Exploring the influence of management practice on mesopredator and herbivore occupancy and interactions

By

Deborah Jean Winterton

Submitted in fulfilment of the requirements for the degree Magister Scientae in the Faculty of Science at the Nelson Mandela University, George, South Africa

March 2019

Supervisor: Dr J.A. Venter
Co-supervisor: Dr Nicola van Wilgen
Declaration

I, DEBORAH JEAN WINTERTON (218211341), hereby declare that the dissertation for Magister Scientae in the Faculty of Science is my own work and that it has not previously been submitted for assessment or completion of any postgraduate qualification to another University or for another qualification.

__________________       ________________
DEBORAH JEAN WINTERTON       DATE

06/12/2018

Official use:
In accordance with Rule G5.6.3,
5.6.3 A treatise/dissertation/thesis must be accompanied by a written declaration on the part of the candidate to the effect that it is his/her own work and that it has not previously been submitted for assessment to another University or for another qualification. However, material from publications by the candidate may be embodied in a treatise / dissertation / thesis.
Abstract

Ecological studies need to consider ecological interactions between species and their environment across trophic levels. This complexity not only makes the study of ecology very challenging but it also means that ecosystems are vulnerable to change as a disruption at any of the levels could result in cascading effects through the hierarchy. This sensitivity to change makes it especially important to understand ecosystem function as this is needed for effective and adaptive conservation management. A key way in which humans drive and change ecosystem function is through land use and associated management practice. A primary objective of many protected areas is restoration of natural function through re-introduction of large ungulates, which are often fenced and small, thus requiring intensive management that can influence ecosystem function. This is true of the West Coast National Park (the park). Small antelope abundance, and associated drivers, in the contractual Postberg section of the park have been a long-term management question. Postberg is a small (1800 ha) fenced and isolated section of the park which was historically used for agriculture (livestock grazing and some cultivation) and later large wild ungulate species were re-introduced and kept at high densities. The perception of a lower abundance of small antelope has been attributed to predation by a mesopredator (Caracal caracal), however interspecific competition and habitat quality is also known to influence species abundance. Therefore, I aimed to explore the potential mechanisms of small antelope occurrence in the region and how this might differ across three sites with different management practices.

Using 18 camera traps, I documented the occurrence of small, medium and large ungulates and caracal. My study spanned across three areas that each represented different forms of management practice with regards to fencing, and stocking rates of managed ungulate species. I made use of single-season, single-species occupancy models in R to assess occupancy of small antelope and caracal and I used the abundance induced heterogeneity model to estimate abundance of managed ungulates. I employed the single-season, two-species occupancy model in PRESENCE to explore species co-occurrence and interactions. Activity patterns and temporal overlap between managed ungulates, small antelope and caracal were assessed using the overlap and activity packages in R.

Vegetation height appears to be an important driver of common duiker occupancy. Fallow lands were strongly favoured by managed ungulates suggesting that they may be utilising these patches for foraging. Small antelope occupancy was highest outside of the park and caracal detections were lowest outside of the park. The low detection of caracal across all areas, along with the known diet of caracals, suggests that predation is not likely the driver of small antelope occurrence. Our data suggest that co-occurrence between small antelope and
managed ungulates is high and that these sympatric species have probably partitioned food resources. I found that small antelope were mostly crepuscular, managed ungulates more diurnal while caracal were primarily nocturnal. There was a high overlap between small antelope and managed ungulate activity while overlap between caracal and small antelope indicates some temporal partitioning.

Overall I found some effects of inter-specific interactions at the local scale. There was, however, no consistent pattern across the areas which, in line with literature, suggests large scale ecological trends are difficult to detect at local scales. Due to the heterogeneity of the region’s vegetation, coupled with the small size of the biome and extensive fragmentation by land use, there are few areas which adequately represent the biome to test how large ungulates would utilise the area at a large scale. This has important implications for the management of small protected areas in the region who are mandated to restore these areas to their historical and natural function. The ability of conservation managers to meet objectives of restoring parks to their historical function, and maintaining these systems as such, may be questioned if our protected areas are not meeting the spatial requirements of re-introduced species.
Publication and presentations related to this research

**Papers in preparation**
Chapter 2: Winterton, D.J., van Wilgen, N.J. and Venter J.A. How management practice influences small antelope and mesopredator occupancy and detection in the West Coast, South Africa. In prep for submission

Chapter 3: Winterton, D.J., van Wilgen, N.J. and Venter J.A. Exploring how the presence of large-bodied managed ungulates influences occupancy and temporal activity of small antelope. In prep for submission

**Presentations**


Authors contributions:
DJW, NvW and JV conceptualized the research project. DJW collected, processed and analysed the data, designed and wrote the dissertation and manuscripts. NvW drafted initial R code and assisted with data analysis. JV and NvW provided valuable comments on the dissertation and manuscripts.
# Table of Contents

Declaration ..................................................................................... i  
Abstract .................................................................................. ii  
Publication and presentations related to this research ...................... iv  
   Papers in preparation ................................................................ iv  
   Presentations ........................................................................ iv  
List of Figures ............................................................................... viii  
List of Tables ............................................................................ xi  
Supplementary material ................................................................. xii  
Acknowledgments ................................................................. xiii

Chapter 1: General introduction .................................................. 1  
   Introduction ........................................................................... 2  
   Populations .......................................................................... 2  
   Interactions ........................................................................... 3  
   Communities and ecosystems ................................................... 5  
   People and nature: Anthropogenic impacts on ecosystem function .......... 6  
      Land use and management practice: impacts on species occupancy and activity .... 7  
   Methods for detecting species .................................................. 9  
   Study area and focal species ................................................. 10  
      Study area ........................................................................ 10  
      Focal Species ................................................................... 12  
   Aims and objectives ................................................................ 15  
   Outline of dissertation ........................................................... 17  
   References ............................................................................ 19  

Chapter 2: How management practice influences small antelope and mesopredator occupancy and detection in the West Coast, South Africa .............................................. 26  
   Abstract ................................................................................ 27  
   Introduction ........................................................................... 28  
   Materials and methods ............................................................. 30  
      Study area ......................................................................... 30
Can you tell what’s for dinner?
List of Figures

Chapter 1:

Figure 1: Map of the study area, showing the three management scenarios and underlying vegetation types. ................................................................. 12

Figure 2: Predictions diagram illustrating my predictions across the three scenarios. I predicted that the higher managed ungulate abundance would result in increased competition between small antelope and managed ungulates at Posterg and the farm. I predicted a lower overall vegetation height and abundance of small antelope at both Postberg and the farm attributed to the higher abundance of managed ungulates and I expected a lower abundance of mesopredators at the farm due to the surrounding predator suppression. ............................................................. 17

Chapter 2:

Figure 1: Map of the study area, showing the three management scenarios and underlying vegetation types. ................................................................. 30

Figure 2: Study species; A = subset of the most common managed ungulates encountered (A1 = eland, A2 = bonsmara cattle, A3 = sheep), B = mesopredator (caracal), C = small antelope (C1 = steenbok, C2 = common duiker). ................................................ 32

Figure 3: Medium ungulate abundance across sites for each of the management scenarios. Significant differences (p < 0.05) are indicated by * between groups that differ and NS indicates no significant difference. Significance is displayed in the middle of the two groups being compared. ................................................................. 39

Figure 4: Large ungulate abundance across sites for each of the management scenarios. Significant differences (p < 0.05) are indicated by * between groups that differ and NS indicates no significant difference. Significance is displayed in the middle of the two groups being compared. ................................................................. 39

Figure 5: Caracal detection probability (± SE bars) across sites for each of the management scenarios. Since no co-variates were useful predictors the output value was constant across all sites therefore results could not be plotted with a box plot. Significant differences (p < 0.001) are indicated by *** between groups that differ. Significance is displayed in the middle of the two groups being compared. .... 41

Figure 6: Duiker occupancy across sites for each of the management scenarios. Significant differences (p < 0.001) are indicated by *** between groups that differ. Significance is displayed in the middle of the two groups being compared. ...................... 41

Figure 7: The influence of vegetation height on common duiker occupancy in Langebaan and Postberg. Note that it was not possible to model the effect of covariates on common duiker occurrence in Lambert’s Bay due to 100% occupancy. ....................... 42
Figure 8: Steenbok occupancy (± SE bars) across sites for each of the management scenarios. Significant differences (p < 0.001) are indicated by *** between groups that differ. Significance is displayed in the middle of the two groups being compared. .......................... 43

Figure 9: Cumulative photographic captures of common duiker across management scenarios. ................................................................. 43

Chapter 3:

Figure 1: Map of the study area. ................................................................. 66

Figure 2: Managed ungulate temporal activity level of across the different areas (A) and overlap between the Langebaan and Postberg areas (B). Time of day is displayed on the x-axes with midday in the middle and the fitted kernel-density on y-axes. In B the coefficient of overlap (Δ) and the associated estimator used (number in subscript), along with the 95% confidence intervals in parentheses, is illustrated by the grey shaded area which shows the period of overlap. The vertical dotted lines represent the earliest and latest sunrise and sunset times across the study period. The dashed vertical lines along the x-axes indicates the sample size of time-of-day observations. ρ is derived based on a Watson-Wheeler test of homogeneity for circular data. ................................................................. 74

Figure 3: Small antelope temporal activity levels across the different areas. No absolute differences in temporal data distribution were detected. Overlap between areas ranged between 84% and 89%. The vertical dotted lines represent the earliest and latest sunrise and sunset times across the study period. The dashed lines along the x-axis indicate the sample size of time-of-day observations for each area. Time of day is displayed on the x-axis with midday in the middle and the fitted kernel-density on y-axis. ................................................................. 75

Figure 4: Temporal overlap estimates between small antelope and managed ungulates at the three areas with time of day starting and ending at midnight on the x-axes and the fitted kernel-density on y-axes. The grey shaded area indicates overlap and is described by the coefficient of overlap (Δ) and the associated estimator used (number in subscript) along with the 95% confidence intervals in parentheses. The vertical dotted lines represent the earliest and latest sunrise and sunset times across the study period. ρ is derived based on a Watson-Wheeler test of homogeneity for circular data. Dashed lines along the x-axes indicate the sample size of time-of-day observations. ................................................................. 76

Figure 5: Caracal activity across Postberg and Langebaan areas with time of day starting and ending at midnight on the x-axis and the fitted kernel-density on y-axis. Vertical
dotted lines illustrates sunrise and sunset periods during the study. Vertical lines along the x-axis show the sampled time-of-day observations across the diel cycle.

Figure 6: Overlap between caracal, steenbok and common duiker activity in the Langebaan area. Time of day starting and ending at midnight on the x-axes and the fitted kernel-density on y-axes. The grey shaded area indicates overlap and is described by the coefficient of overlap (Δ) and the associated estimator used (number in subscript) along with the 95% confidence intervals in parentheses. The vertical dotted lines represent the earliest and latest sunrise and sunset times across the study period. ρ is derived based on a Watson-Wheeler test of homogeneity for circular data. The dashed lines along the x-axes indicate the sample size of time-of-day observations. Time of day is displayed on the x-axes with midday in the middle and the fitted kernel-density on y-axis.
List of Tables

Chapter 2:

Table 1: Data collected on potential site- and observation-level co-variates that were used to model detection ($\rho$) and occupancy ($\psi$) for the different species as well as the source of the data. Effort was the only observation level co-variates considered. 34

Table 2: Model selection for estimating large and medium ungulate abundance across sites, $\rho =$ detection probability and $\psi =$ probability of occurrence. Co-variates used in the model are indicated in brackets while ( ) indicates no co-variates were used. 37

Table 3: Top three models for common duiker, the third best model was used to estimate occupancy across sites and included effort for detection and scenario and height for occupancy, $\rho =$ detection probability and $\psi =$ probability of occurrence. ........... 42

Chapter 3:

Table 1: Occupancy parameters that were assessed for the two-species occupancy models in PRESENCE. ................................................................. 69

Table 2: Time-of-day observations for the species of interest across the three areas. ... 70

Table 3: Site occupancy and associated standard error (SE) for managed ungulates (LU = large ungulate, MU = medium ungulate, LV = livestock) and small antelope (SA = small antelope, SB = steenbok, CD = common duiker) interactions at two scenarios (Langebaan and Lamberts Bay). Managed ungulates are modelled as the dominant species while small antelope as the subordinate. Parameters are described in table 1. ................................................................. 72
Supplementary material

Chapter 2:
Postberg pre-cull camera survey methods. ................................................................. 53
Supplementary Figure 1: Co-variate correlation matrix. ........................................... 54
Supplementary Figure 2: Managed ungulate (large and medium) and small antelope
detections (y-axis) on fallow (1) versus non-fallow (0) lands (x-axis) in the park.
There was no 2016 data available for the Langebaan section and no detections of
small antelope were made in Postberg in 2017. No fallow lands were present on the
farm. ....................................................................................................................... 55
Supplementary Figure 3: Estimated eland abundance pre (Postberg 2016) and post
(Postberg 2017) removal of eland and kudu, significant differences (p < 0.001) are
indicated by *** between groups. ....................................................................... 55
Supplementary Figure 4: Vegetation height across management scenarios showing no
significant difference (NS) between groups, but lower variation at Lamberts Bay.
.......................................................................................................................... 56
Supplementary Figure 5: Slope across management scenarios showing significant
difference (p < 0.05) which are indicated by * between groups that differ. ...... 56
Supplementary Table 1: Model performance for steenbok occupancy. The top model (mod1)
only included effort for detection and scenario for occupancy. ......................... 57

Chapter 3:
Supplementary Figure 1: Detection maps of small antelope and managed ungulates across
the three study areas. Points represent camera sites and the size of the black dots represents
the frequency of detection at each site. Red circles indicate sites which were fallow lands. X-
axes are longitude while y-axes are latitude. ......................................................... 84
Acknowledgments

Firstly, I thank my animals. To my dog, River, who has been with me for almost 10 years; thank you for not disowning me during this difficult time. You are a wise old hound and I know that you always knew why I couldn’t leave my desk to take you for a walk. To my horse, Crusader, who has been with me for 6 years; thank you for giving me those epic gallops down Noordhoek beach which kept me alive, both mentally and physically. To my cat, Jess, who has been with me for an unknown amount of time; thank you for catching rats (sometimes).

Secondly, I thank Guy Chaston, best barrister in the south, your amazing coffee and hugs prepared me for each and every day.

Most of all, I must thank my co-supervisor, colleague and friend, Dr Nicola van Wilgen. Thank you for being my support in every way. It’s not easy doing a degree part time where you lack the support, discussion and camaraderie that you get at a university. You were all that for me and more. Thank you for the much needed attitude adjustments. Of all your student children (still to come) I will probably always be the problem child. Thanks for sticking with and believing in me. You are the best and I owe you.

To my supervisor, Dr Jan Venter; thank you for your dedication, especially towards the end. Thank you also for your insightful comments which encouraged me to think laterally.

To my family; thank you for understanding why I declined so many braai invites – we can braai again soon. To my mom; thank you for offering to type out my dissertation, but thank God I didn’t have to write it out by hand (I’ve come a long way since my diploma)!! 😊

Towards the end I started referring to this document as the swampland of my soul and it really was. So thanks to everyone who helped me get out – I appreciate it.

Peace and love to all!
Chapter 1: General introduction
Chapter 1

Introduction
Individual organisms have evolved physiological, behavioural and anatomical traits according to variation within their environment. Individuals compensate for environmental variation, across space and time, through regulating body temperature, water content and by optimizing foraging to maintain levels of energy intake (Molles 1999). Thus, the environment essentially determines species distribution and abundance, which shapes populations (Molles 1999) and social organisation (through individual traits in animals) (Jarman 1974). Different species populations interact with and sustain one another through the provision of nutrients. These interactions, such as predation, herbivory and competition, play a fundamental role in shaping communities and regulating populations (Duffy 2003; Schmitz et al. 2000; Woodward et al. 2005). A community is described as an association of interacting species (populations) within a defined area (Molles 1999), where each of the species fall on a specific level of the food chain (depending on whether they are classified as producers or consumers), which are also known as trophic levels. The collective communities of organisms that occur together within an area, and the complex set of interactions between individuals, populations and their environment, form what are known as ecosystems (Molles 1999; Tansley 1935).

Populations
Environmental conditions play a pivotal role in species occurrence, distribution and abundance (the fundamental characteristics of populations) and are, essentially, an enabler of reproduction (Molles 1999). Individual species occupy a specific niche; some species can tolerate a wide range of environmental conditions while other species have a low tolerance for environmental variation and require specific conditions (Rabinowitz 1981). The adaptation of the individuals to their environment dictates the population size and social organisation of the species. Population size (abundance or density) and how it changes is an essential concept of ecology (Molles 1999) and monitoring associated vital rates (birth and death rates, immigration and emigration) is important for assessing population status and change (O’Connell and Bailey 2011).

Body size and physiology shape populations
An animal’s anatomical and physiological characteristics affect its diet and food choice, determining animal intake (carnivores) versus plant intake (herbivores) (Shipley 1999). The cellular structure of plants make them difficult to digest and extract required nutrients and therefore herbivores rely not only on specialised digestive tracts, but also on symbiotic gut microbes that provide assistance by fermenting plant material and breaking down cell walls. Grass and browse also have different digestibility and thus the digestive systems of grazers and browsers differ (Demment and van Soest 1985; Jarman 1974). Body size of herbivores
influences diet and food choices. Larger herbivores have longer gut retention times, thus enabling them to process lower quality forage. However, they require large quantities of food whereas the inverse is true for small herbivores (Hopcraft 2010). Mouth morphology also differs between grazers and bowser (Shipley 2007). Grazers have wide mouths and this maximizes their bite size (i.e. how much food can fit in their mouth with one bite) for grazing a continuous distribution of grasses. Browsers, instead, have narrower mouths with unevenly sized incisors which are quite upright and this promotes more selectivity (Shipley 1999).

Body size often dictates spatial requirements as well as social organisation and intraspecific co-existence (Hopcraft et al. 2010; Illius and Gordon 1992; Jarman 1974). Selective feeders (generally with a smaller body size) are often solitary or occur in pairs since their food is scarce and needs to be sought out, whereas the generalist feeders (generally having a larger body size) can occur in larger groups (Jarman 1974). The solitary species are often territorial and these populations then tend be evenly distributed across the landscape because each individual occupies a defined home range, whereas those species that congregate in large groups tend to be distributed in clumps (Molles 1999).

**Interactions**

Populations of different organisms that occur within the same area interact with one another in the form of competition, exploitation (herbivory, predation, parasitism and disease) and mutualism (Molles 1999). Individuals are subject to intra- and interspecific competition where individuals compete for resources; whether it be food, space, the right to reproduce or all of these factors. Intraspecific competition shapes individual characteristics, but is driven by the resource requirements of the individual and the resource availability (Lott 1984), which plays an important role in population regulation (Begon et al. 1990; Molles 1999).

**Competition**

Competition not only plays an important role in regulating populations and social structure but is also considered a strong driver of evolution (Murray and Illius 2000; Stauffer 1957), since the fittest individual ‘wins’, enabling them to reproduce and passing on the ‘winning genes’ to the next generation. Because the feeding style of small ungulates is not conducive to group living, they encounter significant intraspecific competition in defending territories (Jarman 1974), but subsequently less intraspecific competition for food. Whereas the larger generalist ungulates are more social and move at similar average foraging speeds (because their food source is more evenly distributed) they therefore encounter significant intraspecific competition in food acquisition (Jarman 1974). However, since larger ungulates have a larger bite size it allows them time to move away from competitors while chewing, thus not reducing
their intake rates (Shipley 2007). Due to body and bite size, large herbivores are generally feeding on a more abundant lower quality forage at higher vegetative levels that are out of the reach of the small ones. Therefore small ungulates tend to spend more time looking for the less abundant, sparsely distributed higher quality forage such as new shoots and leaves (Jarman 1974; Shipley 2007) and this promotes co-existence as there is evidence of resource partitioning (Anderwald et al. 2015; Herfindal et al. 2017) between body sizes. However, overabundance of large herbivores can result in overgrazing (Mysterud 2006) and, since their bite size is bigger and they are not restricted by forage quality, they can outcompete the smaller antelope simply by consuming the high quality parts along with the rest of the plant (Belovsky 1997). This, along with the consequent habitat modification, could impact the behaviour and abundance of smaller antelope either by facilitation or competition (Bakker et al. 2009) or by forcing the smaller antelope to utilise areas of high predation risk in their search for food (Owen-Smith 2015; Owen-Smith and Traill 2017).

