University of Venda

Industrial landscapes promote small carnivore diversity and modulate the predation experienced by small mammals

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DECLARATION

I **KEVIN WADE EMSLIE**, hereby declare that the dissertation; Industrial landscapes promote small carnivore diversity and modulate the predation experienced by small mammals, for the degree of Master of Zoology at the University of Venda, hereby submitted by me, has not been previously submitted for a degree at this or any other university, that it is my own work in design and execution and that all reference material contained herein has been duly acknowledged.

Signature Date: 2 February 2018

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ABSTRACT

The adverse ecological effects of landscape modification by humans are well known and continue to be studied. Habitat disturbances arising from such modifications result in various levels of biodiversity loss. Amongst mammals, large carnivores are usually the first to disappear, leaving a gap in the trophic pyramid. However, ecologically adaptive small carnivores, free from the effects of intraguild predation can readily fill this gap (i.e. mesopredator release). In highly productive disturbed habitats, small mammals may thrive, reaching densities that can support an abundant and diverse suite of small carnivores.

After frequent sightings of serval (*Leptailurus serval*) on the highly disturbed Sasol Synfuels Operations property, three camera trap surveys were conducted between 2014 and 2015 to study its ecology. The resulting data was subsequently used to study the site's small carnivores. Multispecies occupancy modelling was used to determine detection (p) and occupancy (ψ) probabilities and estimate species richness across the study area. Site-specific covariates were then modelled against abundance values to identify any correlations. Out of 23 small carnivore species predicted to occur on the site, 11 were detected. Spatially, estimated species richness was highest in disturbed habitats, while it was slightly lower in Grassland possibly due to undersampling. Detection and occupancy probabilities were low (except for serval), with interspecies variations. It is suspected that this is the result of survey bias towards serval. The only covariate showing any significant effect was livestock presence, negatively affecting serval occupancy.

Estimated species richness was used as a proxy to identify high- or low-predation areas. Within these areas, three vegetation treatments were selected (low, medium and high cover). Small mammal foraging behaviour under varying predation pressures within these treatments was then studied using the giving-up density (GUD) framework. Differences in GUDs were examined using generalised linear mixed models (GLMM). Small mammal trapping in the study area showed that four-striped grass mouse (*Rhabdomys* sp.; diurnal) and multimammate mouse (*Mastomys* sp.; nocturnal) were dominant. Nocturnal GUDs were lower than diurnal, which is interesting as four-striped grass mice are more abundant than multimammate mice. This indicates that density alone does not influence GUDs. Additionally, no significant difference in GUDs was observed between predation and vegetation treatments. I suggest that observed GUDs are linked to individual or combined impacts of interspecific differences in foraging behaviour, metabolic requirements or temporal variations in perceived predation pressure. GUDs also varied between surveys, being lower in mid- compared to early winter. This might be attributable to decreased availability of food and greater metabolic requirements in mid-winter.

The results show that modified landscapes (such as the study site) can contribute to biodiversity conservation, especially of small carnivores, the adaptability of which allows them to flourish in disturbed habitats. Under favourable conditions, ecologically flexible small mammal species seem to be unaffected by the risks associated with an abundance of small carnivores. While the processes governing the dynamics of predator and prey communities in disturbed systems are not entirely clear, the conservation potential of such areas cannot be ignored and deserves more attention from researchers.

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CHAPTER 1: INTRODUCTION

The world is home to 150 extant small carnivore species. Most of these species are either in decline (39%) or are unclassified due to lack of data (37%; IUCN/SSC Small Carnivore Specialist Group 2018). Of the unclassified species, most are found in Africa with little known about their ecological role, distribution and conservation status. Species richness data across the continent is also minimal (Do Linh San *et al*. 2013). At the global-level, small carnivores have received much attention, with the considerable ecological impacts of many of these species being well known. For example, introduced American minks (*Neovison vison*) are known to influence the location of bird breeding sites on Baltic Sea islands (Nordström & Korpimäki 2004) and compete with indigenous species in the United Kingdom (Harrington & Macdonald 2008). Small carnivores also play a major role in the regulation of small mammal and invertebrate communities through predation (Virgós *et al*. 1999), with potential secondary effects on higher trophic levels (Do Linh San *et al*. 2013).

Across the guild, small carnivore prey includes small mammals, birds, amphibians, reptiles, crustaceans and insects. Consequently, in highly productive landscapes where these prey species are plentiful, small carnivore abundance and richness are expected to benefit (Do Linh San *et al*. 2013). Such correlations between the densities of small carnivores and their prey are especially evident in specialist species (such as those that mainly hunt small mammals; Erlinge 1974). Generalist predators, however, make use of a large variety of food items, and prey on small mammals when available in abundance (Englund 1970). Additional factors affecting small carnivore density and diversity include habitat variety and intraguild interactions (Fox & Fox 2000), while the impact of humans, including landscape modification, is also of major significance (Ordeñana *et al*. 2010).

