (Table 6.5). Overall fence richness decreased in section 3 between 2018 and 2019, as well as the number of species seen using holes (Table 6.5). The overall fence richness in section 2 remained similar between surveys while the number of species seen using holes increased (Table 6.5). Overall species richness along fences, as well as the number of species seen using holes decreased in section 1 between 2018 and 2019 on both sides of the fence (Table 6.5). Overall, the proportion of species using holes compared to farm richness increased on both side of the fences (Table 6.5). The proportion of overall fence species richness compared to farm richness decreased on the core side of the fence but increased on the edge side (Table 6.5).

Similar to 2018, over 60% of overall farm mammal richness was seen along fences in 2019 (Table 6.5). Fence section 1 consistently had the lowest proportion of overall farm richness seen using holes as well as seen along fences in general (Table 6.5). For species using holes Chao 1 estimates were highest (further from S_{obs}) for section 2 on the core side (12.68 ± 5.76) and the edge side (20.18 ± 9.98) (Table 6.5). Chao 1 estimates were lowest (closed to S_{obs}) for section 3 on the edge side (10.57 ± 1.15) (Table 6.5). During both 2018 and 2019 rarefaction curves reached their asymptote from approximately 25 active camera traps on edge side of the boundary fence (Figure 6.8A and B). While on the core side of the boundary fence rarefaction curves only reached their asymptote during 2019 (at approximately 25 active cameras) (Figure 6.8B). During 2018 rarefaction curves for the core side of the fence only see to begin flattening around approximately 45 active cameras (Figure 6.8A).

Table 6.5: Species richness (S_{obs}), Chao 1 richness estimates (± SE) and percentage (%) of overall farm richness calculated for each farm type on either side of three SKA boundary fence sections (between core and edge farms) during two fence surveys before (2018) and after (2019) the cessation of farming on core farms. Bold values indicate mean (± standard error) measurements between the three sections for each year. Measurements were separated into two categories, "using hole" represents only the species detected using a fence hole while, "moving along fence" represents all species detected along the fence on a specific farm types including species using holes.

Year	**Fence Section**	**Farm Type**	**# of Cameras**	**S_{obs}**		**Chao 1 (± SE)**		**% of overall spp. richness on farm**	
				Using hole	*Moving along fence*	*Using hole*	*Moving along fence*	*Using hole*	*Moving along fence*
2018	Section 1	Core	6	7	12	13.66 (± 9.77)	15.75 (± 4.07)	25.93	44.44
		Edge	6	11	14	31.41 (25.98)	24.20 (± 11.03)	40.74	51.85
	Section 2	Core	4	6	10	15.37 (12.94)	34.00 (± 29.79)	22.22	37.04
		Edge	4	4	11	7.37 (5.47)	29.37 (± 23.42)	14.81	40.74
	Section 3	Core	10	13	17	14.35 (2.09)	17.30 (± 0.70)	48.15	62.96
		Edge	10	14	16	19.62 (6.83)	19.75 (± 4.43)	51.85	59.26
	Combined sections	**Core**	**20**	**14**	**21**	**15.42 (2.19)**	**25.27 (± 4.58)**	**51.85**	**77.78**
		Edge	**20**	**15**	**17**	**17.13 (3.24)**	**17.15 (± 0.51)**	**55.56**	**62.96**
2019	Section 1	Core	3	7	9	11.16 (5.17)	11.77 (± 3.39)	25.93	33.33
		Edge	3	6	9	8.66 (3.65)	11.77 (± 3.39)	22.22	33.33
	Section 2	Core	4	8	12	12.68 (5.76)	18.12 (± 6.32)	29.63	44.44
		Edge	4	11	12	20.18 (9.98)	16.50 (± 4.97)	40.74	44.44
	Section 3	Core	7	11	14	14.42 (4.58)	16.28 (± 3.04)	40.74	51.85
		Edge	7	10	12	10.57 (1.15)	13.28 (± 2.01)	37.04	44.44
	Combined sections	**Core**	**14**	**16**	**18**	**20.17 (4.49)**	**19.04 (± 1.66)**	**59.26**	**66.67**
		Edge	**14**	**16**	**17**	**24.35 (9.47)**	**18.04 (± 1.66)**	**59.26**	**62.96**

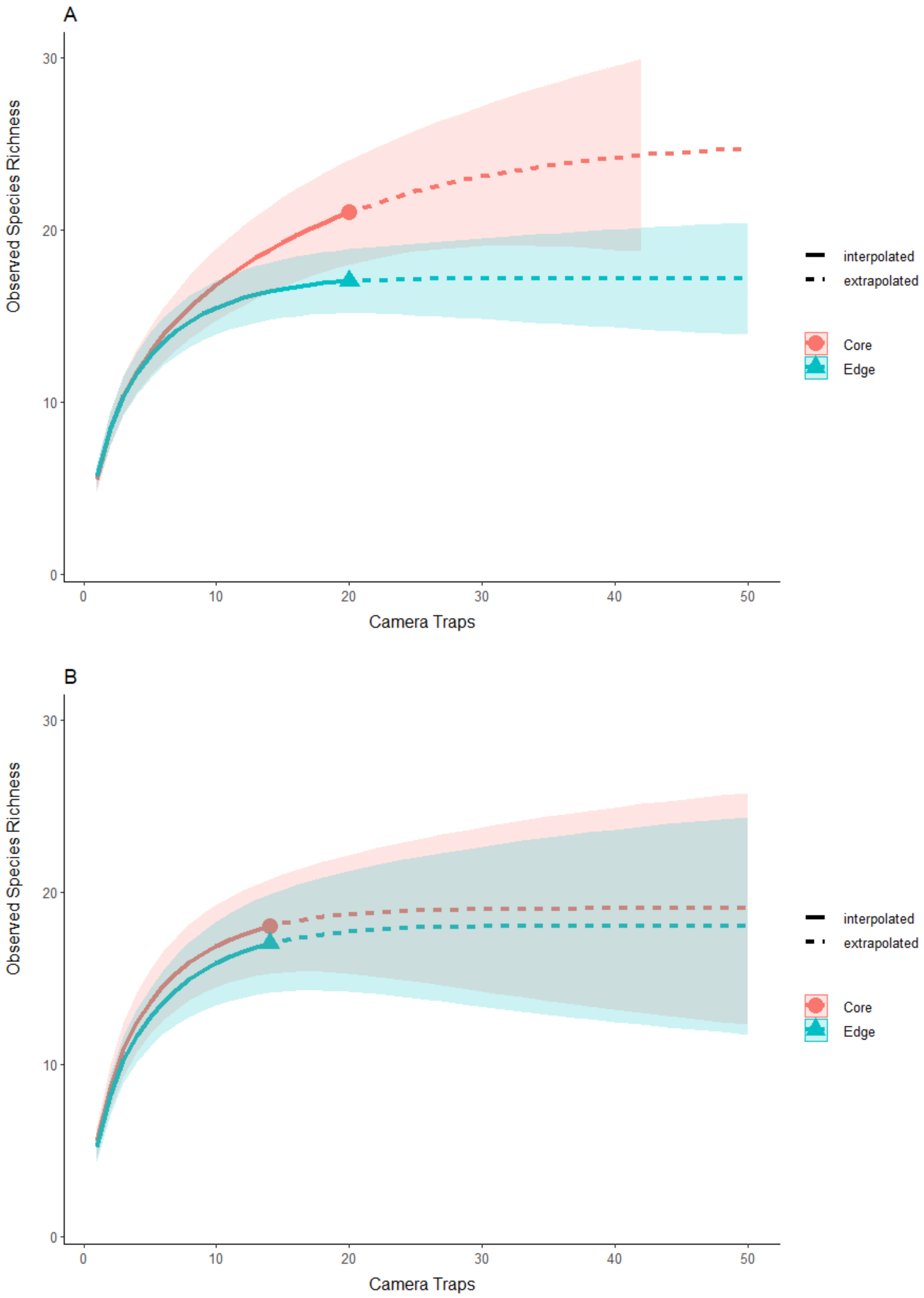


Figure 6.8: Sample-based rarefaction curves of wild mammals captured moving along SKA boundary fences on both the core and edge sides of the fence during two different survey years (A = 2018 before farming activities were terminated on core farms, and B = 2019 twelve months after farming activities were terminated on core farms). Shaded areas represent 95% confidence interval drawn from 1000 randomisations performed with replacement. Solid lines indicate observed richness, while dotted lines indicate expected species richness.

Relative abundance of mammal species detected along fences

For both core and edge sides of the fence hare spp. (*Lepus* spp.) had the highest number of independent captures during 2018 (n = 231.7 on the core side and n = 194.6 on the edge side) and 2019 (n = 200 on the core side and n = 229 on the edge side) (Table 6.6). Canidae had the second highest capture rate overall for both 2018 and 2019 largely due to bat-eared fox (*Otocyon megalotis*) and cape fox (*Vulpes chama*) (Table 6.6). The greater kudu (*Tragelaphus strepsiceros*) and small spotted cat (*Felis nigripes*) had the least number of captures on either side of the fence for both 2018 and 2019 (Table 6.6). Black-backed jackal (*Canis mesomelas*) were detected more on the core side of the fence for both years (Table 6.6). Caracal (*Caracal caracal*) where only captured on the edge side of the fence for both survey years (2018 n = 2.8 and 2019 n = 1) however capture rates were much lower than for jackal (Table 6.6).

GLMs show that overall mammal RAI along fences was significantly influenced by fence section (RAI was higher along section 3 where fence maintenance was low) (Table 6.7). During 2018 overall species RAI was highest along fence section 3 on both the core and edge side of the fence (Figure 6.9). The core side had a lower overall species RAI along both section 1 and section 2 and was highest along section 3 compared to the edge side (Figure 6.9). During 2019 the RAI of all mammals was slightly higher along fence section 3 for both core and edge farms (Figure 6.9). Large deviations between mean and median values for fence section 2 during 2019 is the result of high captures of hare spp. (Figure 6.9).

Table 6.6: Summarised results for overall fence use (both species seen along fences and seen using fence holes) over two years (2018 and 2019) along three sections of SKA boundary fence (core and edge side) presented per family and species. Predator species considered to be a threat to small livestock in the area are highlighted in grey. Number of independent captures was standardised to 14 cameras. Photographic rate (also known as relative abundance index) indicates the trapping rate of a species per 30 trap nights.

Family *Species*	**Number of independent captures (per 14 cameras)**				**Photographic rate (RAI) (per 30 trap nights)**			
	2018		**2019**		**2018**		**2019**	
	Core	*Edge*	*Core*	*Edge*	*Core*	*Edge*	*Core*	*Edge*
Bovidae	57.40	72.10	27.00	21.00	4.10	5.15	1.93	1.50
Greater kudu *Tragelaphus strepsiceros*	1.40	0.00	0.00	0.00	0.10	0.00	0.00	0.00
Springbok *Antidorcas marsupialis*	6.30	4.20	7.00	1.00	0.45	0.30	0.50	0.07
Steenbok *Raphicerus campestris*	49.70	67.90	20.00	20.00	3.55	4.85	1.43	1.43
Canidae	86.10	50.40	74.00	77.00	6.15	3.60	5.29	5.50
Black-backed jackal *Canis mesomelas*	12.60	1.40	19.00	13.00	0.90	0.10	1.36	0.93
Bat-eared fox *Otocyon megalotis*	46.90	29.40	30.00	34.00	3.35	2.10	2.14	2.43
Cape fox *Vulpes chama*	26.60	19.60	25.00	30.00	1.90	1.40	1.79	2.14
Felidae	3.50	6.30	4.00	12.00	0.25	0.45	0.29	0.86
African wildcat *Felis sylvestris*	2.80	3.50	4.00	11.00	0.20	0.25	0.29	0.79
Small-spotted cat *Felis nigripes*	0.70	0.00	0.00	0.00	0.05	0.00	0.00	0.00
Caracal *Caracal caracal*	0.00	2.80	0.00	1.00	0.00	0.20	0.00	0.07
Herpestidae	9.10	14.70	9.00	10.00	0.65	1.05	0.64	0.71
Cape grey mongoose *Galerella pulverulenta*	2.10	9.10	4.00	6.00	0.15	0.65	0.29	0.43
Meerkat *Suricata suricata*	0.70	2.10	2.00	0.00	0.05	0.15	0.14	0.00
Yellow mongoose *Cynictis penicillata*	6.30	3.50	3.00	4.00	0.45	0.25	0.21	0.29
Hyaenidae	14.00	11.90	23.00	29.00	1.00	0.85	1.64	2.07
Aardwolf *Proteles cristata*	14.00	11.90	23.00	29.00	1.00	0.85	1.64	2.07
Hystricidae	7.70	9.10	4.00	3.00	0.55	0.65	0.29	0.21
Cape porcupine *Hystrix africaeaustralis*	7.70	9.10	4.00	3.00	0.55	0.65	0.29	0.21
Leporidae	232.40	194.60	201.00	230.00	16.60	13.90	14.36	16.43
Hare spp. *Lepus* spp.	231.70	194.60	200.00	229.00	16.55	13.90	14.29	16.36
Rock rabbit spp. *Pronolagus* spp.	0.70	0.00	1.00	1.00	0.05	0.00	0.07	0.07
Mustelidae	1.40	3.50	4.00	2.00	0.10	0.25	0.29	0.14
Striped polecat *Ictonyx striatus*	1.40	3.50	4.00	2.00	0.10	0.25	0.29	0.14
Orycteropodidae	15.40	9.10	14.00	20.00	1.10	0.65	1.00	1.43
Aardvark *Orycteropus afer*	15.40	9.10	14.00	20.00	1.10	0.65	1.00	1.43
Procaviidae	4.20	9.10	6.00	5.00	0.30	0.65	0.43	0.36
Rock hyrax *Procavia capensis*	4.20	9.10	6.00	5.00	0.30	0.65	0.43	0.36
Sciuridae	1.40	1.40	1.00	0.00	0.10	0.10	0.07	0.00
Cape ground squirrel *Xerus inauris*	1.40	1.40	1.00	0.00	0.10	0.10	0.07	0.00
Viverridae	1.40	0.00	1.00	4.00	0.10	0.00	0.07	0.29
Small-spotted genet *Genetta genetta*	1.40	0.00	1.00	4.00	0.10	0.00	0.07	0.29

Table 6.7: Summary statistics of multivariate GLMs summarising significance of covariables on changes in the relative abundance of all mammal species and the relative abundance of predators only moving along fences. p values were calculated using 999 resampling. *$p \leq 0.05$; **$p \leq 0.001$. Total relative abundance follows a Poisson distribution (link = "log"), and predator presence follows a negative binomial distribution.

Response variable	Covariate	Estimate (± SE)	z value	Pr (>|z|)
Total species relative abundance (along fences)	(Intercept)	16.57 (± 104.51)	0.15	0.87
	Year	-0.006 (± 0.05)	-0.13	0.89
	Section 1 vs Section 3	0.61 (± 0.10)	5.80	<0.001*
	Section 2 vs. Section 3	0.11 (± 0.06)	1.76	0.05*
	Side of fence: Edge vs. Core	-0.02 (± 0.04)	-0.58	0.55
Predator presence or absence (along fences)	(Intercept)	-21.78 (± 148.70)	-0.001	0.99
	Year	1.06 (± 0.72)	1.46	0.14
	Sheep: Presence vs Absence	1.23 (± 0.95)	1.29	0.19
	Section 1 vs. Section 3	28.64 (± 148.70)	0.00	1.00
	Section 2 vs. Section 3	1.73 (± 1.16)	1.49	0.13

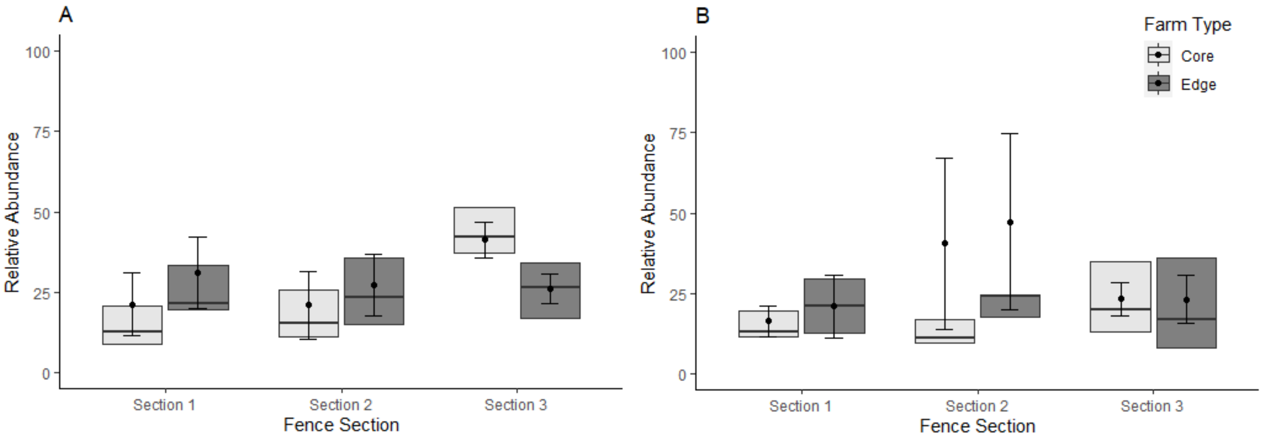


Figure 6.9: Boxplots representing the RAI of all mammals on either side (core and edge) of three SKA boundary fence sections (section 1, 2 and 3) over two survey years (A = 2018 and B = 2019). Shaded boxes indicate lower quartile, median (thick black line) and upper quartile for height and width, while black dots indicate mean RAI with error bars representing standard error.

Predator (black-backed jackal and caracal) presence or absence was not significantly influenced by year, fence section or sheep presence (Table 6.7). Overall (all sections combined) predator RAI was higher along the core side of the fence for both 2018 and 2019 (0.90 and 1.35 respectively) compared to the edge side of the fence (2018 = 0.42 and 2019 = 1.00) (see App 6.1). Predator RAI was highest along fence section 3 for both survey years on both the core and edge side of the fence (Figure 6.10 and App 6.1). Section 2 had the lowest predator RAI during 2018 and 2019 (Figure 6.10 and App 6.1).

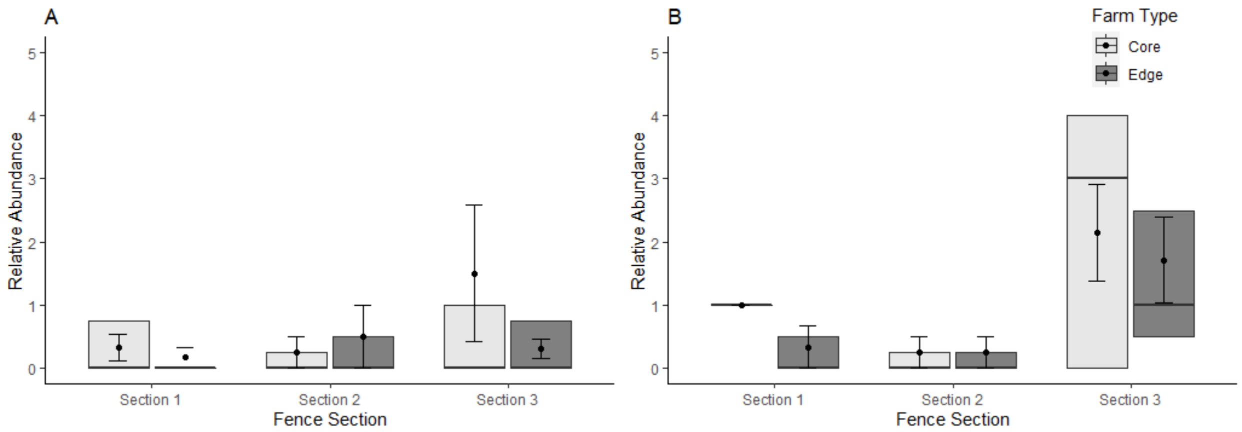


Figure 6.10: Boxplots representing overall predator (jackal and caracal) RAI on either side (core and edge) of three SKA boundary fence sections (section 1, 2 and 3) over two survey years (2018 and 2019). Shaded boxes indicate lower quartile, median (thick black line) and upper quartile for height and width, while black dots indicate mean RAI with error bars representing standard error.