**Predation**

All antelope are vulnerable to predation (Jarman 1974). Predator-prey relationships are dynamic and for prey species to persist they need refuges and therefore they employ different strategies to avoid predation. These strategies involve a) avoidance b) flight at detection or c) flight at attack (Jarman 1974). The small solitary antelope tend to rely on an avoidance strategy through crypsis. They occur in habitat that provides sufficient cover to hide and if they are detected they either freeze or dart off through the vegetation, stop and freeze or lie down (Jarman 1974). It has been suggested that group living reduces the risk of predation but increases intraspecific competition for food (Lott 1984). Ungulates that occur in large groups have the benefit of increased vigilance to detect predators, as well as the benefit of safety in numbers, also known as group dilution, and these ungulates tend to flee upon detecting a predator (Hopcraft et al. 2010; Jarman 1974). Large ungulates are also known to defend themselves by pursuing predators as a group (Jarman 1974). It is argued that predation has the greatest influence on prey abundance when the prey species falls within a nested prey base of both large and medium sized carnivores which maximizes predation risk by a higher number of enemies (Hopcraft et al. 2010; Jarman 1974). However, this is most prominent in areas that have a high predator species diversity. For example, leopard (*Panthera pardus*), cheetah (*Acinonyx Jubatus*) and wild dog (*Lycaon pictus*) all showed a high prey preference for impala in Kruger National Park (Owen-Smith and Mills 2008), however this research also argued that each predator displayed a preference for prey that is equal to or slightly larger than its own size and that the top-down effect that predation has on prey abundance cannot be assessed solely on the number of predator species present in a system. The effect that predators have on prey species is not only lethal. Predators also affect prey species by driving
the development of avoidance or defensive strategies, the costs of which can include: reduced energy income for increased vigilance, increased vulnerability to other predators due to a shift in habitat use or reduced mating success (Preisser et al. 2005). Therefore it is also important to consider the non-lethal influence that predators have on prey species (Lima 1998).

Finally, it is important to consider that predation and competition act synergistically in shaping ecosystems. It is argued that abiotic resources (which dictate quality and quantity of forage), trade-offs related to body size, and adaptive behaviours (e.g. migration and group vigilance) and the extent and frequency of disturbances, all affect how predation and competition structure communities (Hopcraft et al. 2010). To summarise, each species within an ecosystem plays a role in determining the persistence of and competitive forces that may act on other species, sometimes across the different trophic levels. As such, the removal of or introduction of a species or the contraction or expansion of a population, can have marked effects on communities and ecosystem function.

Communities and ecosystems
A community is defined as groups of organisms living in the same place at the same time, delimited by geography (Fauth et al. 1996). Exploitation is an important driver that shapes communities and the simplest way of summarising feeding relationships (i.e., who eats who) within a community is through a food web which can be complex, especially in communities of high species diversity (Molles 1999). The traditional food chain signifies a top-down or bottom-up relationship between the trophic levels where abiotic factors (such as climatic conditions) govern primary production, which sustains herbivores which, in turn, are consumed by carnivores. As such, herbivores are regulated by either primary production (bottom-up) or predation (top-down) processes (Hopcraft et al. 2010; Jarman 1974). Top down and bottom up regulation are both influenced by fundamental components i.e. abiotic factors, disturbances, quality and quantity of forage and body size (Hopcraft et al. 2010). The quality and quantity of primary production are constrained by soil nutrient content along with rainfall (Fritz et al. 2002; Hopcraft et al. 2010) and are known to drive the spatial variability of ungulate abundance and community structure (Radloff 2008). This would suggest that ungulate populations that occur in nutrient-poor systems would be limited by resources and that these communities are likely shaped by competition, since the competitive influence is often stronger in ecosystems with poor nutrient status (Fritz et al. 2002).

Within the food web, there are keystone species. These are species that may constitute a low biomass within the web but nevertheless have a strong influence on (and may even control) the structure of communities through their feeding activities (Molles 1999). Top predators are
an example of keystones species within communities (Leibold 1996) and it has been suggested that some predators may encourage species richness by reducing the chance of competitive exclusion (Molles 1999). Top predators interact with herbivores, and consequently plants, in ways that are so profound that the loss of the predator can result in a cascade at the trophic levels below it (Fortin et al. 2005). A trophic cascade is a reciprocal consequence of predator prey interactions that result in altered abundance, biomass or productivity across trophic levels within a community, affecting numerous links in the food web and even extending to nutrient cycling (Pace et al. 1999).

**People and nature: Anthropogenic impacts on ecosystem function**

Humans (*Homo sapiens*) are probably the most influential species on earth, with profound influences on ecosystem function through alteration of habitat structure and resource availability (Blaum 2007; Burgi et al. 2017; Šálek, Drahníková and Tkadlec 2015). The global human population exceeds seven billion individuals (Lutz et al. 2017) and is distributed across the majority of the earth’s land surface. The actions of humans have important consequences at local and global scales. Land use, habitat fragmentation, conversion and degradation are all major global environmental change drivers (Chapin et al. 2000; Kiffner et al. 2015; Newbold et al. 2015). For instance, urbanisation and urban development result in some of the greatest local extinction rates (Mckinney 2002).

An important way in which humans drive change in ecosystem function is through land use and associated management practices. The removal of apex predators from natural systems is a critical action which could be responsible for cascades at multiple trophic levels in numerous systems (Fortin et al. 2005; Suraci et al. 2016). Apex predators regulate prey populations by exerting top-down pressure (Hopcraft et al. 2010). However, it is not just direct predation that matters in shaping communities. For example, the fear of large carnivores (“landscape of fear” hypothesis) alone can alter the foraging behaviour of mesocarnivores (medium sized carnivore) (Suraci et al. 2016). Similarly the removal of apex predators can results in a release of middle ranked predators, i.e. ‘mesopredator release’ (Soulé et al. 1988), which can often cause a decline in abundance of the mesocarnivore’s prey species (Prugh et al. 2009). The release of herbivores from top-down predation pressure can result in increased grazing pressure, thus altering the structure of habitats. The “green world hypothesis” says that predation limits herbivore abundance (which reduces grazing pressure) and therefore, where significant predation pressure is present the main limitation on vegetation is abiotic, whereas in the absence of predation pressure, herbivory plays a mediating role (Hopcraft et al. 2010). For example, the re-introduction of wolves to Yellowstone National Park resulted in the regeneration of aspen trees that had been over-browsed by elk (Fortin et al. 2005).
Due to the human-induced absence of apex predators from numerous systems, there are many areas where large herbivores persist, or have been re-introduced (Penzhorn 1971) and excel both on private land and in protected areas. In South Africa, many of the protected areas where ungulates have been re-introduced are small in comparison to the spatial requirements of the re-introduced species and, since they are fenced, management becomes very intensive (Mysterud 2010), potentially resulting in overabundance and consequent overgrazing or inbreeding and isolation (Hayward and Kerley 2009). Some wild ungulate populations are actively managed to the extent that some question whether they are approaching a semi-domestic state (Mysterud 2010). Large herbivores impact vegetation and ecosystem function through browsing, grazing, trampling and nitrification through urine and faeces (Mysterud 2006). Overgrazing, however, is generally associated with livestock agriculture because domestic livestock are supplied with fodder through the lean season enabling them to be kept at higher densities (Mysterud 2006), as is also the case with some wild ungulates. Traditional nomadic pastoralism has been perceived as destructive to ecosystems but literature suggests that it may have promoted sustainability, especially when compared to established ranches where livestock are spatially restricted and carrying capacity easily exceeded (Coughenour 1991). The impact of keeping livestock at high densities within established farms led to the implementation of grazing systems (Coughenour 1991). Studies have indicated that the stocking of livestock at low densities, under free ranging conditions, can facilitate high quality grazing by promoting herbaceous diversity, which can benefit wild ungulates by creating nutrient hotspots in the landscape (Charles et al. 2017; Fyn et al. 2016; Herfindall et al. 2017). However, direct impacts of livestock on wild ungulates are more commonly negative than positive (Schieltz and Rubenstein 2016). Finally, it is important to consider the influence of interactions between ungulate movement and abundance, plant growth, plant response to grazing and the topography of the landscape (Coughenour 1991). The re-introduction of large herbivores, which inherently have large spatial requirements, into small, fenced protected areas can create instability in ecosystem function due to the restriction of natural herbivore movement, the resultant over-abundance, the consequent overgrazing and habitat degradation (Coughenour 1991; Venter et al. 2015).

Land use and management practice: impacts on species occupancy and activity

Land use influences species diversity and occurrence which has functional consequences for ecosystems (Chapin et al. 2000). Of all land uses, urbanisation is arguably the most consequential as it frequently results in the elimination of the majority of native species, often replacing them with non-native species, and the habitat loss is longer lasting (McKinney 2002). Urban-gradient studies show, for example, that native species diversity decreases towards
urban centres while non-native species increase (McKinney 2002). This trend extends to rural and agricultural areas, although often not as drastically. For instance, species richness decreases along a gradient from protected area to settled farmland in Tanzania (Kiffner et al. 2014).

Although humans have historically had an impact on natural systems, the increasing human population and accelerating land use change are putting these systems under critical strain (Hopcraft et al. 2010). Measuring the impact of human induced changes on ecosystems requires information on population size (abundance or density), animal activity patterns and species interactions (Frey et al. 2017; O'Connell and Bailey 2011). Estimating population and species interaction parameters is a core component of ecology. Occupancy is one such population parameter (Fiske and Chandler 2011), while activity level (the proportion of time that animals are active) is an important behavioural metric (Rowcliffe et al. 2014). Occupancy can broadly be described as the probability that a site or patch is occupied by a target species. As such, occupancy is fundamentally a function of abundance making it a popular method for monitoring populations of species that are not individually recognisable and / or where capture-mark-recapture is not possible (O'Connell and Bailey 2011). The activity levels of species and how they overlap with one another are important for understanding the energy trade-off between activity and rest (Rowcliffe et al. 2014) as well as for assessing co-existence between species and how they partition their time (Ridout and Linkie 2009). Furthermore, activity often means increased risk (i.e. predation and thermal stress) for many species and therefore animals need to augment the time allocated to certain activities to minimise costs but also to meet basic needs (Rowcliffe et al. 2014).

The impact of land use on species abundance, occupancy and richness has been the topic of numerous studies (Kinnaaird and O'Brien 2011; Kok 2016; Ramesh and Downs 2015; Randa and Yunger 2006; Schuette et al. 2013 and Wallgren et al. 2009) and many have found that land use and management practice do indeed influence species abundance and occupancy. For example, serval have been found to be negatively impacted by high cropland use in the Kwazulu-Natal Midlands (Ramesh and Downs 2015). Large herbivores and carnivores are also negatively impacted by land use in the Botswana Kalahari (Wallgren et al. 2009) and many of the larger carnivores are absent from the communal rangelands when compared to freehold rangelands in Namibia (Kauffman et al. 2007). Land use not only impacts species but also species communities and structure (Ramesh and Downs 2015; Wallgren et al. 2009). Researchers are warned of using the response of flagship species alone to make assumptions of how other species may be influenced by land use (Wallgren et al. 2009) as animal interactions can be an important determinant of species distribution and abundance (Lazenby
Chapter 1

and Dickman 2013), highlighting the importance of studying communities rather than individuals.

**Methods for detecting species**

Experiments and observations of behaviour that explore the response of co-occurring species to one another have contributed important information to the understanding of the interactions between predator species as well as between predators and their prey species (Lazenby and Dickman 2013). For example, if two species show inverse spatial and temporal patterns, it may indicate that one species is dominant over the other (Lazenby and Dickman 2013). How prey species respond to predators is fundamental to understanding how, why and where species occur (Tambling et al. 2015). Species interactions are also important when assessing the impact of land use and management practices since habitat can be an important explanatory variable for observed patterns (Lazenby and Dickman 2013). Within the context of the “landscape of fear hypothesis”, prey respond to spatial variations in predation risk by avoiding high risk areas at several spatial scales relating to resource acquisition and range use (Tambling et al. 2015). Likewise, predation risk also varies across temporal scales such as diel cycles, lunar cycles, hourly variation and climatic and seasonal cycles (Tambling et al. 2015). Assessing how prey species' diel patterns change may reveal how species manage resource acquisition and evade predation. The influence of predation risk or resource acquisition on prey space occupancy can be assessed by comparing day and night activity patterns of predator and prey species, since the risk of predation may decline if the prey reduce their activity during peak predator activity (Tambling et al. 2015). For instance the absence of predators correlated with increased nocturnal activity of buffalo (*Syncerus caffer*) and kudu (*Tragelaphus strepsiceros*) in comparison to areas where predators have been re-introduced (Tambling et al. 2015).

Spatial variation and detectability are two important considerations, when sampling animal populations, for proper estimation of state variables and making inference about their change over time and space (MacKenzie et al. 2006). Traditional methods of surveying animal populations and estimating activity include observational counts along transects (Avenant 1993; Owen-Smith and Mason 2005), scat surveys, scent stations, physical capture, harvest per unit effort (O’Connell et al. 2006), track counts (Silveira et al. 2003), or the use of laboratory apparatus such as running wheels (Rowcliffe et al. 2014). These methods however all have limitations to the situations in which they can be applied. More recently, the advent of telemetry, GPS radio collars and camera traps allow for the collection of continuous 24 hour animal activity data (Rowcliffe et al. 2014). Camera traps are especially useful for both population and behavioural observations as they are non-invasive and can record multiple
species over spatial and temporal scales (Lazenby and Dickman 2013) in areas that are difficult to traverse as well as for detecting cryptic and elusive species that can be difficult to study (O'Connell et al. 2011; Tobler et al. 2008). Camera traps are therefore becoming increasingly popular for surveying animal populations.

The use of camera traps explicitly for scientific research can be traced back to the 1920s when Frank M. Chapman (Curator of Ornithology at The American Museum of Natural History in New York) used trip wire cameras to document species on Barro Colorado Island, Panama. Since then, technology has advanced and camera traps have become cheaper, more accessible and available to researchers. Camera traps can be used to estimate occupancy (O’Connell and Bailey 2011), behaviour and activity patterns (Bridges and Noss 2011), density, abundance (O’Brien 2011), as well as to measure species richness and community dynamics (Kery 2011). Camera traps have been used to study numerous carnivore species (Balme et al. 2009; Harmsen et al. 2009; Karanth and Nichols 1998; Long et al. 2010). Further, camera traps are not only useful for monitoring individual species populations but also entire terrestrial vertebrate communities (Kauffman et al. 2007).

Study area and focal species

Study area

Our study was conducted along the west coast of South Africa in the nutrient-poor Fynbos biome. Annual average rainfall varies between 175 mm in the north and 265 mm in the south of the study region, falling predominantly during the winter months. West Strandveld is the predominant vegetation type of the region, within which my study areas are located. It occurs on sandy soils and is characterised by communities of medium dense to closed shrublands and is dominated by sclerophyllous, broad-leaved shrubs (Mucina and Rutherford 2012). This area provides for an interesting case study of community dynamics due to the long history of grazing (regionally) and the variety of management practices employed, particularly the juxtaposition of protected area and managed agricultural land. The vegetation of this greater West Coast area has been exposed to livestock grazing for approximately 2000 years, first by indigenous pastoralists and then later by European settlers (Mucina and Rutherford 2012).

I had three study areas (scenarios) defined by their different management practices, using the ‘stocking rate’ and different species of managed ungulates, as well as the degree of movement restriction imposed by fences and isolation, at each area as a proxy for ‘management practice’. Two areas were within the West Coast National Park (hereafter referred to as the WCNP or park), at the Postberg and Langebaan sections respectively, and the third was on the Nortier agricultural research farm (Lamberts Bay, hereafter referred to as the farm). The park is
located approximately 100 km north-west of Cape Town, while the farm is just outside of the town Lamberts Bay, approximately 100 km north of the park (Fig. 1). Postberg (the northern portion of the Langebaan peninsula) is comprised primarily of elevated granite outcrops (the highest being 193 m above sea level) while the Langebaan section (east of the Langebaan lagoon) consists largely of calcified and unconsolidated sands with the occasional granite outcrop. Surface water in the park is scarce and of a seasonal nature, however the Elandsfontein Aquifer is a source of freshwater to the marshlands of the lagoon (Hanekom et al. 2009) and water points have been constructed for use by animals. The park was originally proclaimed in 1985 to conserve the Langebaan Lagoon and off-shore islands and has since expanded to its current size of approximately 47 000 ha (SANParks 2013). The primary land use within the buffer zone of the park is agricultural (crop cultivation and some livestock), with ever increasing industrial and mining activity (van Wilgen and Herbst 2017).

The Nortier research farm falls under the management of the Department of Agriculture (Elsenburg), Western Cape Government and is 2 780 ha in size and consists of consolidated sand dune fields with deep sandy soils with a low organic carbon content (Mucina and Rutherford 2012). Several resource flocks and herds are kept for the Directorate: Animal Sciences, while it is also the site of veld rehabilitation projects run by the Directorate: Plant Sciences. The sheep (Ovis aries) flock consists of three breeds (namaqua afrikaner, dorper and SA mutton merino), the beef cattle (Bos taurus) are of the bonsmara breed, while there is also a bio-secure ostrich (Struthio camelus) flock, although this flock is restricted to camps that were not surveyed. The farm was selected due to it being in the same bioregion as the areas in the park and of comparable size. The majority of commercial farms along the west coast are predominantly used for crop production with little livestock and are therefore not of a comparable size to the areas within the protected area. The research farm is located in a matrix of other farms where predator control is known to take place. The Postberg scenario has historically been characterised by intensive management of large and medium sized herbivores in a small area (1 800 ha). Postberg was originally acquired in the early 1800s by a group of farmers and was used primarily for winter grazing, but the land was also ploughed. Postberg was proclaimed as a private nature reserve in the 1960s, after which it was contractually included into the WCNP in 1987. Many indigenous and extra-limital large and medium sized ungulate species were introduced to Postberg since the 1960s which perpetuated overgrazing of the small, fenced area. The extent of overgrazing in Postberg is so severe that wild ungulates have been provided with fodder during the lean season to ensure survival of individuals, highlighting the extent of intensive management. The Langebaan section of the park is more open, with few extra-limital or non-native species and less active management of ungulates takes place in this area. This scenario is therefore characterised by
more natural species movement and processes, albeit in the absence of large predators. Here managed ungulates are not confined to a small area, are free ranging and occur at lower density. Historically this area was also used for agriculture which included small livestock and crop production and different portions were proclaimed as part of the park in 1989 and 1996 respectively.

**Figure 1**: Map of the study area, showing the three management scenarios and underlying vegetation types

**Focal Species**

**Small antelope**

Three small antelope species are known to occur in the area, the common duiker, *Sylvicapra grimmia*, the steenbok, *Raphicerus campestris*, and the Cape grysbok, *Raphicerus melanotis*. Both the common duiker and steenbok are common along the west coast of South Africa. Because the grysbok was detected exceptionally infrequently across sites, I focus only on the former two species. Common duiker are widespread throughout Africa south of the Sahara and are not too selective in their habitat requirements. They do not occur in forests and are absent from desert regions, however they can penetrate these areas along water courses that
support enough vegetative cover (Skinner and Chimimba 2005). The presence of shrubs is an essential habitat requirement for common duiker and previous research within the park established that they prefer to inhabit areas where vegetation is higher than 60cm (Heydenrych 1995). Steenbok occur across Southern Africa (Namibia, Botswana, Zimbabwe, Western and Southern Mozambique and South Africa). In South Africa they are widespread through all provinces except Kwazulu-Natal (Skinner and Chimimba 2005). Steenbok inhabit open country and are less dependent on vegetation cover compared to the common duiker. Both steenbok and common duikers are considered browsers (Skinner and Chimimba 2005). They forage very selectively on a wide range of plant species, focussing on very specific plant parts, often restricted to a particular vegetation type and occupying a small home range. Heydenrych (1995) found that both steenbok and common duikers utilise a wide spectrum of plants in the park. It is not certain how steenbok and common duikers partition their resources, but they are frequently observed utilising the same areas (pers. obs.). Both species are solitary, except during breeding, and are thus territorial (Jarman 1974). It is believed that common duikers and steenbok rely on a similar strategy to avoid predation whereby they remain inconspicuous by either temporal partitioning or by relying on vegetation cover (Jarman 1974).