1.1 Background information

Small carnivores (weighing less than 15 kg) rely on a variety of prey species for food. Those whose prey includes small mammals are often referred to as mesopredators, which can broadly be defined as midranking predators in a food web, irrespective of size, weight or taxonomy (Prugh *et al*. 2009)[1]. As such, a mesopredator in one system could be an apex predator in another, and several mesopredators (such as small carnivores) may inhabit one ecosystem (Crooks & Soulé 1999, Bergstrom *et al*. 2009, Roemer *et al*. 2009). Several functional types of mesopredators prey on rodents and can be differentiated according to their degree of specialisation and mobility (Andersson & Erlinge 1977). Some small mammal predators are classified as specialists (e.g., weasels, *Mustela* sp.), as they are adapted to hunt and kill rodent prey (Watson 1957, Erlinge 1975). The densities of these specialists are closely related to those of their small mammal prey (Erlinge 1974). Such specialists seem to rely on their prey to breed successfully and may seek alternative prey, usually with little success, when small mammal numbers are low (Andersson 1976, Andersson & Erlinge 1977). Other small mammal predators are known as generalists (e.g., serval, *Leptailurus serval*). Generalists make use of a large variety of food items, and prey on small mammals when available in abundance. When their small mammal prey becomes scarce, they are easily able to use alternate food sources. This change to other food sources may happen at higher small mammal densities than it does with specialists (Andersson & Erlinge 1977). In areas with multiple food sources, changes

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[1] From henceforth, any mention of mesopredators in this document includes small carnivores.

in small mammal density may have a minimal effect on generalist numbers. However, when alternative food sources are rare, generalist numbers may also fluctuate with changing small mammal densities, due to their dependence on this food source for survival and reproduction (Englund 1970).

Mesopredators which are resident species are forced to find alternative food sources and will show increased movements in search of prey when small mammal densities are low (Erlinge 1975). Under the same conditions, other species (such as generalists) will not move out of a defined territory, even though they can travel long distances (Southern 1954). Some nomadic specialists will migrate from an area without breeding when small mammals are scarce (Gross 1947). If small mammal densities return to high enough levels, nomadic species may return and breed (Andersson 1976). These nomadic movements and migrations can result in rapid predator increases where small mammals are abundant (Lockie 1955, Galushin 1974). A rise in mesopredator numbers resulting from an increase in small mammal prey populations is termed a numerical response (Sinclair *et al*. 1990), which can lead to increased predation pressure. This may have both direct (through predation) and indirect (through the costs of behavioural changes or risk effects) impacts on small mammals (e.g., Creel & Christianson 2008).

The direct effects of mesopredators include the suppression of small mammal population densities and reproductive success, which can adversely influence ecosystem processes and cause local extinctions of prey (Prugh *et al*. 2009, Ritchie & Johnson 2009, Salo *et al*. 2010). However, such effects are density dependent, and when there is a hyperabundance of prey, predation rates cannot keep up with prey population increases. In this case, prey populations will not be directly affected (Fischer *et al*. 2012), and the indirect effects of predation may be more apparent. This includes the amplification of the landscape of fear for small mammals under high predator densities (Mahlaba *et al*. 2017), which can, for example, impact prey foraging behaviour (Lima & Bednekoff 1999) with prey sacrificing food for safety (Matassa & Trussell 2011).

A landscape of fear[2] may be particularly prominent in human-modified landscapes, where larger apex predators are usually absent, resulting in the irruption of mesopredators, i.e. mesopredator release (Prugh *et al*. 2009, Fischer *et al*. 2012). The disturbed habitats of human-modified landscapes often provide the ideal conditions (such as food and cover) for high densities of small mammals (e.g., Ferreira & van Aarde 1996, Keesing 1998). Such conditions allow ecologically adaptable mesopredators to thrive (Ordeñana *et al*. 2010, Do Linh San *et al*. 2013, Caruso *et al*. 2016, Gálvez *et al*. 2018), having positive effects on abundances and species richness, indicating the potential of such modified landscapes for small carnivore conservation.

1.2 Literature review

The world is familiar with large mammalian carnivores, most of whom play important ecological roles as apex predators (Estes *et al*. 2011). Only a few individuals can cause strong predation-driven direct or fear-driven indirect effects on prey communities and ecosystems (Ripple & Beschta 2004, Ray *et al*. 2005). This, along

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[2] The landscape of fear represents relative levels of predation risk as peaks and valleys that reflect the level of fear of predation a prey experiences in different parts of its area of use (Laundré *et al*. 2010).

with their potential for conflict with humans has made them the subjects of many studies (Estes *et al*. 1998, Gittlemann *et al*. 2001, Ripple *et al*. 2014). However, most of the world's carnivores are not large apex predators. Instead, they are small, weighing up to 15 kg (Roemer *et al*. 2009). While large carnivores (such as lion; *Panthera leo*) command respect and invoke fear in humans, smaller carnivores (such as serval), in contrast, are often seen as pests whose impacts on human activities are to be mitigated. Consequently, research focussing on their ecological role is minimal, especially in Africa (Roemer *et al*. 1999, Do Linh San *et al*. 2013). Although dissimilar to large carnivores, there is also considerable variation in their behaviour and ecology (Roemer *et al*. 2009) with them playing a considerable role in influencing the structure of their prey communities (Jedrzejewska & Jedrzejewska 1998, Virgós *et al*. 1999). Furthermore, small carnivores provide essential ecosystem services such as seed dispersal, influencing the diversity and coverage of plant communities in the habitats that they occupy (Jordano *et al*. 2007, Nakashima & Sukor 2009, Mudappa *et al*. 2010).