Species utilisation of holes and direction of movement

GLMs show that overall wildlife RAI using holes was influenced by fence section (RAI was higher along section 3 where fence maintenance was low) (Table 6.8). During 2018 there was higher fence utilisation along fence section 3 compared to section 1 and 2 (Figure 6.11A). There was no significant difference in species RAI moving from core to edge or moving edge to core (Table 6.8 and Figure 6.11). There was no significant difference in species RAI moving in a particular direction between 2018 and 2019 (Table 6.8 and Table 6.9). Low incidence of predators (black-backed jackal and caracal) using holes resulted in poor model performance and unlike GLMs focusing on movement along fences the predator specific hole use GLM was dropped from analysis.

Table 6.8: ANOVA table summarising statistical significance of the most parsimonious multivariate GLMs for the relative abundance of all mammal species using fence holes. Total relative abundance follows a Poisson distribution (link = “log”), *p* values were calculated using 999 resampling. **p* ≤ 0.05; ***p* ≤ 0.001.

Response variable	Covariate	Deviance Resid.	Df	Resid. Dev	Est.	z	Pr (>|z|)
Total species relative abundance (using holes)	Year	1.35	66	895.31	0.08	1.15	0.24
	Section 1 vs Section 3	92.91	64	802.40	1.11	5.91	>0.001**
	Section 2 vs. Section 3	92.91	64	802.40	0.68	6.10	>0.001**
	Direction of movement	0.17	63	802.22	0.02	0.41	0.60

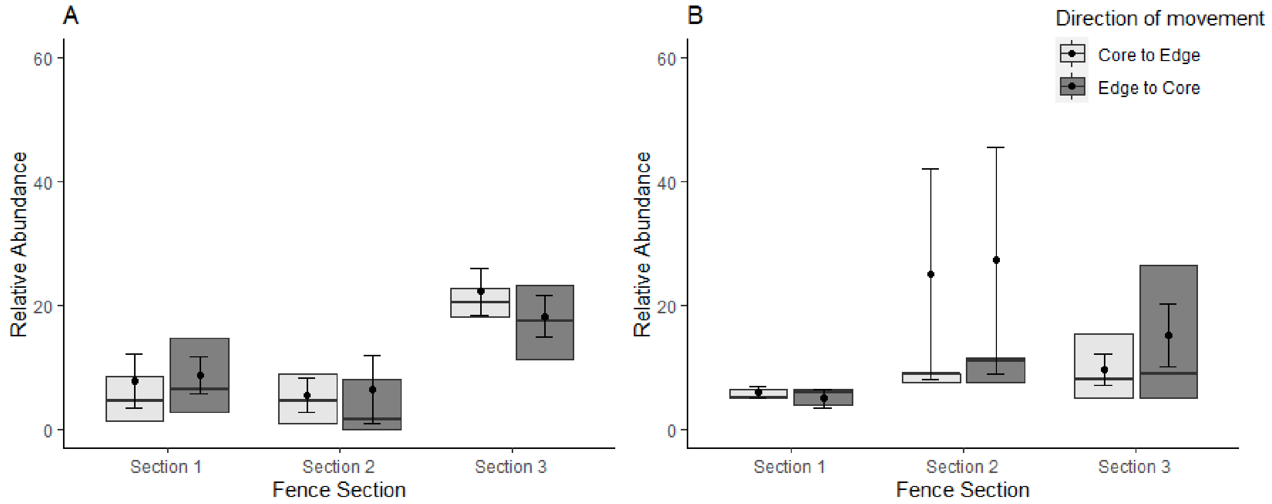


Figure 6.11: Boxplots showing the RAI of all mammal species using holes over two survey years (A = 2018 and B = 2019). Direction of movement indicates which farm type a species originated from and towards which farm type the species was moving. Shaded boxes indicate lower quartile, median (thick black line) and upper quartile for height and width, while black dots indicate mean RAI with error bars representing standard error.

Table 6.9: Results from both paired and unpaired Wilcox tests comparing total RAI and predator RAI based off hole use only abundance over two survey years (2018 and 2019). Comparisons are considered significantly different when p.adjust ≤ 0.05 and are marked with an asterisk.

Variable	**Comparison**	**All species**			**Predator species**		
		statistic	*n*	*p.adjust*	*statistic*	*n*	*p.adjust*
Direction	***Year***	**Wilcox rank-sum test (unpaired)**					
Core to edge	2018 – 2019	162	34	0.45	136	34	0.80
Edge to core	2018 - 2019	141	34	0.98	99.5	34	0.06
Year	***Direction***	**Wilcox sign-rank test (paired)**					
2018	Core to Edge – Edge to Core	115	20	0.20	7	20	0.58
2019	Core to Edge – Edge to Core	21	14	0.09	3.5	14	0.07

Overall fewer species and individuals were captured using fence holes compared to overall fence utilisation (movement along fences and using holes) (Table 6.6 and Table 6.10). Greater kudu and some rodent species did not use fence holes throughout the study period (Table 6.10, Figure 6.12 and Figure 6.12). During 2018 four species (bat-eared fox, cape fox, aardwolf and aardvark) had a higher incidence of hole use compared to simple movement along fences (without using holes) (Figure 6.12) while during 2019 this increased to eight species (bat-eared fox, cape fox, caracal, yellow mongoose, aardwolf, cape porcupine, hare spp. and rock rabbit spp.) (Figure 6.13). Hare spp. had the highest incidence of hole utilisation during 2018 and 2019 (Table 6.10). During 2018 hare spp. were captured moving more frequently from the core to the edge, while in 2019 hare spp. were captured moving more from the edge to the core (Table 6.10). Muridae were captured the least using fence holes for both 2018 and 2019 as well as Viverridae (Table 6.10). Black-backed jackal were more frequently captured moving from core to edge farms during 2018, but were captured more moving from edge to core during 2019 (Table 6.10). Caracal were only captured moving from edge to core through fence holes for both 2018 and 2019 (Table 6.10). Major deviations between mean and median values were detected during the 2019 survey on fence section 2 as a result of hare spp. captures (Figure 6.13B).

Table 6.10: Summarised results for fence hole use (only species seen using fence holes) over two years (2018 and 2019) along three sections of SKA boundary fence presented per family and species. Number of independent capture and photographic rate for each year is separated into two categories indication direction of movement through holes (C to E = core to edge, E to C = edge to core). Problematic predator species are highlighted in grey. Number of independent captures was standardised to 14 cameras. Photographic rate (also known as relative abundance index) indicates the trapping rate of a species per 30 trap nights.

Family Species	**Number of independent captures (per 14 cameras)**				**Photographic rate (RAI) (per 30 trap nights)**			
	2018		**2019**		**2018**		**2019**	
	C to E	*E to C*	*C to E*	*E to C*	*C to E*	*E to C*	*C to E*	*E to C*
Bovidae	18.20	23.80	6.00	8.00	1.30	1.70	0.43	0.57
Greater kudu *Tragelaphus strepsiceros*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Springbok *Antidorcas marsupialis*	0.00	1.40	1.00	0.00	0.00	0.10	0.07	0.00
Steenbok *Raphicerus campestris*	18.20	22.40	5.00	8.00	1.30	1.60	0.36	0.57
Canidae	56.00	35.70	45.00	53.00	4.00	2.55	3.21	3.79
Black-backed jackal *Canis mesomelas*	5.60	0.70	3.00	8.00	0.40	0.05	0.21	0.57
Bat-eared fox *Otocyon megalotis*	33.60	23.80	23.00	24.00	2.40	1.70	1.64	1.71
Cape fox *Vulpes chama*	16.80	11.20	19.00	21.00	1.20	0.80	1.36	1.50
Felidae	2.10	3.50	2.00	5.00	0.15	0.25	0.14	0.36
African wildcat *Felis sylvestris*	1.40	2.10	2.00	4.00	0.10	0.15	0.14	0.29
Small-spotted cat *Felis nigripes*	0.70	0.00	0.00	0.00	0.05	0.00	0.00	0.00
Caracal *Caracal caracal*	0.00	1.40	0.00	1.00	0.00	0.10	0.00	0.07
Herpestidae	5.60	2.80	5.00	6.00	0.40	0.20	0.36	0.43
Cape grey mongoose *Galerella pulverulenta*	1.40	2.10	2.00	3.00	0.10	0.15	0.14	0.21
Meerkat *Suricata suricata*	0.70	0.00	1.00	0.00	0.05	0.00	0.07	0.00
Yellow mongoose *Cynictis penicillata*	3.50	0.70	2.00	3.00	0.25	0.05	0.14	0.21
Hyaenidae	9.80	9.10	11.00	25.00	0.70	0.65	0.79	1.79
Aardwolf *Proteles cristata*	9.80	9.10	11.00	25.00	0.70	0.65	0.79	1.79
Hystricidae	3.50	4.90	2.00	3.00	0.25	0.35	0.14	0.21
Cape porcupine *Hystrix africaenustralis*	3.50	4.90	2.00	3.00	0.25	0.35	0.14	0.21
Leporidae	94.50	86.80	105.00	115.00	6.75	6.20	7.50	8.21
Hare spp. *Lepus* spp.	94.50	86.80	104.00	114.00	6.75	6.20	7.43	8.14
Rock rabbit spp. *Pronolagus* spp.	0.00	0.00	1.00	1.00	0.00	0.00	0.07	0.07
Mustelidae	0.00	2.80	0.00	1.00	0.00	0.20	0.00	0.07
Striped polecat *Ictonyx striatus*	0.00	2.80	0.00	1.00	0.00	0.20	0.00	0.07
Orycteropodidae	11.20	7.70	6.00	10.00	0.80	0.55	0.43	0.71
Aardvark *Orycteropus afer*	11.20	7.70	6.00	10.00	0.80	0.55	0.43	0.71
Procaviidae	0.00	2.10	1.00	2.00	0.00	0.15	0.07	0.14
Rock hyrax *Procavia capensis*	0.00	2.10	1.00	2.00	0.00	0.15	0.07	0.14
Sciuridae	1.40	0.00	1.00	0.00	0.10	0.00	0.07	0.00
Cape ground squirrel *Xerus inauris*	1.40	0.00	1.00	0.00	0.10	0.00	0.07	0.00
Viverridae	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.07
Small-spotted genet *Genetta genetta*	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.07

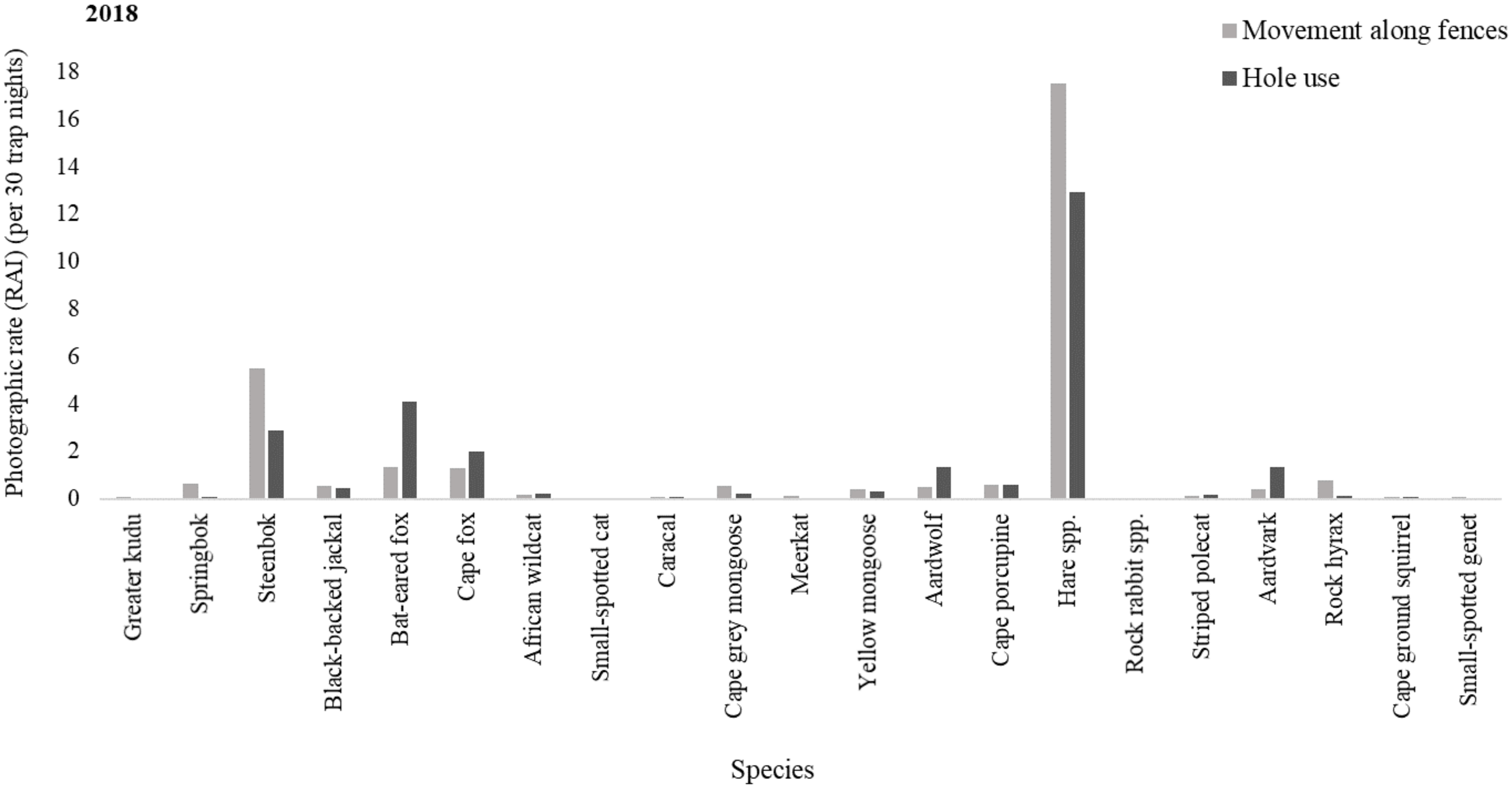


Figure 6.12: Relative abundance (per 30 trap nights) of mammal species moving along fences compared to relative abundance of species using fence holes along three fence sections of SKA boundary fence during 2018 (before the cessation of farming activities on core farms). RAI represents combination of both core and edge side of the fence.

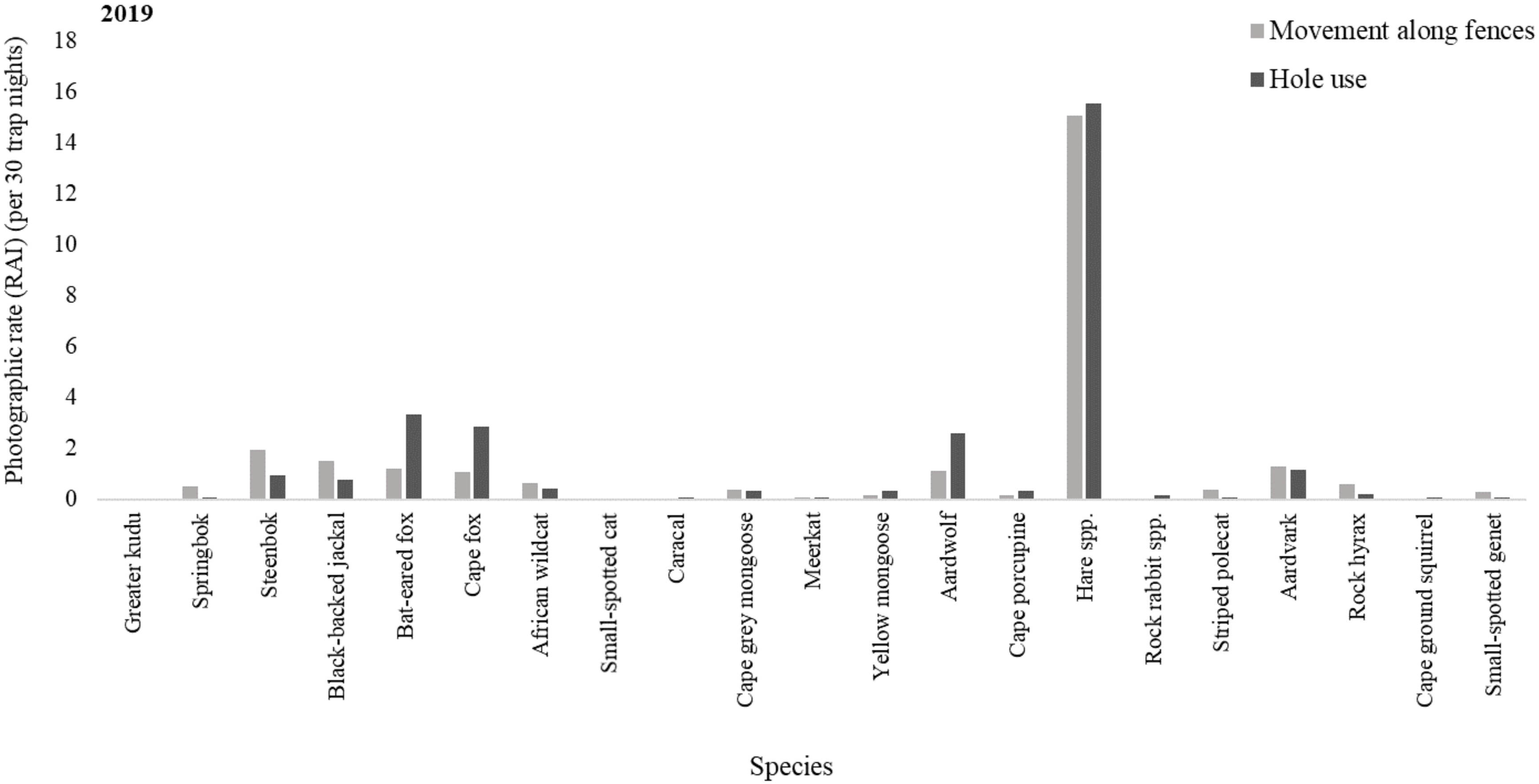


Figure 6.13: Relative abundance (per 30 trap nights) of mammal species moving along fences compared to relative abundance of species using fence holes along three fence sections of SKA boundary fence during 2019 (after the cessation of farming activities on core farms). RAI represents combination of both core and edge side of the fence.

During both 2018 and 2019 predators (jackal and caracal) moving from core farms to edge farms were only captured along fence section 3 (Figure 6.14 and App 6.2). Predators moving from edge to core farms were recorded along section 1 and 3 during 2018, and fence section 2 and 3 during 2019 (Figure 6.14 and App 6.2). Predator RAI (using fence holes) was highest along sections 3, and highest for movements from edge farms to core farms (Figure 6.14 and App 6.2). There was no significant difference in predator hole utilisation in terms of direction of movement (core to edge and edge to core) within a specific year (2018: statistic = 7, p = 0.58 and 2019: statistic = 3.5, p = 0.07), or between years when focusing on a specific direction of movement (Core to edge: statistic = 136, p = 0.80 and edge to core: statistic = 99.5, p = 0.06) (Table 6.9).

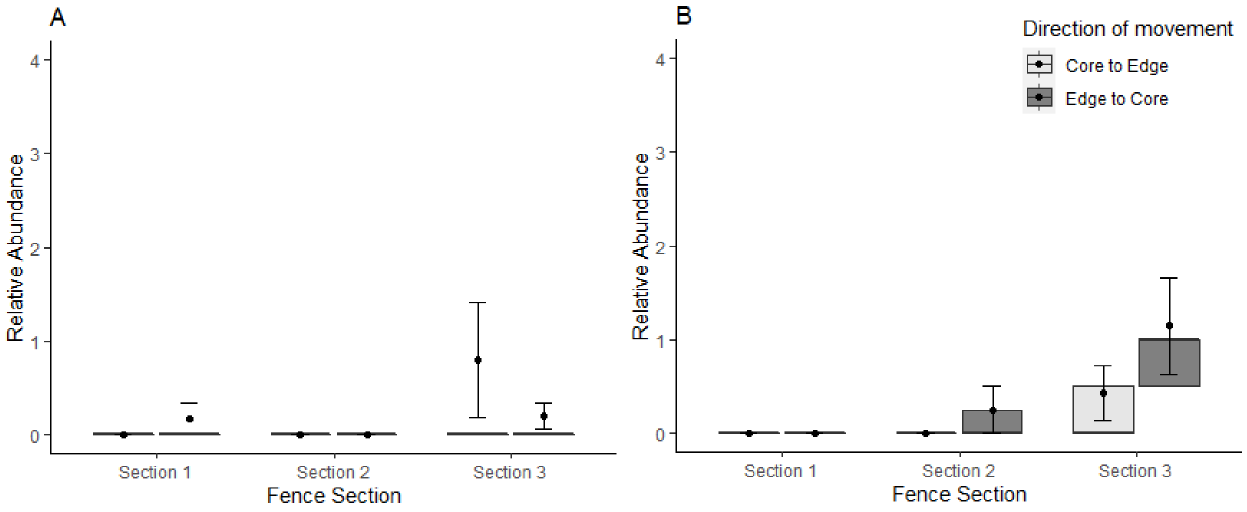


Figure 6.14: Boxplots representing RAI of predator species (jackal and caracal) using holes over two survey years (2018 and 2019). Direction of movement indicates which farm type a species originated from and towards which farm type the predator was moving. Shaded boxes indicate lower quartile, median (thick black line) and upper quartile for height and width, while black dots indicate mean RAI with error bars representing standard error.