Managed ungulates
I considered ungulates that require the intervention of people to manage or control the population dynamics e.g. through removal, rotation, food provision, introduction or culling on the basis of game census or veld assessment as 'managed species'. Managed species were classified into different size classes according to the weight ranges of the species present at the areas. When mapped the weight ranges naturally segregated into three groups which were classified as follows; animals <25 kg were classified as small herbivores, between 26 – 200 kg were classified as medium herbivores and anything >201 kg was classified as a large herbivore. No managed species was classified in the small herbivore class. Managed species differed across scenarios with bontebok (*Damaliscus pygargus pygargus*), Cape mountain zebra (*Equus zebra zebra*), red hartebeest (*Alcelaphus buselaphus caama*), eland (*Taurotragus oryx*), blue wildebeest (*Connochaetes taurinus*), kudu (*Tragelaphus strepsiceros*), springbok (*Antidorcas marsupialis*) and gemsbok (*Oryx gazelle*) occurring in the Postberg scenario. Managed species at the Langebaan scenario were eland, bontebok and red hartebeest. Of the managed species in the park, only the red hartebeest would have been resident in the area throughout the year prior to human intervention. Cape mountain zebra, bontebok, kudu, gemsbok and springbok are considered extra-limital species (i.e. species that were unlikely to occur in the area historically except potentially as vagrants or for short lived and rare incursions) (Boshoff and Kerley 2001), with the blue wildebeest being a true alien to
the locality. Eland would most likely have occurred in the area historically, but probably on an ephemeral and seasonal basis or they may have occurred in small populations in patchy habitat refugia since the broad habitat unit is unlikely to support a significant resident population (Boshoff and Kerley 2001). The managed species at the farm were primarily livestock i.e. namaqua afrikaner, dorper and merino sheep, bonsmara cattle, while the introduced extra-limital impala (*Aepyceros melampus*) and nyala (*Tragelaphus angasii*) were present. Sheep and cattle are primarily grazers and they are also provided with feed and forage.

Estimated density of managed ungulates were approximately 11.3 managed animals per km² in Postberg and 7.6 managed animals per km² in both Langebaan and on the research farm. These stocking rates are, however, based on data from 2015 which were collected prior to a significant removal of large managed ungulates from the Postberg section in 2016. Nevertheless, it is important to consider the legacy effects, albeit indirect, that humans have on ecosystems, such as modifying processes like natural fire and browsing / grazing regimes (Burgi *et al.* 2017).

**Caracal**

Since the extirpation of large apex predators (Cruz-Uribe and Schrire 1991), the caracal (*Caracal caracal*) is the largest predator present in the study system. Few studies have been conducted on the abundance of caracals (Singh *et al.* 2014) across their range, with studies limited to diet ecology and home range estimation (Avenant and Nel 1998; Braczkowski *et al.* 2012). Caracals have a wide distribution, occurring throughout most of Africa to the Middle East and Southwestern Asia (Skinner and Chimimba 2005). Although they are particularly widespread and common across Southern Africa, little is known about their ecology (Avenant and Nel 1998). They are adaptable to a wide range of habitats including Fynbos, Savannah, Arid Karoo and Afro-temperate forests (Braczkowski *et al.* 2012) as well as urban and agricultural areas (Skinner and Chimimba 2005). Habitat use, home range and diet of caracals were studied in the Postberg section of the park in the early 1990s (Avenant 1993; Avenant and Nel 1998). Two adult male and three adult female caracals were tracked for 1 year over a 130 day period for each caracal and uninterrupted for 120 hours at a time. It was found that adult male caracals had much larger home ranges (27 ± 0.8 km²) than females (7 ± 1.7 km²). Overall, 14 individual caracals were captured of which 9 were classified as sub adult (and possibly dispersing). Diet was studied by analysing caracal scat that was collected over a 12 month period in the Postberg (*n*=201) section of the park as well as from the sand dunes (*n*=38) and marshes (*n*=104) outside of Postberg but within the park (Avenant 1993; Avenant and Nel 1997). The results of the diet study showed that no less than 80% of scat from all
areas contained small mammal remains and that the use of specific plant communities by caracal had a positive relationship to rodent biomass (Avenant 1993; Avenant and Nel 1997; Avenant and Nel 1998).

The abundance of a meso-predator such as caracal, and its regulating influence on small antelope in the contractual Postberg section of the park has been an ongoing management question since the early 1990s and was the topic of two MSc theses (Avenant 1993; Heydenrych 1995). Avenant (1993) investigated space use and diet of caracal and Heydenrych (1995) investigated plant communities and how they influence the occurrence and density of small antelope within Postberg. Both of these studies indicated that caracals are responsible for some small antelope losses but neither study had concrete evidence that caracals were solely responsible for a decline in small antelope abundance. Avenant (1993) did however find that caracals were responsible for a significant number of springbok losses between 1990/91, which may have been a reflection of the inability of springbok to adapt to the area (since they are not native to this area of the West Coast). Because both studies (Avenant 1993 and Heydenrych 1995) were restricted to a very small privately managed area, it is uncertain to what extent the perceived high predation trend holds outside of this area, where different management practices prevail. The private landowners of Postberg are currently concerned that caracal abundance may be responsible for a decline in small antelope abundance. While this concern may be valid, predation is not the only process that could result in a decrease in abundance of small antelope. Historical and current land use and management practice within Postberg also include agriculture (livestock and crop cultivation) and more recently the overstocking of large wild herbivores (as well as historical stocking of domestic herbivores) which have resulted in extensive habitat degradation, through overgrazing and trampling.

**Aims and objectives**

Through this study I aimed to investigate the potential drivers of small antelope occurrence in the region and how this might differ across the three areas with different management practices. I considered three potential drivers; predation, competition and habitat. I did this by investigating occupancy of steenbok, common duiker and caracal using site abundance of managed (wild re-introduced and domestic) ungulates, estimates of vegetation height and cover as well as other site specific co-variates as potential predictors for occupancy. I also explored species interactions and temporal activity and overlap between managed ungulates, small antelope and caracal. The study spanned across two primary land uses in the area i.e. protected area and agriculture, where each study area represented a different scenario in
terms of top-down and bottom-up processes that could potentially influence the focal species and habitat in different ways. I made the following predictions (Fig. 2):

I hypothesised that vegetation height and percentage cover (i.e. habitat structure) would be negatively associated with managed (wild and domestic) ungulates. I expected to find the greatest influence on vegetation at Postberg and the farm due to the higher densities, restricted movements (via isolation and fencing) of managed ungulates and the consequent overgrazing which is known to cause habitat degradation (Du Toit and Cumming 1999). Conversely, I expected vegetation structure to be more intact in the Langebaan area which is more open where there are less restrictions on the movements of managed ungulates.

I expected the (assumed) habitat alteration at Postberg and the farm to have a negative effect on the occupancy of small antelope (steenbok and common duiker) as both are known to rely on vegetation cover (Heydenrych 1995; Skinner and Chimimba 2005), whereas I expected higher occupancy at Langebaan due to (assumed) more intact habitat. Since caracal have been “released” from competition with (historically) extirpated apex predators in the park, I anticipated that they would occur at higher frequencies in the park (Postberg and Langebaan) than at the farm where predator persecution takes place. I did not expect to find a difference in caracal occurrence between Postberg and Langebaan since the species is managed uniformly across these areas.

I hypothesised that managed ungulates would interact strongly with small antelope and that their presence would negatively influence occurrence probabilities of small antelope at Postberg and the farm due to either direct competition for resources with, or due to habitat modification by, the more abundant larger managed ungulates (Fritz et al. 2002) whose movements are restricted. I expected managed ungulates to have less influence on the occurrence of small antelope at Langebaan due to the more free ranging behaviour of managed ungulates at the site.

I predicted significant temporal overlap between managed ungulates and small antelope in Postberg and the farm when compared to more natural area (Langebaan) due to the higher abundance of managed ungulates within a restricted area and thus forcing the small antelope to spend more time looking for appropriate resources. Finally, I hypothesised that small antelope would display greater avoidance behaviour at Postberg and the farm by being active during the times that caracal are least active due to the increased predation risk (Tambling et al. 2015) associated with the expected decrease in vegetation structure.
Figure 2: Predictions diagram illustrating my predictions across the three scenarios. I predicted that the higher managed ungulate abundance would result in increased competition between small antelope and managed ungulates at Posterg and the farm. I predicted a lower overall vegetation height and abundance of small antelope at both Postberg and the farm attributed to the higher abundance of managed ungulates and I expected a lower abundance of mesopredators at the farm due to the surrounding predator suppression.

Outline of dissertation

In this dissertation I explore the influence of management practice on small antelope occurrence and activity. I first investigate how management practice influences occurrence and detection of small antelope and caracal where I address the following questions in Chapter 2:

1) Is there a difference in the detection probability, occupancy levels and/or abundance of (a) caracal, (b) small antelope and (c) managed ungulates across the different management scenarios?

2) Does vegetation structure (height and cover) influence the abundance/occupancy of (a) managed ungulates, (b) caracal and/or (c) small antelope?

In Chapter 3 I use two-species occupancy and temporal activity models to investigate how the presence of large managed ungulates influences occurrence and temporal activity of small antelope by asking the following questions;
3) How does the presence or absence of managed ungulates affect the occupancy of steenbok and common duiker between management scenarios?
4) Is there evidence of temporal niche partitioning between managed ungulates and small antelope?
5) Is there a temporal difference in activity patterns between steenbok and common duiker and their predator, the caracal?

In Chapter 4 I discuss the overall findings and synthesise the processes which could be at play within the different systems as well as the caveats that constrain my interpretation.

Chapters 3 and 4 were both written as independent papers to be submitted for scientific publication which has resulted in some repetition of information across the chapters. Each chapter, however, contributes to the overall theme of the dissertation.
Chapter 1

References


Chapter 1


McKinney, M.L. (2002). Urbanization, Biodiversity, and Conservation. The impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. *Bioscience*, 52(10), 883-890.


Chapter 1


Chapter 1


Chapter 1


Chapter 2: How management practice influences small antelope and mesopredator occupancy and detection in the West Coast, South Africa

Deborah J. Winterton¹,², Nicola J. van Wilgen¹,³ and Jan A. Venter²,⁴

¹ Cape Research Centre, SANParks Scientific Services, Western Cape, South Africa
² School of Natural Resource Management, Faculty of Science, Nelson Mandela Metropolitan University, George Campus, Western Cape, South Africa
³ Centre for Invasion Biology, Stellenbosch University, Western Cape, South Africa
⁴ Eugène Marais Chair of Wildlife Management, Mammal Research Institute, University of Pretoria, Pretoria, South Africa

Word count: 8164 (excluding supplementary material)
Abstract

Land use change and management practice have significant effects on ecosystem function. Herbivore abundance is regulated by either top-down (predation) or bottom-up (primary production) processes, disturbance of which can result in ecological cascades at multiple trophic levels. Predation as a regulator of small antelope abundance, as opposed to land-use practice, has been an ongoing question within the Postberg section of the West Coast National Park (the park) since its proclamation. We investigated how management practice, defined by the abundance of large managed ungulates, and the presence of caracal, *Caracal caracal*, (the largest predator in the system) influences the occurrence of small antelope (common duiker, *Sylvicapra grimmia*, and steenbok, *Raphicerus campestris*) on the West Coast of South Africa. Occupancy is an important ecological state variable and is useful for monitoring animal populations, especially when individuals are not uniquely identifiable. Camera traps are especially useful for these types of observations as they can record multiple species over space with time-of-detection data. We used 18 camera traps to systematically survey three areas with different management practices between May-October 2017. We found that small antelope have lower probability (p < 0.001) of occurrence in Postberg compared to other parts of the park and the agricultural site. Common duiker occurrence was positively associated with vegetation height while steenbok occurrence had a negative association with slope. Caracal detection probability was significantly different across all areas with the lowest chance of detection on the agricultural site. The most interesting finding of this study was the much higher occurrence (100%) of small antelope outside of the protected area. While the mechanism for this is not clear, it is unlikely that predation is the driver due to low detection and known diet. While there was no difference in mean vegetation height between the sites, it was significantly at the farm providing more even cover for species which could be driving the high occurrence of small antelope. Therefore we postulate that small antelope are regulated by bottom-up processes.

*Keywords: caracal, steenbok, duiker, camera traps, managed ungulate, ecosystem regulation*
Introduction

Land use change is a major driver of global environmental change (Kiffner et al. 2015) and is known to alter species abundance, occupancy and richness (Kok 2016; Ramesh and Downs 2015; Schuette et al. 2013). The impacts that humans have on landscapes influence ecosystem function as different land uses alter habitat structure and resource availability differently (Blaum 2007; Šálek, Drahniková and Tkadlec 2015). Importantly, human activities also impact top down and bottom-up landscape-level ecosystem processes (Burgi et al. 2017). Herbivore abundance is regulated by either top down processes, such as predation or by bottom up constraints on primary production, such as soil fertility (Hopcraft et al. 2010). The removal of apex predators from natural systems can lead to a trophic cascade (Fortin et al. 2005, Suraci et al. 2016). The “green world hypothesis” postulates that predation limits herbivore abundance, which releases pressure on grazing, with top predators thereby playing a regulatory role in ecosystem function (Hopcraft et al. 2010). For example, the re-introduction of wolves in the Yellowstone National Park resulted in the regeneration of aspen trees that were released from foraging pressure by deer (Fortin et al. 2005). “Mesopredator release” (Soulé et al. 1988), the ecological phenomenon where the removal of apex predators results in competitive release of middle-ranked predators, can often cause a decline in prey species abundance (Prugh et al. 2009). Hopcraft et al. (2010) argue that predation has the greatest influence on abundance when prey species fall within a nested prey base of both large and medium sized carnivores as they then have more enemies and are exposed to a higher risk of predation. Aside from predation, the overabundance of large ungulates can also alter bottom-up processes. Overgrazing and altered habitat structure influence the behaviour and abundance of smaller antelope, either by altering their resource availability or by forcing them to utilise high risk areas in their search for food (Hopcraft et al. 2010). Change of habitat use may also result when an absence of large predators alters the “landscape of fear” (Suraci et al. 2016), where the fear of large carnivores formerly acted to alter the foraging behaviour of mesocarnivores (medium sized carnivores) as well as herbivores.

Information on population size (abundance or density) and associated vital rates (birth and death rates, immigration and emigration) is important when assessing population status and necessary for monitoring population change (O’Connell and Bailey 2011), and understanding how free-ranging populations impact ecosystem function. Estimating these population parameters has been a key focus of faunal research. However, in situations where animals are not individually recognisable and capture-mark-recapture is not possible, occupancy is a useful alternative (O’Connell and Bailey 2011). Occupancy is broadly described as the probability that a site or patch is occupied by a target species, thus it is fundamentally a function of abundance (O’Connell and Bailey 2011) and an important state variable in
Chapter 2

ecological research (Fiske and Chandler 2011). Camera traps are useful tools for estimating occupancy and associated parameters and are becoming increasingly popular to address research questions because they allow non-invasive sampling of species that can be difficult to study (O’Connell et al. 2011; Tobler et al. 2008). For example numerous carnivore species have been studied with the use of camera traps (Balme et al. 2010; Harmsen et al. 2009; Karanth and Nichols 1998; Long et al. 2010). Camera traps have been used to estimate species density, abundance (O’Brien 2011), occupancy (O’Connell and Bailey 2011), behaviour and activity patterns (Bridges and Noss 2011), as well as to measure species richness and community dynamics (Kauffman et al. 2007; Kery 2011) and the influence of land use. For example, Ramesh and Downs (2015) used camera traps to show that serval occupancy was negatively influenced by high cropland use in the Kwazulu-Natal Midlands. Similarly, Wallgren et al. (2009) found that large herbivore and large carnivore densities were negatively impacted by communal grazing areas and fenced ranches in the Botswana Kalahari. This correlates closely to Kauffman et al.’s 2007 finding that many of the larger carnivores were absent from the communal lands (managed for livestock only) in Namibia when compared to privately owned lands (managed for livestock and game populations).

Mesopredator (caracal) abundance and their regulating influence on small antelope in the contractual Postberg section of the West Coast National Park (hereafter referred to as the park) has been a management concern since the early 1990s (Avenant 1993 and Heydenrych 1995). The caracal (Caracal caracal) is the largest predator in the system following the historical extirpation of apex predators and may have been “released” from top down competition that would have occurred in the presence of large predators prior to extirpation (Cruz-Uribe and Schrire 1991). Landowners are concerned that caracal abundance may be responsible for a perceived decline in small antelope abundance. While this concern of the land-owners may be valid, predation is not the only process that could result in a decrease in abundance of small antelope. Historical land use and management practice within Postberg includes agriculture (livestock and crop cultivation) and more recently the overstocking of large herbivores which have resulted in extensive habitat degradation. The aim of this study was to assess large and medium herbivore (key ecosystem regulators in these systems), mesopredator (Caracal caracal) and small antelope (common duiker, Sylvicapra grimmia, and steenbok, Raphicerus campestris) occupancy across three different management practice scenarios. We expected habitat structure (vegetation height and cover) to be significantly altered in Postberg when compared to more natural areas within the park. Due to overgrazing and trampling associated with livestock we also expected habitat structure and food availability to be altered in the nearby agricultural areas. This, we predicted, would negatively influence small antelope, since both steenbok and common duiker require adequate shrub for cover and
forage (Heydenrych 1995; Skinner and Chimimba 2005). The main research questions were; (1) is there a difference in the detection probability, occupancy levels and or abundance of (a) caracal, (b) small antelope and (c) managed ungulates across the different management scenarios? (2) Does vegetation structure (height and cover) influence the abundance/occupancy of (a) managed ungulates, (b) caracal and/or (c) small antelope?

Materials and methods

Study area

Our study was conducted along the west coast of South Africa (Fig. 1), in the nutrient-poor Fynbos Biome, where annual average rainfall varies between 152 mm in the north and 265 mm in the south. Strandveld is the predominant vegetation type of the region and is characterised by communities of medium density to closed shrublands dominated by sclerophyllous, broad-leaved shrubs (Mucina and Rutherford 2012).

Figure 1: Map of the study area, showing the three management scenarios and underlying vegetation types
We had three study areas (scenarios) defined by their different management practices, using the ‘stocking rate’ and species of managed ungulates at each scenario as a proxy for ‘management practice’. Two areas were within a protected area (Postberg and Langebaan sections of the West Coast National Park) and the third was on an agricultural research farm (Lamberts Bay, hereafter referred to as the farm). The park is located approximately 100 km North West of Cape Town and the Nortier research farm is just outside of the town Lamberts Bay which is approximately 100 km north of the park. The park was proclaimed in 1985 and since then it has expanded to its current size of approximately 47 000 ha (SANParks 2013). The farm falls under the management of the Department of Agriculture (Elsenburg), Western Cape Government and is 2 780 ha in size. The farm was selected due to the similar vegetation type and because its size. Since the majority of commercial farms along the west coast are predominantly used for crop production with little livestock they are therefore not of a comparable size to the areas within the park. Managed species included only herbivores and were defined as those species which require the intervention of people to manage the populations e.g. feed supplementation and population removals and or introductions. Managed ungulates were classified into different size classes according to weight. When mapped, the weight ranges on the ungulates present at our study areas naturally segregated into three groups which were grouped as follows: animals <25 kg (small herbivores), between 26 – 200 kg (medium herbivores) and anything >200 kg was designated as large herbivore. No managed ungulate species were classified in the small herbivore class. Managed ungulates differed across scenarios with bontebok (Damaliscus pygargus pygargus), Cape mountain zebra (Equus zebra zebra), red hartebeest (Alcelaphus buselaphus caama), eland (Taurotragus oryx) (Fig. 2), blue wildebeest (Connochaetes taurinus), kudu (Tragelaphus strepsiceros), springbok (Antidorcas marsupialis) and gemsbok (Oryx gazelle) occurring in the Postberg scenario. Managed species at the Langebaan scenario were eland, bontebok and red hartebeest, while sheep, Ovis aries, ( namaqua afrikaner, dorper and merino breeds), Bonsmara cattle (Bos taurus) (Fig. 2), impala (Aepyceros melampus) and nyala (Tragelaphus angasii) were present at the farm. Estimated density of managed ungulates was approximately 11.3 managed animals per km² in Postberg and 7.6 managed animals per km² in both Langebaan, based on aerial census data (unpublished SANParks data), and stocking information on the research farm (C. Rheeder, research farm manager, pers. comms.).