Ironically, while given more research attention, large carnivores are in decline because of anthropomorphic actions (Ripple *et al*. 2014). This decline has, in many instances, led to increases of small carnivores (e.g., mesocarnivore release; Soulé *et al*. 1988). In the absence of large carnivores, many of these species have become apex predators (Crooks & Soulé 1999, Roemer *et al*. 2009), altering their ecological roles in the affected systems (Do Linh San *et al*. 2013).

In Africa (home to 34% of the world's small carnivores), most small carnivore research has concentrated on a few diurnal, social species, including suricate (*Suricata* *suricatta*) and banded mongoose (*Mungos mungo*). Others, such as the large-grey mongoose (*Herpestes ichneumon*) have received minimal attention. As a result, the behaviour and ecology of this guild across Africa are poorly understood. Although the overall conservation status of African small carnivores seems healthy, in general, fauna across the continent are declining. Without the prioritisation of their conservation, existing (e.g. habitat degradation) and new threats (e.g. wildlife trade and climate change) may push many small carnivore species onto the threatened list (Do Linh San *et al*. 2013).

Small carnivores occur at relatively greater densities, exhibiting enhanced social variability (such as smaller home ranges and increased home range overlap) in areas with high prey biomass (Eide *et al*. 2004). Such areas include human-modified landscapes, which are usually devoid of large carnivores, providing prime conditions for many small carnivore species to flourish (especially ecologically flexible generalist species, which can live in close proximity to people; Roemer *et al*. 2009, Caruso *et al*. 2016). Therefore, the potential value of human-modified landscapes (for example, urban and industrial areas or farming matrices; Ordeñana *et al*. 2010, Caruso *et al*. 2016, Williams *et al*. 2018) in small carnivore conservation cannot be ignored and should be afforded further research attention.

While increased small carnivore densities and diversities in modified landscapes might be positive for the conservation of some species, such changes may negatively impact other species, and alter ecosystem functioning. For example, a rise in small carnivore density and diversity is expected to alter the ecosystem state at a local level, such as reducing the abundance of small mammal prey (Smith & Quin 1996). Such declines can destabilise ecosystems and lead to local extinctions of prey, decreasing diversity (Prugh *et al.* 2009, Ritchie & Johnson 2009). This may, in turn, impact ecosystem processes that are reliant on small mammals, including services like seed dispersal. Understanding the impact of small carnivore abundance and diversity changes on ecosystems should, as a result, not be overlooked.

Predator impact on prey is often mediated through a landscape of fear (Matassa & Trussell, 2011). It has been suggested that escalations in predator abundance and richness could exacerbate the landscape of fear for small mammal prey (Mahlaba *et al*. 2017). As such, a landscape of fear concept might be an ideal model to investigate the effects of varying small carnivore densities and diversities on small mammal communities. In a landscape of fear, prey animals are expected to sacrifice food for safety (Matassa & Trussell 2011). Such effects of predation on foraging behaviour can be measured using the giving-up density (GUD) framework. The optimisation of foraging time is essential for any animal to compete and survive effectively, particularly under the risk of predation (Mahlaba *et al*. 2017). GUD, first described by Brown in 1988, is an experimental and mathematical approach used to quantitatively determine the foraging decisions of an animal in the wild based on patch characteristics. The GUD framework is dependent on the existence of food patches as a finite food source that foragers use differently to maximise fitness. Essentially, the GUD is the amount of food left in a patch by foragers, indicating the apparent cost of foraging at that patch, such that a lower GUD reflects a lower net cost (Bedoya-Perez *et al*. 2013).

Small mammals, for example, can assess the risk of predation while foraging *via* indirect signs (for example, light levels) or direct signs (such as predator urine; Orrock

2004). The GUD framework is a valuable tool for researching predator-prey dynamics in a landscape of fear (Willems & Hill 2009, Schmidt & Kuijper 2015). Theoretically, foragers should vacate a patch when fitness gains from feeding no longer exceed the costs of potential predation (Brown 1999, Brown & Kotler 2004). Where the potential for predation is high, a forager's GUD should be higher than in a low-risk environment (Brown 1988). Such data can be used to illustrate a prey animal's landscape of fear, providing important ecological information on how animals perceive and use complex habitats (e.g., modified landscapes), and informing management decisions (Morris & Davidson 2000, Schmitz 2005). For example, the GUDs of grey squirrels (*Sciurus carolinensis*) were found to be higher in areas without trees and where domestic pets/predators (i.e., cats and dogs) were present nearby (Bowers & Breland 1996). Similarly, Mahlaba *et al*. (2017) observed rodents leaving higher GUDs in rural homesteads where cats and dogs were both present, compared to those with only cats or dogs, or neither of the two. In replicated maize field plots in Tanzania, Mohr *et al*. (2003) used GUDs to determine the effect of avian predation pressure on the foraging behaviour of multimammate mice (*Mastomys natalensis*). Results indicated that GUDs were lower for covered (artificial and natural) feeding trays, but not significantly affected by predation pressure. The researchers concluded that multimammate mice can assess ambient predation pressure and make foraging adaptations relative to the feeding patch. Additionally, a strong positive correlation was found between small mammal density and GUD, potentially masking variations in predation pressure/landscape of fear.