When combining all independent hole use events across all species within a multivariate GLM there was a significant effect of fence section and year (Table 6.11). Fence section had a greater effect on number of hole use events during 2019 (p = 0.01) compared to 2018 (p = 0.03) (Table 6.11). Neither ear nor the number of holes repaired per kilometre had a significant effect on the total number of hole use events (Table 6.11). Bat-eared fox and springbok hole use were significantly influenced by fence section but not year or number of repaired holes (Table 6.12). There were no effects of year, fence section or the number of repaired holes per kilometre on the number of times both black-backed jackal and caracal used holes (Table 6.12).

Table 6.11: ANOVA table summarising statistical significance of the most parsimonious multivariate GLMs for total number of hole use events and number of hole use events per year. *p* values were calculated using 999 resampling. $^*p \leq 0.05$; $^{**}p \leq 0.001$.

Response variable	Covariate	Res.Df	Df.diff	Val (Dev)	Pr (> F)
Number of use events	Year	32	1	20.70	0.62
	Fence section	30	2	102.51	0.002**
	Repaired holes per km	29	1	25.42	0.29
Number of use events (per year)	Fence section during 2018	17	2	64.51	0.09
	Fence section during 2019	11	2	84.64	0.02*

Table 6.12: Univariate statistic from multivariate GLMs for hole use events showing which mammal species (with specific focus on predator species) contributed significantly to changes in number of use events between different covariates (year, section and repaired holes per km). Dev = deviance explained by each species. $^*p \leq 0.05$; $^{**}p \leq 0.001$.

Species	Year		Fence section		Repaired holes (per km)	
	Dev	*p*	*Dev*	*p*	*Dev*	*p*
Black-backed jackal *Canis mesomelas*	1.74	0.98	8.60	0.27	0.06	1.00
Caracal *Caracal caracal*	0.79	0.99	3.08	0.95	0.01	1.00
Bat-eared fox *Otocyon megalotis*	0.08	1.00	12.99	0.04*	0.15	1.00
Springbok *Antidorcas marsupialis*	0.07	1.00	13.33	0.04*	0.00	0.99

nMDS ordination plots showed significant clustering of hole use events for fence section 3, while fence section 1 and 2 were clustered together (Figure 6.15). There was a strong separation of fence sections along a repaired hole per km gradient (Figure 6.15). Fence section 3 clustered at lower repaired hole per km values, and section 2 tended more towards higher numbers of repaired holes per km (Figure 6.15).

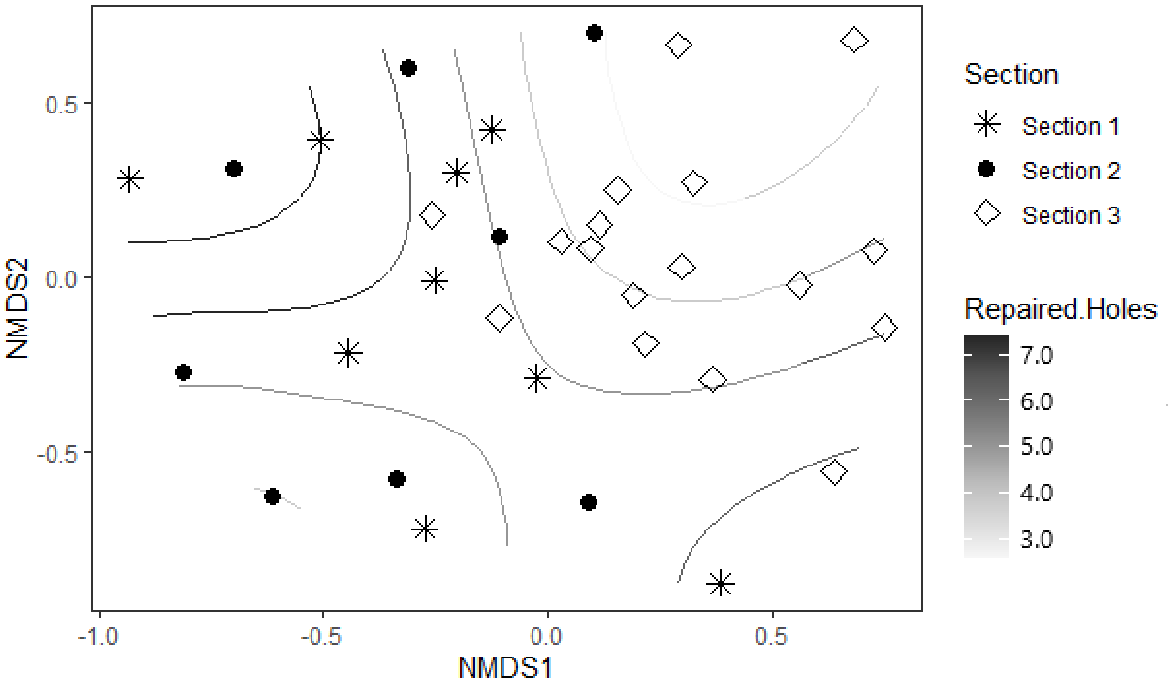


Figure 6.15: nMDS based on Jaccard-index of similarity of number of hole use events of all 34 camera trapped holes across three SKA boundary fence sections for two survey years (2018 and 2019), overlaid with a repaired holes per km surface (grey contour lines) (Stress value = 0.23). Fence section is indicated by distinct symbols.

Discussion

Despite extensive fencing across the Karoo, there has been very little research on how successful it is at restricting the movement of both domestic and wild mammals (Cozzi *et al.* 2013, Smith *et al.* 2020a). Similarly, there is little research investigating how fence condition (quality) and maintenance influences which wildlife species move along fences and how often they move through holes in fences between PAs and farmland (Cozzi *et al.* 2013, Pirie *et al.* 2017). Given fences are the most pervasive non-lethal method for separating potential predators and competitors from livestock in South Africa (Hayward & Somers 2012) it is vital to understand their efficacy, particularly when farmers are forced to live adjacent to a protected area. Most farmers consider fences to be an essential first line of defence against livestock depredation (du Plessis *et al.* 2018) but they also perceive PAs as a source of potential predators despite being separated from them by a fence. Presumably this contradiction pertains to how well such fences are maintained with the assumption that routine patrolling and closing of holes along fence lines constitutes essential predation management by farmers who believe in the role of ‘good’ fences in mitigating livestock losses.

Fence condition and permeability

Fence structure (height, length between posts and placement of rocks along the apron) along the border between the SKA core farms and edge farms was similar, but quality was highly variable with significantly more open versus repaired holes along section 3 of the fence line. By contrast section 2 had a higher number of repaired holes and a lower number of open holes suggesting more effort on both monitoring and repairing. This may be explained by the edge farmer having permanent employees on his farm compared to section 3 whose labour was more ephemeral. Importantly section 3 had the highest species richness of mammals moving along it and using the holes (Figure 6.12 and 6.13) in both 2018 and 2019. Additionally, the ratio of repaired versus open holes decreased from 2018 to 2019 along section 3, suggesting a decline in hole maintenance, while section 1 improved to a similar level to what was the best maintained section viz., section 2 (Figure 6.6). The improvement in fence maintenance along section 1 may be explained by the increased presence of workers and farmers who began renting on edge farm 1 during 2019 (see Chapter 2). Despite this all sections had open holes in both study years confirming the theory that agricultural fences within the Karoo should be considered semi-permeable as opposed to full exclusion barriers (Connolly *et al.* 2009, Pirie *et al.* 2017). The degree of permeability is therefore primarily determined by the initial fence construction and thereafter its' condition linked to routine maintenance (Connolly *et al*. 2009, McInturff *et al.* 2020).

Shifts in species richness relative to fence section and year

Fence camera trap surveys showed that 60% of all mammal species recorded on farms (including small mammals) interacted with fences, either moving along them as a linear structure or moving through them using holes. While fence surveys were not matched to the summer months of the extensive camera trap surveys the period between a fence survey and the corresponding camera trap survey (six months prior to a fence survey) was relatively short and slow community change seen within the Karoo suggested that the mismatch in timings would not have an effect on comparisons made between the surveys (Dean & Milton 1999, Hoffman *et al.* 2018). It should however be noted that while sampling mammal communities at fence holes can provide sufficient data in less time, fences were not an accurate representation of all habitats on a farm. This was evident in Chao1 estimates and rarefaction curves were species richness estimates indicated that not all species present in the area were detected within the fence sampling period.

Between 50 and 60% of all mammals detected overall on farms were recorded using fence holes. Fence permeability is determined by two main factors, fence conditions and what species are able to move through fences (Connolly *et al.* 2009, Pirie *et al.* 2017). Within the SKA region of the Karoo the majority of mammal species present are of small to medium body size with very few species being considered large (e.g., greater kudu). Consequently, most of the mammals detected along the fences are of a size that can use the holes to move between farms. While camera traps showed a reduced number of species using holes compared to the overall richness seen along fences, almost all species recorded along the fence used at least one hole along the three sections during the survey period. Only one species was seen not to use fence holes at all during the survey period, namely greater kudu. This is likely due to the fact that kudu are jumping antelope and fence height was relatively low compared to other types of fences aimed at containing jumping species. Contrary to my original prediction (P1) poorly maintained fences (e.g., section 3) did not have a higher species richness either moving along the fence or through the holes. Furthermore, the removal of sheep on core farms did not result in more species using holes or moving from core to edge farms to either seek food (e.g., predators seeking livestock) or water (e.g., obligate drinkers seeking artificial water points) as predicted by most farmers (Terblanche 2020). The lack of a change in wild mammals either adjacent to or moving through fences aligns with previous results (see Chapter 4) in which the change in land use including the removal of sheep did not significantly impact mammalian species richness within the time frames of the study.

Mammal interaction with fences and shifts in fence utilisation

Farm type (core side of the fence versus edge) and year did not significantly impact overall mammal species RAI along fence section 1 and 2. This aligned with results from extensive grid camera surveys which showed that overall species RAI did not change between farm types or between survey years (see Chapter 4). Results did, however, provide evidence that species abundance along fences was significantly influenced by fence quality supporting (prediction 2, P2). Fence section 3 was determined to have low fence quality (poor condition) and during the 2018 survey (before farming activities were terminated) this section of the fence had significantly higher overall species interactions compared to section 1 and 2 (based on relative abundance as opposed to richness which did not change significantly between sections). Therefore, while there were a similar number of species interacting with fences at each section the number of individuals at each section differed. This was particularly evident on the core side of the fence, where species were more abundant than the edge side.

Changes in species abundance between fence sections may be a result of how each section is managed. Section 1 and 2 were considered well maintained fences, with the number of repaired holes outnumbering open holes. One can assume with improved fence maintenance the presence of humans was higher along these sections. Camera trap data reflected this trend as over the two survey years there were seven incidents of human activity along section 1 (low – medium maintenance), 23 incidents along section 2 (high maintenance) and only four incidents of human activity along section 3 (low maintenance). Most mammals living in a landscape where they overlap with humans are known to avoid areas with high human presence (Whittaker & Knight 1998, Festa-Bianchet & Apollonio 2003, George & Crooks 2006, Ünal *et al.* 2020). This is reflected in the results were fence sections that were better maintained, and hence likely had higher human presence linked to patrolling and maintenance activities had lower species abundance. This suggests that the activities associated with fence maintenance are driving down the number of species observations. A similar trend was seen during 2019, however the differences in relative abundance between fence sections were not significant. A likely cause for this result is the very high abundance of hare species that were detected along fence section 2 during the 2019 survey, while the abundance of all other species decreased. The decrease in the relative abundance of most species during 2019 was consistent with results from the farm level camera trap surveys which suggested that persistent drought conditions had a negative overall impact on the abundance of all wild animals in the region (see Chapter 4) (Davimes *et al*. 2017, Levy *et al.* 2018, Abraham *et al.* 2019, Gedir *et al.* 2020).

Interestingly predator species that pose a significant risk to livestock (i.e., jackal and caracal) did not follow the same patterns as other species seen along fences. Predator RAI only increased significantly on the edge side of fence section 3. These results suggest that like other mammal species generally year and farm types did not influence changes in predator abundance, however unlike other mammals there was no significant influence of fence quality on the likelihood that more predator individuals would interact with fences. After farming activities were terminated on the core farms the abundance of predators seen on either side of the fence did not change, suggesting that the cessation of farming activities and in particular sheep presence or absence did not influence the abundance of predators along fences. Overall, there was no clear link between overall predator abundance on a farm and predator abundance along fences. This suggested that increases in predators along fences cannot be explained by changes in relative abundance of predators within an area. Predator abundance was generally higher along fences than seen overall on each farm which may be the result of a bias in detection between random camera trap surveys (i.e., 2 x 2 km grid) and targeted camera trap surveys (e.g., along roads, fences, water holes). Jackal are known to travel along roads and other linear structures to move through their territory (Hayward & Hayward 2009). Roads were often constructed along boundary fences to provide access by landowners, suggesting that these areas may be biased towards the detection of jackal. Furthermore, extensive grid surveys carried out during the same period saw a higher detection of jackal at cameras placed along the edge of a farm compared to cameras on the farm interior, providing support for the argument of a bias in detection associated with trapping close to linear structures (see Chapter 5).

Hole utilisation and direction of movement

The RAI of mammals using holes was markedly lower than the RAI detected along fences. Despite this almost every mammal species that was detected along fences used holes (Table 6.10) including larger herbivores (springbok *Antidorcas marsupialis*) as well as larger insectivores (aardvark *Orycteropus afer* and aardwolf *Proteles cristata*), the latter which are known to use larger holes to traverse fence lines (Stullken & Kirkpatrick 1953, Pirie *et al.* 2017).

Overall hole use (by all species) was higher along fence section 3 compared to section 1 and 2 during the 2018 survey. This matched the patterns of abundance along the fence with more species detected along fence section 3 compared to section 1 and 2. Again, this supports the prediction (P2) that fence condition influences the abundance of mammals' movement along fences and ultimately hole utilisation. More open holes indicate lower maintenance and hence reduced human presence favouring movement along and across farm fences. There was a slight overall increase in hole use along all three sections between 2018 and 2019 which mirrored the slight increase in species RAI along fences seen in 2019. A possible explanation for these increases may be the impact of increased drought conditions during 2019 (see Chapter 4). As drought conditions increased animals likely increased the distance travelled to find limited resources. These patterns were more pronounced when focusing on predator hole utilisation which was highest along section 3 for both survey years. However, contrary to predictions the direction of movement by all mammals (P3) and predators specifically (P4) was not significantly skewed towards a farm with livestock and more artificial water.

Predators were equally likely to move from core to edge as they were to move from edge to core. It may be argued that the lack of significant differences between the direction of movement during 2019 is the result of predators sleeping on core farms but hunting on edge farms (where sheep are present), resulting in equal directional movement between farms. In the absence of individually identified individuals or the use of GPS collars to remotely track movement it is not possible to support or refute this theory using the available data. Irrespective, the RAI of predators both moving along fences and through holes is extremely low despite the constant presence of holes and if predators are using the core as a refuge and attacking livestock on edge farms then there are very few of them doing so.

Contrary to my predictions (P4) the cessation of farming activities did not influence hole utilisation by predators or the direction of movement. Despite the RAI of predators along fence section 1 and 2 being relatively high compared to the RAI of predators detected on farms, hole utilisation by predators was nevertheless extremely low (in some cases no predators used fence holes). Many farmers set traps along fence lines and particularly within holes (du Plessis *et al*. 2018) and tend to stage dead predators on or near fences (Figure 6.16) (Swanepoel 2016), however jackals are renowned for learning to avoid both traps and human interference more generally. This low rate of hole use may explain why none of the results from the GLMs exploring hole utilisation were significant, and why only section 3 which had the least maintenance had a higher RAI of predators.

Several studies have suggested that for predator proof fencing to be effective maintenance must be rigorous and regular (Pickard 2007, Pirie *et al*. 2017, Du Plessis *et al.* 2018). Pickard (2007) showed that dingoes were most successfully excluded from sheep production zone where fence maintenance was high. Pirie *et al.* (2017) found direct evidence that hole utilisation by wild animals increased with decreasing fence condition (determined by number of holes in fence).

The differences in fence quality between three sections sampled along the same boundary fence highlights the importance of fence maintenance being coordinated to ensure equal effort on both sides of the fence line. It has been suggested that SANParks will construct a new much higher fence along the core/edge farms boundary and both the design and maintenance of the fence should exceed the current fence line to limit the movement of wildlife onto edge farms and livestock onto the core.

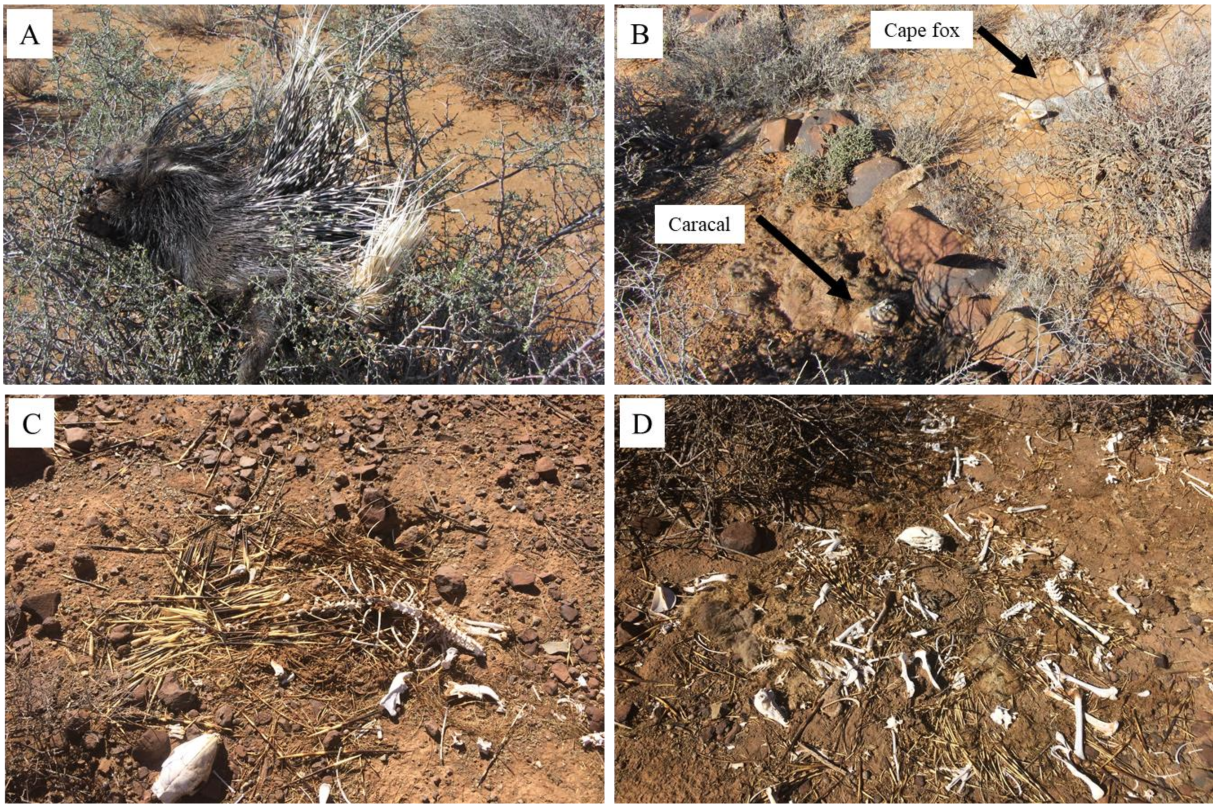


Figure 6.16: Incidence of 'problem' mammal species found dead along fence section 1 (top images) and section 3 (bottom images) as a result of trapping or hunting by humans. Animals were often staged on top of bushes (A – cape porcupine *Hystrix africaenustralis*), near old holes (B - caracal *Caracal caracal* and cape fox *Vulpes chama*) or placed in one common area near fences (C – multiple porcupine skeletons, and D – pile of black-backed jackal *Canis mesomelas* and cape fox bones) (© Michelle Blanckenberg).