The Postberg scenario has historically been characterised by intensive management of large and medium sized herbivores in a small area (1800 ha), which is isolated by the Langebaan lagoon in the east, the Atlantic ocean in the west and a fence in south. Postberg was originally acquired in the early 1800’s by a group of farmers and was used primarily for winter grazing, but the land was also ploughed. Postberg was proclaimed as a private nature reserve in the
Chapter 2

1960s, after which it was contractually included into the park in 1987. Many indigenous and extra-limital medium and large herbivore species were introduced to Postberg since the 1960s which resulted in overgrazing of the small area. The Langebaan scenario is characterised by the management of medium and large herbivore species in a larger, more open section of the park. Here large herbivores are not confined to a small area, are free ranging and occur at lower density. Historically this area was also used for agriculture which included small livestock and crop production and different portions were proclaimed as part of the park in 1989 and 1996. The Lamberts Bay scenario is a research farm where several resource domestic flocks and herds are kept for the Directorate: Animal Sciences, while it is also the site of veld rehabilitation projects run by the Directorate: Plant Sciences. The sheep resource flock consists of three breeds (namaqua afrikaner, dorper and SA mutton merino), the beef cattle resource herd (bonsmara) and the bio-secure ostrich (Struthio camelus) flock. The ostrich flock is restricted to camps that were not surveyed. The research farm is located in a matrix of other farms where predator control is known to take place.

![Figure 2: Study species; A = subset of the most common managed ungulates encountered (A1 = eland, A2 = bonsmara cattle, A3 = sheep), B = mesopredator (caracal), C = small antelope (C1 = steenbok, C2 = common duiker).](image)

**Survey design and in-field methods**

The Postberg scenario was surveyed between May - July, followed by the Langebaan scenario between July – August and the farm from August – October 2017 respectively. We used 18 Cuddeback®, model C3 blackflash (Non Typical, De Pere, WI), to survey each scenario. Each area was overlaid with a grid of 18 1 km² cells in Arc GIS which corresponded to the total Postberg area. We then calculated the centroid for each cell which served as the camera location. Once we had navigated to the centroid we spiralled outward to identify the first location where two or more signs of animal activity were detected but within 120 m from the centroid (Colyn 2017). Once the location was identified we set the camera. Cameras were
mounted approximately 40 – 50 cm above ground level, onto a wooden stake and faced in a southerly direction so that the sun moved behind the camera to prevent false triggers and overexposure (Glen et al. 2014). Cameras were programmed to capture three burst photographs when triggered with a 30 second delay between photographs. Cameras were mounted and programmed in a standardised way across all surveys.

Trail type, a categorical value of either game trail or road (management track, private road or tourist road), was assessed visually in-field (Table 1). Vegetation height and cover was measured at each site according to the protocol described in Colyn (2016), i.e. by taking a measurement at one and two meter distances from the camera trap location in a north, south, east and west direction (eight measurements in total). The vegetation height measurements were recorded in the field at the prescribed 1 m and 2 m distances with a measuring tape. Using a densitometer (Li et al. 2000), we also measured the percentage cover at each point where vegetation height was measured. Elevation was extracted at site level from the CGIAR-CSI SRTM 90 m Digital Elevation Data (Jarvis et al. 2008) using the spatial analyst tool within ArcGIS. Similarly, slope was calculated using a digital slope model from the same DEM using the spatial analyst tool within ArcGIS (ESRI 2012).

**Data analysis**

Camera trap images were downloaded after each management scenario was surveyed. Image data were processed and captured using the TimeLapse2 Image Analyzer software (Saul Greenberg, University of Calgary, Calgary, Alberta) and then exported to excel per camera station. Image databases of camera stations were then merged to create an image database per management scenario. Animal photographs were separated from non-animal photographs and when more than one species was captured in a single photograph, entries were duplicated and edited to capture the number of individuals of each detected species as a separate record.

Starting with a blank database, image data were binned into independent capture events using a loop in R (R Development Core Team, 2015). The loop grouped all captures of a particular species, at a particular location, and then calculated the time difference between each picture and assigned those that occurred within 30 minutes of one another to a particular group and then from this group, selected the photograph with the highest number of individuals of that species and appended it to the analysis database as an independent capture.
Table 1: Data collected on potential site- and observation-level co-variates that were used to model detection ($\rho$) and occupancy ($\psi$) for the different species as well as the source of the data. Effort was the only observation level co-variate considered.

<table>
<thead>
<tr>
<th>Co-variate</th>
<th>Variable type</th>
<th>Response variable</th>
<th>Source of data</th>
</tr>
</thead>
<tbody>
<tr>
<td>Management scenario</td>
<td>3-level factor: Postberg, Langebaan, Lamberts Bay</td>
<td>$\rho$ &amp; $\psi$</td>
<td>Component of study design</td>
</tr>
<tr>
<td>Effort</td>
<td>Continuous variable, starting at 0</td>
<td>$\rho$</td>
<td>Camera traps</td>
</tr>
<tr>
<td>Vegetation height</td>
<td>Continuous variable, starting at 0</td>
<td>$\psi$</td>
<td>Field data collection</td>
</tr>
<tr>
<td>Fallow land</td>
<td>2 level factor: yes, 0 - no</td>
<td>$\psi$</td>
<td>Field data collection</td>
</tr>
<tr>
<td>Elevation</td>
<td>Continuous variable</td>
<td>$\psi$</td>
<td>Digital Elevation Model (DEM) depicting elevation (m) at 90m resolution (Jarvis et al. 2008)</td>
</tr>
<tr>
<td>Slope</td>
<td>Continuous variable</td>
<td>$\psi$</td>
<td>Digital slope model depicting slope (°) at 90m resolution (Jarvis et al. 2008)</td>
</tr>
<tr>
<td>Trail type</td>
<td>2-level factor: road &amp; game trail</td>
<td>$\rho$</td>
<td>Field data collection</td>
</tr>
<tr>
<td>Large managed ungulate abundance</td>
<td>Continuous variable, starting at 0</td>
<td>$\psi$</td>
<td>Royle-Nichols Occupancy model output, based on data from camera traps</td>
</tr>
<tr>
<td>Medium managed ungulate abundance</td>
<td>Continuous variable, starting at 0</td>
<td>$\psi$</td>
<td>Royle-Nichols Occupancy model output, based on data from camera traps</td>
</tr>
</tbody>
</table>
Site specific co-variates were captured in a separate sites database in excel and correlations assessed for those variables with numeric / continuous values (Supplementary Fig. 1). There was a strong positive correlation between vegetation height and cover (0.75) and therefore we only used vegetation height in models as a proxy for vegetation structure.

We used the *camtrapR* package (Niedballa et al. 2016) in R to create a camera operation matrix and a detection history for individual species / or suites of species of interest (e.g. managed species). Temporal replication was defined per species by dividing the camera survey into sampling occasions which can range from 1- 15 days (Kok 2016). Occasion length varied for different species depending on their detectability. Shorter occasion lengths are better for assessing occupancy of species that are frequently detected, while longer occasion lengths are better for assessing occupancy of species that are less abundant and that have low detection probabilities.

Occupancy and abundance were analysed using the *unmarked* package in R (R Development Core Team, 2015) by creating occupancy frameworks, for the species of interest, using the detection history, observation level and site specific co-variates. Large and medium herbivore abundance per site was estimated using the abundance-induced heterogeneity model (Royle and Nichols 2003) using the *occurRN* function in the *unmarked* package in R (R Development Core Team, 2015). Data were pooled for all three areas; effort was used to explain detection probability and scenario to explain occupancy with an occasion length of 2 days (Table 2). Small antelope and caracal occupancy was estimated using the single season, single species occupancy model (MacKenzie et al. 2002) using the *occu* function. Data across areas were pooled to estimate small antelope occupancy and therefore scenario was always included in the models to explain occupancy and effort was always included to explain detection for all species. The large and medium managed ungulate species’ abundance estimates along with other site specific co-variates were used as predictors of small antelope occupancy (Table 1). The best models were selected using the *modsel* and *fitlist* functions which produce a table of AIC and R$^2$ values for null and more complex models. Models were assessed for relative goodness of fit by scrutinising the AIC, delta and R$^2$ values in the model summaries.

The “best” model is considered the model which produces the lowest AIC value. However it is only best in relation to other models and not necessarily to reality (Burnham et al. 2011). Therefore we also considered the delta value, which is the difference in AIC value between a model and the model with the lowest AIC. Earlier literature on this topic suggested that models with a delta value of >2 were poor, however this notion is now known to be weak and models...
with a delta value in the range of 2 – 7 and do have some support and should be considered (Burnham et al. 2011). We made predictions based on the top models and inspected the 95% confidence intervals of the predictions. Models that produced lower and upper occupancy confidence estimates ranging between 0 (complete absence) and 1 (100% occupancy) were not considered to be informative or have any predictive power. If there were no co-variates that provided strong predictive power, we made predictions based on either the null model or a model that used effort to explain detection and scenario to explain occupancy, depending on comparative AIC values.

Because many of the occupancy models did not have sufficient data to converge, we also tested particular hypotheses directly. We hypothesised that managed ungulates would show preference for fallow lands and as such would be detected more often, with a shorter time between captures than recorded elsewhere. Conversely, we expected small antelope to avoid these areas, and thus their time between captures on fallow lands would be higher. To assess this we calculated the number of detections for small, medium and large ungulates at each vegetated site and compared the number of detections on fallow versus natural lands across areas for an equal number of days (33). We also compared the average time between independent captures for species from each group (small / medium / large) between fallow and natural lands across areas. These analyses were not conducted for the farm as no fallow lands are present there.

All data were non-parametric (tested using the Shapiro-Wilk test of normality). We used the Pairwise Wilcox Test to compare abundance, occupancy, vegetation height, detections and slope across the different areas. The tidyverse package (Wickham 2017) in R was used to manipulate databases and produce summaries where necessary, and the ggplot2 package was used to produce plots (Wickham 2016).
Table 2: Model selection for estimating large and medium ungulate abundance across sites, $\rho = \text{detection probability}$ and $\psi = \text{probability of occurrence}$. Co-variates used in the model are indicated in brackets while (.) indicates no co-variates were used. Modelled outputs per site were used as co-variates in small antelope occupancy models.

<table>
<thead>
<tr>
<th>Model</th>
<th>nPars</th>
<th>AIC</th>
<th>delta</th>
<th>AICwt</th>
<th>cumltvWt</th>
<th>Rsq</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\rho$ (effort), $\psi$ (scenario)</td>
<td>5</td>
<td>629.05</td>
<td>0</td>
<td>1.00</td>
<td>1.00</td>
<td>0.61</td>
</tr>
<tr>
<td>$\rho$ (.), $\psi$ (.)</td>
<td>2</td>
<td>673.56</td>
<td>44.51</td>
<td>0.00</td>
<td>1.00</td>
<td>0</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Model</th>
<th>nPars</th>
<th>AIC</th>
<th>delta</th>
<th>AICwt</th>
<th>cumltvWt</th>
<th>Rsq</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\rho$ (effort), $\psi$ (scenario)</td>
<td>5</td>
<td>894.5</td>
<td>0</td>
<td>1.00E+00</td>
<td>1.00E+00</td>
<td>0.37</td>
</tr>
<tr>
<td>$\rho$ (.), $\psi$ (.)</td>
<td>2</td>
<td>913.18</td>
<td>18.68</td>
<td>8.80E-05</td>
<td>1.00E+00</td>
<td>0</td>
</tr>
</tbody>
</table>
Chapter 2

Results

Sampling effort (i.e. number of active trap nights per survey and occasion) differed across areas. Camera trap nights per survey were 542, 602 and 561 for the Postberg, Langebaan and the farm respectively, with an overall effort of 1705 camera days across all three areas. The Postberg site had one camera failure which resulted in fewer camera days. Both Postberg and Langebaan were surveyed for approximately 30 days while the farm site was surveyed for 60 days, however the data for the farm were partitioned and only the data generated within the first 30 days of the survey were used for comparisons across areas.

There was no significant difference in vegetation height between the areas (ρ = 0.1627), however, vegetation height on the farm was significantly less variable than in the park (ρ = 0.002, using an asymptotic test in the `cvequality` package in R (Marwick and Krishnamoorthy, 2018). This was driven by the very high variation in vegetation height within the Postberg and Langebaan scenarios, both of which included sites with no vegetation (former fallow lands) and well vegetated sites with high vegetation height, whereas sites on the farm were more evenly vegetated. We found a moderate negative correlation of -0.49 between vegetation height and large managed ungulate species abundance and -0.47 between vegetation height and medium managed ungulates species abundance (Supplementary Fig. 1).

Large herbivores were captured significantly more often on fallow lands (p = 0.02, Wilcoxon test), which were visited on average every 2.8 days while natural lands were visited every 8.2 days across areas. This pattern was particularly prevalent in Langebaan. Overall, there was no difference in small antelope detections between fallow and non-fallow lands however, 32 detections at one fallow land site in Langebaan likely obscured any potential patterns. There were no fallow land detections in 2017 for small antelope in Postberg (Supplementary Fig. 2).

Significant differences were detected in managed species abundance across areas. Medium sized ungulate abundance was significantly higher at the Langebaan site when compared to the Postberg site (ρ = 0.014) as well as the farm site (ρ = 0.015) with a mean site abundance of 2.79 individuals per site. There was no significant difference in site abundance of managed medium sized ungulates between Postberg and the farm (ρ = 0.856) with a mean of 1.56 and 1.48 individuals per site respectively (Fig. 3). Estimated managed large ungulate site abundance was significantly lower at the farm when compared to Postberg (ρ = <0.001) and Langebaan (ρ = <0.001), while there was no difference between Langebaan and Postberg (ρ = 0.22; Fig. 4). Large sized managed ungulates had a mean abundance of 2.65, 0.072 and 3.12 individuals per site for the Langebaan, farm and Postberg areas respectively.
Figure 3: Medium ungulate abundance across sites for each of the management scenarios. Significant differences (p < 0.05) are indicated by * between groups that differ and NS indicates no significant difference. Significance is displayed in the middle of the two groups being compared.

Figure 4: Large ungulate abundance across sites for each of the management scenarios. Significant differences (p < 0.05) are indicated by * between groups that differ and NS indicates no significant difference. Significance is displayed in the middle of the two groups being compared.
Chapter 2

We found that when detection probability was <0.1, occupancy could not be estimated, and therefore we could not make any confident predictions for caracal occupancy for either Postberg or the farm. We were, however, able to model caracal detection probabilities across sites. As we found no informative co-variates for detection, we used a null model thus producing one constant prediction for each study area. We used an occasion length of 5 days and detection probabilities were significantly different across all three areas. Detection probability was highest at Langebaan (0.178 ± 0.103 SE, Fig. 5) followed by Postberg (0.025 ± 0.014 SE) and then the farm (0.0159 ± 0.003 SE). We used an occasion length of 7 days and found significant differences in common duiker occupancy (ψ) across scenarios with the farm having the highest occupancy of 1 (± 0 SE), followed by Langebaan (ψ = 0.889 ± 0.052 SE) and Postberg (ψ = 0.473 ± 0.098 SE, Fig. 6). The best model included effort to explain detection with scenario, vegetation height and elevation to explain occupancy (Table 3). However, this model did not produce confident predictions with 95% confidence intervals including zero (complete absence) and one (100% occupancy). This was also the case with the second best model that used trail type to explain detection in addition to the variables used in the top model. My predictions were therefore made using the third best model (Δ AIC = 4.09, Table 3), that included effort to explain detection and vegetation height to explain occupancy (Fig. 7), but produced much more stable estimates of common duiker occupancy for both Postberg and Langebaan. Estimates of co-variates for the farm however remained uninformative due to 100% occupancy at all sites (Fig. 6).

Steenbok occupancy was significantly different across all three areas with the farm having the highest probability of occurrence (ψ = 0.871 ± 0.116 SE), followed by Langebaan (ψ = 0.487 ± 0.129 SE) and then Postberg (ψ = 0.196 ± 0.103 SE, Fig. 8). We used an occasion length of 7 days to estimate steenbok occupancy. The best model included effort to explain detection and only management scenario to explain occupancy. No covariates proved to be strong predictors for occupancy and all models had R² ≤0.30, but fallow land, vegetation height and slope appeared to have a weak influence on occupancy (Supplementary Table 1).

The cumulative photographic captures of steenbok and common duiker were also assessed across the management scenarios and steenbok captures (five in Postberg, 35 in Langebaan and 40 at the farm) were significantly lower than common duiker (21 in Postberg, 142 in Langebaan and 299 at the farm) captures across all sites which correlates closely with the probability of occurrence for the two species. Captures for both steenbok and common duiker were consistently lower in Postberg and highest at the farm (Fig. 9).
Figure 5: Caracal detection probability (± SE bars) across sites for each of the management scenarios. Since no co-variates were useful predictors the output value was constant across all sites therefore results could not be plotted with a box plot. Significant differences (p < 0.001) are indicated by *** between groups that differ. Significance is displayed in the middle of the two groups being compared.

Figure 6: Duiker occupancy across sites for each of the management scenarios. Significant differences (p < 0.001) are indicated by *** between groups that differ. Significance is displayed in the middle of the two groups being compared.
Table 3: Top three models for common duiker, the third best model was used to estimate occupancy across sites and included effort for detection and scenario and height for occupancy, \( \rho \) = detection probability and \( \psi \) = probability of occurrence.

<table>
<thead>
<tr>
<th>Model</th>
<th>nPars</th>
<th>AIC</th>
<th>delta</th>
<th>AICwt</th>
<th>cumltvWt</th>
<th>Rsq</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \rho ) (effort, ( \psi ) (scenario, veg height, elevation))</td>
<td>7</td>
<td>288</td>
<td>0</td>
<td>0.36</td>
<td>0.36</td>
<td>0.59</td>
</tr>
<tr>
<td>( \rho ) (effort, trail type), ( \psi ) (scenario, veg height, elevation)</td>
<td>8</td>
<td>289.98</td>
<td>1.97</td>
<td>0.13</td>
<td>0.63</td>
<td>0.59</td>
</tr>
<tr>
<td>( \rho ) (effort), ( \psi ) (scenario, veg height)</td>
<td>6</td>
<td>292.09</td>
<td>4.09</td>
<td>0.05</td>
<td>0.73</td>
<td>0.54</td>
</tr>
</tbody>
</table>

Figure 7: The influence of vegetation height on common duiker occupancy in Langebaan and Postberg. Note that it was not possible to model the effect of covariates on common duiker occurrence in Lambert’s Bay due to 100% occupancy.
Figure 8: Steenbok occupancy (± SE bars) across sites for each of the management scenarios. Significant differences (p < 0.001) are indicated by *** between groups that differ. Significance is displayed in the middle of the two groups being compared.

Figure 9: Cumulative photographic captures of common duiker across management scenarios
Discussion

This study examined the influence of management practice on the occupancy and abundance of mammalian ungulates and a mesopredator, with a view to identify potential impacts on vegetation structure and the resultant occupancy and detection probabilities of small antelope and caracals. The protected area was found to have higher abundance of managed ungulates than the site outside of the park, likely because livestock are kept for research at the Lambert’s Bay farm rather than for commercial purposes. While we hypothesised that managed ungulate abundance would be negatively correlated with vegetation structure, we found no difference in overall vegetation height across areas. Small antelope occupancy was significantly higher outside of the protected area. Although this was an unexpected finding, higher densities of small antelope outside of protected areas has also been observed in Tanzania (Caro et al. 1998). Caracal detections were low across all sites and this confounded my ability to estimate probability of occurrence.

*Top down regulation of small antelope – the role of predation*

Initially, the lower abundance of small antelope in Postberg was believed to be due to predation by caracal. While top-down regulation may be a regulating influence on small antelope populations, predation has the greatest influence when the prey species falls in a nested prey base of both large and medium sized carnivores (Hopcraft et al. 2009). Caracals are however the only predators currently extant in the system. Further, caracal diet within the park consists primarily of rodents (84% occurrence in scat), while small antelope are less important with a 6.5% occurrence in scat (Avenant and Nell 2002). Caracal detection was considerably lower in Postberg when compared to the Langebaan section and therefore not consistent with the perceived higher abundance, and most likely not the reason for the lower small antelope occupancy. Caracal detection probability was lowest at the farm site, which was expected and presumed to be associated with the potentially high levels of predator persecution on the surrounding small livestock farms. Therefore, considering all evidence it is unlikely that predation is the driver for small antelope abundance.