Predation risk, food availability, habitat characteristics (often determined by land use and associated modifications), interspecific competitive relationships and environmental conditions are some of the factors that influence the landscape of fear, and consequently, small mammal feeding behaviour (e.g., Brown 1988). The role played by each factor, particularly predation risk and habitat characteristics, is debatable and their individual effects do not work in isolation on an animal. It is, rather, a combination of the effects of such factors together with a prey animal's level of fitness (competitive ability), which determine how it optimises the amount of time it spends foraging (e.g., Kotler *et al*. 1991, Mahlaba *et al*. 2017).

1.3 Overview of methods

1.3.1 Study area

The research was conducted in the secondary area of the Sasol Synfuels Operations property in Secunda, Mpumalanga. This heavily industrialised area is a matrix of industrial infrastructure, disturbed Grassland and Wetland, and undisturbed Grassland.

1.3.2 Camera trapping

Three 40-day camera trapping surveys were conducted between August 2014 and July 2015 within the study area. The surveys included the deployment of 34 camera traps in a 1 km^2 grid over a total area of 79.4 km^2. The main objective of the surveys was to determine habitat usage and population size of serval within the study area (Goodman & Matthews 2017). For the study, I used the images of all small carnivores captured to determine occupancy, detection probabilities and estimate species richness across the site.

1.3.3 Giving-up density experiments

Using the small carnivore species estimates from the camera trap surveys as a proxy, high- and two low-predation sites were selected in the study area. Within these sites, GUD experiments were conducted in three vegetation treatments: high, medium and low cover. Artificial feeding stations (trays with a mixture of sand and sunflower seed) were placed across the vegetation treatments to measure the effects of several variables (including predation pressure and vegetation treatment) on small mammal foraging behaviour.

1.4 Research questions

- What is the effect of disturbed vegetation on small carnivore diversity and density?
- What are the effects of vegetation structure and predation pressure on small mammal foraging behaviour?

1.5 Research aims

This research project aimed to investigate the effects of habitat disturbance on small carnivore abundance and diversity, and how such changes, in combination with vegetation structure, impact small mammal foraging behaviour.

1.6 Null hypotheses

Several hypotheses were tested by the research, each related to a specific chapter. A broad overview of these hypotheses is presented below, with more details available in the respective chapters.

- Vegetation disturbance does not affect small carnivore diversity and density.
- Predation pressure will not affect small mammal foraging behaviour.

CHAPTER 2: THE IMPORTANCE OF INDUSTRIAL SITES IN SMALL CARNIVORE CONSERVATION: THE CASE OF THE SASOL SYNFUELS OPERATIONS PROPERTY IN SECUNDA, SOUTH AFRICA

2.1 Introduction

The industrial and mining sectors are key drivers of economic progress in many countries. In South Africa, the petrochemical (~5%; Brand South Africa 2017) and mining (~8%) sectors are two of the most important contributors to the annual Gross Domestic Product (GDP; Statistics South Africa 2017). Additionally, thousands of South Africans rely on these sectors for jobs. For example, the mining sector supplied ~490,000 jobs in 2015 (Statistics South Africa 2017). The national importance and nature of such sectors mean that future growth is likely. Therefore, the area that they occupy (e.g., 328,973 ha for the mining sector; Department of Environmental Affairs 2016) is also expected to increase, accompanied by the associated landscape modifications.

50 to 70% of the earth's terrestrial surface has already been modified by humans (Barnosky *et al*. 2012). Such landscape modifications include those related to industrial and mining development, which is a major cause of biodiversity loss, biotic homogenisation and alteration of ecosystem function (e.g. Foley *et al*. 2005, Pauchard *et al*. 2006, Snep *et al*. 2011).The causes of these impacts include: i) degradation or fragmentation of natural habitats; ii) alteration of ecological processes, sometimes irreversibly (e.g., disruption of species movement patterns); iii) pollution of air, soil and water; iv) soil damage and erosion; v) siltation of surface water sources; vi) introduction of invasive alien species; and vii) overexploitation of natural resources (e.g., Foley *et al*. 2005). Such environmental degradation decreases the capacity of

ecosystems to supply goods and services (e.g., water purification and waste mediation; Costanza *et al*. 2017), while biodiversity is lost through habitat fragmentation, species declines and local extinctions (Pimm & Raven 2000). Species declines related to landscape modification have been observed in birds (Clergeau *et al*. 2006), butterflies (Ramírez Restrepo & Halffter 2013), many other species (McKinney 2006, 2008).

Dmochowski and Dmochowska (2011) found that the build-up of heavy metals in bottom sediments of surface water sources affects the occurrence of gastropods and bivalves. Similarly, the erection of roads in wetlands destroys habitats used by amphibians (Lewin *et al*. 2015). The city of Concepción, Chile, was developed in an area of high biodiversity. The associated development, as well as pollution in the area's riparian and wetland habitats, severely impacted biodiversity (Pauchard *et al*. 2006). For example, reduced habitat heterogeneity including the loss of complex wetland plant communities has led to declines in bird species (Riffo & Villarroel 2000). Native fish species have also been affected by the proliferation of alien invasive species (e.g., rainbow trout; *Oncorhynchus mykiss*; Campos *et al*. 1993, Habit & Parra 2001).