Conclusion and implications for future fence management

These findings suggest that currently the SKA boundary fence should be classified as semi-permeable as there is at least one open hole along every fence section sampled. However, regular fence maintenance did reduce the movement of mammal species between farms, especially jackal and caracal, despite occasional open holes. Edge farmers are thus correct in suggesting that good quality fences that are well maintained are an important part of managing livestock depredation. Consequently, improved relationships between the SKA and the edge farmers begins with the quality and level of maintenance of the boundary fence that separates the two land uses. A constant source of discontent expressed by edge farmers with whom we worked was the failure of the SKA to upgrade the boundary fence and routinely patrol it for holes. While we were not privy to the original agreements and could not verify the farmers claims it was apparent that fence quality varied significantly with section of the fence suggesting the absence of a coordinated approach with maintenance being left to individual edge farmers. It has been suggested that SANParks will commence with a more substantive fence that includes both anti-dig and anti-climb features in addition to more routine patrols and maintenance. It is my perception that this will be the single most important contribution to reducing conflict between edge farmers and the SKA.

Despite the low abundance of predators on both core and edge farms (Chapter 4), the low abundance of predators both moving along fences and using holes and the absence of any directional bias in direction of movement (i.e., core to edge), farmers nevertheless perceive fences as the first and most important step in limiting livestock depredation (Terblanche 2020). It will require more data than that presented here and by Drouilly *et al.* (2018) to convince farmers that being neighbours with a PA does not equate to higher rates of livestock depredation. It is my recommendation therefore that these fence surveys are conducted every two years to monitor changes in wildlife movement along and through this barrier and the proposed upgrades. It is only through long-term monitoring that we will understand the importance of fences around PAs to limiting wildlife movement onto farms and domestic livestock into PAs. My findings suggest however that increased monitoring and hole repair still allows some species to move through holes but influences predator hole utilisation, providing a possible win-win scenario. This scenario however relies heavily on the buy in from all stakeholders to invest time and money into sustained fence maintenance and monitoring.

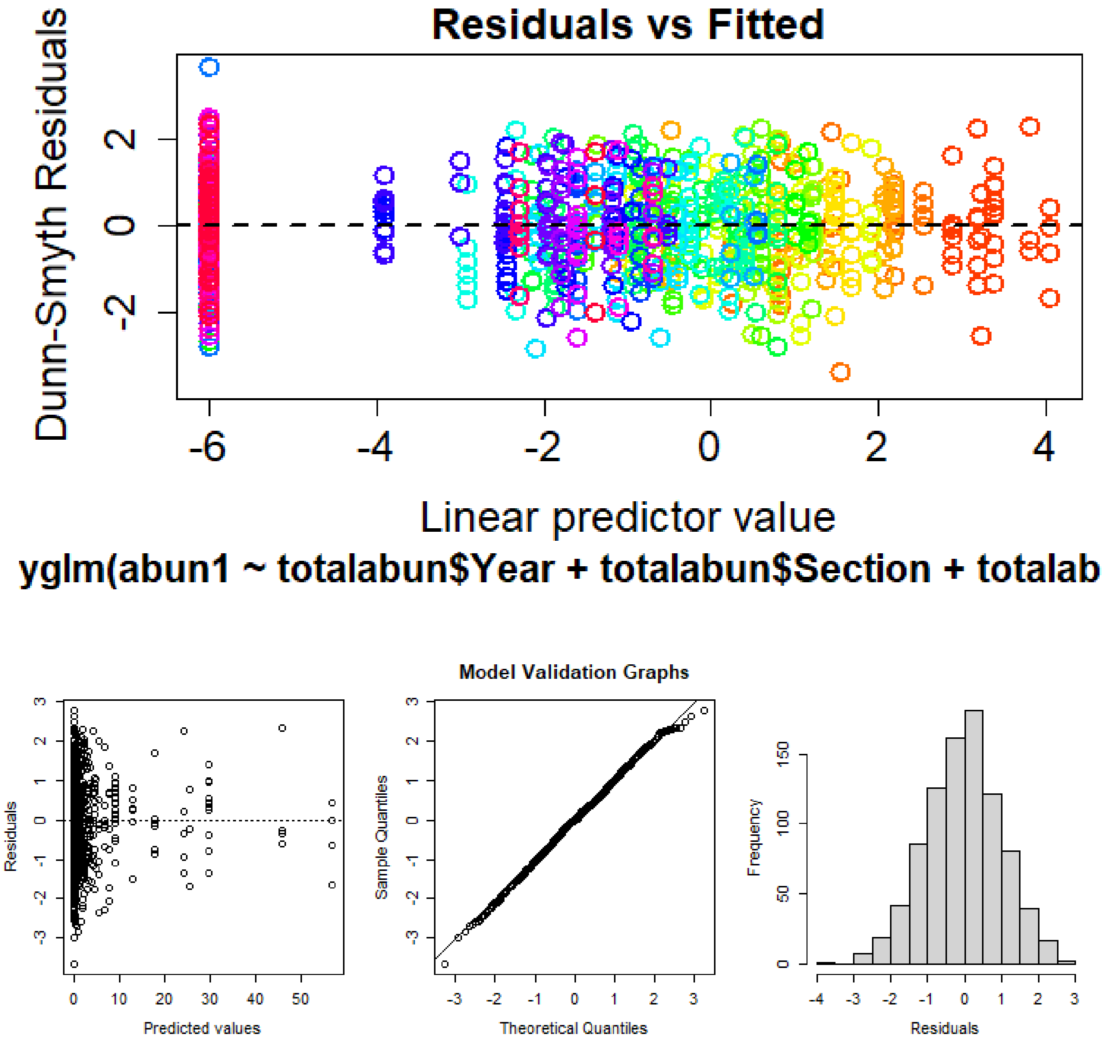
Appendix 6: Mammal utilisation of fences appendices

App 6.1: Summarised results for black-backed jackal and caracal seen along fences during two survey years (2018 and 2019) along three sections of SKA boundary fence (core and edge side). Photographic rate (also known as relative abundance index) indicates the trapping rate of a species per 30 trap nights.

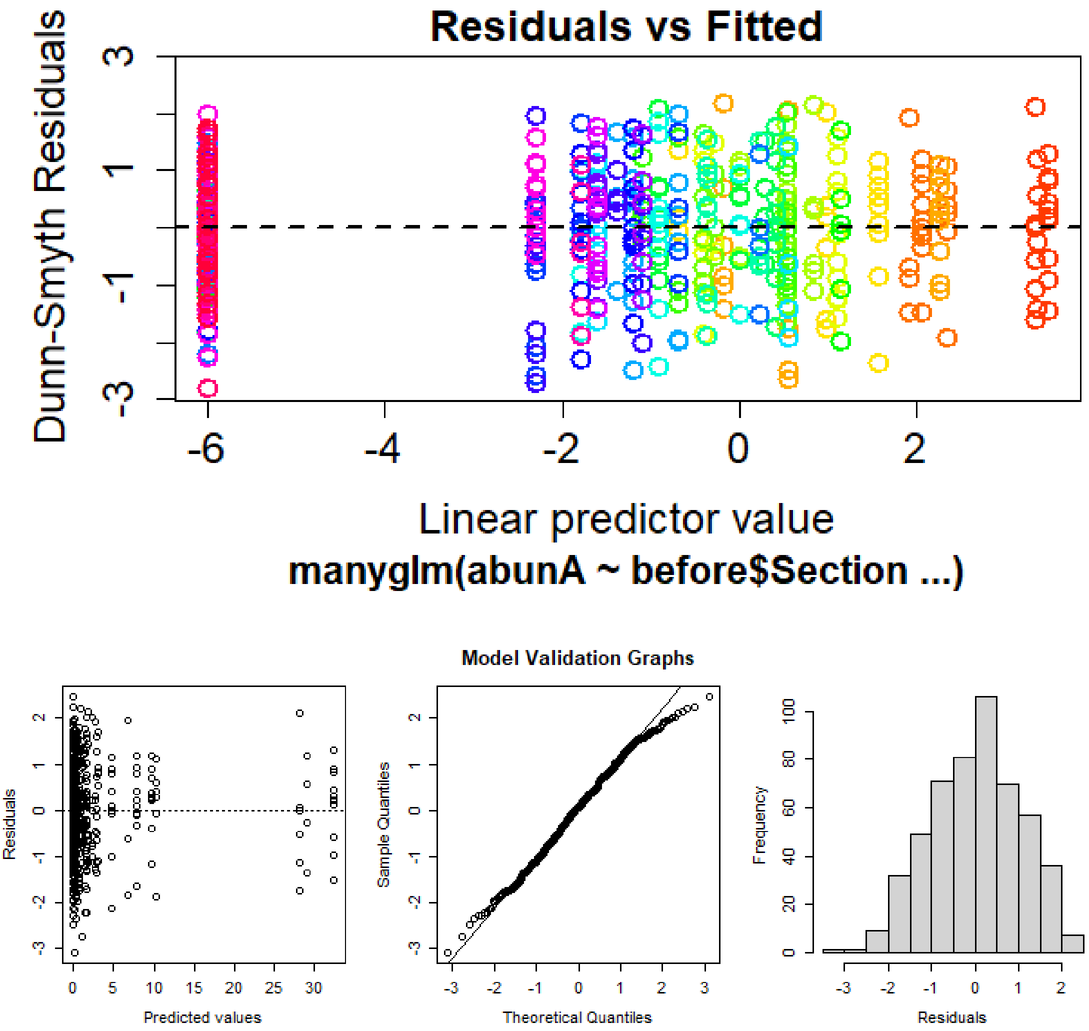
Year	**Section**	***Core side***		***Edge side***	
		Number of Captures	*RAI*	*Number of Captures*	*RAI*
2018	Section 1	2	0.33	1	0.16
	Section 2	1	0.25	2	0.50
	Section 3	15	1.50	3	0.30
	Combined sections	**18**	**0.90**	**6**	**0.42**
2019	Section 1	3	1.00	1	0.33
	Section 2	1	0.25	1	0.25
	Section 3	15	2.14	12	1.71
	Combined sections	**19**	**1.35**	**14**	**1.00**

App 6.2: Summarised results for black-backed jackal and caracal using fence holes over two years (2018 and 2019) along three sections of SKA boundary fence (core and edge side). Photographic rate (also known as relative abundance index) indicates the trapping rate of a species per 30 trap nights.

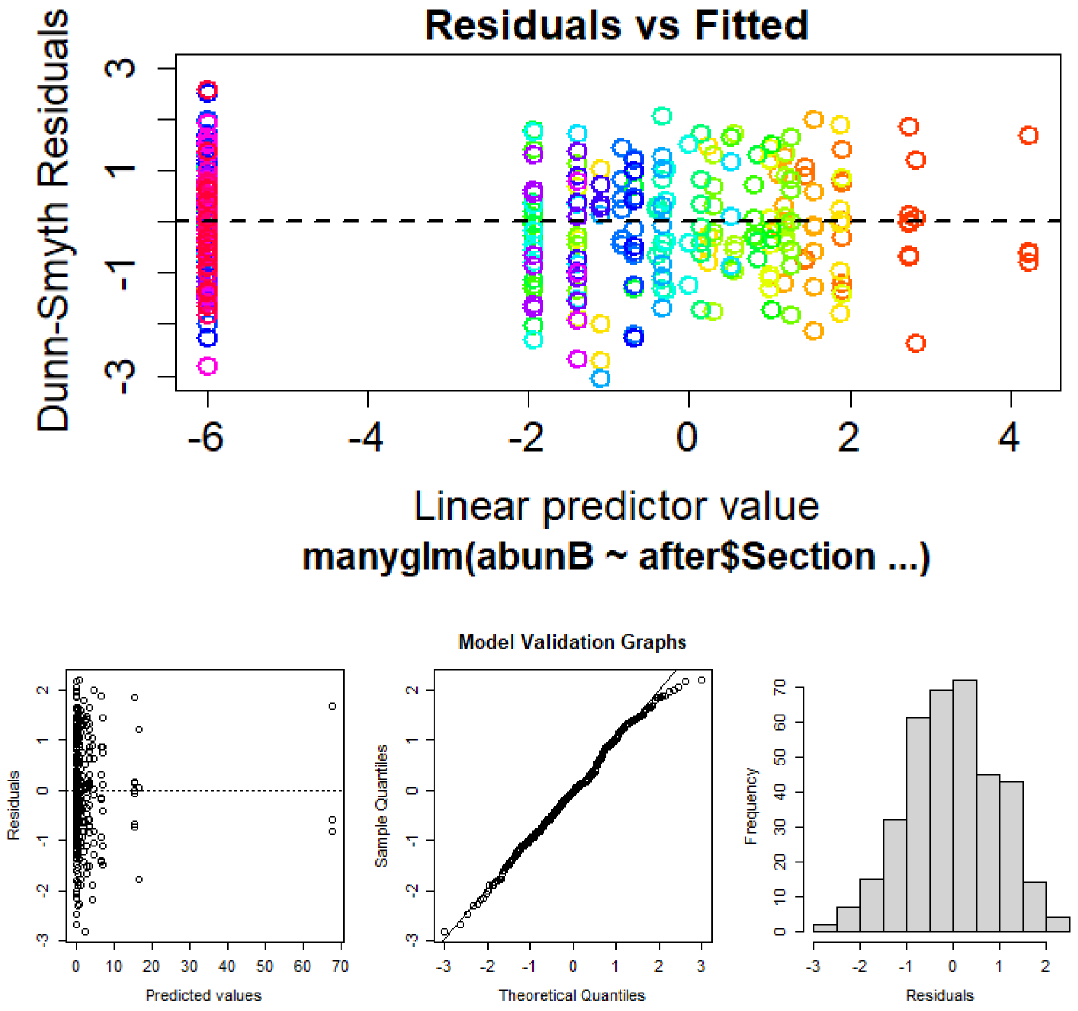
Year	**Section**	***Core to Edge***		***Edge to Core***	
		Number of Captures	*RAI*	*Number of Captures*	*RAI*
2018	Section 1	0	0	1	0.16
	Section 2	0	0	0	0
	Section 3	8	0.80	2	0.20
	Combined sections	**8**	**0.40**	**3**	**0.15**
2019	Section 1	0	0	0	0
	Section 2	0	0	1	0.25
	Section 3	3	0.42	8	1.14
	Combined sections	**3**	**0.21**	**9**	**0.64**



App 6.3: Model validation graph for top ‘number of fence hole use events’ model showing predicted versus fitted residuals (top graph), residual versus predicted values spread (bottom left), sample versus theoretical quantile spread (bottom middle) and distribution of data (bottom right).



App 6.4: Model validation graph for top 'number of fence hole use events in 2018' model showing predicted versus fitted residuals (top graph), residual versus predicted values spread (bottom left), sample versus theoretical quantile spread (bottom middle) and distribution of data (bottom right).



App 6.5: Model validation graph for top 'number of fence hole use events in 2019' model showing predicted versus fitted residuals (top graph), residual versus predicted values spread (bottom left), sample versus theoretical quantile spread (bottom middle) and distribution of data (bottom right).

CHAPTER 7

SYNTHESIS

Typical Karoo landscapes at sunset (top and middle) with dorper sheep (bottom) taken in the SKA region of the Karoo (© Michelle Blanckenberg).

The impacts of livestock on a landscape can range from drivers of desertification, to competitive exclusion of wild herbivores (Kraaij & Milton 2006, Tessema *et al.* 2011, Hempson *et al.* 2017, Hoffman *et al.* 2018, van der Merwe *et al.* 2018) as well as, acting as an abundant food source for native predators (Zimmermann *et al.* 2005, Holmern *et al.* 2007, Gusset *et al.* 2009, Kinnaird & O'Brien 2012, Perry *et al.* 2020). The interactions are complex and often generate conflict amongst diverse stakeholders on how best to mitigate negative interactions between livestock and the landscape (Treves & Kananth 2003, Graham *et al.* 2005, du Plessis *et al.* 2018). There is little doubt that agriculture has fuelled both global and local extinctions of fauna and flora (Madhusudan 2004, Green 2005, Drouilly & O'Riain 2019). However, there is also a growing realisation that extensive livestock farming in semi-arid rangelands is compatible with significant levels of local biodiversity and thus private landowners are important stakeholders for meeting global biodiversity targets (de Leeuw *et al.* 2001, O'Brien *et al.* 2003, Krausman *et al*. 2009, Schieltz & Rubenstein 2016). Realising this objective requires a better understanding of the impacts of different agricultural practices on biodiversity and natural ecosystem functions (Madhusudan 2004, Riginos *et al.* 2012).

It was my goal to contribute to the dearth of scientific data on not only the impacts of small livestock farming on wildlife in a semi-arid range land of South Africa but how a change to protected area status will influence aspects of mammalian abundance and community structure. In the absence of baseline data prior to the onset of farming, most studies investigating the impacts of livestock on biodiversity have compared active farmland with land used historically for farming but are now protected (where livestock is naturally excluded) (e.g., Drouilly *et al*. 2018a and Drouilly & O'Riain 2019). The establishment of a protected area associated within the SKA radio telescope core area provided a unique opportunity to use a BACI design for understanding how the cessation of small livestock farming within the semi-arid Karoo might influence both the vegetation and native wildlife. In this chapter I aim to contextualise the key findings of my study with the existing literature at a local and international scale in addition to discussing how the findings of this thesis may contribute to the importance of protected areas and private landowners in semi-arid rangelands to meeting national and international biodiversity targets.

An important baseline database of vegetation and mammals in the SKA

While the intervention of shifting land use from farmland to a protected area did not result in many significant changes in vegetation and mammal populations this study nevertheless provides the largest survey of small and medium to large mammals in the Northern Karoo region of South Africa. This region was classified as data deficient in the Strategic Environmental Assessment (SEA) (Todd & Henschel 2016, van der Merwe 2020). My data provide a critical baseline dataset on vegetation cover and mammal richness and relative abundance within the SKA region of the Karoo for long term monitoring of change linked to both land use and climate.

Within the SKA protected area there has only been one study that looked at vegetation cover and while this study provided valuable baseline data for the SKA, the study only looked at a single farm unit (Losberg) (van der Merwe 2020). The results from my study provided a much broader assessment of vegetation cover across multiple farms and habitats. Results from my study aligned with those recorded in the van der Merwe (2020) study where shrubs were dominant across the landscape (specifically *Rhigozum trichotomum, Salsola tuberculata* and *Salsola aphylla*). Before the cessation of farming activities, and similar to other studies investigating the impact of grazing on Karoo vegetation, there was a dominance of unpalatable spinescent species with little grass and forb cover (Hoffman 2000, Kraaij & Milton 2006, O'Connor *et al.* 2014, Hempson *et al.* 2017, Hoffman *et al.* 2018, van der Merwe *et al.* 2018). Results from van der Merwe (2020) saw increased cover of palatable forb and grass species largely due to the long-term exclusion of livestock from the two original farms (Losberg and Meysdam) that were purchased as part of the core area (more than seven years ago, see Chapter 2). While results from the 2019 vegetation surveys saw an increase in both forb and grass cover on core farms, these trends were statistically non-significant, and only forb cover seemed to significantly influence the overall changes in vegetation between 2017 and 2019. These results aligned with other studies within the Karoo which showed changes in vegetation were only statistically significant after long periods (e.g., > 20 years) of recovery (Boardman *et al.* 2010, Rahlao *et al.* 2008, van Rooyen *et al.* 2015, McManus *et al.* 2018). Results from vegetation surveys provided the most definitive evidence that the timescale over which the study occurred was too short for noticeable landscape recovery (van der Merwe *et al.* 2018).

The eight small mammal taxa recorded during the study were typical arid region generalists (e.g., *Gerbilliscus paeba* and *Desmodillus auricularis*) recorded in other studies throughout the Karoo (Kerley 1992a, Eccard *et al*. 2000, Bösing *et al.* 2014, Aboul-Hassan 2020). Small mammal richness was however lower than previous studies in the southern Karoo with noticeable absence of both the pygmy mouse (*Mus minutoides*) and pouched mouse (*Saccostomus campestris*) (Aboul-Hassan 2020). These lower measures of richness are expected for the drier northern regions (van Deventer & Nel 2006).