*Competition*

An alternative hypothesis was that small antelope abundance may be driven by interspecific competition since the Postberg section is known to be overstocked with large herbivores at the time. Six months prior to this survey, however, there was a large-scale removal of eland and kudu from the Postberg section in November 2016 (Supplementary Fig. 3 and the pre cull survey methods). This made it challenging to test the hypothesis. However, due to slow reproduction rates of ungulates and recovery of vegetation, the past overabundance of large herbivores in the Postberg section would leave a legacy effect of potential disturbance on
vegetation and small antelope. For example, vegetation cover improved with time following removal of grazing pressure by livestock in the Succulent Karoo (Van Rooyen et al. 2014) and roan antelope population recovery was gradual after the impact of zebra and wildebeest was reduced in the Kruger National Park (Harrington et al. 1999). Interspecific competition between ungulates can range between facilitation and exclusion, but for one species to competitively exclude another there must be an overlap in either resource or space use, of which one or both of the shared resources must be limiting (Anderwald et al. 2015). It has also been suggested that although larger ungulates are unselective grazers, it does not necessarily stop them from consuming high quality forage (Belovsky 1997), thus an overabundance of large herbivores could also result in decreased food availability for selective feeders. Since each of the study areas are enclosed and space is limited, it is also important to consider historical distributions and abundances of ungulates in the region as the current situation may not be a true reflection of how this system functioned historically. Large apex predators would have also, historically, predated on large ungulates utilising the area which would have assisted in regulating their populations too (Boshoff and Kerley 2001). However, it is believed that large ungulate species historically occurring at the study areas would have most likely been regulated by bottom-up processes due to the low nutritive value of the Fynbos vegetation (Boshoff and Kerley 2001; Campbell 1986). My data does show that small antelope occupancy is higher at areas where managed ungulate abundance is lower (Figs. 3, 4, 6 and 8), although managed ungulate abundance did not prove to be a good predictive variable as a site specific co-variate. These results could suggest that competition with larger herbivores for forage and space may be influencing occurrence and distribution of small antelope.

Bottom up regulation of small antelope – the role of forage, habitat and topography
The overstocking of ungulates can also result in altered vegetation and habitat structure through overgrazing. Yet the greatest impact of overgrazing may not always present in decreased vegetation structure but rather in a decrease of plant species diversity resulting in an altered food availability for other species (Rooney and Waller 2003) which we unfortunately did not measure. It has been suggested that keeping livestock at low densities could improve habitat and forage for wild ungulates (Charles et al. 2017) which could also be driving the high occurrence of small antelope at the farm. Vegetation structure and habitat are important drivers for small antelope occurrence and distribution (Belton 2008; Brashares and Arcese 2002; Jarman 1974). We found that vegetation height was a good predictor for common duiker occupancy within the park, which is consistent with previous research conducted on this topic in the area (Heydenrych 1995). There was no difference in mean vegetation height between the sites, but vegetation height on the farm was significantly less variable than in the park (where both areas included several fallow lands with no cover), providing more even cover for
species potentially facilitating higher small antelope occupancy. While fallow land was not an informative site co-variate for small antelope occurrence we found that it was an important indicator of habitat use for managed ungulates. Large managed ungulates spent significantly ($p = 0.02$) more time on fallow lands versus non-fallow lands which suggests fallow lands are preferred for foraging (Supp. Fig. 2). Small antelope did not show any clear preference, however potential patterns are obscured by high detections at one fallow land site at Langebaan, though this is most likely due to the close proximity of the camera to more natural lands (pers. obs.). Small antelope were not detected on fallow lands at all in Postberg during 2017 which is noteworthy as this occurred after the removal of a significant number of managed ungulates. There was no strong correlation between vegetation height and steenbok occurrence, but it is known that steenbok are less reliant on cover than common duiker (Skinner and Chimimba 2005). A significantly steeper slope was recorded at Postberg which may also be driving small antelope occurrence there since there was a weak correlation between slope and steenbok occurrence (Supplementary Fig. 5).

**Caveats**

Small antelope, specifically steenbok, occurrence varied across sites with very low probabilities in Postberg and very high probabilities at the farm with little variation between sites within areas. This made identifying potential drivers of their occurrence difficult. The influence of measured variables on small antelope occupancy could not be assessed for the farm because the species was present at all sites.

Caracal occupancy across the different management scenarios was one of the primary questions in this study but there was not enough data to accurately estimate this. However, species detection probabilities differ depending on camera placement and carnivores are more likely to be detected on prominent trails (Cusack *et al.* 2015; Mann *et al.* 2014). Caracals are known to be elusive and to occur at naturally low densities and are consistently reported to have little detection when compared to other species (Cusack *et al.* 2015; Ramesh and Downs 2015; Schuette *et al.* 2013; Singh *et al.* 2015) and thus the low probability of detection during this study was not unusual. Furthermore, research suggests that caracal detection could be negatively influenced by dense vegetation (Cusack *et al.* 2015). It is therefore possible that camera placement during my study negatively influenced caracal detection. We therefore recommended that survey effort should be >1 400 trap nights (Cusack *et al.* 2015) which should be achieved by increasing the number of cameras rather than the length of the survey.
Chapter 2

Although overgrazing has the potential to alter vegetation and habitat, it has been insinuated that climate has a greater impact on vegetation than overgrazing (Coughenour 1991). Therefore alternative methods for assessing vegetation cover such as NDVI/EVI could provide further insights into overall cover and habitat suitability of the three areas at a landscape level.

Conclusions and recommendations

In line with landowner observations, small antelope species do have a lower probability of occurrence in Postberg compared to other parts of the park and areas outside of the park. While the data collected here appear insufficient to determine a mechanism for this, it is unlikely that high predation by caracals is the driver, both because caracals were not detected at higher frequencies in Postberg and because their diet in the area has been shown to include a much higher proportion of rodents compared to ungulates. The most surprising finding of this study was the very high probability of small antelope occurrence outside of the protected area (Fig. 6, Fig. 8, and Fig. 9) which warrants further investigation. Assessment of small antelope occurrence over time is recommended to determine whether or not numbers start to increase following the reduction in large ungulate abundance and the associated regeneration of vegetation. Further research is required to identify environmental variables which are meaningful in determining species occupancy dynamics.

Acknowledgements

We would like to thank Mila Truter, Trevor Adams, Chanel Williams, Zishan Ebrahim and Toni Dyers for their assistance with field data collection. Thanks to Mila Truter and Alexis Bierman for their assistance with data capture. We appreciate the invaluable advice from Matthew Rogan and Res Altwegg with regards to the occupancy analyses. Nicola van Wilgen and Matthew Rogan (drafting of initial generic code) and Robert Schlegel (determining independent captures) provided advice and inputs into R script, for which we are grateful. This work would not have been possible without the funding and support from South African National Parks and West Coast National Park management. We would also like to thank the Elsenburg Provincial department of agriculture for their support, specifically, Christie Rheeder, the Nortier Research farm manager, and for permitting us to work on their farm.
Chapter 2

References
Chapter 2


Chapter 2


**Supplementary material:**

Postberg pre-cull camera survey methods:

The Postberg scenario was surveyed prior to a large herbivore cull from the August to October of 2016. Using ArcGIS we created a grid of 1 km² cells over Postberg and three random points were generated per cell which served as camera stations with no more than one camera per cell at any given time. We navigated to the chosen point (per cell) and set the camera at the closest most suitable site (within 100 meters of the point) which contained signs of animal activity, the majority of which were on game trails. Twelve Cuddeback®, model C3 blackflash (Non Typical, De Pere, WI), were thus randomly distributed in 46 single-camera stations over the survey period that operated for seven (12 stations) or 14 days (34 stations) generating a total of 644 trap-days.
Supplementary Figure 1: Co-variate correlation matrix
Supplementary Figure 2: Managed ungulate (large and medium) and small antelope detections (y-axis) on fallow (1) versus non-fallow (0) lands (x-axis) in the park. There was no 2016 data available for the Langebaan section and no detections of small antelope were made in Postberg in 2017. No fallow lands were present on the farm.

Supplementary Figure 3: Estimated eland abundance pre (Postberg 2016) and post (Postberg 2017) removal of eland and kudu, significant differences (p < 0.001) are indicated by *** between groups.
Supplementary Figure 4: Vegetation height across management scenarios showing no significant difference (NS) between groups, but lower variation at Lamberts Bay.

Supplementary Figure 5: Slope across management scenarios showing significant difference ($p < 0.05$) are indicated by * between groups that differ.
**Supplementary Table 1**: Model performance for steenbok occupancy. The top model (mod1) only included effort for detection and scenario for occupancy

<table>
<thead>
<tr>
<th>Model</th>
<th>nPars</th>
<th>AIC</th>
<th>delta</th>
<th>AICwt</th>
<th>cumWt</th>
<th>Rsq</th>
</tr>
</thead>
<tbody>
<tr>
<td>mod1</td>
<td>5</td>
<td>232.59</td>
<td>0</td>
<td>0.07</td>
<td>0.067</td>
<td>0.25</td>
</tr>
<tr>
<td>mod13</td>
<td>6</td>
<td>233.49</td>
<td>0.9</td>
<td>0.04</td>
<td>0.11</td>
<td>0.27</td>
</tr>
<tr>
<td>mod12</td>
<td>6</td>
<td>233.73</td>
<td>1.14</td>
<td>0.04</td>
<td>0.148</td>
<td>1</td>
</tr>
<tr>
<td>mod15</td>
<td>6</td>
<td>234.33</td>
<td>1.74</td>
<td>0.03</td>
<td>0.235</td>
<td>0.26</td>
</tr>
<tr>
<td>mod16</td>
<td>6</td>
<td>234.43</td>
<td>1.84</td>
<td>0.03</td>
<td>0.261</td>
<td>0.26</td>
</tr>
<tr>
<td>mod14</td>
<td>6</td>
<td>234.45</td>
<td>1.86</td>
<td>0.03</td>
<td>0.288</td>
<td>0.26</td>
</tr>
<tr>
<td>mod2</td>
<td>6</td>
<td>234.48</td>
<td>1.89</td>
<td>0.03</td>
<td>0.314</td>
<td>0.26</td>
</tr>
<tr>
<td>mod11</td>
<td>6</td>
<td>234.56</td>
<td>1.97</td>
<td>0.02</td>
<td>0.364</td>
<td>0.25</td>
</tr>
<tr>
<td>mod41</td>
<td>7</td>
<td>234.65</td>
<td>2.06</td>
<td>0.02</td>
<td>0.388</td>
<td>0.28</td>
</tr>
<tr>
<td>mod39</td>
<td>7</td>
<td>234.84</td>
<td>2.25</td>
<td>0.02</td>
<td>0.41</td>
<td>0.28</td>
</tr>
<tr>
<td>mod51</td>
<td>7</td>
<td>235.17</td>
<td>2.58</td>
<td>0.02</td>
<td>0.428</td>
<td>0.27</td>
</tr>
<tr>
<td>mod40</td>
<td>7</td>
<td>235.36</td>
<td>2.77</td>
<td>0.02</td>
<td>0.445</td>
<td>0.27</td>
</tr>
<tr>
<td>mod5</td>
<td>7</td>
<td>235.37</td>
<td>2.78</td>
<td>0.02</td>
<td>0.462</td>
<td>0.27</td>
</tr>
<tr>
<td>mod52</td>
<td>7</td>
<td>235.46</td>
<td>2.87</td>
<td>0.02</td>
<td>0.478</td>
<td>0.27</td>
</tr>
<tr>
<td>mod27</td>
<td>7</td>
<td>235.47</td>
<td>2.88</td>
<td>0.02</td>
<td>0.493</td>
<td>0.27</td>
</tr>
<tr>
<td>mod50</td>
<td>7</td>
<td>235.48</td>
<td>2.89</td>
<td>0.02</td>
<td>0.509</td>
<td>0.27</td>
</tr>
<tr>
<td>mod4</td>
<td>7</td>
<td>235.59</td>
<td>3</td>
<td>0.01</td>
<td>0.524</td>
<td>0.27</td>
</tr>
<tr>
<td>mod93</td>
<td>8</td>
<td>235.81</td>
<td>3.21</td>
<td>0.01</td>
<td>0.552</td>
<td>0.29</td>
</tr>
<tr>
<td>mod94</td>
<td>8</td>
<td>235.99</td>
<td>3.4</td>
<td>0.01</td>
<td>0.589</td>
<td>0.29</td>
</tr>
<tr>
<td>mod36</td>
<td>8</td>
<td>236.05</td>
<td>3.46</td>
<td>0.01</td>
<td>0.601</td>
<td>0.29</td>
</tr>
<tr>
<td>mod43</td>
<td>9</td>
<td>236.21</td>
<td>3.62</td>
<td>0.01</td>
<td>0.623</td>
<td>0.31</td>
</tr>
<tr>
<td>mod17</td>
<td>8</td>
<td>236.26</td>
<td>3.67</td>
<td>0.01</td>
<td>0.633</td>
<td>0.29</td>
</tr>
<tr>
<td>mod67</td>
<td>8</td>
<td>236.26</td>
<td>3.67</td>
<td>0.01</td>
<td>0.644</td>
<td>0.29</td>
</tr>
<tr>
<td>mod59</td>
<td>7</td>
<td>236.28</td>
<td>3.69</td>
<td>0.01</td>
<td>0.665</td>
<td>0.26</td>
</tr>
<tr>
<td>mod66</td>
<td>7</td>
<td>236.28</td>
<td>3.69</td>
<td>0.01</td>
<td>0.676</td>
<td>0.26</td>
</tr>
<tr>
<td>mod7</td>
<td>7</td>
<td>236.3</td>
<td>3.71</td>
<td>0.01</td>
<td>0.686</td>
<td>0.26</td>
</tr>
<tr>
<td>mod29</td>
<td>7</td>
<td>236.31</td>
<td>3.72</td>
<td>0.01</td>
<td>0.697</td>
<td>0.26</td>
</tr>
<tr>
<td>mod</td>
<td>236.32</td>
<td>3.73</td>
<td>0.01</td>
<td>0.707</td>
<td>0.26</td>
<td>1</td>
</tr>
<tr>
<td>-----</td>
<td>--------</td>
<td>------</td>
<td>------</td>
<td>--------</td>
<td>------</td>
<td>---</td>
</tr>
<tr>
<td>mod8</td>
<td>236.33</td>
<td>3.74</td>
<td>0.01</td>
<td>0.718</td>
<td>0.26</td>
<td>1</td>
</tr>
<tr>
<td>mod60</td>
<td>236.36</td>
<td>3.77</td>
<td>0.01</td>
<td>0.728</td>
<td>0.26</td>
<td>1</td>
</tr>
<tr>
<td>mod3</td>
<td>236.45</td>
<td>3.86</td>
<td>0.01</td>
<td>0.747</td>
<td>0.26</td>
<td>1</td>
</tr>
<tr>
<td>mod28</td>
<td>236.45</td>
<td>3.86</td>
<td>0.01</td>
<td>0.757</td>
<td>0.26</td>
<td>1</td>
</tr>
<tr>
<td>mod35</td>
<td>236.64</td>
<td>4.05</td>
<td>0.01</td>
<td>0.766</td>
<td>0.28</td>
<td>1</td>
</tr>
<tr>
<td>mod33</td>
<td>236.7</td>
<td>4.11</td>
<td>0.01</td>
<td>0.775</td>
<td>0.28</td>
<td>1</td>
</tr>
<tr>
<td>mod92</td>
<td>236.76</td>
<td>4.17</td>
<td>0.01</td>
<td>0.783</td>
<td>0.28</td>
<td>1</td>
</tr>
<tr>
<td>mod46</td>
<td>237.14</td>
<td>4.55</td>
<td>0.01</td>
<td>0.79</td>
<td>0.27</td>
<td>1</td>
</tr>
<tr>
<td>mod101</td>
<td>237.16</td>
<td>4.57</td>
<td>0.01</td>
<td>0.789</td>
<td>0.27</td>
<td>1</td>
</tr>
<tr>
<td>mod34</td>
<td>237.17</td>
<td>4.58</td>
<td>0.01</td>
<td>0.803</td>
<td>0.27</td>
<td>1</td>
</tr>
<tr>
<td>mod44</td>
<td>237.26</td>
<td>4.66</td>
<td>0.01</td>
<td>0.817</td>
<td>0.3</td>
<td>1</td>
</tr>
<tr>
<td>mod47</td>
<td>237.35</td>
<td>4.75</td>
<td>0.01</td>
<td>0.823</td>
<td>0.27</td>
<td>1</td>
</tr>
<tr>
<td>mod20</td>
<td>237.35</td>
<td>4.76</td>
<td>0.01</td>
<td>0.829</td>
<td>0.27</td>
<td>1</td>
</tr>
<tr>
<td>mod45</td>
<td>237.36</td>
<td>4.77</td>
<td>0.01</td>
<td>0.835</td>
<td>0.27</td>
<td>1</td>
</tr>
<tr>
<td>mod53</td>
<td>237.46</td>
<td>4.87</td>
<td>0.01</td>
<td>0.841</td>
<td>0.3</td>
<td>1</td>
</tr>
<tr>
<td>mod102</td>
<td>237.46</td>
<td>4.87</td>
<td>0.01</td>
<td>0.847</td>
<td>0.27</td>
<td>1</td>
</tr>
<tr>
<td>mod95</td>
<td>237.57</td>
<td>4.98</td>
<td>0.01</td>
<td>0.858</td>
<td>0.32</td>
<td>1</td>
</tr>
<tr>
<td>mod88</td>
<td>237.62</td>
<td>5.03</td>
<td>0.01</td>
<td>0.864</td>
<td>0.3</td>
<td>1</td>
</tr>
<tr>
<td>mod89</td>
<td>237.82</td>
<td>5.23</td>
<td>0.00</td>
<td>0.874</td>
<td>0.29</td>
<td>1</td>
</tr>
<tr>
<td>mod18</td>
<td>238.11</td>
<td>5.52</td>
<td>0.00</td>
<td>0.887</td>
<td>0.26</td>
<td>1</td>
</tr>
<tr>
<td>mod72</td>
<td>238.11</td>
<td>5.52</td>
<td>0.00</td>
<td>0.891</td>
<td>0.26</td>
<td>1</td>
</tr>
<tr>
<td>mod9</td>
<td>238.14</td>
<td>5.55</td>
<td>0.00</td>
<td>0.895</td>
<td>0.29</td>
<td>1</td>
</tr>
<tr>
<td>mod64</td>
<td>238.14</td>
<td>5.55</td>
<td>0.00</td>
<td>0.899</td>
<td>0.29</td>
<td>1</td>
</tr>
<tr>
<td>mod37</td>
<td>238.19</td>
<td>5.6</td>
<td>0.00</td>
<td>0.903</td>
<td>0.31</td>
<td>1</td>
</tr>
<tr>
<td>mod61</td>
<td>238.2</td>
<td>5.61</td>
<td>0.00</td>
<td>0.908</td>
<td>0.29</td>
<td>1</td>
</tr>
<tr>
<td>mod109</td>
<td>238.2</td>
<td>5.61</td>
<td>0.00</td>
<td>0.912</td>
<td>0.29</td>
<td>1</td>
</tr>
<tr>
<td>mod55</td>
<td>238.22</td>
<td>5.63</td>
<td>0.00</td>
<td>0.916</td>
<td>0.26</td>
<td>1</td>
</tr>
<tr>
<td>mod56</td>
<td>238.24</td>
<td>5.65</td>
<td>0.00</td>
<td>0.92</td>
<td>0.26</td>
<td>1</td>
</tr>
<tr>
<td>mod63</td>
<td>238.24</td>
<td>5.65</td>
<td>0.00</td>
<td>0.924</td>
<td>0.26</td>
<td>1</td>
</tr>
<tr>
<td>mod108</td>
<td>238.25</td>
<td>5.66</td>
<td>0.00</td>
<td>0.928</td>
<td>0.26</td>
<td>1</td>
</tr>
<tr>
<td>mod31</td>
<td>238.26</td>
<td>5.67</td>
<td>0.00</td>
<td>0.931</td>
<td>0.29</td>
<td>1</td>
</tr>
<tr>
<td>mod22</td>
<td>238.29</td>
<td>5.7</td>
<td>0.00</td>
<td>0.935</td>
<td>0.26</td>
<td>1</td>
</tr>
<tr>
<td>mod21</td>
<td>238.32</td>
<td>5.72</td>
<td>0.00</td>
<td>0.939</td>
<td>0.26</td>
<td>1</td>
</tr>
<tr>
<td>mod87</td>
<td>238.58</td>
<td>5.99</td>
<td>0.00</td>
<td>0.946</td>
<td>0.28</td>
<td>1</td>
</tr>
<tr>
<td>mod38</td>
<td>239.05</td>
<td>6.46</td>
<td>0.00</td>
<td>0.952</td>
<td>0.3</td>
<td>1</td>
</tr>
<tr>
<td>mod96</td>
<td>239.06</td>
<td>6.46</td>
<td>0.00</td>
<td>0.954</td>
<td>0.3</td>
<td>1</td>
</tr>
<tr>
<td>mod97</td>
<td>239.14</td>
<td>6.54</td>
<td>0.00</td>
<td>0.957</td>
<td>0.27</td>
<td>1</td>
</tr>
<tr>
<td>mod54</td>
<td>239.18</td>
<td>6.59</td>
<td>0.00</td>
<td>0.959</td>
<td>0.27</td>
<td>1</td>
</tr>
<tr>
<td>mod48</td>
<td>239.3</td>
<td>6.71</td>
<td>0.00</td>
<td>0.962</td>
<td>0.3</td>
<td>1</td>
</tr>
<tr>
<td>mod98</td>
<td>239.34</td>
<td>6.75</td>
<td>0.00</td>
<td>0.964</td>
<td>0.27</td>
<td>1</td>
</tr>
<tr>
<td>mod103</td>
<td>239.45</td>
<td>6.86</td>
<td>0.00</td>
<td>0.966</td>
<td>0.3</td>
<td>1</td>
</tr>
</tbody>
</table>
Chapter 3: Exploring how the presence of large-bodied managed ungulates influences occupancy and temporal activity of small antelope