Clearly, landscape modification alters terrestrial and aquatic environments, causing species losses in both plant and animal communities (Batty 2005). As a result, most research in these landscapes has focused on biodiversity loss, with limited emphasis on their conservation potential (Miller & Hobbs 2002). Occasionally, landscape modification leads to the formation of unique and ecologically important communities, dependent on altered conditions – such as elevated concentrations of metals (Batty

2005). For example, true metallophytes are plants that have adapted to metal contaminated soils (Baker 1987). These include rare and threatened species such as *Viola calaminaria*, which is present at sites in Belgium contaminated by atmospheric deposits of zinc (Zn), lead (Pb) and cadmium (Cd) (Bizoux *et al*. 2004).

Modified landscapes may also support substantial populations of animals (Batty 2005). The highest known density of serval (*Leptailurus serval*) was reported on the highly degraded Sasol Synfuels Operations site in South Africa (Loock *et al*. in review)[3]. In Mexico, Lopez-Gonzalez and Torres-Morales (2004) found multiple bat species (including long-eared bats; *Corynorhinus* spp.) roosting in abandoned mines. Research in Australia found threatened beetle species on mining land adjacent to agricultural areas where they were rare or absent (Brändle *et al*. 2000). Transformed aquatic ecosystems and newly created (usually polluted) reservoirs on industrial sites (Jeffries 2012) often serve as refuges for many plants and animals (Wood *et al*. 2003). These ecosystems may provide the only local breeding habitats for amphibians, dragonflies and molluscs (Le Viol *et al*. 2012, Lewin *et al*. 2015).

Green spaces within developed sites also hold ecological potential. Such spaces can reduce biodiversity loss by maintaining gene flow among populations (Kong *et al*. 2010). However, few studies have evaluated their ecological potential. Snep *et al*. (2011) studied their conservation value for endangered butterfly populations in Holland. The study found that additional habitat provided by green spaces supported a significant proportion (19–33%) of vulnerable butterfly populations at a national scale, suggesting that such spaces have considerable potential to contribute to the

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[3] The study site where research for this project was undertaken.

biodiversity conservation. In South Africa, an example of the contribution of green spaces to biodiversity conservation is the Royal Canin Eco Industrial Park. The four-hectare site, once completely degraded, is now a functioning ecosystem through watershed and wetland restoration. The site's biodiversity has increased, with bird species rising from 10 to 175 and a population of endangered African bullfrogs (*Pyxicephalus adspersus*) being re-established. Since then, the park has observed some of the highest breeding frequencies of African bullfrog within human-modified landscapes (Posthumus 2017).

Most ecosystems in industrial landscapes, like the Royal Canin Eco Industrial Park, can only support animal species up to a certain size, such as small carnivores. However, some of these areas have the capacity to support a wide variety of animals (including larger mammals). For example, game reserves surrounding the Venetia (South Africa) and Jwaneng (Botswana) diamond mines are home to a suite of species ranging from rodents to the big five (Smallie & O' Connor 2000, Kamler *et al*. 2007, Houser *et al*. 2009, Jackson *et al*. 2014). Additionally, the Sperrgebiet exclusion zone in Namibia, initially established to protect diamond deposits (Edwards *et al*. 2014), is now a National Park (Wiesel 2010). Gálvez *et al*. (2018) identified that human-modified landscapes with large intensive farms can be of conservation value, given that an appropriate network of habitat patches is maintained within the matrix.

In this study, small mammalian carnivores were focused on as model species to investigate the conservation potential of industrial sites. This choice is guided by conservation needs, ecological theory and ecosystem processes. Firstly, small carnivores is one of least studied mammalian guilds in Africa (Do Linh San *et al*. 2013), with little known about their distribution. Secondly, based on the "mesocarnivore release" concept (Soulé *et al*. 1988), it is hypothesised that in the absence of large carnivores, small carnivores should thrive. Given the small size of many industrial sites (such as the Sasol Synfuels Operations site; 3,000 ha), I believe that this is a realistic scenario. Thirdly, it is believed that ecological processes will change under conditions of mesopredator release (i.e. in the absence of large carnivores) with mesopredators assuming the role of apex predators, particularly in a system with low species diversity (Roemer *et al*. 2009). Also, in mesocarnivore dominated systems, seeds and seedlings of various plant species may be protected from rodent granivory and herbivory respectively. This will enhance seedling emergence and recruitment, improving population growth rates and abundance (Kauffman & Maron 2006). Finally, South Africa's petrochemical sector is a critical economic asset (e.g., supplying 40% of the country's fuel; Majozi & Veldhuizen 2015), and it is likely that such industries will continue expanding throughout Africa. With one-tenth (3.3 million km^2) of global wilderness being lost over the last two decades and just 30.1 million km^2 of these areas left (23% of the earth's land area; Watson *et al*. 2016), understanding the impacts of modified landscapes (including industrial sites) on and their role in biodiversity conservation is, therefore, a necessity.