Small mammal abundance was similar to that seen in Eccard *et al.* (2000) and, while low, are nevertheless expected for semi-arid to arid environments (Joubert & Ryan 1999, Hoffman & Zeller 2005, Muck & Zeller 2006, Bösing *et al.* 2014). Todd & Henschel (2016) predicted at least 10 small mammal species (excluding bats and cryptic rodent species within rocky habitats) within the SKA protected area. This study provided the first evidence of the extent and richness of these cryptic species. Most notably this study provided valuable genetic information on cryptic *Micaelamys* spp. (*Micaelamys namaquensis* and *Micaelamys granti*) and Macroscelididae species (*Macroscelides proboscideus*, *Elephantulus rupestris* and *Elephantulus pilicaudus*) some of which were not previously thought to extend so far north into the Bushmanland biome (Main *et al.* 2019). Other small mammal species predicted to occur but not captured within the region included Karoo bush rat (*Otomys unisulcatus*) and subterranean taxa (Family Bathyergidae*)*, both of which are seldom captured using Sherman live traps (Harkins *et al.* 2019, Motro *et al.* 2019, Thomas *et al.* 2020). Personal field observations however, confirmed that there was evidence that these species were present, (e.g., bush rat nests, observations from farmers and mole-rat mounds) and highlights the importance of an additional small mammal survey utilising multiple trapping techniques.

Species richness of medium and large mammals within the SKA protected area and surrounding farmland (n = 27) was similar to other studies within the Karoo (Mann 2014, Drouilly *et al.* 2018, Woodgate *et al.* 2018). This however was less than the predicted 40 species by Todd & Henschel (2016), who suggested species such as brown hyena (*Hyaena brunnea*), leopard (*Panthera pardus*), honey badger (*Mellivora capensis*), eland (*Taurotragus oryx*), common duiker (*Sylvicapra grimmia*) and riverine rabbit (*Bunolagus monticularis*) would be present, but none of which were recorded in the 6 251 independent photographs taken in my study. Many of these species have been recorded in other Karoo studies suggesting their potential occurrence in the SKA (Collins & du Toit 2016, Drouilly *et al.* 2018a, Woodgate *et al.* 2018), but most studies were on populations in the Southern Karoo which is more mesic and mountainous than the SKA region. The lack of detection of honey badger and common duiker was surprising, especially because of their wide reported distribution within South Africa (including the SKA region) and their detection in other Karoo studies (Woodgate *et al.* 2018). However, honey badgers were similarly not detected by Drouilly *et al.* (2018a). The drier climate of northern Karoo systems may explain why these species were absent from the study, compounded by the impact of extensive livestock production.

The relative abundance of species was similar to those seen in other Karoo farmland areas (Yeo *et al.* 1993, Blaum *et al.* 2009, Georgiadis *et al*. 2007, Kiffner *et al*. 2015, Schieltz & Rubenstein 2016, Woodgate *et al*. 2018) for all three survey years, despite the establishment of the protected area in 2018 and 2019. While other studies suggest that relative abundance of mammals is typically higher in protected areas (Kinnaird & O'Brien 2012), the lack of change on core farms over the study period confirms the idea that due to slow recovery within the area the three-year time scale combined with drought conditions during the study may have precluded detecting a measurable effect of the intervention (Prins 2000, Mishra *et al.* 2002). Bat-eared fox, yellow mongoose, cape fox, small-spotted genet and hare spp. are all species recorded to have higher abundance on farmlands where vegetation cover has decreased through livestock grazing (Blaum *et al.* 2009, Kurberg 2005, Kamler & Macdonald 2014, Drouilly 2019). This was supported by my findings where bat-eared fox, cape fox and hare spp. all have high RAIs compared to other species across all farm types and survey years. These species prefer drier open habitats (Blaum *et al.* 2009, Kurberg 2005, Kamler & Macdonald 2014, Drouilly 2019) which was reflected in the results of my vegetation surveys which revealed low vegetation cover relative to bare ground in several areas (Chapter 3, Table 3.5A). Lagomorph RAI decreased on core farms over the survey period despite slight increases (albeit non-significant) in grass cover and significant increases in grass height (a preferred habitat characteristic, Farmer 2006). The decrease in lagomorph RAI was similarly observed on edge and control farms, suggesting these species were more impacted by overall region wide drought than shifts in grass characteristics (more cover and significantly higher grass on core farms). Overall relative abundance of species on core farms consistently reflected patterns of abundance seen on farmlands rather than protected areas.

Slow recovery in Karoo systems

Small isolated protected areas within the Karoo, similar to the new SKA protected area, exhibit key differences in vegetation and mammal communities compared to the surrounding farmland (Hoffman *et al.* 2009, Drouilly 2019). Vegetation richness and cover for example is often higher in protected areas compared to farmland owing to the lack of overgrazing by domestic herbivores (Hoffman *et al.* 2009, van der Merwe 2020). On the other hand, several studies comparing mammal communities between farmland and protected areas highlighted that species richness may not change significantly (Kinnaird & O'Brien 2012, Mann 2014, Kiffner *et al.* 2015, Drouilly *et al.* 2018a) between the two land uses but community structure and abundance does shift (Drouilly 2019). While protected areas may never return to a pre-colonisation state (due to the eradication of large migrating mega herbivores and associated carnivores) (Morris 2018), one would expect a protected area within the Karoo to have increased vegetation cover and richness (Hoffman *et al.* 2009, van der Merwe 2020), as well as increased mammal abundance with shifts towards a more evenly spread community structure (Drouilly *et al.* 2018a). This ecological state however was not observed within the new SKA protected area, suggesting recovery of the vegetation and mammal communities, to match what was expected for a protected area in the Karoo, was not recorded during the study period.

The lack of significant changes in vegetation and small mammal populations (Chapter 3) is likely explained by the slow recovery typical of the semi-arid landscapes that have been subject to prolonged anthropogenic impacts (Boardman *et al.* 2010, Rahlao *et al.* 2008, van Rooyen *et al.* 2015, McManus *et al.* 2018). While there were slight increases in the abundance of forb species on core farms (Chapter 3, Table 3.23) these changes were unlikely to enable bottom-up changes to higher trophic levels. Vegetation in the core was allowed to recover passively from decreased livestock herbivory for roughly 18 months before the repeated surveys. However as with other semi-arid systems (Weber *et al.* 1998, Diouf & Lambin 2001, Rahlao *et al.* 2008, Hoffman *et al.* 2009) this period was too brief to allow for significant changes and likely further suppressed by the serious and prolonged drought conditions that prevailed throughout the study (see Chapter 2, Figure 2.3).

Abandoned agricultural land in semi-arid regions of Spain (Carcavo basin) showed slow signs of vegetation recovery, taking ca. 40 years to see significant changes (Lesschen *et al*. 2008).

van der Merwe *et al.* (2018) showed very slow changes in species composition ca. 27 years after sheep stocking rates were reduced on Karoo farms. My results also aligned with another recent study (McManus *et al.* 2018) that reported no significant shift in shrub cover or diversity following the passive recovery of vegetation in the Karoo over a one year period following rainfall. Grass height was the only vegetation characteristic that shifted significantly between survey years. Grasses were significantly taller on core farms after the cessation of farming activities and were significantly taller than grasses on edge and control farms which decreased in height over the years. The trends in shorter grass height may have reflected continued livestock grazing on these farms as grasses and forb cover are likely to recover first after the removal of livestock (van der Merwe 2020). The significant increase in grass height on core farms but the lack of significantly increasing grass cover suggests that if rainfall increased during the study there may have been a flourish in grass cover (du Toit *et al.* 2018), boosting grazing for wild herbivores and providing cover and seeds for rodents (Riginos & Grace 2008, Kuiper & Parker 2013).

Small mammal communities did not change significantly during the study, with only habitat type having a significant influence on community composition. Predictably rocky habitats were dominated by rock rat spp. (*Micaelamys* spp.) while sandy flat open areas were dominated by hairy footed gerbil (*Gerbillurus paeba*). This was similar to results from Aboul-Hassan (2020) who looked at small mammal richness and abundance in the Karoo Shale Gas Development Area. Habitat dependent responses of small mammal communities to ecosystem changes has been recorded in other arid landscapes with the degree of response largely depended on rainfall (Frank *et al.* 2014). In environments with higher rainfall small mammal communities showed significant increases after the removal of livestock in a shorter timeframe (6 – 19 months) (Schmidt *et al.* 2005, Frank *et al.* 2014), however significant changes in small mammal communities in arid landscapes were only observed after three years (Haby & Brandle 2018). Small mammal communities (diversity and abundance) are closely linked to changes in vegetation (Valone & Sauter 2005, Torre *et al.* 2007, Rosi *et al.* 2009, Wallgren *et al.* 2009) and in the absence of significant rainfall during my study period my results resemble those obtained in arid regions with no significant change in plant cover and small mammal abundance.

Additionally, my results highlighted the importance of looking at individual species responses as well as overall community changes. Different species are likely to have different responses to the removal of livestock (either speed of response or degree of response) suggesting that monitoring at a species level may show earlier signs of passive recovery (Schmidt *et al.* 2005). This trend was evident with *G. paeba* (hairy-footed gerbil) which showed greater variability in abundance over the survey period compared to other species. Gerbil species typically dominate disturbed arid landscapes and have been recorded to thrive where livestock are present, responding faster to changes in vegetation than other small mammal species (Eccard *et al.* 2000, Aboul-Hassan 2020). The removal of livestock may result in the decreasing dominance of generalist species like *G. paeba* and allow species which are more specialised to increase through succession which tracks the succession of vegetation (Kruger & Bigalke 1984, Briani *et al.* 2004, Torre & Díaz 2004, Rebelo *et al.* 2019). While, *G. paeba* did show greater variability in abundance with time this species remained dominant in all farm types throughout the study period, possibly benefiting from the increased aridification linked to the drought despite the absence of livestock on core farms (Piers *et al.* 2020).

The importance of rainfall and vegetation for mammal recovery

Bottom-up processes are highly influential in arid landscapes, with rainfall and vegetation being a major predictor of mammal species abundance and diversity (Snyder & Tartowski 2006, Kelly *et al.* 2013). While several studies have clearly outlined the negative impact of livestock on mammal species (Stephens *et al.* 2001, Schieltz & Rubenstein 2016, Soofi *et al.* 2018) and the positive effects of removing livestock from a landscape (Hoffman & Zeller 2005, Jeddi & Chaieb 2010, Legge *et al*. 2011, Filazzola *et al.* 2020) there was no clear effect of livestock removal in my study area. I attribute this to the prolonged drought conditions that persisted throughout the study period which prevented vegetation recovery even under conditions of reduced grazing pressure (Valone *et al.* 2002, Filazzola *et al.* 2020). Drought plays an important role in arid regions like the Karoo (Milton *et al*. 1995, Kraaij & Milton 2006), however predicted increase in drought conditions as a results of climate change is threatening to push the system over a threshold (Cook *et al.* 2018, Ahmadalipour *et al.* 2019). Interestingly results from surveys after the removal of sheep on core farms provided some evidence for the competitive release theory. While mammal community structure shifted significantly on edge and control farms during increased drought conditions (i.e., decreases in carnivore and herbivore RAI), these trends were not observed on core farms which were more similar to baseline surveys (i.e., no decreases in RAI that would result in community shifts despite drought). This suggests the removal of sheep provided some buffer to drought for mammal communities on core farms. Evidence of protected areas acting as buffer zones from drought has been provided for other areas where species abundance (particularly herbivores) was protected from impacts of decreased rainfall after vegetation was protected from overgrazing and/or deforestation (Acosta Salvatierra *et al.* 2017, Smit & van Rensburg 2020).

Impacts of human disturbance on wildlife

Camera trapping surveys on farms provided evidence that human absence impacted daily activity patterns of several mammal species (App 7.1). Typically, in areas with high levels of human disturbance wildlife were more nocturnal presumably to avoid "risks" associated with humans (Clinchy *et al.* 2016), as corollary mammals have been recorded shifting from diurnal to nocturnal where human disturbance (i.e. hunting, hiking, vehicles) increased (Di Bitetti *et al*. 2008, Crosmary *et al.* 2012, Gaynor *et al.* 2018, Smith *et al.* 2018a). The results from the daily activity analysis in this study aligned with the theory of nocturnal flexibility (Murray & St. Clair 2015) and suggests that while human presence may impact temporal activity these impacts can be significantly reduced where human presence is reduced.

Carnivores (black-backed jackal *Canis mesomelas*, cape fox *Vulpes chama*, and yellow mongoose *Cynictis penicillata*) showed significant responses to decreased human disturbance through shifting activity patterns. Activity shifts are common for highly persecuted species (such as carnivores) as an avoidance response towards humans (Mendes *et al.* 2020). Reduced diurnal activity where human presence is high was evident for both large and small carnivores in California (i.e., pumas *Puma concolor*, bobcats *Lynx rufus*, coyotes *Canis latrans*, striped skunks *Mephitis mephitis*, and Virginia opossums *Didelphis virginiana*) (Nickel *et al*. 2020), as well as mesopredator species is Israel (i.e., golden jackal *Canis aureus* and red fox *Vulpes vulpes*) (Shamoon *et al.* 2018). These studies aligned with the activity patterns of predators seen on both edge and control farms (where persecution was still high) however increased nocturnal/diurnal flexibility was observed on core farms after persecution in these areas was reduced. My results provide evidence, through behavioural shifts, of passive mammal recovery of predators and some herbivores from anthropogenic influences after the cessation of farming activities.

Perceived versus observed threat of changes in predator abundance

Black-backed jackal and caracal (*Caracal caracal*) were the dominant "problem" mesopredator species in my study area, aligning with findings from other South African dryland systems. However, unlike established protected areas in the Karoo (Collins & du Toit 2016, Drouilly *et al.* 2018a), leopard was not detected, possibly because of limited mountain refugia within the study area (Swanepoel *et al.* 2013, Mann *et al.* 2020). During the study period there was one incidence of a reported leopard sighting to the north of core and edge farm 3 suggesting that over time dispersal may see the return of leopards to the southern more mountainous section of the PA.

Black-backed jackal and caracal populations did not increase significantly within the SKA protected area compared to surrounding farmland as predicted by various landowners. This finding was also contradictory to the original predictions of SEAs for the core area which suggested mesopredator populations would rapidly increase before stabilising with knock-on effects for fox and wild prey populations (Milton *et al.* 2016). Protected areas do allow for the recovery of predator populations as seen in North America (mountain lion, Davenport *et al.* 2010 and cougar LaRue *et al*. 2012) and Europe (grey wolves, Chapron *et al.* 2014, Fabbri *et al.* 2014 and golden jackal, Arnold *et al.* 2012) and I would predict that following the end of the drought predator RAI will increase within the SKA core.

Furthermore, contrary to results from the Drouilly *et al.* (2018a) study, caracal had slightly higher RAI and naïve occupancy on core farms after the establishment of the protected area compared to surrounding farmland. This may be because of the absence of larger predators in the SKA core which coupled with the absence of farmers may have provided a release from top-down effects. In Drouilly *et al.* (2018a) leopards were present in the PA and were assumed to suppress caracal numbers. The different response of predator species to the establishment of a protected areas has been observed in Nepal, where tiger (*Panthera tigris*) populations increased due to the establishment of a protected area while leopards (*Panthera pardus*) remained constant (Wegge *et al*. 2009). Reintroductions of predators in various conservation areas within the Eastern Cape, South Africa, saw similar variability in success. Lions (*Panthera* *leo*), hyaena (*Crocuta crocuta*) (Hayward *et al.* 2007a, Davies *et al.* 2016) and wild dog (*Lycaon pictus*) (Hayward *et al.* 2007a) all had marked success when reintroduced to protected areas, highlighting prey abundance as the major factor influencing space use by predators within a PA. Leopards and cheetah (*Acinonyx jubatus*) had relative success after reintroduction to protected areas, however the degree of success depended on the PA and the population dynamics of other large predators (Hayward *et al.* 2007a & 2007b, Tambling *et al.* 2012). Studies with Eastern Cape protected areas, particularly Addo Elephant National Park, once again highlighted the important of prey abundance as a major determinant for predator space use within a PA (Hayward *et al.* 2009). As Drouilly *et al.* (2018c) highlighted, predators within protected areas will likely predate on wild prey population rather than moving onto farmland and hunting domestic prey. Results from this study showed that wild prey populations were similar to those seen in the Drouilly *et al.* (2018a & 2018c) study area, suggesting prey populations within the SKA PA are sufficient to support predators without the need to predate livestock on surrounding farms.

While jackal and caracal did not show significant responses to the cessation of farming activities, farmers (and some researchers) nevertheless maintain the narrative that predator numbers would increase within the core and ultimately spill onto edge farms (Humphries *et al.* 2015, Minnie *et al.* 2015, Minnie *et al.* 2018). Farmers on edge farms did report higher livestock losses as the study progressed and consequently more retaliatory killing of predators. These changes were not however mirrored by increasing numbers of potential livestock predators on edge farms, but it is possible that ongoing lethal management on edge farms suppressed predator numbers effectively masking any changes in camera trap estimates of RAI. Furthermore, some farmers revealed that they would shoot predators on core farms while patrolling their borders and while hunting on the core was markedly lower than on the edge this too may have impacted the overall results for predator RAI on all farm types. Irrespective of these confounding effects it is clear that the abundance of potential livestock predators in this region of the Karoo is exceptionally low with naïve occupancy lower than recently reported by both Drouilly *et al*. (2018) and Woodgate *et al.* (2018). While it could be argued that the reduced densities of jackal on edge and control farms were the result of intensive jackal control (Kamler *et al.* 2013), the similarly reduced densities of jackal on core farms contradicted this theory. It was apparent throughout the study that there is a strong disconnect between ecological data (no observed increase in predators) and socio-economic pressures (drought, historic negative attitudes and economic loss) that are used to inform predator management. Pressure has mounted on the SKA to actively hunt jackals and caracal within the core despite my data providing no evidence for a growing population or one that regularly traverses fence lines to hunt livestock on edge farms. Minnie *et al.* (2015) suggested that removal of jackal through lethal management resulted in an expanding population, most likely a result of compensatory immigration. Fence surveys determined that the movement of predators from the PA to neighbouring farms did not increase over the survey period. This was contrary to the source-sink dynamic described by Minnie *et al.* (2018). However, as suggested above the stable state of predator populations in both the PA and farmland may be the result of drought dampening the effects of the land-use intervention. Research from Minnie *et al.* (2015) suggest source-sink dynamic could occur within the SKA PA, similar to the Karoo National Park, over time and for this reason we urged the SKA to focus on improving the quality and maintenance of the SKA/edge farm fences as the only broadly acceptable non-lethal management tool accepted by farmers in the region.

Fencing is considered one of the more effective non-lethal predator management techniques (van Bommel & Johnson 2014), and where human-predator conflict is high the benefits of fencing outweigh the ecological risks as the preferred alternative would be lethal management (Scasta *et al.* 2017). While the results of this study provided evidence that fencing can successfully limit the movement of predators between farms, the importance of fence quality was also highlighted (Chapter 6). Notably where fence monitoring and fence hole repair was high predator hole utilisation was lowest. Interestingly while fence quality did impact hole utilisation for non-predator species, all fences provided a level of permeability to mammals. This suggests that the semi-permeable nature of Karoo fences may still benefit the ecological needs of mammal species while providing effective barriers to predators (see Chapter 6). The success of well-maintained fences as effective exclusion barriers to predators is evident across various arid landscape, suggesting these results provide additional support for the use of fences as non-lethal management tools. Australia has seen successful exclusion of predators using fencing decreasing depredation of livestock by carnivores (Burns *et al.* 2012, Dickman 2012, Clark *et al.* 2018). Studies in southern Africa further highlight the need for well-maintained fences as human-wildlife conflict increases rapidly when fencing show signs of permeability (Durant *et al.* 2015, Pekor *et al.* 2019). This study highlights the importance of collaborative management between the SKA and surrounding landowners especially with regards to fence maintenance (Humphries *et al.* 2015).