Deborah J. Winterton¹,², Nicola J. van Wilgen¹,³ and Jan A. Venter²,⁴

¹ Cape Research Centre, SANParks Scientific Services, Western Cape, South Africa
² School of Natural Resource Management, Faculty of Science, Nelson Mandela Metropolitan University, George Campus, Western Cape, South Africa
³ Centre for Invasion Biology, Stellenbosch University, Western Cape, South Africa
⁴ Eugène Marais Chair of Wildlife Management, Mammal Research Institute, University of Pretoria, Pretoria, South Africa

Word count: 9635
Chapter 3

Abstract
Substantial knowledge gaps related to the local effects of global environmental change drivers persist, particularly those that do not manifest in obvious ways. The more subtle and cascading effects that anthropogenic stressors have on local ecological assemblages, in the form of altered interspecific interactions, are particularly concerning given their importance in ecosystem function. Small antelope abundance in the contractual Postberg section of the West Coast National Park has been an ongoing management concern. The perception of a lower abundance of small antelope has been attributed to predation by a mesopredator (caracal, *Caracal caracal*). However interspecific competition is also known to influence species abundance. Since Postberg has been influenced by the overstocking, and consequent overgrazing, of larger -bodied managed ungulates, we aimed to assess the influence of different management practices on interspecific interactions. Using camera traps we investigated species co-occurrence and temporal activity and overlap between small antelope and managed ungulates, as well as caracal. Results suggest that small antelope and managed ungulates have a high degree of spatial and temporal overlap, while temporal partitioning between small antelope and caracal is apparent, with caracal being significantly more nocturnal. This is indicative of anti-predator behaviour portrayed by small antelope. The results also suggest that small antelope and managed ungulates occur independently of one another. Small antelope were noticeably crepuscular in activity, whereas managed ungulate activity was higher throughout the day with both groups being significantly less active at night. Ecological systems are complex and interactions can be influenced by multiple factors which makes elucidating patterns from a small sample size difficult. However we did find some evidence of interspecific interactions and ecosystem process at the local scale. Therefore we recommend continued monitoring over the long term and over a wider area to establish important drivers of ecosystem function to inform management of small protected areas.

*Keywords: steenbok, common duiker, caracal, resource partitioning*
Introduction

Land use results in habitat conversion, degradation and fragmentation which have, along with climate change, altered the biodiversity and ecosystems of the earth (Chapin et al. 2000; Newbold et al. 2015). Substantial knowledge gaps related to the local effects of global environmental change drivers persist, particularly those that do not manifest in obvious ways like land cover conversions and wildlife population declines (Newbold et al. 2015). The more subtle and cascading effects that anthropogenic stressors have on local ecological assemblages, in the form of altered interspecific interactions and species behaviours, are particularly concerning given their importance in ecosystem function (Erb et al. 2017; Frey et al. 2017). Niche partitioning between species at the same trophic level is an important facilitator of coexistence (Frey et al. 2017; Herfindal et al. 2017). Understanding how environmental stressors influence niche partitioning between species is critical for informing management decisions as well as for improving my understanding of how local assemblages respond to anthropogenic changes (Frey et al. 2017).

Resource partitioning is commonly observed in diet segregation, habitat use, spatial aggregation or timing of peak activity which is needed for sympatric species to co-exist (Herfindal et al. 2017; Marti et al. 1993). Resource partitioning amongst ungulates is usually driven by body size, due to differing metabolic rates, (Cromsigt and Olf 2006), competition and resource availability (Gordon and Illius 1989). For example, larger ungulates have a lower per mass metabolic rate and therefore require quantity of forage rather than the quality which the smaller antelope require due to their higher per mass metabolic rate (Cromsigt and Olf 2006). As such, resources are partitioned along a niche axis of quantity versus quality (Cromsigt and Olf 2006). Variability of forage quantity has been ascribed to variation of the vertical component where large and small ungulates target different parts of the plant according to height, but there is also, however, a horizontal component to consider and that is heterogeneity of vegetation and patch size which influences foraging behaviour differently (Cromsigt and Olf 2006; Venter et al. 2014). Alternatively, resource partitioning occurs when there is a mutually preferred resource which is more effectively utilised by the dominant species, thereby excluding the subordinate, hence, for co-existence to transpire, the subordinate species needs to be able to utilise a less preferred resource which the dominant species does not (Gordon and Illius 1989). When there is an overlap in resource use between species, but resources are readily available, then competition is likely to be low, whereas when there is overlap and resources are scarce competition is likely to be high (Voeten and Prins 1999). When there is high overlap the dominant species will have a greater impact on the subordinate since the dominant can exclude the subordinate from the preferred resource (Gordon and Illius 1989). On the other hand, the dominant species may benefit the subordinate
by facilitating access to forage by reducing plant biomass of a lower digestibility (Arsenault and Owen-Smith 2002).

Time spent on one activity is a lost opportunity for beneficial gains of another activity, which has associated energetic costs. Therefore animals need to carefully balance fitness trade-offs between forage intake, risk of predation and thermoregulation (Owen-Smith and Goodall 2014; Rowcliffe et al. 2014). For example, foraging theory suggests that if fitness increases with net energy gains, then animals should spend the maximum amount of allowable time foraging, but if animals are at a high risk of predation it may be more worthwhile to spend the minimum amount of time foraging to meet their basic energy and nutrient requirements (Schoener 1971). Therefore, variation in activity patterns is expected across the diel cycle, seasons, and between animals that differ physiologically, in social structure and susceptibility to predation (Owen-Smith and Traill 2017). The proportion of time that animals spend active (hereafter referred to as activity level) is a good indicator of species energetics, foraging effort and risk exposure, all of which are poorly understood due to the challenges of quantifying activity in the field (Rowcliffe et al. 2014). For instance, if two species show inverted spatial and temporal patterns, it may indicate that one species is dominant over the other (Lazenby and Dickman 2013) or it could suggest resource partitioning when time is considered a resource (Frey et al. 2017). However, temporal niches are driven not only by competition but also by predation risk (Díaz-Ruiz et al. 2016; Tambling et al. 2015).

Animal interactions can be an important determinant of species distribution and abundance (Lazenby and Dickman 2013). Experiments and observations of behaviour that explore the responses of co-occurring species have contributed important information to understanding the interactions between not only predators and prey, but also between species of the same trophic level (Herfindal et al. 2017; Lazenby and Dickman 2013). Species interactions are also important when assessing the impact of land use and management practices since habitat can be an important explanatory variable for observed patterns (Lazenby and Dickman 2013). Furthermore, alteration of species abundance and composition through direct management could influence free ranging species through facilitative or competitive interactions. For example, domestic ungulates kept at a low abundance improve foraging for wild ungulates but the effect becomes negative as densities increase (Herfindal et al. 2017). In Mpala Conservancy, Laikipia County, Kenya, cattle were the main driver of increased mean productivity and wild ungulates were the main drivers of spatially and temporally steady productivity, suggesting that replacing wildlife with cattle (at moderate densities) could lead to greater heterogeneity of herbaceous plant communities with a similar productivity level as that maintained by wildlife (Charles et al. 2017). The response of wild ungulates to grazing by
livestock varies and while some research shows positive responses, the majority of studies indicate that wild ungulates are negatively impacted by livestock, with the greatest negative responses being due to competition and a change in forage quantity and quality (Schieltz and Rubenstein 2016).

Small antelope (common duiker, *Sylvicapra grimmia*, and steenbok, *Raphicerus campestris*) abundance in the contractual Postberg section of the West Coast National Park (hereafter referred to as the park) have been a management concern since the early 1990s (Avenant 1993 and Heydenrych 1995). There is a perception of a lower abundance of these two species in the contractual section of the park, when compared to other sections, which landowners have attributed to predation by a mesopredator (caracal, *Caracal caracal*) (Postberg owners consortium, pers. comm.). Caracals are the largest predator in the system following the historical extirpation of apex predators. The caracal’s “release” from the top down competition that would have occurred in the presence of large predators prior to extirpation (Cruz-Uribe and Schrire 1991) may have enhanced its impact on small antelope populations in the area. However, while the predation threat may be realistic, it is not the only process that could result in low abundance of small antelope. Historical land use and management practice within Postberg includes agriculture (livestock and crop cultivation) and more recently the overstocking of large ungulates which has resulted in extensive habitat degradation.

Using camera traps we aimed to assess co-occurrence and temporal activity overlap between managed ungulates and small antelope with a view to establish how land management (in the form of stocking rates of different ungulate species and fencing) influences species interactions. Camera traps are especially useful tools for observing animal interactions as they provide 24 hour surveillance that can record multiple species over space with time-of-detection (Lazenby and Dickman 2013; Rowcliffe *et al.* 2014), which is important for assessing interactions between co-occurring species. Furthermore, camera traps are instrumental in estimating species distribution and abundances in relation to anthropogenic change and stressors (Frey *et al.* 2017) as they are very effective at detecting medium to large sized terrestrial mammals (Reilly *et al.* 2017). We used data from cameras in three areas with different management practices and managed ungulate abundances (two within the park, Postberg and Langebaan, and one on a research livestock farm) to assess how the presence or absence of managed ungulates affects the occupancy of small antelope (steenbok and common duiker) and whether there is a difference in temporal activity patterns between the two groups. A secondary aim was to investigate temporal activity overlap between caracal and small antelope to ascertain the extent to which the only predator in the study system could be driving temporal activity of a potential prey species in the park. We expected the presence of
managed ungulates to negatively influence occurrence probabilities of small antelope in Postberg due to either direct competition for resources with, or due to habitat modification by, the more abundant larger managed ungulates (Fritz et al. 2002). We also predicted a greater temporal overlap between managed ungulates and small antelope in Postberg when compared to more natural areas within the park due to the higher abundance of managed ungulates, thus forcing the small antelope to spend more time looking for appropriate resources. To add scope to the comparisons and influence of managed ungulates on small antelope we also investigated co-occurrence and temporal overlap between managed ungulates on a research farm where livestock are restricted to fenced camps. Here, as with Postberg, we expected the presence of livestock to have a negative influence on the occupancy of small antelope as well as to have higher temporal activity overlap when compared to the larger more natural area in the park where ungulates are free ranging. Finally, we expected a significant temporal niche partitioning between small antelope and caracal, due to lower their predation risk (Tambling et al. 2015).

**Materials and methods**

**Study area**

This study took place in the nutrient-poor Fynbos Biome, along the west coast of South Africa, where annual average rainfall varies between 152 mm in the north and 265 mm in the south. The predominant vegetation type of the region is Strandveld which is dominated by sclerophyllous, broad-leaved shrubs that form communities of medium density to closed shrublands (Mucina and Rutherford 2012).

We defined three study areas (scenarios) by their different management practices where the ‘stocking rate’ and species of managed ungulates at each site acted as a proxy for ‘management practice’. Managed ungulates were defined as those species which require the intervention of people to manage the populations e.g. removals, introductions, feed supplementation and census. Ungulates were classified into different size classes according to weight, where animals <25 kg were classified as small, between 26 – 200 kg were classified as medium and anything >200 kg was classified as a large, based on the natural segregation of weight ranges between the managed ungulates. No managed ungulate was classified in the small class. Two areas were within a protected area (Postberg and Langebaan sections of the park) and the third was on a research farm (Lamberts Bay, hereafter referred to as the farm). The park is located approximately 100 km north-west of Cape Town and was proclaimed in 1985 and since then it has expanded to its current size of approximately 47 000 ha (SANParks 2013). The farm is located outside of the town Lamberts Bay which is approximately 100 km north of the park (Fig. 1). The park was proclaimed in 1985 and since
then it has expanded to its current size of approximately 47 000 ha (SANParks 2013). The farm was selected due to its size since the majority of commercial farms along the west coast are predominantly used for crop production with little livestock and are therefore not of a comparable size to the areas within the protected area and also because it is within the same bioregion so the vegetation types were comparable.

**Postberg**
The Postberg scenario has historically been characterised by intensive management of large and medium sized herbivores in a small area (1 800 ha). Postberg was originally acquired in the early 1800s by a group of farmers and was used primarily for winter grazing, but the land was also ploughed. Postberg was proclaimed as a private nature reserve in the 1960s, after which it was contractually included into the park in 1987. Many indigenous and extra-limital large and medium sized ungulate species were introduced to Postberg since the 1960s which resulted in overgrazing of the small, fenced area. Managed ungulates at this site were: bontebok (*Damaliscus pygargus pygargus*), Cape mountain zebra (*Equus zebra zebra*), red hartebeest (*Alcelaphus buselaphus caama*), eland (*Taurotragus oryx*), blue wildebeest (*Connochaetes taurinus*), kudu (*Tragelaphus strepsiceros*), springbok (*Antidorcas marsupialis*) and gemsbok (*Oryx gazelle*) and occurred at an estimated density of approximately 11.3 managed ungulates per km² (SANParks unpublished data). Although there have been consistent removal efforts of extra-limital and re-introduced ungulates since Postberg's inclusion into the park, November 2016 (6 months prior to the study) saw a significant removal of these species from the area, resulting in slightly lower densities during this study. However, due to slow reproduction rates of the removed managed ungulates (and associated delay in observable response) and recovery of vegetation, the high stocking rate would have a legacy effect on small antelope abundance and vegetation structure that would extend through the duration of this research.

**Langebaan**
The Langebaan scenario is characterised by the management of large and medium sized herbivores in a larger, more open section of the park. Here, large herbivores are not confined to a small area, are free ranging and occur at lower densities. Historically this area was also used for agriculture, which included livestock and crop production and different portions were proclaimed as part of the park in 1989 and 1996. Managed ungulates at the Langebaan scenario were eland, bontebok and red hartebeest and occurred at an estimated density of 7.6 managed ungulates per km² (SANParks unpublished data).
Chapter 3

*Lamberts Bay (the farm)*

The farm scenario made use of the Nortier research farm that falls under the management of the Department of Agriculture (Elsenburg), Western Cape Government and is 2780 ha in size. Several resource flocks and herds are kept on the farm for the Directorate: Animal Sciences, while it is also the site of veld rehabilitation projects run by the Directorate: Plant Sciences. The livestock present include the sheep (*Ovis aries*) resource flock, consisting of three breeds (namaqua afrikaner, dorper and SA mutton merino), the beef cattle (*Bos taurus*) resource herd (bonsmara). The research farm is located in a matrix of other farms where predator control is known to take place (C. Rheeder, research farm manager, pers comms). Managed ungulates at this site were namaqua afrikaner, dorper and merino sheep, bonsmara cattle, impala (*Aepyceros melampus*) and nyala (*Tragelaphus angasii*). Estimated density of managed ungulates were was 7.6 animals per km$^2$ (C. Rheeder, research farm manager, pers comms).

![Figure 1: Map of the study area.](image-url)
Survey design and in-field methods

The three scenarios were surveyed over the winter of 2017 using 18 Cuddeback®, model C3 blackflash (Non Typical, De Pere, WI) camera traps. The Postberg scenario was surveyed between May - July, followed by the Langebaan scenario between July – August and the farm from August – October 2017. We overlaid each area with a grid of 1 km² cells in Arc GIS, and selected the centroid of each of the 18 cells, which served as the camera locations. Once we were in the field myself and field assistants used a handheld GPS to navigate to the centroid after which we walked outward in a spiral fashion for up to 120 m from the centroid, seeking the first location where two or more signs of animal activity were detected (Colyn 2017). The camera was set at this point. Cameras were mounted approximately 40 – 50 cm above ground level, onto a wooden stake and faced in a southerly direction, away from the sun, to prevent false triggers and over exposure (Glen et al. 2014). We programmed the cameras to capture three burst photographs when triggered, with a 30 second delay between photographs.

Vegetation height and cover were measured at each site according the protocol described in Colyn (2016), i.e. by taking a measurement at one and two meter distances from the camera trap location in a North, South, East and West direction (eight measurements in total). Vegetation height was recorded at the prescribed 1 m and 2 m distances with a measuring tape and percentage cover was also measure at these points using a densitometer (Li et al. 2000). Height and cover were averaged across the eight measurements for use in analyses. Elevation was extracted at site level from the CGIAR-CSI SRTM 90m Digital Elevation Data (Jarvis et al. 2008) using the spatial analyst tool within ArcGIS. Similarly, slope was calculated using a digital slope model from the same DEM using the spatial analyst tool within ArcGIS (ESRI 2012).

Data analysis

Camera trap images were downloaded and image data were processed and captured using the TimeLapse2 Image Analyzer software (Saul Greenberg, University of Calgary, Calgary, Alberta) and then exported to excel per camera station. Image databases of camera stations were merged for each management scenario. Non-animal photographs were removed from the database and when more than one species was captured in a single photograph, entries were duplicated and edited to capture the number of individuals of each species as separate records. If a photographed animal was not recognisable to species level, but could be classified as either a small antelope or managed ungulate, then it was captured as such. Image data were binned into independent capture events using a loop in R (R Development Core Team, 2015) which grouped all captures of a particular species, at a particular location. It then calculated the time difference between each picture and assigned those that occurred
within 30 minutes of one another to a particular group. From this group it then selected the photograph with the highest number of individuals of that species and appended it to the analysis database as an independent capture. We used the tidyverse package (Wickham 2017) in R to manipulate databases and produce summaries where necessary and we used the camtrapR package (Niedballa et al. 2018) to produce detection maps.

**Two-species occupancy**

To assess how the presence of managed ungulates influences the occurrence of small antelope we conducted single season, two-species occupancy analyses in PRESENCE (Hines 2006). Detection histories for the species of interest were created using an occasion length of five days in R (R Development Core Team, 2015) using the camtrapR package (Niedballa et al. 2018). The two-species model that we used included three occupancy parameters, five detection parameters and a species interaction factor (SIF) that was assessed using the occupancy estimates (Table 1). A SIF <1 suggests avoidance, SIF = 1 suggests that the two species occur independently of one another and a SIF >1 suggests that the two species tend co-occur together more frequently than expected under independence (Mackenzie et al. 2004). We assessed co-occurrence between the species of interest separately for each management scenario. Probability of occurrence and detection were kept constant across sites and surveys with no site specific co-variates used to explain detection or occurrence. For the protected area we analysed the influence of medium and large managed ungulates on steenbok and common duiker where managed ungulates were considered the dominant species (species A) and small antelope as the subordinate species (species B). We performed these analyses using presence-absence data of medium and large managed ungulates separately and pooled (managed ungulates), and of common duiker and steenbok separately and pooled (small antelope). For the farm we only looked at the influence of livestock on steenbok occurrence due to high occurrence of common duiker and the pooled data for managed ungulates confounding my ability to make accurate occurrence and interaction estimates.