2.2 Methods

2.2.1 Study area

The study was conducted in the secondary area of the Sasol Synfuels Operations property just outside the town of Secunda (26° 33'S, 29° 10'E), Mpumalanga, South Africa (Figure 1). Approximately 3,000 ha in size (total size of the property is 8,445 ha), this is the land that surrounds the Sasol Synfuels plant (Matthews 2016). The secondary area is situated on the Highveld plateau at ~1,590 m above sea level; the landscape is a mix of gentle and moderate undulations. This previously disturbed area supports a variety of short to medium-high, dense, tufted grasses. The Grassland vegetation is interrupted by scattered small Wetlands (man-made and natural), narrow stream alluvia (part of the upper catchment of the Waterval River), and occasional ridges or rocky outcrops (Matthews 2016). Mean annual precipitation of this summer rainfall (October to March) area is 772 mm (Burger 2013). The climate is cool-temperate with thermic continentality – high extremes between maximum summer and minimum winter temperatures, frost is common, and there are large thermic diurnal differences (Mucina & Rutherford 2006).

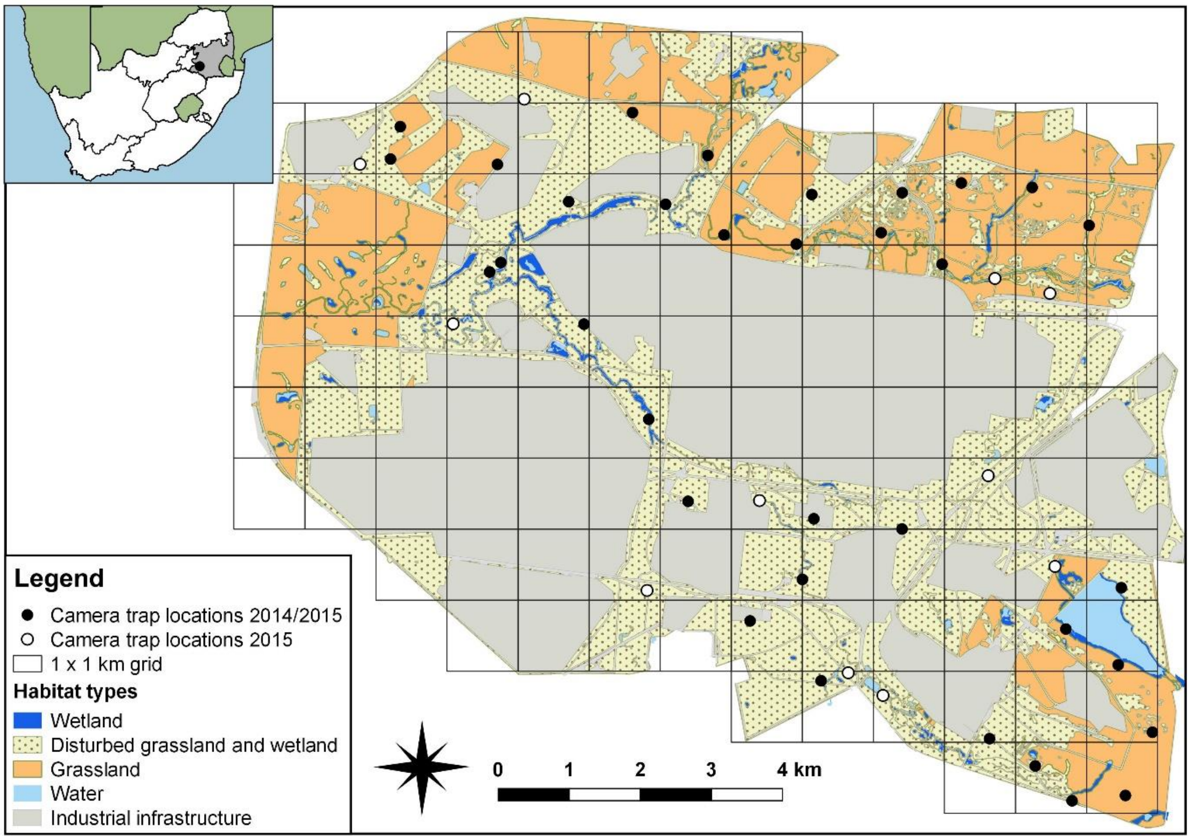

Figure 1. Map of South Africa showing the location of the study area, its habitat types and the camera trap locations. Adapted from Matthews 2016.

Initial mapping of the site classifies the property's landcover as follows: i) 4,042.7 ha (48%) transformed; ii) 2,350.2 ha (28%) degraded/disturbed; iii) 1,920 ha (23%) untransformed/undisturbed; and iv) 132 ha (2%) water. Of the untransformed areas, 245.4 ha (3%) is classified as Wetland and 1,674.6 ha (20%) as dry land (Grassland; Figure 1; Matthews 2016).

The study area is located within the Soweto Highveld Grassland vegetation unit (classified as a vulnerable ecosystem; SANBI 2011), which is part of the Mesic Highveld Grassland Bioregion of the Grassland Biome (Mucina & Rutherford 2006). Broad plant communities, as described by Matthews 2016, of Soweto Highveld Grassland occurring in the secondary area, include:

- *Themeda triandra – Cymbopogon pospischilii* relatively unspoiled grassland;
- *Setaria nigrirostris – Eragrostis plana* relatively unspoiled moist grassland;
- *Hyparrhenia tamba – Verbena bonariensis* relatively disturbed tall grassland;
- *Schkuhria pinnata – Aristida bipartita* disturbed grassland; and
- *Bidens pilosa – Cosmos bipinnatus*[4] transformed disturbed flats and floodplains.