Study limitations

The single greatest limitation to the findings of this study was the duration (3 years) which when coupled with a prolonged drought limited the likelihood of measuring meaningful change in the transition of land use from small livestock farming to protected area. Furthermore, the timing of the intervention itself (a cessation of farming activity) was delayed leading to my extending the duration of my fieldwork by a year. This highlights the challenges of working on real-world situations at the level of the landscape where most timelines linked to planned interventions are beyond the control of researchers. Despite this it is my hope that this study will provide a critical baseline dataset for ongoing long-term monitoring of this site by Square Kilometre Array Environmental Observation Network (SKAEON – a derivative of SAEON). SKAEON did not have the capacity or resources to obtain baseline data but have committed to long term monitoring of a subset of my study sites to track the changes linked to the formation of the SKA protected area.

A further major limitation to this study were the restrictions imposed by the SKA telescopes which effectively constrained the number of farms of each type which could be included in the study. For each telescope a five km buffer was designated within which no camera trap was permitted. Only five farms within the core fell outside the no-go buffers and of these only three were situated on the boundary allowing for a paired comparison with an edge farm. Ultimately this restriction limited the sample size of the study (n = 3 for each treatment), limiting the likelihood of finding statistically "significant" trends. This studies overall sample size of 9 is lower than other recent studies in the Karoo exploring biodiversity on farmland (i.e., n = 22 farms; Drouilly *et al.* 2018a, n = 23 farms; Woodgate *et al.* 2018). However, unlike these studies, and despite the small sample size, I was able to use a BACI design (providing temporal replication) that almost certainly provides improved understanding of the impact of an intervention such as land use change (Brits *et al.* 2002, Drouilly 2019).

High spatial variability among farms within each category (core, edge and control) was a design feature of the BACI study with the goal of capturing the topographic and environmental variation within the study site. Furthermore, for small mammal and vegetation transects we deliberately selected different habitat types on each farm to ensure representativity of habitat diversity. This made comparisons between farms within a category undesirable and high variability and/or patchiness calculated throughout the study was not only expected but desirable (as it meant I captured the variation well). However, this also contributed to the observed high coefficients of variability > 0.3 in both vegetation and small mammal attributes within each farm type in each survey year. It should be noted that this level of variability may have masked significant trends and reduced the resolution of statistical tests, perhaps even leading to Type 1/2 statistical errors.

Implications for management and future research

Despite research illustrating that the removal of sheep and a cessation of hunting can have significant, mostly positive, impacts on flora and fauna (i.e., increase in vegetation cover and/or wildlife abundance) (Olff *et al.* 2002, Benayas & Bullock 2015, Kartzinel *et al*. 2017) my study failed to show any short-term changes in species richness or relative abundance of mammals. Ultimately passive recovery is predicted for the core region (Haby & Brandle 2017, Condon *et al.* 2020) but more time (10-50 years) is required before differences between farmland and protected areas will become evident (Kinnaird & O'Brien 2012, Mann 2014, Kiffner *et al.* 2015, Drouilly *et al.* 2018a).

While my results showed no evidence of predator abundance increasing on core or edge farms once the protected area was established and as predicted by farmers, the perceived threat of predators to farmer livelihoods was strongly evident in farmer interviews (Chapter 5). Terblanche (2020) surveyed several farmers within the SKA region investigating the sociological impact of predator conflict and reported that the establishment of the SKA protected area exacerbated the stress associated with the management of predation risk to livestock for many surrounding farmers (regardless of ecological evidence). This stress compounded tensions between the farmers and the SKA with the former focussing on both the absence of an improved boundary fence or any lethal management of predators within the SKA to suppress their numbers. Farmers consider effective predator management in the region to require the buy-in from all stakeholders involved if the suppression of predation is to be effective. Retaliatory killings of predators on edge farms increased over the study period, with farmers citing increased livestock losses as the reason. I was not able to independently verify either the extent of their losses or the causes, but it is possible that predators (particularly jackal) were subject to lethal management at least in part as a result of frustration (from the drought, the SKA and historic predator conflict) as "(farmers) feel they still have agency over (jackals)" (Terblanche 2020).

Throughout the study period various stakeholders recommended the routine lethal management of predators within the SKA PA as essential to preventing excess livestock losses on edge farms. As discussed in Chapter 5, lethal management is widely used as a method to suppress predator populations within the Karoo. While fencing and the clean-up of predators within fenced farms was initially very successful in the Karoo (Beinart 2018) it has had limited success at reducing livestock depredation by jackal and caracal in the last 20 years with most farmers reporting increased predator sightings and livestock losses (Drouilly & O'Riain 2019) and still other research suggesting higher losses in the year after extensive lethal culls (Bailey & Conradie 2013, Nattrass *et al.* 2020). Furthermore, other studies comparing lethal and non-lethal methods suggest greater success with the latter both locally (McManus *et al.* 2015, Treves *et al.* 2016), as well as in Australia (Pickard 2007, Smith & Appleby 2018, Smith *et al.* 2020c), Europe (Angst 2001, Jackson & Wangchuk 2001, Rigg *et al.* 2011) and the USA (Allen & Flemming 2004, Conner *et al.* 2008).

Despite the growing support for non-lethal interventions and the mounting evidence that lethal methods provide only short-term relief (Breck *et al.* 2017, Lennox *et al.* 2018) and may even exacerbate losses (Nattrass *et al.* 2020), farmers throughout the Karoo still engage in lethal management particularly in the form of night hunting (Drouilly 2019, Terblanche 2020). While my data provide no evidence of an increase in predator numbers either on core, edge or control farms during the study, it is possible that this reflects the outcome of both top-down and bottom-up effects. Continued culling on edge and control farms may suppress predator numbers and the loss of prey biomass on core farms when sheep were removed, may have deprived predators of an accessible and abundant food resource. Together these top-down and bottom-up factors could have ensured predator numbers remain consistently low. The absence of domestic prey for predators on the core also needs to be tempered by their release from farmer persecution. Untangling these confounding effects was not possible with the data I was permitted to collect (GPS collaring was not permitted) and mark recapture of individual predators to allow for density estimates was unfeasible in the time frames of the study. Despite the uncertainties in the causative factors it is clear that potential livestock predators in this region of the Karoo have a very low relative abundance index and seldom move across fences (especially where fence quality is high). I can thus recommend to the SKA and edge farmers that lethal management of predators in the core is not a scientifically defendable position.

Suggested future research

This study has provided a critical baseline data set which includes not only data from land before and immediately after it was used for small livestock farming but also the first comprehensive mammal survey in this region of the Karoo, South Africa. As discussed above only a subset (%) of the species that were assumed to be here (Todd & Henschel 2016) were recorded and reveal a similar subset to Drouilly *et al.* (2018a) and Woodgate *et al.* (2018) of the original fauna documented in the Karoo. This subset is comprised mostly of small and medium sized generalist species that neither compete extensively with small livestock for grazing nor pose a threat to their lives (e.g., aardwolf, aardvark, porcupine) and which may benefit from modification of the ecology on farmland through for example the removal of apex predators (e.g., mesopredators, kudu) and the provision of permanent water supplies (e.g., baboons). It is likely that over time new species will immigrate into the SKA core including brown hyaena, honey badger and duiker. If the SKA PA continues to recover passively and they resist calls to 'manage predators' then it will be an important study site for assessing how floral and faunal components respond to the landscape level change in land use. Repeating the surveys set up during this study at regular timescales after my study (i.e., 5 years, 10 years, 20 years after the establishment of the protected area) will provide important insights into the value of existing marginal rangelands that are increasingly being allowed to 'rewild' for realising national and global biodiversity targets (Republic of South Africa 2004). It may further reveal whether active restoration is required both to stimulate primary productivity and restore plant diversity and to restore important ecosystem functions such as the introduction of apex predators that are easily curbed by fences (e.g., cheetah) (Hayward & Kerley 2009).

As with other Karoo farmlands (i.e., succulent karoo outside of Ceres) livestock and agriculture have likely resulted in altered soil properties and poor soil conditions constraining potential passive recovery of vegetation (Beukes & Cowling 2003, Saaed 2018). While the SKA PA productivity may remain in a stable state over the long term, improved NDVI/productivity and vegetation diversity will require active rehabilitation as was evident in the Tankwa Karoo National Park (TKNP (Saaed 2018). This may include active seed dispersal and/or mulching of bare areas for better rainfall retention to facilitate natural seedling emergence (Beukes & Cowling 2003, Saaed 2018). However, Beukes & Cowling (2003) stated that active restoration of Karoo landscapes is risky largely due to low natural follow up rainfall reducing seedling survival. Long term monitoring will help to elucidate the short-term effects of rainfall on passive and/or active recovery (Beukes & Cowling 2003) in addition to the long term impacts of climate change in the Karoo and the proposed importance of south versus north facing slopes (Todd & Henschel 2016, Milton *et al.* 2016) SEA). As part of development and construction of the SKA telescopes, active habitat and vegetation restoration has been highlighted as a key mitigation and maintenance measure for the project, especially where temporary camps and roads are built during construction phases (Milton *et al.* 2016). The monitoring of these rehabilitation measures would provide valuable insights into the efficiency of larger scale active protected area rehabilitation within Karoo landscapes.

Alternately the reintroduction of apex predators as an active measure of recovery has been successful in other Karoo protected areas (i.e., lion reintroduction in KNP) (Hayward *et al.* 2007c, Fourie *et al.* 2015). The benefit of reintroduction within the SKA PA would need to be heavily weighed against the original goals of the area (i.e., to provide a space for astronomical research) especially because the carrying capacity of these arid regions is typically low for large apex predators suggesting contribution to conservation of these populations would be minimal (Hayward *et al.* 2007c). Lindenmayer *et al.* (2012) explained that long term monitoring programs are essential to providing data at scales that are relevant to decision makers and management and helps avoid making decisions based on shifting baselines. This will overall benefit landscape level ecological processes as well as long term socio-economic decisions.

The potential closing of artificial water points and the removal of interior farm fences will also need to be closely monitored (Milton *et al.* 2016). Farmland within the Karoo is characterised by multiple artificial water points for livestock, typically one per camp (a camp referring to fenced off areas within the external predator proof boundary fence of a farm) (Figure 7.1) (Beinart 2018). Internal fences may restrict the movement of wildlife within a farm, although not as much as the more robust predator proof fences, however these fences may still impact access to resources (Beinart 2018, Dean *et al.* 2018).

Figure 7.1: Lefthand image shows example of artificial water point on control farm 2, including wind pump and water reservoir. Troughs are typically attached to reservoirs with a pump so animals can access water. Righthand image shows interior farm fence and gate on control farm 3. These fences are typically a series of single wire strands (ca. four strands) and are not predator proof (© Michelle Blanckenberg).

As farming activities cease within the SKA PA, maintenance and monitoring of all these structures (typically done by farmers) will likely fall away. Internal farm fences are already being removed, and while the majority of water points have remained active the large number of water points per farms suggests not all pumps will be regularly checked and repaired if damaged (pers. obs.). Low rainfall and its natural variability within the arid landscapes suggests surface water-dependent wildlife heavily utilise artificial water points within farmlands (Dean & Milton 1999, James *et al.* 1999). Milton *et al.* (2016) suggested the termination of artificial water points would ensure wildlife populations (especially those dependent on surface water) would remain at sustainable densities. However, the increasing drought conditions, and climate change related rainfall fluctuations suggests the removal of these water points may limit growth of wildlife populations and influence the way in which species use the landscape (Smit *et al.* 2007). As the SKA PA already has extremely low wildlife densities this may further hinder recovery of mammal populations, not to mention bird populations that may also rely on these water points. Research on which species are most reliant on artificial water points and how systematic closure of these points impacts species distribution will be increasingly valuable.

Overall the increase in vegetation cover predicted for the SKA PA in the coming years (see van der Merwe 2020 for examples of how the vegetation may recover) will provide an essential resource for the majority of mammal species reliant on this vegetation especially with predicted increases in drought frequency and intensity. The results from this study provide a necessary baseline set of data for monitoring how this new protected area may improve and sustain mammal abundance within the Karoo, especially for rarer species like black-footed cat and springhare (see App 7.1). Furthermore this study highlights the importance of the social aspects of this region and how this may influence the management of its wildlife. While fencing may have deleterious effects on the natural processes of a landscape (Hayward & Kerley 2009, Jakes *et al.* 2018), in this case fencing can be effectively utilised as a human-human, as well as a human-predator, conflict mitigating tool, especially where maintenance and monitoring of the boundary fence is frequent (see App 7.1).

Appendix 7: Synthesis appendices

App 7.1: Summary of major findings from different survey techniques (i.e. vegetation, small mammal, camera trap, longitudinal and fence) of the research presented in this thesis, as well as limitations specific to each survey.

Survey method	Major findings	Survey limitations
Wheel-point (vegetation)	• PFG richness and diversity was not significantly different between farm types or over survey years • No significant difference in vegetation cover between farm types or survey years • Forbs were significantly more abundant in 2019 versus 2017	• Low rainfall resulted in dry vegetation which was difficult to identify to species level
Sherman traps (small mammal)	• Total of seven species recorded • Richness and diversity were not significantly different between farm types or survey years • Abundance was not significant different between survey years • Habitat (rocky areas) and shrub cover significantly influenced small mammal communities in both survey years	• Sherman trapping had a species bias therefore, surveys may have excluded more trap shy species (i.e. Karoo bush rat)
Camera traps (medium and large mammals)	• No significant change in mammal species richness, diversity or abundance between farm types and survey years • Community structure differed on core sites compared to edge and control sites after the cessation of farming activities, suggesting removal of sheep provided a buffer to drought conditions • Human presence significantly impacted species daily activity patterns on core sites after cessation of farming activities • Predator abundance was not influenced by sheep abundance but rather a factor of increasing drought conditions	• Very low detection and density of mammals within arid landscape ∴ could not perform occupancy modelling
Questionnaire (farmer interviews)	• Farmers' negative perception of jackal and caracal did not change between survey years • Reported livestock losses and killings of predators had no correlation to actual predator abundance	• Records for livestock losses and depredation were not rigorous • Number of surveys limited to farmers involved in study
Fence with camera traps (fence use and quality)	• Fence quality relates to the frequency of maintenance and monitoring • Fence quality significantly influences overall hole utilisation → good fence quality = less hole utilisation • Predator are more likely to use holes along poor quality fences • Human presence along fences significantly impact the time at which animals were seen along and used holes in fences → good quality fences = high human disturbance = exclusive nocturnal fence utilisation	• Number of cameras set at holes limited by camera availability

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LIST OF TABLES

Table 2.1: Summary description of each study farm, showing farm size, major biomes, general topography, soil type, approximate number of permanent water sources (subject to change), approximate number of sheep per year (during the study period), management style and month/year of removal of sheep from core farms. All data was gathered through a series of interviews with the owners of each farm. **36**

Table 3.1: Summary of total trap nights, trap failures and trap nights per habitat for nine study farms within three farm type (core, edge and control) during the 2017 small mammal trapping survey. Values in bold indicate totals within a column. **49**

Table 3.2: Description of landscape-level environmental covariates and site-specific vegetation predictor variables used to assess differences in small mammal communities within the SKA region of the Karoo. The predicted effect (+/-) describes how we predict each variable to affect small mammal abundance and vegetation, positively, negatively or no effect (na). SM = small mammal, NDVI = normalised difference vegetation index. **55**

Table 3.3: Description of most parsimonious models based on the Akaike Information criterion (AIC) (with negative binomial distributions) used for three response variables small mammal abundance (per farm type), small mammal abundance (per farm type and habitat) and vegetation cover. Covariates include survey year, farm type, sheep presence (presence/absence), habitat type, NDVI, rock cover, shrub cover and shrub basal cover. **56**

Table 3.4: Summary of environmental and PFG parameters (% ± standard error) per farm type over two survey years, 2017 (before cessation of farming activities on the core) and 2019 (after cessation of farming activities on the core). Both total cover as well as cover for each plant functional group is reported. Cover indicates abundance or count of a particular plant functional group expressed as a percentage. Coefficient of variation (CV = sd/mean) indicated by [ ] and italicised. CV ≥ 0.3 indicates a relatively high variation and is highlighted in bold. **59**

Table 3.5: Summary statistics for post-hoc Tukey tests comparing total vegetation cover, grass cover and shrub cover within each farm type (core, edge and control) between 2017 (before cessation of farming activities on core farms) and 2019 (after cessation of farming activities on core farms). For each comparison n = 9. ‘Est.’ indicates model output estimate with standard error. **60**

Table 3.6: Summary statistics for post-hoc Tukey tests comparing total vegetation cover, grass cover and shrub cover between farm types (core, edge and control) within 2017 (before cessation of farming activities on core farms) and 2019 (after cessation of farming activities on core farms). For each comparison n = 9. ‘Est.’ indicates model output estimate with standard error. **60**

Table 3.7: Vegetation diversity measures averaged (± standard error) for each farm type during two different surveys, 2017 (before sheep removed) and 2019 (after sheep were removed) Diversity values include alpha diversity (observed PFG richness), effective number of species (e^H), Shannon-Wiener diversity index (H’), Pielou’s evenness (J’), habitat complexity (Hab. comp) and NDVI. Coefficient of variation (CV = sd/mean) indicated by [ ] and italicised. CV ≥ 0.3 indicates a relatively high variation and is highlighted in bold. **62**

Table 3.8: Summary statistics for post-hoc Tukey tests comparing effective number of PFGs (e^H), Shannon-Wiener diversity index (H’), Pielou’s evenness (J’) and habitat complexity (Hab. comp) within each farm type (core, edge and control) between 2017 (before cessation of farming activities on core farms) and 2019 (after cessation of farming activities on core farms). ‘Est.’ indicates model output estimate with standard error. **63**

Table 3.9: Summary statistics post-hoc Tukey tests comparing effective number of PFGs (e^H), Shannon-Wiener diversity index (H’), Pielou’s evenness (J’) and habitat complexity (Hab. comp) between farm types (core, edge and control) within 2017 (before cessation of farming activities on core farms) and 2019 (after cessation of farming activities on core farms). ‘Est.’ indicates model output estimate with standard error. **63**

Table 3.10: Summary table comparing results of small mammal trapping in three different farm types (core, edge and control) over two different survey years (2017 and 2019). Values in bold indicate totals **66**

within each farm type in each year, while values in bold italics indicated averages (± standard error) for each farm type. Coefficient of variation ($CV = sd/mean$) indicated by [ ] and italicised. $CV \geq 0.3$ indicates a relatively high variation and is highlighted in bold.