The two-species occupancy analysis was performed using a data set produced by a systematic survey of the three areas between May – September 2017. The Postberg site had one camera failure which resulted in fewer camera days. Both Postberg and Langebaan areas were surveyed for approximately 30 days while the farm was surveyed for 60 days, however the data for the farm were partitioned and only the data generated within the first 30 days of the survey were used for the two-species occupancy. This generated 542, 602 and 561 trap nights for the Postberg, Langebaan and the farm respectively.
Table 1: Occupancy parameters that were assessed for the two-species occupancy models in PRESENCE

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>PsiA</td>
<td>Probability of site occupancy of dominant species (managed ungulates).</td>
</tr>
<tr>
<td>PsiBA</td>
<td>Probability of site occupancy of subordinate species (small antelope), where dominant species (managed ungulates) are present.</td>
</tr>
<tr>
<td>PsiBa</td>
<td>Probability of site occupancy of subordinate species (small antelope), where dominant species (managed ungulates) are not present.</td>
</tr>
<tr>
<td>SIF</td>
<td>Species interaction factor: likelihood ratio of co-occurrence, SIF = psiAB/(psiA*psiB)</td>
</tr>
</tbody>
</table>

Temporal activity and overlap
Activity level and overlap of small antelope and managed ungulates were assessed using the overlap (Ridout and Linkie 2009) and activity (Rowcliffe 2016) packages in R (R Development Core Team, 2015). Prior to activity and overlap analyses the data were structured into the required format by converting time to decimal numbers. The time of sunrise and sunset was calculated and stored for each record based on the date and GPS coordinate of each photograph, using the StreamMetabolism package (Sefick 2016). Data were then partitioned by time into 24 different time bins representing the 24 hours of the day. Hourly data were used to plot accumulation curves of hours that the species of interest was detected at using the specaccum function in the package vegan (Oksanen et al. 2018) to assess how well well-represented the hours of activity were within the data for each species of interest.

The analysis of circular data is a specialised, but well established field (Ridout and Linkie 2009). However, since circular data is acquired by measuring arrival times or direction in reference to a point on the unit circle (Taşdan and Yeniay 2013), problems with time-of-day data arise due to the arbitrariness of the time origin (Ridout and Linkie 2009). For example a species activity could be centred on midday but if that is shifted by 12 hours, the distribution inverses entirely. It is, thus, important for any analysis to recognise that the difference between 23h50 - 00h01 is the same as the difference between 11h50 – 12h01 and therefore standard statistical measure such as mean and variance, and procedures such as regression are not appropriate (Ridout and Linkie 2009). Time was converted to radians, a requirement of the overlap package. Activity was broadly depicted by non-parametrically estimating activity patterns using kernel density estimation with the bandwidth concentration parameter set at the maximum of 3 (Ridout and Linkie 2009). This was further multiplied and adjusted by 1.5 as per Rowcliffe et al. (2014) who noted that bandwidth adjustment of 1.5 gave the most
robust and minimally biased activity level estimations. The degree of overlap in temporal use of different species groups was estimated using the coefficient of overlap, $\Delta$, where $0 = \text{complete separation}$ and $1 = \text{complete overlap}$. If there were less than 75 observations for one of the species, we used the $D_{hat1}$ overlap estimator whereas if the sample size was greater than 75 for both species, $D_{hat4}$ was used (Ridout and Linkie 2009). We compared the activity overlap of the species of interest across areas first to assess whether they displayed any difference in activity patterns in the different areas. Following this we compared the overlap between managed ungulates and small antelope at each area to determine if there is any evidence of temporal niche partitioning between species groups. Data were bootstrapped and resampled 500 times for each overlap estimate to generate 95% confidence intervals. To test whether activity patterns differed between species, we tested for significance between the distributions of the respective data across the diel cycle (Taşdan and Yeniay 2013), using the Watson-Wheeler test of homogeneity for circular data on non-bootstrapped data in circular package in R (Agostinelli and Lund 2017). Activity levels and overlap were plotted using the overlap package.

To increase the available sample size for the temporal activity and overlap analyses, we lumped the data generated by the systematic survey described above with camera trap data that was opportunistically collected in the Postberg and Langebaan sections of the park between June 2016 and February 2017, where cameras were set on management tracks using the same camera settings as above as well as data generated from the full 60 days for which the farm was surveyed. This resulted in 1150, 1159 and 1213 trap nights for the Postberg, Langebaan and the farm respectively. We did not have enough time-of-day observations (Table 2) for caracal at the farm and Postberg to assess temporal activity and overlap with small antelope, so this analysis was restricted to the Langebaan site.

**Table 2: Time-of-day observations for the species of interest across the three areas**

<table>
<thead>
<tr>
<th>Species</th>
<th>Postberg</th>
<th>Langebaan</th>
<th>Lamberts Bay</th>
</tr>
</thead>
<tbody>
<tr>
<td>caracal</td>
<td>17</td>
<td>56</td>
<td>4</td>
</tr>
<tr>
<td>steenbok</td>
<td>9</td>
<td>89</td>
<td>97</td>
</tr>
<tr>
<td>common duiker</td>
<td>50</td>
<td>196</td>
<td>577</td>
</tr>
<tr>
<td>Small antelope</td>
<td>59</td>
<td>292</td>
<td>691</td>
</tr>
<tr>
<td>Managed ungulates</td>
<td>649</td>
<td>828</td>
<td>276</td>
</tr>
</tbody>
</table>
Chapter 3

Results

Two-species occupancy

Langbeaan

Large herbivore occupancy estimates (psiA) were high as determined by interaction models with small antelope (0.957 ± 0.055 SE) and common duiker (0.985 ± 0.061 SE). Small antelope (0.942 ± 0.056 SE) and common duiker (0.887 ± 0.075 SE) had high probability of occurrence in the presence of large herbivores (psiBA). The species interaction factor (SIF) between large ungulates was close to one for both small antelope (0.997 ± 0.004 SE) and common duiker (0.998 ± 0.008 SE) (Table 3).

Medium ungulate occupancy estimates (psiA) in the interaction models with small antelope (0.611 ± 0.123 SE) and common duiker (0.579 ± 0.182 SE) were lower than the estimates for large ungulates. Small antelope (0.909 ± 0.087 SE) and common duiker (0.808 ± 0.130 SE) however, still had high probability of occurrence in the presence of medium sized ungulates (psiBA). The SIF between medium ungulates was also close to one for both small antelope (0.963 ± 0.040 SE) and common duiker (0.909 ± 0.086 SE) (Table 3).

Lamberts Bay (farm)

The only viable interaction model for the farm was between livestock and steenbok where livestock probability of occurrence (psiA) was 0.286 (± 0.109 SE). The probability of steenbok occurring in the presence of livestock (psiBA) was 0.809 (± 0.176 SE) while in the absence (psiBa), it was 0.921 (± 0.173 SE). Similar to the Langebaan site, SIF between livestock and steenbok was close to one (0.910 ± 0.195 SE) (Table 3).
Table 3: Site occupancy and associated standard error (SE) for managed (LU = large ungulate, MU = medium ungulate, LV = livestock) and small antelope (SA = small antelope, SB = steenbok, CD = common duiker) interaction at two areas (Langebaan and Lamberts Bay). Managed ungulates are modelled as the dominant species while small antelope as the subordinate. Parameters are described in table 1.

<table>
<thead>
<tr>
<th></th>
<th>psiA</th>
<th>SE</th>
<th>psiBA</th>
<th>SE</th>
<th>psiBa</th>
<th>SE</th>
<th>SIF</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Langebaan</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LU-SA</td>
<td>0.957</td>
<td>0.055</td>
<td>0.942</td>
<td>0.056</td>
<td>NA</td>
<td>NA</td>
<td>0.997</td>
<td>0.004</td>
</tr>
<tr>
<td>LU-C</td>
<td>0.985</td>
<td>0.061</td>
<td>0.887</td>
<td>0.075</td>
<td>NA</td>
<td>NA</td>
<td>0.998</td>
<td>0.008</td>
</tr>
<tr>
<td>MU-SA</td>
<td>0.611</td>
<td>0.123</td>
<td>0.909</td>
<td>0.087</td>
<td>NA</td>
<td>NA</td>
<td>0.963</td>
<td>0.040</td>
</tr>
<tr>
<td>MU-C</td>
<td>0.579</td>
<td>0.182</td>
<td>0.808</td>
<td>0.130</td>
<td>NA</td>
<td>NA</td>
<td>0.909</td>
<td>0.086</td>
</tr>
<tr>
<td><strong>Lamberts Bay</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LV-SB</td>
<td>0.286</td>
<td>0.109</td>
<td>0.809</td>
<td>0.176</td>
<td>0.921</td>
<td>0.173</td>
<td>0.910</td>
<td>0.195</td>
</tr>
</tbody>
</table>
Chapter 3

**Temporal activity and overlap**

*Managed ungulate and small antelope activity across areas*

Prior to assessing temporal overlap between managed ungulates and small antelope, we were interested to see whether the activity patterns of the two species groups differed across the three areas. Managed ungulates were most active during the day with much less activity at night across all areas. Despite having a high degree of overall overlap in activity times, (86%, 95% confidence interval (CI) 0.82 - 0.89), the distribution of time-of-detection data across the diel cycle differed significantly for managed ungulates between the Langebaan and Postberg areas (p = <0.001). No other differences in activity were detected. Managed ungulate activity, at Postberg and the farm, peaked after sunrise and before sunset but there is a clear drop in activity at midday. The drop in activity level at midday is not observed in the Langebaan area, rather activity peaks at this time (Fig. 2). The farm and Postberg had an overlap coefficient of 84% (CI: 0.78 – 0.88). The farm and Langebaan areas had the lowest level of overlap of 80% (CI: 0.73 – 0.86). Small antelope activity overlap was high across all areas and these animals were most active in the mornings and evenings with an obvious drop in activity at midday. Small antelope activity did not peak as obviously during sunrise at Langebaan when compared to the other areas. Small antelope were more active at night at the farm when compared to the Langebaan and Postberg areas (Fig. 3).
Figure 2: Managed ungulate temporal activity level of across the different areas (A) and overlap between the Langebaan and Postberg areas (B). Time of day is displayed on the x-axes with midday in the middle and the fitted kernel-density on y-axes. In B the coefficient of overlap ($\Delta$) and the associated estimator used (number in subscript), along with the 95% confidence intervals in parentheses, is illustrated by the grey shaded area which shows the period of overlap. The vertical dotted lines represent the earliest and latest sunrise and sunset times across the study period. The dashed vertical lines along the x-axes indicates the sample size of time-of-day observations. $\rho$ is derived based on a Watson-Wheeler test of homogeneity for circular data.
Figure 3: Small antelope temporal activity levels across the different areas. No absolute differences in temporal data distribution were detected. Overlap between areas ranged between 84% and 89%. The vertical dotted lines represent the earliest and latest sunrise and sunset times across the study period. The dashed lines along the x-axis indicate the sample size of time-of-day observations for each area. Time of day is displayed on the x-axis with midday in the middle and the fitted kernel-density on y-axis.

Activity overlap between managed ungulates and small antelope
Activity overlap between managed ungulates and small antelope was assessed at the area level (Fig. 4). There was a significant difference in the distribution of the activity data between small antelope and managed ungulates at the farm (p < 0.001) and Langebaan (ρ = <0.001) areas, while there was no difference at the Postberg site (ρ = 0.089). Overlap was highest at the Postberg site (86%, CI: 0.77 – 0.93), followed by 79% (CI: 0.73 – 0.84) at Langebaan and 74% (CI: 0.68 – 0.79) at the farm. Small antelope tended to be more active at night but had a more defined drop in activity at midday compared to managed ungulates.
Figure 4: Temporal overlap estimates between small antelope and managed ungulates at the three areas with time of day starting and ending at midnight on the x-axes and the fitted kernel-density on y-axes. The grey shaded area indicates overlap and is described by the coefficient of overlap (Δ) and the associated estimator used (number in subscript) along with the 95% confidence intervals in parentheses. The vertical dotted lines represent the earliest and latest sunrise and sunset times across the study period. ρ is derived based on a Watson-Wheeler test of homogeneity for circular data. Dashed lines along the x-axes indicate the sample size of time-of-day observations.
Time-of-day observations for caracal and steenbok in Postberg were insufficient to assess temporal overlap, therefore we only performed this analysis for the Langebaan section. Despite the small sample for Postberg, however, the activity pattern appeared similar to that observed at Langebaan (Fig. 5).

**Figure 5**: Caracal activity across the Postberg and Langebaan areas with time of day starting and ending at midnight on the x-axis and the fitted kernel-density on y-axis. Vertical dotted lines illustrate sunrise and sunset periods during the study. Vertical lines along the x-axis show the sampled time-of-day observations across the diel cycle.

We assessed temporal overlap between caracal and small antelope (common duiker and steenbok independently as well as pooled) at the Langebaan site (Fig. 6). The overall trend across the overlap analyses is that small antelope activity peaks when caracal activity drops. Caracal are significantly more nocturnal while small antelope tend to be more crepuscular. Caracal activity was consistently low between sunrise and midday and then started picking up just after midday. The distribution of activity data across the diel cycle was significantly (<0.001) different between caracal and duiker, steenbok and small antelope. Caracals had the highest overlap with steenbok activity (58%, CI: 0.46 – 0.70), followed by 55% (CI: 0.45 – 0.64) with small antelope and 53% (CI: 0.42 – 0.63) overlap with common duikers.
Figure 6: Overlap between caracal, steenbok and common duiker activity at the Langebaan site. Time of day starting and ending at midnight on the x-axes and the fitted kernel-density on y-axes. The grey shaded area indicates overlap and is described by the coefficient of overlap (Δ) and the associated estimator used (number in subscript) along with the 95% confidence intervals in parentheses. The vertical dotted lines represent the earliest and latest sunrise and sunset times across the study period. ρ is derived based on a Watson-Wheeler test of homogeneity for circular data. The dashed lines along the x-axes indicate the sample size of time-of-day observations. Time of day is displayed on the x-axes with midday in the middle and the fitted kernel-density on y-axis.
Discussion

Co-existence between sympatric species requires segregation of resources such as food, habitat use, spatial distribution and temporal activity to facilitate niche partitioning (Frey et al. 2017; Herfindal et al. 2017). Adjusting temporal activity is also a way for prey species to avoid predation and escape risk (Owen-Smith 2015). In this study we explored the influence of different management practices on interspecific interactions by investigating species co-occurrence and temporal activity and overlap between small antelope and managed ungulates as well as a potential predator, the caracal. Results suggest that small antelope and managed ungulates have a high degree of spatial and temporal overlap, while temporal partitioning between small antelope and caracal is apparent.

Two-species occupancy

The results suggest that small antelope occurrence is not influenced by the presence of managed ungulates and that the two species groups occur independently of one another since the 95% CIs for the species interaction factor encompassed one. However, the very high occurrence of managed ungulates at Langebaan and steenbok at Lamberts Bay may have confounded the ability of the models to effectively estimate the different parameters. Although we expected to see avoidance behaviour by the small antelope, due to competition with managed ungulates at the sites with higher densities, it is not unusual to find sympatric species occurring independently of one-another. Amin et al. (2014) found a positive correlation in camera trap rates of different species of forest antelope, suggesting a positive spatial association between ungulate species. The ecological theory of resource partitioning suggests that for sympatric species to co-exist, the subordinate species needs to be able exploit a resource which is not available to the dominant species (Gordon and Illius 1989). It is therefore likely that small antelope and managed ungulates have segregated food resources at our study site. This segregation is most likely due to the difference in body size that dictates forage requirements and forage availability on the vertical and horizontal planes (Cromsigt and Olff 2006). Small antelope, due to their small size and muzzle width would be able to access new growth that is located at a low level or within the shrub itself, whereas the large ungulates are most likely utilising the outer and higher parts of the shrub component. Also, the larger ungulates have more access along the horizontal plane as they are not restricted to home ranges (Jarman 1974) and therefore can move greater distances between suitable foraging patches (Venter et al. 2015).

There is often a relationship between the available forage quantity and quality in an area and the amount of time that a large herbivore spends there (Venter et al. 2015), therefore, although managed ungulates were detected at a high proportion of sites, they may be transient at many
Chapter 3

of them and merely passing through. This is supported by the much higher detection of managed ungulates at sites that were classified as fallow lands when compared to the more vegetated sites within the park (Chapter 2). Research has also suggested that habitat heterogeneity may drive movement scales of larger herbivores as they move between suitable foraging patches (Venter et al. 2015), which would be applicable to the current study site given the heterogeneity of vegetation. We considered the potential of managed ungulates facilitating forage opportunities for small antelope. However, it is not likely to be occurring here due to the nutrient-poor soils and slow growth rates of the vegetation which often encourages competition between ungulates (Fritz et al. 2002). In addition, small antelope occurrence is lowest in the areas with the highest densities of managed ungulates which may indicate competition (see Chapter 2 and Supplementary Fig. 1). For example, it was suggested that small antelope were released from competition from buffalo (*Syncerus caffer*) when they were eliminated from the Serengeti National Park which resulted in their increased abundance (Arsenault and Owen-Smith 2002). While there seems to be little interspecific competition at the local level this might not be the case at a larger scale. For example, roe deer and wild boar have been seen to occur independently of cattle at the habitat level in China but displayed segregation at the landscape level (Wang et al. 2018). Further, research in the Kruger National Park suggests that interspecific interactions may have effects on the distribution of African megafauna, but that this may not be evident at the local scale (Ryan and Ladau 2017).

Temporal niche partitioning

Species temporal activity is influenced by temperature, forage availability, predation risk, reproduction and competition (Maloney et al. 2005; Owen-Smith 2015; Tambling et al. 2015; Wronski et al. 2015). Small antelope had noticeable peaks in activity in the mornings and evenings and a distinct drop in activity at midday, whereas managed ungulate activity was higher throughout the day, with both groups being significantly less active at night which is consistent with what has been found in other areas (Amin et al. 2014; Du Toit and Yetman 2004; Wronski et al. 2015). Small antelope, however, were more active at night compared to managed ungulates, suggesting that they spend more time foraging at night to make up for the lowered activity at midday. Interestingly, managed ungulate activity at the Langebaan site did not drop and actually peaked at midday. The reason for this is not clear, but may be attributed to the bigger size of the area and therefore a need for them to spend more time moving between forage patches and water sources (Du Toit and Yetman 2004; Venter et al. 2015). An important driver of activity patterns in ungulates is ambient temperature and animals will adjust activity to avoid thermal stress (Maloney et al. 2005). Since a behavioural adjustment is less (energetically) costly than the physiological process of thermoregulation, ungulate activity usually drops during the hottest part of the day and peaks at times with mild
thermal conditions, like mornings and evenings (Maloney et al. 2005). Body size is also important for ungulate thermo-regulation since larger ungulates have a smaller surface to volume ratio than smaller species and thus have a reduced heat dissipation capacity (Shrestha et al. 2014). However, research suggests contrasting influences of body size on activity patterns. For example, some suggest that larger ungulates spend more time foraging due to greater metabolic (Du Toit and Yetman 2004) and nutritional requirements (Demment and Van Soest 1985), while the Jarman-Bell principal suggests that due to a shorter gut retention time, smaller antelope would need to spend more time foraging than larger antelope (Bell 1971; Jarman 1974). On the other hand, there are those who propose that neither feeding style nor body size have a significant influence on activity patterns (Hetem et al. 2012), which could be the case during this study as it was conducted in the winter months and since ambient temperatures were mild it is unlikely that the animals were influenced by thermal stress.

**Predator avoidance**

Caracal activity in the park is typical of that observed in other felids (Ramesh and Downs 2015; Reilly et al. 2017), being predominantly nocturnal, with a distinct drop in activity between sunrise and midday after which activity picked up again. Small antelope showed a largely inverse, diurnal pattern. This is indicative of anti-predator behaviour portrayed by small antelope. However, there is a degree of temporal overlap between the species (delta ~0.5) and this might suggest that caracals do not present a significant risk as a predator, which is corroborated by previous research which found that caracal diet within the park consists primarily of rodents (84% occurrence in scat), while small antelope were less important with a 6.5% occurrence in scat (Avenant and Nell 2002). Large managed ungulates were less active at night than small antelope. Since there is no predation threat to large herbivores at the study site it could be postulated that they would capitalise on this time for foraging as is displayed by buffalo in the Kruger National Park (Owen-Smith and Goodall 2014). Alternatively, the lower predation risk might enable the large ungulates to meet their foraging requirements during the day due to less time devoted to vigilance.