The area's Wetlands are dominated by the indigenous common reed (*Phragmites australis*). Scattered amongst this vegetation in places is various industrial infrastructure including roads, process water dams, ash heaps and powerline pylons. The Sasol Synfuels Operations property is surrounded by urban and semi-urban settlements, as well as agricultural land. As a National Keypoint[5], the property is highly

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[4] Some of the many naturalised alien invasive plant species occurring on the site (Bromilow 2010).
[5] A site of national strategic importance.

secure, with strict access control measures in place. Consequently, there is minimal human activity in the secondary area.

2.2.2 General camera trapping

Between August 2014 and July 2015, an intensive population study of serval in the study area was conducted (Loock *et al*. in review). This consisted of three surveys; summer 2014, autumn 2015 and winter 2015. The objective of this study was to determine the approximate population size, density and habitat usage of serval across the secondary area. For each survey, 34 Reconyx^{TM} Hyperfire^{TM} HC600 camera traps (black flash) were deployed for a minimum of 40 days across an area of 79.4 km^2 in a 1 km^2 grid (Figure 1). The survey design was constrained by access limitations to various restricted areas on the site and the number of available cameras. Camera trap sites were selected with the aim of capturing serval and were placed at an average of 1.2 km (maximum 2.1 km) apart. These distances were based on serval home range size (Ramesh *et al*. 2015). As a result, most camera traps were placed in and around the tall grass and reed beds of the Wetlands, a habitat that is predominantly used by serval (Ramesh *et al*. 2015). Other habitats where camera traps were placed included disturbed Grassland and Wetland, and Grassland. After gaps in the sampling coverage of study area and overlapping some camera trap sites were identified during the first survey (summer 2014), 11 of the camera traps were moved to increase coverage across the site and increase the probability of detecting additional serval during the following two surveys (autumn and winter 2015; Figure 1). On the ground, the camera traps were set up at a height of 50 cm alongside (~2 m away) dirt tracks, game paths and other natural pathways in the veld. The camera height was explicitly selected to capture photos of serval, which are relatively tall compared with many other small carnivore species. As a result, all other species captured during the survey were incidental. The camera traps were set on Trail mode – when triggered by movement, the camera trap takes three photos with a one-second interval between photos.

Camera traps were checked weekly during each survey period. These checks included the: i) downloading of photos; ii) changing of batteries; iii) repositioning of cameras that had been dislodged by cattle or for any other reason; and iv) clearing of vegetation within two to five metres of the cameras to prevent any blank detections. Once downloaded, the photos generated during the surveys were managed using CameraBase© version 1.6.1. (Tobler 2014). Management of images consisted of the identification of species and individuals (when possible). The 40-day survey periods were then divided into eight (K = 8, temporal replication) sampling occasions of five days for each of the 34 (N = 34, spatial replication) camera trap locations. Detection/non-detection of all species was then recorded at every camera trap station during each of the sampling occasions.

Sampling effort per camera trap station was calculated as the number of days that a camera was active (i.e. that is was fully functional). Total effort across the 45 stations over the three surveys was 3,381 trap days (mean = 25.6, 37.9, 27.4; SD = 12.1, 5.2, 13; range = 0–40, 19–40, 0–40 for the summer 2014, autumn 2015 and winter 2015 surveys respectively; Table 1). Detection or non-detection of small carnivore species was recorded at each station for every trap day. This resulted in a response variable representing a naïve estimate of small carnivore occurrence across the camera trap sites (MacKenzie 2006).

Table 1. Camera trapping effort per survey.

Survey	**Dates**	**Camera trap days**	**Total photos**	**Total small carnivore photos**	**Total small carnivore detections***	**Total small carnivore species**[6]
Summer 2014	5 August – 13 September 2014	971	124,550	1,845	284	8
Autumn 2015	1 March – 9 April 2015	1,289	73,140	1,532	258	11
Winter 2015	20 May – 28 June 2015	1,121	51,459	2,028	258	9

* Total photos and detections per species are presented in Appendix A.

2.2.3 Statistical methodology

2.2.3.1 *Sampling completeness*

The iNEXT package for R (Chao *et al*. 2014, Hsieh *et al*. 2016, R Core Team 2017) was used to determine sampling completeness of the camera trap surveys across the three habitat types (disturbed Grassland and Wetland, Wetland and Grassland). Using the iNEXT package, small carnivore diversity was compared using sample coverage (the proportion of all the individuals in a community belonging to the species that are in the sample) rather than sample size, as comparisons based on size underestimate the true diversity of more diverse communities as compared to assemblages that are less diverse (Chao & Jost 2012). To compare sites with similar sample sizes but differing small carnivore diversities, as well as to avoid discarding data from camera trap sites with low diversities and species with minimal detections, the iNEXT package uses incidence-based rarefaction and extrapolation sampling curves that can be rarefied to smaller sample sizes or extrapolated to a larger sample size, guided by an estimated asymptotic species richness (Colwell *et al*. 2012).

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[6] Carnivore species weighing less than 15 kg.

Alpha diversity metrics following the Hill numbers were calculated for the three communities organised in three orders (q) as follows: i) species richness (S) (q = 0), ii) the exponential Shannon-Wiener index (exp H´) (q = 1); and iii) the inverse of Simpson´s concentration index (1/D) (q = 2). The Hill numbers combine knowledge on species richness, species rarity and species dominance, offering several advantages over other diversity indices (Chao *et al*. 2014).