Table 3.11: Summary results of the number of small mammal individuals captured per taxon (excluding recaptures, hereafter referred to MNA = Minimum Number Alive) and per habitat in three farm types (core, edge and control) over two survey years (2017 and 2019). Overall trapping success per habitat and per farm type in each survey year indicated in bold. Individuals captured was standardised per 300 trap nights per habitat type and standardised per 1000 trap nights for total captures in each farm type to account for slight variations in sampling effort. **67**

Table 3.12: Summary statistics for unpaired and paired t-tests comparing both trapping success and recapture rate of small mammal communities between three farm types (core, edge and control) within each survey year, and within each farm type over two survey years (2017 and 2019). Significant p-values are indicated by an asterisk. **68**

Table 3.13: Small mammal diversity measures averaged (± standard error) for each farm type during two different surveys, 2017 (before any sheep were removed from farms) and 2019 (after sheep were removed from core farms). Diversity values include alpha diversity (observed number of taxa), Chao 1 estimates, effective number of taxa (e^H), Shannon-Wiener taxon diversity index (H'), Pielou's evenness (J'), and % inventory (taxonomic) completeness (Staxa/Chao1*100). **71**

Table 3.14: Summary statistics for post-hoc Tukey tests comparing effective number of small mammal taxa (e^H), Shannon-Wiener taxon diversity index (SWI), and Pielou's evenness within each farm type (core, edge and control) between 2017 (before cessation of farming activities on core farms) and 2019 (after cessation of farming activities on core farms). 'Est.' indicates model output estimate with standard error. **72**

Table 3.15: Summary statistics for post-hoc Tukey tests comparing effective number of small mammal taxa (e^H), Shannon-Wiener taxon diversity index (SWI), and Pielou's evenness between farm types (core, edge and control) within 2017 (before cessation of farming activities on core farms) and 2019 (after cessation of farming activities on core farms). 'Est.' indicates model output estimate with standard error. **72**

Table 3.16: Summary statistics for post-hoc Tukey tests comparing both relative abundance (per 1000 trap nights) and overall standing biomass (g) of small mammal communities between three farm types (core, edge and control) within a survey year, and within a farm type between two survey years (2017, before sheep were removed and 2019, after sheep were removed from core farms). 'Est.' indicates model output estimate with standard error. **74**

Table 3.17: ANOVA table summarising statistical significance of the most parsimonious multivariate GLMs for small mammal taxon abundances and plant functional group abundances (vegetation cover). p values were calculated using 999 resampling. *$p \leq 0.05$; **$p \leq 0.001$. **78**

Table 3.18: Univariate statistic from multivariate GLMs for small mammal abundances (MNA) showing which specific taxa significantly influenced changes in overall abundance between different significant covariates (habitat, shrub (0.5 < 1m) cover and shrub (1.5 < 2m) basal cover). Dev = deviance explained by each taxon. *$p \leq 0.05$; **$p \leq 0.001$. **79**

Table 3.19: Univariate statistic from multivariate GLMs for plant functional group abundances showing which PFG contributed significantly to changes in abundance between different significant covariates (survey, farm type and habitat). Dev = deviance explained by each PFG. * $p \leq 0.05$. **82**

Table 4.1: Trophic guild, persecution level and body mass (grams) (Stuart & Stuart 2007) for 25 wild mammal species recorded on the three farm types (core, edge and control) over three survey years in the SKA region of the Karoo, South Africa. **123**

Table 4.2: Camera trapping effort including the number of camera traps, number of trap nights and the duration of the survey on three farm types (core, edge and control) over three survey periods (A, B and C) in the SKA region of the Karoo, Northern Cape, South Africa. **125**

Table 4.3: Number of wildlife captures, and number of species recorded during three extensive camera trap surveys (A = 2017/18, B = 2018/19 and C = 2019/20) across three different farm types (core, edge and control). **126**

Table 4.4: Summarised results of the number of independent captures of individual species grouped by family for three camera trap surveys (A = 2017/18, B = 2018/19 and C = 2019/20) on core farms. Species completely absent (not detected) on a specific farm type are highlighted in grey. Naïve occupancy indicates the proportion of camera stations where a species was detected, while photographic rate (also known as relative abundance index) indicates the trapping rate of a species per 100 trap nights. **128**

Table 4.5: Summarised results of the number of independent captures of individual species grouped by family for three camera trap surveys (A = 2017/18, B = 2018/19 and C = 2019/20) on edge farms. Species completely absent (not detected) on a specific farm type are highlighted in grey. Naïve occupancy indicates the proportion of camera stations where a species was detected, while photographic rate (also known as relative abundance index) indicates the trapping rate of a species per 100 trap nights. **129**

Table 4.6: Summarised results of the number of independent captures of individual species grouped by family for three camera trap surveys (A = 2017/18, B = 2018/19 and C = 2019/20) on control farms. Species completely absent (not detected) on a specific farm type are highlighted in grey. Naïve occupancy indicates the proportion of camera stations where a species was detected, while photographic rate (also known as relative abundance index) indicates the trapping rate of a species per 100 trap nights. **131**

Table 4.7: Pooled observed (Sobs) and estimated (± SE) species richness of wild mammals detected during three different surveys (A = 2017/18, B = 2018/19 and C = 2019/20) across three different farm types. Species richness estimates include Chao 1, first order Jackknife (Jack 1) and bootstrap. Total number of camera trap nights per year indicated by n. **133**

Table 4.8: Observed (S_{obs}) and asymptotic estimated (± SE) species richness of wild mammals detected during three different surveys (A = 2017/18, B = 2018/19 and C = 2019/20) on three different farm types (core, edge and control). 95% confidence intervals drawn from 1000 randomisations performed with replacement. **134**

Table 4.9A: Summary statistics for negative binomial GLMER summarising significance of survey year and farm type on changes in effective number of species (ENS). *p* values were calculated using 999 resampling, significantly different values (< 0.05) were indicated with an asterisk. **138**

Table 4.9B: Summary statistics for Wilcox rank sum and signed-rank tests comparing effective number of species (ENS) within core, edge and control communities between three survey years (A = 2017/18, B = 2018/19 and C = 2019/20). P-values were adjusted using the holm method, significantly different values (< 0.05) were indicated with an asterisk. **139**

Table 4.10: Rank abundance curve changes between year A and B and year A and C for each farm type. Richness and evenness change bound between -1 and 1 (larger values indicate greater increases or decreases). Rank change bound between 0 and 0.5 (0.5 represents the maximum rank changes allowed). Turnover bound between 0 and 1 (larger values represent a high proportion of species lost). **140**

Table 4.11: ANOVA results showing the difference between rank abundance curve (RAC) change measures between farm types in survey C. All ANOVAs were tested for normality using a Shapiro-Wilk's test with all results showing a p value > 0.05, therefore assuming normality for all tests. **140**

Table 4.12: Functional dispersion index (FDis) indicating the weighted mean distance of a particular mammal species (using RAIs) in a multidimensional space, to the centroid of all species within that space. FDis values were calculated for each farm type (core, edge and control) in three different survey years (A = 2017/18, B = 2018/19 and C = 2019/20). **145**

Table 4.13: Results from both paired Wilcox signed-rank and unpaired Wilcox rank-sum tests comparing RAIs for different trophic levels found within core, edge and control communities between survey A (2017/18) and survey C (2019/20). Comparisons are considered significantly different when p.adjust < 0.05. **147**

Table 4.14: Results for Kruskal-Wallis test with post-hoc pairwise wilcox test comparing RAIs for different trophic levels found within survey A (2017/18) and survey B (2019/20) community between three farm types (core, edge and control). Comparisons are considered significantly different when p.adjust < 0.05. **147**

Table 4.15: Overlapping coefficients (Δ) with 95% bootstrap confidence intervals for top ten most abundant mammal species across three farm types (core, edge and control) over three survey years (A = 2017/18, B = 2018/19 and C = 2019/20). Value in bold indicate a significant shift in daily temporal activity. Shaded grey blocks indicate species where detection was too low to calculate delta. **149**

Table 5.1: Functional group, persecution level and mean body mass (grams) of select predators and their main prey species recorded in three farm types (core, edge and control) over three survey years in the SKA region of the Karoo, South Africa. **176**

Table 5.2: Key questions discussed with eight landowners during three different wildlife surveys across three different farm types in the SKA region of the Karoo, South Africa. **178**

Table 5.3: The number of independent photographic captures for four predator species on nine different farms in three surveys A, B and C (A = 2017/18, B = 2018/19 and C = 2019/20). Farms were categorised according to their geographical location as either within the SKA protected area (core), on the edge of the protected area (edge) or at least 50km from the edge of the protected area (control). Data extracted from Chapter 4 **-** Table 4.4, 4.5 and 4.6. **180**

Table 5.4: Results from both paired and unpaired Wilcox tests comparing RAIs for black-backed jackal, caracal and combined predators found within core, edge and control farms between survey A (2017/18) and survey C (2019/20). Comparisons are considered significantly different when p.adjust < 0.05 and are indicated with an asterisk. **181**

Table 5.5: Results for Kruskal-Wallis test with post-hoc pairwise Wilcox test comparing RAIs for different predators found within survey A (2017/18) and survey B (2019/20) communities between three farm types (core, edge and control). Comparisons are considered significantly different when p < 0.05*. **182**

Table 5.6: Overlapping coefficients (Δ) with 95% bootstrap confidence intervals for black-backed jackal across three farm types (core, edge and control) over three survey years (A = 2017/18, B = 2018/19 and C = 2019/20). Values in bold indicate a significant shift in daily temporal activity. **184**

Table 5.7: Overlapping coefficients (Δ) with 95% bootstrap confidence intervals for combined target predator species (excluding baboon) across three farm types (core, edge and control) over three survey years (A = 2017/18, B = 2018/19 and C = 2019/20). Values in bold indicate a significant shift in daily temporal activity. **188**

Table 5.8: ANOVA table summarising statistical significance of the most parsimonious multivariate GLMs for black-backed jackal RAI, caracal RAI and combined predator (jackal and caracal) RAIs. p values were calculated using 999 resampling. Significant p values ($p \leq 0.05$) marked with an asterisk. **193**

Table 6.1: Length of each SKA boundary fence section surveyed as well as number of paired cameras set up along each section per survey year. The number of paired cameras varied with the size, number and use of holes. **218**

Table 6.2: Description of categorical covariates used to assess differences in overall mammal abundance and predator abundance using fences along the SKA boundary fence within the SKA region of the Karoo. The predicted response describes for each covariate is described as increasing (+), decreasing (-) or remaining constant (+/-). **221**

Table 6.3: Summary characteristics of three sections of the SKA boundary fence (between core and edge farms) during two fence surveys before (2018) and after (2019) the cessation of farming activity on core farms. Bold values indicate mean (± standard error, SE) measurements between the three sections for each year. **224**

Table 6.4: Number of repaired and open holes found along three SKA boundary fence sections (between core and edge farms) during two fence surveys before (2018) and after (2019) sheep were removed from core farms. Bold values indicate the mean (± standard error) measurements for all three sections for each year. **225**

Table 6.5: Species richness (S_{obs}), Chao 1 richness estimates (± SE) and percentage (%) of overall farm richness calculated for each farm type on either side of three SKA boundary fence sections (between core and edge farms) during two fence surveys before (2018) and after (2019) the cessation of farming on core farms. Bold values indicate mean (± standard error) measurements between the three sections for each year. Measurements were separated into two categories, “using hole” represents only the **228**

species detected using a fence hole while, "moving along fence" represents all species detected along the fence on a specific farm types including species using holes.

Table 6.6: Summarised results for overall fence use (both species seen along fences and seen using fence holes) over two years (2018 and 2019) along three sections of SKA boundary fence (core and edge side) presented per family and species. Predator species considered to be a threat to small livestock in the area are highlighted in grey. Number of independent captures was standardised to 14 cameras. Photographic rate (also known as relative abundance index) indicates the trapping rate of a species per 30 trap nights. **231**

Table 6.7: Summary statistics of multivariate GLMs summarising significance of covariables on changes in the relative abundance of all mammal species and the relative abundance of predators only moving along fences. p values were calculated using 999 resampling. $*p \leq 0.05$; $**p \leq 0.001$. Total relative abundance follows a Poisson distribution (link = "log"), and predator presence follows a negative binomial distribution. **232**

Table 6.8: ANOVA table summarising statistical significance of the most parsimonious multivariate GLMs for the relative abundance of all mammal species using fence holes. Total relative abundance follows a Poisson distribution (link = "log"), p values were calculated using 999 resampling. $*p \leq 0.05$; $**p \leq 0.001$. **233**

Table 6.9: Results from both paired and unpaired Wilcox tests comparing total RAI and predator RAI based off hole use only abundance over two survey years (2018 and 2019). Comparisons are considered significantly different when p.adjust ≤ 0.05 and are marked with an asterisk. **234**

Table 6.10: Summarised results for fence hole use (only species seen using fence holes) over two years (2018 and 2019) along three sections of SKA boundary fence presented per family and species. Number of independent capture and photographic rate for each year is separated into two categories indication direction of movement through holes (C to E = core to edge, E to C = edge to core). Problematic predator species are highlighted in grey. Number of independent captures was standardised to 14 cameras. Photographic rate (also known as relative abundance index) indicates the trapping rate of a species per 30 trap nights. **236**

Table 6.11: ANOVA table summarising statistical significance of the most parsimonious multivariate GLMs for total number of hole use events and number of hole use events per year. p values were calculated using 999 resampling. $*p \leq 0.05$; $**p \leq 0.001$. **240**

Table 6.12: Univariate statistic from multivariate GLMs for hole use events showing which mammal species (with specific focus on predator species) contributed significantly to changes in number of use events between different covariates (year, section and repaired holes per km). Dev = deviance explained by each species. $*p \leq 0.05$; $**p \leq 0.001$. **240**

LIST OF FIGURES

Figure 1.1: Potential ecological support areas (light green areas) found within the SKA region in relation to current critical biodiversity areas (dark green areas) (sourced from Milton *et al.* 2016). Red dots indicate the position of individual telescopes (current and future) and the black polygon shows the border of the SKA core area. **11**

Figure 1.2: Square Kilometre Array Protected Area (black polygon) within the Karoo region in relation to the current South African protected areas network (green polygons), specifically Augrabies Falls National Park, Tankwa-Karoo National Park and Karoo National Park. White dots indicate major cities relevant to the study. **12**

Figure 2.1: The cadastral boundaries of the farms that together comprise the core, edge and spiral arms of the Square Kilometre Array (SKA) relative to the three nearest towns (black circles), Carnarvon, Brandvlei and Williston within the Northern Cape province of South Africa. Black dots within shaded circles indicate the position of the radio dishes across the SKA with a 5 km buffer, relative to nine **22**

farms (black outline) used as individual study sites within the core (green polygons), edge (grey polygons) and spiral (white polygons) areas of the SKA zone.

Figure 2.2: Mean monthly temperature range (°C) and mean monthly rainfall (mm) for the SKA region in the Karoo based off temperature measures taken in Brandvlei and Williston (averaged) over a three year period (2017-2019). **23**

Figure 2.3: Standardised precipitation and evaporation index values for the SKA region on the Karoo between 1988 and 2019. Drought conditions between 2016 and 2018 indicated by red circle (Data sourced from SPEI 2021). **24**

Figure 2.4: Map showing the different biomes making up the SKA core region and surrounding farmland. Labelled white dots indicate major towns (Carnarvon, Brandvlei, Williston and Calvinia), while black dots indicate original two MeerKAT farms (Losberg and Meysdam). Black polygon indicates SKA core boundary. Biome layer sourced from SANBI VEGMAP 2012. **25**

Figure 2.5: Typical landscapes in the SKA core Bushmanland bioregion featuring low and spiny shrubs (*Rhigozum*, *Salsola*, *Pentzia*, *Eriocephalus)* (top left and right), rocky landscape with more small-leaved shrubs and shrubby succulents (*Brownanthus*, *Drosanthemum*, *Ruschia*) (bottom left) and dolerite boulders found scattered within the region (bottom right) (© Michelle Blanckenberg). **26**

Figure 2.6: Adult black headed dorper sheep (left) and white headed dorper sheep lamb (right) (*Ovis aries*) typically used for small livestock production in the Karoo (© Michelle Blanckenberg). **30**

Figure 3.1: The cadastral boundaries of the farms that together comprise the core, edge and spiral arms of the Square Kilometre Array (SKA) relative to the three nearest towns (black circles), Carnarvon, Brandvlei and Williston within the Northern Cape province of South Africa. Study farms (bold black outline) represent the nine farms used as individual study sites within the core (green polygons), edge (grey polygons) and spiral (white polygons) areas of the SKA zone. **45**

Figure 3.2: Example of the distribution of small mammal and vegetation transects on one of the core farms within the SKA protected area. SM indicates small mammal transect, while Veg indicates vegetation transect SM 1 and Veg 1 are located in 'plains' habitat, SM 2 and Veg 2 in 'river' habitat, SM 3 within an interesting ecotone (scree landscape with small to large bushes) and SM 4 and Veg 3 are located in 'rock' habitat. Orange line are ~ 600 m long while blue lines are 100 m long. **46**

Figure 3.3: Photograph of myself taking measurements of a shrub species for a vegetation survey. Both the width and the height were recorded, as well as percentage cover of an individual within a one m^2 quadrat (© Michelle Blanckenberg). **48**

Figure 3.4: A schematic of the small mammal trapping survey in a given habitat type. Transects were 600 meters long with 12-meter intervals between adjacent Sherman traps (see image on the right) (© Michelle Blanckenberg). Transects were situated between two camera stations on the 2x2km camera grid (see chapter 4) to facilitate the location of the transect. **50**

Figure 3.5: Example of small mesh (potato) bag used during small mammal processing, the image on the left is of a hairy-footed gerbil while the image on the right is a short-tailed gerbil (© Michelle Blanckenberg). **51**

Figure 3.6: Average vegetation percentage cover per farm type over two survey years, 2017 before sheep are removed from farms and 2019 after sheep are removed from the core. Error bars indicate standard error. **58**

Figure 3.7: Boxplots representing mean grass height (cm) for three farm types (core, edge and control) between two survey years (2017 survey, before cessation of farming activities on the core, 2019 survey, after cessation of farming activities on core farms). Shaded boxes indicate lower quartile, median (thick black line) and upper quartile for grass height, while black dot indicates mean grass height with error bars representing standard error. **61**

Figure 3.8: Taxa incidence (S_{taxa}) of small mammals captured on three farm types (core, edge and control) during two survey years (2017, before sheep were removed for any farm and 2019, after sheep are removed from core farms). **69**

Figure 3.9: Chao 1 taxa rarefaction curves (A and B) and Shannon-Wiener taxon diversity curves (C and D) for small mammal taxa captured on three farm types (core, edge and control) over two survey **70**

years (A and C = 2017, B and D = 2019). Solid lines represent observed richness and diversity, while dotted line represent Chao 1 expected richness and diversity. Shaded polygons indicate 95% confidence intervals.

Figure 3.10: Boxplots representing small mammal mean relative abundances (per 1000 trap nights) for three farm types (core, edge and control) between two survey years (2017 survey, before cessation of farming activities on core farms, 2019 survey, after cessation of farming activities on core farms). Shaded boxes indicate lower quartile, median (thick black line) and upper quartile for relative abundance, while black dot indicates mean relative abundance with error bars representing standard error. **73**

Figure 3.11: Comparison of small mammal mean relative abundance per taxon in three habitat types (plain = light grey, river = medium grey and rock = dark grey) across three farm types (core, edge and control) over two survey years. Error bars represent standard errors. Relative abundance was standardised per 300 trap nights for each habitat and pooled across farm type to account for slight variations in sampling effort. **76**

Figure 3.12: Total standing biomass (g) of small mammal taxa captured across three farm types (core, edge and control) during two surveys years. Light grey bars represent 2017 surveys, and dark grey bars represent 2019 surveys. Standing biomass was standardised per 1000 trap nights. Shaded boxes indicate lower quartile, median (thick black line) and upper quartile for standing biomass with error bars representing standard error. Note different y-axis scales. **77**

Figure 3.13: nMDS of small mammal occurrence (based off abundance) based on Jaccard-index of similarity of all nine sites for two survey years (2017 and 2019), overlaid with a fitted large shrub cover (1.5 > 2 m) surface (grey contour lines) (Stress value for 2017 = 0.072, and for 2019 = 0.100). The habitat type of each site is indicated by distinct symbols. **80**

Figure 3.14: Hierarchal cluster dendrogram showing similarities in small mammal abundances among nine farms (core, edge and control) during two survey years (2017 – before the cessation of farming activities on the core and 2019 – after the cessation of farming activities on the core). Red indicates interesting groupings. **81**

Figure 3.15: Hierarchal cluster dendrogram showing vegetation community associations among nine farms within three farm types (core, edge and control) during two survey years (2017 – before the cessation of farming activities on the core and 2019 – after the cessation of farming activities on the core). **83**

Figure 3.16: Canonical correspondence analysis biplot of the nine study sites (blue triangle; Core *x* = a specific core farm, Edge *x* = a specific edge farm and Control *x* = a specific control site) during 2017 (before sheep were removed from core farms) and five taxa (green triangle; *Desmodillus auricularis*, *Gerbilliscus paeba*, *Rhabdomys pumilio*, Macroscelididae spp. and *Micaelamys* spp.) in the SKA region of the Karoo, based on small mammal relative abundances and environmental data variables (Table 3.4 and 3.8). Arrows represent the most important environmental variables indicating direction of maximum change of that variable across the diagram. Length of arrows is proportional to the rate of change. **86**

Figure 3.17: Canonical correspondence analysis biplot of the nine study sites (blue triangle; Core *x* = a specific core farm, Edge *x* = a specific edge farm and Control *x* = a specific control site) during 2019 (after sheep were removed from core farms) and five taxa (green triangle; *Desmodillus auricularis*, *Gerbilliscus paeba*, *Rhabdomys pumilio*, Macroscelididae spp. and *Micaelamys* spp.) in the SKA region of the Karoo, based on small mammal relative abundance and environmental data variables (Table 3.4 and 3.8). Arrows represent the most important environmental variables indicating direction of maximum change of that variable across the diagram. Length of arrow is proportional to the rate of change. **87**

Figure 4.1: Camera trap (black camera icons) survey design across the nine small livestock farms including core (n=3 with 44 cameras), edge (n=3 with 43 cameras) and control farms (n=3 with 51 cameras). Cameras were placed at regular intervals on a randomly established 2x2 km grid. X refers to stations that were omitted because of extreme terrain and inaccessibility. Core 1 = Janseboom, Core 2 = Jas Kloof, Core 3 = Lovedale, Edge 1 = Hondeblaf, Edge 2 = Rietpoort, Edge 3 = Gannabos Leegte, Control 1 = Hoezar-Wes, Control 2 = Leeuwkrans and Control 3 = Skurwekloof. **115**