**Caveats**

Ecological systems are complex and interactions can be influenced by multiple biotic and abiotic characteristics. The capability of my models were limited due to low variation in the data which made elucidating patterns of interest difficult. Although camera traps are excellent tools for monitoring animal communities, they still have some limitations as they only monitor a fixed point in the landscape. As such, species detectability may have been biased by survey design and dense vegetation which could prevent species detection. Therefore detection probability is a particularly important consideration when conducting camera surveys,
Chapter 3

especially surveys that focus on communities rather than an individual species, since different species often have specific habitat requirements and are thus detected more frequently in areas where other species might not be detected. For this reason, we recommend continued monitoring with more camera traps so that all species and habitats can be targeted appropriately.

Conclusions and recommendations

Although this study had certain limitations, the results suggest a high level of spatial and temporal overlap between managed ungulates and small antelope. Further, there is an indication that the two groups of species likely occur independently of one another, at least at Langebaan and the farm, for which we had sufficient data required for the two-species models. This suggests that competition and facilitation are unlikely drivers of small antelope occurrence, but rather that these sympatric species co-exist due to a segregation of food resources. However, the low occurrence of small antelope in Postberg may be due to competitive exclusion by managed ungulates. Although, we were unable to estimate this due to data limitations and therefore recommend further investigation over the long term to assess whether small antelope populations recover after the removal of managed ungulates. Although managed ungulates were detected at a high proportion of sites in the park we postulate that it is due to them moving between areas of suitable forage. This is supported by the fact that they spent significantly more time on the fallow lands when compared to non-fallow lands (see Chapter 2 and Supplementary Fig. 1), although this could be biased by a lower detection probability of animals in well vegetated areas. Radloff (2008) also concluded that eland and bontebok avoided sandstone and limestone Fynbos, and when they did occur there they mainly utilised grassy microhabitats. The managed ungulates are also water dependant, whereas the small antelope are not (Valeix et al. 2009), and thus would need to travel between water points and forage patches regularly. This made it challenging to assess their influence on small antelope occurrence and how these two groups’ partition resources. It would, therefore, be worthwhile deploying GPS collars on managed ungulates and small antelope in the Langebaan and Postberg sections to gain a finer scale understanding of resource partitioning and co-occurrence of these sympatric species.

Overall we found some effects of inter-specific interactions at the local scale but there was a lack of reliable patterns across areas. This is consistent with literature that suggests large-scale ecological trends are difficult to detect at fine scales (Ryan and Ladau 2017; Wang et al. 2018). This has important implications for the management of small protected areas since many are small, fenced and stock ungulate species that have large spatial requirements. The resultant restriction of natural movement patterns within these protected areas therefore
Chapter 3

confounds our ability to detect ecological processes which makes adaptive management difficult. Considering the financial and human resource capacity of most small protected areas, this study represents a realistic (if not more so) level of ecological monitoring. This begs the question that if this study cannot provide sufficient understanding of how these systems function, how are we supposed to manage them? Having said that, an increased survey effort across the whole park and over the long term will yield a better understanding of species co-occurrence and activity at a larger scale.

Acknowledgements

We would like to thank Mila Truter, Trevor Adams, Chanel Williams, Zishan Ebrahim and Toni Dyers for their assistance with field data collection. Thanks to Mila Truter and Alexis Bierman for their assistance with data capture. Nicola van Wilgen (drafting of initial generic code), and Robert Schlegel (determining independent captures) provided advice and inputs into R script, for which we are grateful. This work would not have been possible without the funding and support from South African National Parks and West Coast National Park management. We would also like to thank the Elsenburg Provincial department of agriculture for their support, specifically, Christie Rheeder, the Nortier Research farm manager, and for permitting us to work on their farm.
Supplementary Figure 1: Detection maps of small antelope and managed ungulates across the three study areas. Points represent camera sites and the size of the black dots represents the frequency of detection at each site. Red circles indicate sites which were fallow lands. X-axes are longitude while y-axes are latitude.
Chapter 3

References


Colyn, R. (2016). Optimising camera trap density and position to determine medium and large mammal species richness and occupancy on the Cape Peninsula, South Africa. MSc thesis. Cape Peninsula University of Technology.


Chapter 3


Chapter 3


Chapter 3


Chapter 4: Conclusion
Introduction

Ecological studies are challenging but important for conservation management. The study of ecology needs to consider three explicit levels, a biological hierarchy, which structure ecosystems: a) the individual organism, b) the populations of these organisms and c) the communities of the different species’ populations (Begon et al. 1990). Importantly, however, these levels cannot be viewed as silos since it is the interaction between these levels and with their environment which defines ecosystem function (Molles 1999). Ecology does not have a simple linear structure, as everything affects everything else and therefore dissecting it to answer an apparently simple question is sometimes an enormous task (Begon et al. 1990). So in my quest to understand relatively simple problems it was not always as easy as separating two or three pieces of the puzzle, but rather, it was like unravelling an intricately woven tapestry of interactions and relationships. The key, is to seek patterns and trends in the complexity rather than being overwhelmed by it. Like Andrewartha and Birch (1986) reminded us; that although ecological models help us simplify the complex, we should heed the physicist Whitehead’s methodological warning to “seek simplicity, but distrust it”.

The simple / complex picture of ecology is no more evident than in a food web. Food webs epitomise ecology and are the simplest way of conceptualising numerous links within the biological hierarchy (Molles 1999). They can be as simple as a basic four level web, where abiotic factors influence primary production which is consumed by herbivores and which are then consumed by carnivores, or they can be far more detailed and specific to a particular community where each species is represented, resulting in hundreds of interactions. When considering ecosystem function and who consumes and regulates who, it is vital to consider the biology of the individual as well as the pervading influences of historical, evolutionary and geological events (Begon et al. 1990). Disturbance or disruption at any level can have cascading effects across the links which can persist over time, ultimately resulting in a novel ecosystem (Barnosky et al. 2012). Most ecosystems today are different to what they were originally, before humans started having a significant impact on them, and these are the systems which conservation management are tasked with managing. Yellowstone, one of the oldest the National Parks in the world, was without its apex predator for more than 60 years (Fortin et al. 2005). However the re-introduction of wolves to Yellowstone provided an excellent opportunity to study how ecosystems respond to change and resulted in numerous studies which produced insightful ideas of trophic cascades and ecosystems function (Berger and Connor 2008; Beschta et al. 2016; Fortin et al. 2005; Newsome and Ripple 2014; Ripple et al. 2014). A primary objective of many protected areas is to restore ecosystems to what they historically were (Venter et al. 2014). In many cases, however, management authorities
do not know how the original system functioned, which makes it difficult to restore and therefore requires ongoing monitoring to inform adaptive management.

This is the case at my study site. The West Coast National Park (hereafter referred to as the park) is situated in the nutrient-poor Fynbos Biome along the west coast of South Africa, where the primary vegetation type is Strandveld. European settlers arrived ±350 years ago and since then have extirpated most large mammals from the area by hunting (Radloff 2008). Prior to the arrival of European settlers, however, the area was inhabited by indigenous people who were pastoralists and it is believed that the west coast area of South Africa has been exposed to livestock grazing for approximately 2000 years (Mucina and Rutherford 2012). The park was originally proclaimed in 1985 with the primary objective of conserving the Langebaan Lagoon and associated marine systems, but it progressively expanded to include a large terrestrial component. Unfortunately the park is fragmented as it is divided by a national road, the N7, and the western section (where this study was conducted) is about 23 000ha. The contractually managed Postberg section is even smaller (1 800 ha) and also isolated by topography and a fence on the southern boundary, where large ungulates (native and extra-limital) were re-introduced and kept at high densities for almost half a century. With a goal to restore the area to its historical function, large ungulates (eland, *Taurotragus oryx*) were later re-introduced to the Langebaan section, although at much lower densities than Postberg. However, the densities at which large ungulates would have historically occurred in the region is not certain (Mucina and Rutherford 2012). Research, based on a survey of available literature and the ecological requirements of species, suggests that the area most likely did not support big resident populations of large herbivores such as eland, but that the smaller solitary antelope occurred as residents (Boshoff and Kerley 2001). This is corroborated by research which postulates that large herbivores favoured the nutrient rich Ronesterveld (Radloff 2008)) and that they largely avoided the nutrient-poor Fynbos and Strandveld (Mucina and Rutherford 2012), but that they did occur as ephemeral migrants or in small habitat refugia (Boshoff and Kerley 2001). Large predators also occurred in the area historically (Boshoff and Kerley 2001; Cruz-Uribe and Schrire 1991) which have since been extirpated. The caracal (*Caracal caracal*) is now the largest predator in the system.

Considering the historical events and the current management practice of the park, major drivers regulating small antelope populations are unknown. Both steenbok (*Raphicerus campestris*) and common duiker (*Sylvicapra grimmia*) are common throughout the park but the Postberg land owners have raised concerns regarding a perceived lower abundance of steenbok in the section with the blame falling on caracal predation. This prompted me to initiate this study to investigate the mammal communities of the park and greater West Coast
region. I was interested in the relationship between small (naturally occurring) antelope, wild re-introduced or domestic managed ungulates and the only remaining predator, the caracal, as well as how these species interact with their environment and whether there is any evidence of influence across these links.

A primary objective of community ecology is to understand the drivers of coexistence between species and to do this it is important to identify how co-occurring species use and share space and resources (Darmon et al. 2011). Therefore, through this study, I aimed to explore the potential drivers of small antelope occurrence in the region and how this might differ across three sites with different management practices, the Langebaan and Postberg sections of the park and the Nortier research farm in Lamberts Bay (hereafter referred to as the farm). I considered three potential drivers being; a) predation, b) competition and c) habitat. This was done by investigating occupancy of steenbok, common duiker and caracal using site abundance of managed ungulates and other site specific co-variates as potential predictors for occupancy. I also explored species interactions and temporal activity and overlap between managed ungulates, small antelope and caracal.

**Key findings**

The primary objective of this study was to investigate whether land management practise influences species occupancy and interactions, the results of which suggest that it does. Management scenario was consistently a strong predictor in all occupancy models, therefore something related (although unmeasured) to management must be driving these differences. It is uncertain whether these drivers are legacy effects of historical land uses (such as old fallow lands) or consequences of current management actions (such as manipulation of ungulate populations), which highlights the need for further investigation.

**Occupancy**

Small antelope occupancy was significantly lower at Postberg when compared to the other two areas. Interestingly small antelope had the highest occupancy at the farm which was an unexpected finding. Langebaan, the most open and natural of the three areas, had occupancy estimates which more closely resembled those at the farm. None of the measured environmental variables had a particularly strong effect on occupancy estimates which challenged my ability to identify a driver. Caracal detections were low across all sites, which confounded my ability to estimate occupancy, but were lowest at the farm and highest at Langebaan. Caracal detections at Postberg were closer to those observed at the farm and were significantly lower than Langebaan. The very low occupancy of small antelope at Postberg substantiates the land owner’s perceived lower abundance, however predation is
unlikely to be the driver of this due to the much lower detection probability of caracal in Postberg compared to a more open area of the park, along with the evidence from previous research which indicates that small antelope constitute a small proportion of caracal diet in the region (Avenant and Nel 2002).

Vegetation structure appears to be an important driver of common duiker occupancy (see Chapter 2) which is consistent with previous research (Heydenrych 1995; Skinner and Chimimba 2005). Overall there was no significant difference in vegetation height across the three areas. However, vegetation at the farm was more uniformly intact, with less variation in height compared to the Langebaan and Postberg areas, which both included sites of old fallow lands (see Chapter 2). The increased cover and better habitat could be driving the much higher occurrence of small antelope at the farm. Fallow land had a significant influence on managed ungulate and small antelope space use in the park. Although managed ungulates were detected at a very high proportion of sites within the park, they spent significantly more time on fallow lands which suggests that fallow lands are preferred foraging sites. This is in line with other research which suggests that eland and bontebok would only utilize grassy micro-habitats within sandstone and limestone Fynbos (Radloff 2008).

It seems that whatever is driving small antelope occurrence has a greater influence on steenbok compared to common duiker since steenbok are consistently detected at lower rates and have lower occurrence probabilities across all the sites. Whether this is driven by competition with common duiker, managed ungulates or habitat suitability is uncertain but research suggests that steenbok naturally occur in the region at lower densities than common duiker (Boshoff and Kerley 2001).

While I expected to see a relationship between managed ungulate abundance and vegetation height I did not detect any strong correlation. Although overgrazing by large ungulates is known to alter vegetation structure (Coughenour 1991; Radloff 2008) the effects on plant diversity may be more pronounced than those on structure (Charles et al. 2017; Herfindal et al. 2017). I did not, however, quantify plant species diversity in this study.

**Co-occurrence and activity**

My investigation into species co-occurrence was hindered by a very high proportion of sites that were occupied by managed ungulates at the Postberg and Langebaan sites and the very high proportion of sites occupied by small antelope at the farm. Therefore any differential occurrence of small antelope must be driven by something else which I did not include in those models. However, large ungulates forage at a courser scale while smaller ungulates at a finer
scale and therefore spatial heterogeneity and patch size of vegetation are important drivers of large ungulate movement (Venter et al. 2015). Hence, the very high occurrence of managed ungulates at the sites in the park may be explained by them interacting with the system at a courser scale. Since they seem to utilize the fallow lands as preferred foraging areas I postulate that managed ungulate movement and space use may be driven by fallow lands and water points, thus explaining the high detection in most habitats.

Daily activity patterns of ungulates and caracal were consistent with what has been found elsewhere with similar species (Amin et al. 2014; Du Toit and Yetman 2004; Ramesh and Downs 2015; Wronski et al. 2015). Small antelope tended to be more crepuscular, managed ungulates were more diurnal and caracal were more nocturnal. Small antelope and managed ungulate activity was, however, markedly different at the Langebaan site where small antelope did not have a prominent activity peak in the morning while managed ungulate activity did not drop at midday, as was observed in the other areas. It is not certain what is influencing this difference, but it may be attributed to the fact that the Langebaan site is the most open and natural of the three areas with the least restrictions on animal movements.

**Caveats**

*Data limitations*

Ecological systems are complex and interactions can be influenced by multiple biotic and abiotic characteristics. This makes elucidating patterns from a small sample size difficult when there are many environmental variables that could be driving patterns. Since modelling relies on differences in key variables between sites, the very high or very low detection probability of managed ungulates and small antelope at the different areas limited my ability to assess relationships of interest. Due to the nature of circular data the ability to statistically test the subtle differences in peak activity times in a biologically meaningful way are limited (see Chapter 3 methods). For example, small antelope and managed ungulate activity was markedly different at Langebaan when compared to the other two areas, when assessed graphically, but this difference did not always reflect in the results of the Watson-Wheeler test. Although the smoothing parameter within the `overlapPlot` (Ridout and Linkie 2009) function may obscure subtle differences in activity further investigation into testing significance between species activity levels is recommended. Further, it is unclear whether the statistical differences that were detected are biologically meaningful in any way.

*Camera trap limitations and species detectability*

Camera traps are excellent tools for monitoring communities as they detect a wide range of species over the diel cycle but they still have some limitations. Species detectability is an
important consideration when conducting camera surveys since camera placement can influence species detections. For example, carnivores are known to be better detected on prominent trails and roads (Mann et al. 2014) which could account for the low caracal detections during this study. This makes it challenging to design camera surveys that focus on the community rather than the species level since different species detection probabilities can vary widely according to habitat preference (Mann et al. 2014). The results of this study suggest a high level of spatial and temporal overlap between managed ungulates and small antelope. However, camera traps only monitor a fixed point in the landscape and this may have biased detection probabilities negatively in more vegetated areas due to the camera being obscured by dense vegetation and thus having a smaller detection zone. This made it challenging to assess the influence of managed ungulates on small antelope and how these two groups partition resources. Having said that, had there been enough cameras to survey the areas simultaneously, resulting in increased camera days, the data might not be as limiting as it was.

**Management implications and future research**

Very little is known about the historical occurrence and densities of large herbivores in the Fynbos Biome and what their impact is on the vegetation (Mucina and Rutherford). It is presumed that large herbivores concentrated in the nutrient rich areas and avoided the nutrient-poor Fynbos and Strandveld (Radloff 2008). This makes it difficult for conservation managers to make decisions with regards to appropriate stocking rates. Since many of the protected areas in the Fynbos Biome are small and fenced, the consequential restriction of large ungulate movement makes it difficult to study and assess natural movements and processes that would have occurred prior to extirpation. This is an important consideration for management as large ungulate re-introductions into the Fynbos Biome need to be treated as testable hypotheses (Boshoff and Kerley 2001).

Management need to be aware that the fallow lands may be supporting the large ungulate populations. This is important for maintaining the state of degradation that produces the spring flower displays, which are an important tourist attraction and revenue generator (SANParks 2013). An increase or decrease of large ungulate densities may, therefore, influence spring flowers.

Considering that we do not have a comprehensive understanding of the natural processes related to large herbivores in Fynbos and since they are restricted to small areas across the biome, we can only attempt to understand how their presence influences ecosystem function at the local level. Essentially this study tried to estimate broad scale patterns in an area the
size of a caracal’s home range, which is unfortunately the reality for protected areas in much of the region. Naturally this area might have seen a pride of lions (*Panthera leo*) or a herd of eland occasionally but now it is the full system which needs to be managed as if it were natural. Therefore the ability to glean a true representation of what would have happened naturally is questionable. Perhaps management should rather focus on current patterns rather than trying to emulate a historical reality for which the spatial requirements are unrealistic.

Having said that I would suggest that management establish a biodiversity monitoring system which measures key environmental variables over the long term to identify what is driving ecosystem processes in the park. This should include extending the camera survey across the whole park, since only a small portion of the Langebaan section was surveyed. It would also be worthwhile deploying GPS collars on managed ungulates and small antelope in the Langebaan and Postberg sections to gain a better and more fine-scale understanding of resource partitioning and co-occurrence of these sympatric species. Since it is uncertain how browsing ungulates influence plant species diversity I suggest including vegetation surveys in addition to measuring height and cover. Although park management do conduct game counts, I recommend doing these counts using a standardised method, combining both vehicle and foot counts, which should be conducted, at least, seasonally. Given that the fallow lands appear to be important drivers of managed ungulate movement and foraging it would be valuable to monitor fallow land size and restoration, especially in Postberg after the removal of managed ungulates. I suggest that no additional game introductions should be considered until the potential impacts are better understood.

**Concluding remarks**

Despite the limitations of this study I found some effects of inter-specific interactions and ecosystem function at the local scale. Although there was a lack of reliable patterns across the areas, literature suggests that large scale ecological trends are difficult to detect at fine scales (Ryan and Ladau 2017; Wang *et al.* 2018). Due to the heterogeneity of the Fynbos Biome, coupled with its small size and extensive fragmentation by land use, there are no areas that are large enough and which adequately represent the biome to test how large herbivores would utilise the biome at the regional level. While research suggests that herbivores would have congregated on the more nutrient rich Renosterveld (Radloff 2008), they still would have utilised the more nutrient-poor Fynbos and Strandveld areas, although the intensity of which is uncertain. This has important implications for the management of small protected areas in the Fynbos Biome who are mandated to restore these areas to their historical and natural function. How is management meant to fulfil management objectives of restoring parks to their
historical function and maintaining these systems as such if we may not even be meeting the spatial requirements of the species which we re-introduce?

Land use and management have important consequences for ecosystem function. Therefore, in the face of global environmental change we need to consider not only how systems are functioning now but also, how vulnerable they are and how they might be able to respond to change. This is especially important in a highly transformed region like the Fynbos Biome where habitats are fragmented with little connectivity overall, since species need to be able to move in order to adapt. Therefore, it is up to us to understand the workings of ecosystems and to encourage more sustainable and integrated land use models so that we can manage ecosystems more effectively, while also taking the interests of society at large into account (Bell 1971).
References
Chapter 4


Chapter 4