Figure 4.2: Setting up camera traps using recycled fence droppers (A). Cameras were ideally placed with the back of the camera against a bush to provide a level of protection from the elements and camouflage (B). **116**

Figure 4.3: Sample-based species accumulation curves of total wild mammals pooled across three farm types (core, edge and control) during three different survey years (A = 2017/18 before intervention on core farms, B = 2018/19 six months after intervention on core farms and C = 2019/20 eighteen months after intervention). Shaded areas represent 95% confidence interval drawn from 1000 randomisations performed with replacement. **133**

Figure 4.4: Sample-based rarefaction curves of wild mammals captured across three farm types, control farms (red line), edge farms (blue line) and core farms (green line) during three different survey years (A: 2017/18 before the intervention on core farms, B: 2018/19 six months after the intervention on core farms and C: 2019/20 eighteen months after the intervention). D shows observed species richness for data pooled across all three farm type in each of the three survey years. Shaded areas represent 95% confidence interval drawn from 1000 randomisations performed with replacement. Solid lines indicate observed richness, while dotted lines indicate expected species richness. X-axis represents number of active camera traps. **135**

Figure 4.5: Sample-based rarefaction curves of wild mammals captured across three farm types during three different survey years (2017/18 before the intervention on core farms, 2018/19 six months after the intervention on core farms and 2019/20 eighteen months after the intervention). 0 represents overall species richness curve (hill number q = 0), and 1 indicates overall Shannon-Weiner diversity curves (hill number q = 1). Shaded areas represent 95% confidence interval drawn from 1000 randomisations performed with replacement. Solid lines indicate observed richness, while dotted lines indicate expected species richness. X-axis represents number of active camera traps. **136**

Figure 4.6: (A) Mean effective number of species (± SE), (B) mean Shannon-Weiner Diversity (± SE) and (C) mean Pielou's evenness (± SE) for three farm types (core, edge and control) between three different survey years (A = 2017/18, B = 2018/19 and C = 2019/20). Shaded boxes indicate lower quartile, median (thick black line) and upper quartile for each measure, while black dot indicates mean values with error bars representing standard error. **137**

Figure 4.7: Best fit distribution models for observed rank abundance distributions of 25 selected species (springhare and bontebok excluded) constructed from farm type level RAIs on three farm types (core, edge and control) during three different survey years (A = 2017/18, B = 2018/19 and C = 2019/20). **142**

Figure 4.8: Jaccard Similarity Index heatmap showing the relative similarity between communities within three farm types (core, edge and control) over three different survey years (A = 2017/18, B = 2018/19 and C = 2019/20). Index bound between 0 and 1, with 1 (white) representing greatest similarity. **143**

Figure 4.9: Hierarchal cluster dendrogram based off Jaccard dissimilarity matrices showing community associations between three farm types (core, edge and control) over three different survey years (A = 2017/18, B = 2018/19 and C = 2019/20). **144**

Figure 4.10: Distribution of 25 wild mammal species on three farm types (core, edge and control) across two survey years (A = 2017/18 and C = 2019/20), along two functional traits, trophic level and log body mass (g). Each circle represents a specific species within a community, while circle size is relative to photographic rate (RAI). Shading of circles indicates level of persecution with a specific farm type and year. **146**

Figure 4.11: Changes in the density of time stamps for four mammal species on core sites during survey A (2017/18, solid line) and survey C (2019/20, dotted line). Grey shaded area indicates the overlap in activity between the two years (also known as delta). **148**

Figure 4.12: Changes in the density of time stamps for three mammal species on edge sites during survey A (2017/18, solid line) and survey C (2019/20, dotted line). Grey shaded area indicates the overlap between activity between the two years (also known as delta). **150**

Figure 4.13: Changes in the density of time stamps for two mammal species on control sites during survey A (2017/18, solid line) and survey C (2019/20, dotted line). Grey shaded area indicates the overlap between activity between the two years (also known as delta). **151**

Figure 5.1: The dominant small livestock species that is farmed in the Karoo, a dorper sheep with her weaned offspring (left). Lambs are often targeted by predator species (right) driving retaliatory measures by farmers and fuelling conflict between stakeholders on how best to reduce predation. Images captured during extensive camera trap surveys in SKA region of the Karoo, South Africa (© Michelle Blanckenberg). **169**

Figure 5.2: The four main predator species that are considered to pose a threat to livestock in SKA region of Karoo. Black-backed jackal (A) and caracal (B) are considered extremely problematic, while chacma baboon (C) and cape fox (D) are considered moderately problematic. Images captured through extensive camera trap surveys in SKA region of the Karoo, South Africa (© Michelle Blanckenberg). **173**

Figure 5.3: Boxplots representing photographic rates (RAIs) for four predator species as well as combined predator RAI on three farm types (core, edge and control) over three survey years (A = 2017/18, B = 2018/19 and C = 2019/20). Shaded boxes indicate lower quartile, median (thick black line) and upper quartile for RAIs, while black dot indicates mean RAI with error bars representing standard error. **181**

Figure 5.4: Camera trap (camera icons) survey design across the nine small livestock farms showing camera station were either black-backed jackal or caracal were captured over the three survey years (red camera icons = survey A only, yellow camera icons = survey B and C collectively, blue camera icons = where survey A, B and C overlap). Map includes core (n=3 with 44 cameras), edge (n=3 with 43 cameras) and control farms (n=3 with 52 cameras) with cameras placed at regular intervals on a randomly situated 2 x 2 km grid. Core 1 = Janseboom, Core 2 = Jas Kloof, Core 3 = Lovedale, Edge 1 = Hondeblaf, Edge 2 = Rietpoort, Edge 3 = Gannabos Leegte, Control 1 = Hoezar-Wes, Control 2 = Leeuwkrans and Control 3 = Skurwekloof. **183**

Figure 5.5: Daily activity patterns of black-backed jackal on core (A), edge (B) and control (C) sites during survey A (2017/18, solid line) and survey C (2019/20, dotted line). Grey shaded area indicates the overlap in activity between the two survey years (also known as delta). **186**

Figure 5.6: Daily activity patterns of black-backed jackal during survey C on three different farm types. A indicates comparisons between core (solid line) and control farms (dotted line), B indicate comparisons between core (solid line) and edge (dotted line) sites and C indicates comparisons between edge (solid line) and control (dotted line) sites. Grey shaded area indicates the overlap between activity between the two years (also known as delta). **187**

Figure 5.7: Daily activity patterns of combined predators (excluding baboon) on core (A), edge (B) and control (C) sites during survey A (2017/18, solid line) and survey C (2019/20, dotted line). Grey shaded area indicates the overlap between activity between the two years (also known as delta). **189**

Figure 5.8: Daily activity patterns of combined predators (excluding baboon) during survey C on three different farm types. A indicates comparisons between core (solid line) and control farms (dotted line), B indicate comparisons between core (solid line) and edge (dotted line) sites and C indicates comparisons between edge (solid line) and control (dotted line) sites. Grey shaded area indicates the overlap in activity between the two years (also known as delta). **190**

Figure 5.9: The functional diversity of four predator species, five wild mammal prey species and one domestic mammal prey species on three farm types (core, edge and control) across three survey years (A = 2017/18, B = 2018/19 and C = 2019/20), grouped according to functional group and log body mass (g). Each circle represents a specific species within a community, circle size reflects photographic rate (RAI). Circle colour indicates level of persecution within a specific farm type and survey year **192**

Figure 5.10: Correlation plots of the number of livestock farmers perceived to have been killed by predators and the relative abundance of predators (jackal and caracal combined) for the baseline period: A (2017/18) and two years following the termination of farming activity: C (2019/20). All nine farms are represented. **194**

Figure 5.11: Correlation plots between combined black-back jackal and caracal RAI and number of predicted predators killed from hunting during two survey years (A = 2017/18 and C = 2019/20). All nine farms are represented. 195

Figure 6.1: Location of three surveyed fence sections (red line) along the SKA boundary that separates core and edge farms (black line) included in the study. Grey circles indicate the proposed position of SKA dishes within the core (white polygons) and edge (grey polygons) farms. 214

Figure 6.2: Example of an open active hole dug below the fence with no repairs effected (A) and a scraped hole dug underneath both the fence and the rocks which were placed at the base of the fence to discourage digging (B). 216

Figure 6.3: Example of holes repaired with rocks (A and C), or branches and poles (B and C). 216

Figure 6.4: Example of how holes were measured. Height (orange line) represents the distance from the lowest point in the ground below the fence to the wire, while width (red line) represents largest side to side diameter of the hole. 217

Figure 6.5: Example of how cameras were set up to determine which mammal species utilise a specific hole in the SKA boundary fence between the core and edge farms. Cameras were placed on either side of the fence facing each other, at least 1.5 m away from the hole. 218

Figure 6.6: Number of repaired and open holes found along three different sections of SKA boundary fence separating core and edge farms, during two survey years. 2018 represents the period before farming activities were terminated on core farms, while 2019 represent 12 months after farming activities were terminated on core farms. 225

Figure 6.7: Boxplots representing the size (height x width) of open holes found along three SKA boundary fence sections (section 1, 2 and 3) over two survey years (2018 and 2019). Shaded boxes indicate lower quartile, median (thick black line) and upper quartile for height x width, while black dots indicate the mean and error bars representing standard error. 226

Figure 6.8: Sample-based rarefaction curves of wild mammals captured moving along SKA boundary fences on both the core and edge sides of the fence during two different survey years (A = 2018 before farming activities were terminated on core farms, and B = 2019 twelve months after farming activities were terminated on core farms). Shaded areas represent 95% confidence interval drawn from 1000 randomisations performed with replacement. Solid lines indicate observed richness, while dotted lines indicate expected species richness. 229

Figure 6.9: Boxplots representing the RAI of all mammals on either side (core and edge) of three SKA boundary fence sections (section 1, 2 and 3) over two survey years (A = 2018 and B = 2019). Shaded boxes indicate lower quartile, median (thick black line) and upper quartile for height and width, while black dots indicate mean RAI with error bars representing standard error. 232

Figure 6.10: Boxplots representing overall predator (jackal and caracal) RAI on either side (core and edge) of three SKA boundary fence sections (section 1, 2 and 3) over two survey years (2018 and 2019). Shaded boxes indicate lower quartile, median (thick black line) and upper quartile for height and width, while black dots indicate mean RAI with error bars representing standard error. 233

Figure 6.11: Boxplots showing the RAI of all mammal species using holes over two survey years (A = 2018 and B = 2019). Direction of movement indicates which farm type a species originated from and towards which farm type the species was moving. Shaded boxes indicate lower quartile, median (thick black line) and upper quartile for height and width, while black dots indicate mean RAI with error bars representing standard error. 234

Figure 6.12: Relative abundance (per 30 trap nights) of mammal species moving along fences compared to relative abundance of species using fence holes along three fence sections of SKA boundary fence during 2018 (before the cessation of farming activities on core farms). RAI represents combination of both core and edge side of the fence. 237

Figure 6.13: Relative abundance (per 30 trap nights) of mammal species moving along fences compared to relative abundance of species using fence holes along three fence sections of SKA boundary fence during 2019 (after the cessation of farming activities on core farms). RAI represents combination of both core and edge side of the fence. 238

Figure 6.14: Boxplots representing RAI of predator species (jackal and caracal) using holes over two survey years (2018 and 2019). Direction of movement indicates which farm type a species originated from and towards which farm type the predator was moving. Shaded boxes indicate lower quartile, median (thick black line) and upper quartile for height and width, while black dots indicate mean RAI with error bars representing standard error. **239**

Figure 6.15: nMDS based on Jaccard-index of similarity of number of hole use events of all 34 camera trapped holes across three SKA boundary fence sections for two survey years (2018 and 2019), overlaid with a repaired holes per km surface (grey contour lines) (Stress value = 0.23). Fence section is indicated by distinct symbols. **241**

Figure 6.16: Incidence of 'problem' mammal species found dead along fence section 1 (top images) and section 3 (bottom images) as a result of trapping or hunting by humans. Animals were often staged on top of bushes (A – cape porcupine *Hystrix africaenustralis*), near old holes (B - caracal *Caracal caracal* and cape fox *Vulpes chama*) or placed in one common area near fences (C – multiple porcupine skeletons, and D – pile of black-backed jackal *Canis mesomelas* and cape fox bones) (© Michelle Blanckenberg). **247**

Figure 7.1: Lefthand image shows example of artificial water point on control farm 2, including wind pump and water reservoir. Troughs are typically attached to reservoirs with a pump so animals can access water. Righthand image shows interior farm fence and gate on control farm 3. These fences are typically a series of single wire strands (ca. four strands) and are not predator proof (© Michelle Blanckenberg). **270**

LIST OF APPENDICES

App 3.1: Pearson's similarity coefficients between continuous environmental covariates. Grey shaded boxes indicate significant correlations (< -0.6 and > 0.6). **98**

App 3.2: Visual representation of Pearson's similarity coefficients between continuous environmental covariates, dark red and blue indicate strong correlations while light red and blue indicate weaker correlations. Habitat complexity = Hab. Comp, PFGs = plant functional group richness, Total.Veg.Cover = overall vegetation cover, Shrub 0.5 = shrubs below 0.5 m in height, Shrub 1 = shrubs between 0.5 and 1 m in height, Shrub 1.5 = shrubs between 1 and 1.5 m in height, Shrub 2 = shrubs between 1.5 and 2 m in height, Cover = above ground plant cover and BC = basal plant cover. **99**

App 3.3: Model validation graph for top small mammal abundance (per farm) model showing predicted versus fitted residuals (top graph), residual versus predicted values spread (bottom left), sample versus theoretical quantile spread (bottom middle) and distribution of data (bottom right). **100**

App 3.4: Model validation graph for top small mammal abundance (per habitat and farm) model showing predicted versus fitted residuals (top graph), residual versus predicted values spread (bottom left), sample versus theoretical quantile spread (bottom middle) and distribution of data (bottom right). **101**

App 3.5: Model validation graph for top vegetation model showing predicted versus fitted residuals (top graph), residual versus predicted values spread (bottom left), sample versus theoretical quantile spread (bottom middle) and distribution of data (bottom right). **102**

App 3.6: Ordination results for the first two axes (Figure 3.16) from canonical correspondence ordination analyses to assess the environmental factors associated with differences in small mammal communities in two different survey years (2017 and 2019). Strong correlations (> ± 0.60) are given in boldface. **103**

App 3.7: Mean shrub cover (%) (± standard error) in different height categories per farm type over two survey years, 2017 (before cessation of farming activities on the core) and 2019 (after cessation of farming activities on the core). Shrub cover is divided into four height group, below 0.5 m, between 0.5 and 1 m, between 1 and 1.5 m and between 1.5 and 2 m. Cover indicates abundance or count (as a **104**

percentage) of a particular shrub height group. Coefficient of variation (CV = sd/mean) indicated by [ ] and italicised. CV ≥ 0.3 indicates a relatively high variation and is highlighted in bold.

App 3.8: Number of positively identified small mammal individuals per cryptic species (based on genetic identification of 2017 samples) as well as overall species richness (including cryptic species and non-cryptic species) for each farm in three different farm types (core, edge and control). **104**

App 3.9: Standardised MNA for small mammal taxa found on nine different farms within three farm types (core, edge and control) during two survey years (2017 = before cessation of farming activities on core farms and 2019 = after cessation of farming activities on core farms). Macroscelididae spp. = *Macro* spp., *Rhabdomys pumilio* = *R. pumilio, Gerbilliscus paeba* = *G. paeba, Micaelamys* spp. = *Mic* spp. and *Desmodillus auricularis* = *D. auricularis*. **105**

App 3.10: Total standing biomass (g) of small mammal taxa captured during two surveys years (2017 and 2019) across three farm types (core, edge and control) as well as total standing biomass per farm type. Values in bold show average standing biomass (± standard error) (referred to as 'Ave. total') per farm type. Standing biomass was standardised per 1000 trap nights. **106**

App 4.1: AIC values for negative binomial GLMER (response variable ENS and J') and LMER (response variable H') and corresponding null models. Where null AIC is less than model AIC variance in data is a result of random variation rather than response variable. **161**

App 4.2: Rank abundance distributions for three farm types (core, edge and control) over three survey years (A = 2017/18 before sheep were removed on core farms, B = 2018/19 six months after sheep were removed on core farms and C = 2019/20 eighteen months after sheep removal). Species are ranked along the x-axis according to decreasing proportion of abundance based on farm type level RAIs. **162**

App 4.3: Deviance criteria for five types of models (null, pre-emption, lognormal, Zipf and Zipf-Mandelbrot) fitted to rank abundance distributions of species seen within three farm types (core, edge and control) across three survey years (A = 2017/18, B = 2018/19 and C = 2019/20). **163**

App 4.4: ANOVA results comparing FDis measures for three different farm types (core, edge and control) during three different survey years (A = 2017/18, B = 2018/19 and C = 2019/20). **163**

App 5.1: Model validation graph for top predator (black-backed jackal only) model showing residual versus predicted values spread (left), sample versus theoretical quantile spread (middle) and distribution of data (right). **204**

App 5.2: Model validation graph for top predator (caracal only) model showing residual versus predicted values spread (left), sample versus theoretical quantile spread (middle) and distribution of data (right). **204**

App 5.3: Model validation graph for top predator (all species combined) model showing residual versus predicted values spread (left), sample versus theoretical quantile spread (middle) and distribution of data (right). **204**

App 5.4: Word cloud illustrating farmer perceptions toward predator species within the SKA region of the Karoo, South Africa. Images were derived from interviews with eight of the nine landowners within the study site that were still actively farming core, edge and control farms during survey A (before sheep were removed on the core farms and a protected area was established). Size of words indicates the frequency the word was used when landowners were asked specific questions. **205**

App 5.5: Word cloud illustrating farmer perceptions toward predator species within the SKA region of the Karoo, South Africa. Images were derived from interviews with eight of the nine landowners within the study site that were still actively farming core, edge and control farms during survey C (eighteen months after sheep were removed on the core farms and a protected area was established). Size of words indicates the frequency the word was used when landowners were asked specific questions. **205**

App 5.6: Naïve occupancy and photographic rate of four predator species on nine different farms in three surveys A, B and C (A = 2017/18, B = 2018/19 and C = 2019/20). Farms were categorised according to their geographical location as either within the SKA protected area (core), on the edge of the protected area (edge) or at least 50km from the edge of the protected area (control). Naïve **206**

occupancy indicates the proportion of camera stations where a species was detected. Data extracted from Chapter 4 - Table 4.4, 4.5 and 4.6.

App 5.7: Estimated number of livestock lost to predators (per year) and estimate number of predators (jackal and jackal) killed by farmers (per year) for nine different farms within the SKA region during two different survey years. **206**

App 6.1: Summarised results for black-backed jackal and caracal seen along fences during two survey years (2018 and 2019) along three sections of SKA boundary fence (core and edge side). Photographic rate (also known as relative abundance index) indicates the trapping rate of a species per 30 trap nights. **249**

App 6.2: Summarised results for black-backed jackal and caracal using fence holes over two years (2018 and 2019) along three sections of SKA boundary fence (core and edge side). Photographic rate (also known as relative abundance index) indicates the trapping rate of a species per 30 trap nights. **249**

App 6.3: Model validation graph for top ‘number of fence hole use events’ model showing predicted versus fitted residuals (top graph), residual versus predicted values spread (bottom left), sample versus theoretical quantile spread (bottom middle) and distribution of data (bottom right). **250**

App 6.3: Model validation graph for top ‘number of fence hole use events in 2018’ model showing predicted versus fitted residuals (top graph), residual versus predicted values spread (bottom left), sample versus theoretical quantile spread (bottom middle) and distribution of data (bottom right). **251**

App 6.4: Model validation graph for top ‘number of fence hole use events in 2019’ model showing predicted versus fitted residuals (top graph), residual versus predicted values spread (bottom left), sample versus theoretical quantile spread (bottom middle) and distribution of data (bottom right). **252**

App 7.1: Summary of major findings from different survey techniques (i.e. vegetation, small mammal, camera trap, longitudinal and fence) of the research presented in this thesis, as well as limitations specific to each survey. **272**