2.2.3.2 *Multispecies occupancy modelling*

A key assumption of occupancy modelling is independence between sampling grids, where movement of individual animals between grid cells is limited, resulting in population closure (e.g., Shannon *et al*. 2014). However, research focusing on small carnivore ecology in South Africa (as well as the rest of Africa) is severely limited (Do Linh San *et al*. 2013). As such, reliable data on small carnivore home ranges could not be assembled to accurately estimate a grid size that would have allowed for population closure. We, therefore, had to consider a possibility other than movement between grid cells that would violate the closure assumption. Under such circumstances, the occupancy parameter (ψ) should be interpreted as the proportion of area used rather than occupied (MacKenzie & Bailey 2004). Since the study was focused on areas used by small carnivores, and hence how such use will affect predation pressure/landscape of fear, it is believed that such an approach was adequate for the analysis.

In this study, a hierarchical formulation of the Dorazio/Royle community occupancy model was used to estimate species-specific occupancy and camera trap site-specific species richness (with data augmentation; Dorazio & Royle 2005). Two processes govern hierarchical occupancy models; a state process (or an ecological process) governing true occupancy and an observation process which governs the probability that a species is detected or not (Fiske & Chandler 2011, 2015). Under a single-species single-season occupancy model the probability that site j is occupied by species Z_j is modelled as a Bernoulli random variable governed by occupancy probability (ψ). Occupancy probability can either be modelled as a constant parameter (on a logit scale) or as a function of some site-specific variable (for example, habitat type of each grid cell). Similarly, the observation process is governed by the detection probability (p) conditioned on the true latent occupancy state of species Z_j. For camera trapping surveys, sites are surveyed on k occasions (occasions = days) where the species observations (γ_{jk}) are modelled as a Bernoulli random variable, either p_{jk}= 1 where z_j = 1 (species detected) or p_{jk}= 0 where z_j = 0 (species not detected). As with occupancy probability, detection probability can also be modelled as a: i) constant using a logit scale; or ii) as a function of either site (for example, habitat type) or occasion (for example, temperature) specific variables.

Community models further extend the single-species single-season model by indexing the latent and model parameters by species (i). Under this formulation, it was assumed that the species-specific parameters come from a common underlying distribution (governed by the hyperparameter, which is the small carnivore community). Consequently, indexing the single species model by species results in a number of linked species-specific models. Estimating species richness at each camera trap site (including those not detected) is achieved by augmenting the data with all-zero observations for the hypothetical number species not detected (Dorazio & Royle 2005). By extracting small carnivore distribution data from the most recent IUCN analysis (IUCN 2016), it was estimated that around 23 species could occur in the study site. The data was, therefore, augmented with 12 species (11 detected + 12 never detected = 23 total community size).

It was hypothesised that small carnivore detection and occupancy would be affected by various environmental variables. Firstly, it was expected that small carnivore occupancy would be affected by black-backed jackal (*Canis mesomelas*) presence or abundance. For example, Kamler *et al*. (2013) found that black-backed jackals had both lethal (suppression of a Cape fox [*Vulpes chama*] population) and sub-lethal (behavioural changes in both Cape and bat-eared foxes [*Otocyon megalotis*]) impacts on small carnivores.

Secondly, I hypothesised that small carnivore density and occupancy would be lower in the natural Grassland habitats of the study site where livestock are present (i.e. in livestock and game camps – representing a relatively high stocking rate), compared to those areas – primarily disturbed Wetland and Grassland – where livestock are not present (i.e. outside of livestock and game camps – representing a relatively low stocking rate). For example, a study in the Kalahari found that the abundance of small- and medium-sized carnivores was lowest on farms where stocking rates were high (i.e. stocking rate was the most important variable driving local carnivore abundance; Blaum *et al*. 2009). This hypothesis is, however, not only linked to the presence of livestock but also to the natural Grassland habitats dominating the livestock and game camps. The structure of this habitat – i.e. Soweto Highveld Grassland – is naturally low, without extensive basal cover, conditions which do not favour high small mammal abundances (Smit *et al*. 2001). As a result, the prey base needed to support a high diversity and abundance of small carnivores is expected to be absent in these areas, compared to the disturbed habitats which consist of taller plant species and extensive basal cover, providing the ideal conditions for small mammals (Smit *et al*. 2001). This is supported by the results of small mammal trapping surveys conducted across the habitats in the study area, which detected lower densities of small mammals in Grassland, compared to disturbed Grassland and Wetland (Swanepoel & Keith 2016). Furthermore, vegetative cover is an important habitat characteristic for some small carnivore species (Caruso *et al*. 2016, Gálvez *et al*. 2018). The lack of extensive vegetative cover within the Grassland habitats of the study site would, therefore, result in the limited use of these areas by small carnivores, especially if nearby disturbed Grassland and Wetland provide the preferred conditions – cover and prey.

Lastly, it was expected that habitat type would play an important role in small carnivore diversity and occupancy. For example, certain habitat types were found to have either positive or negative effects on the occurrence of several carnivore species in Mole National Park, Ghana (Burton *et al.* 2012). The habitat types assigned to each camera station were based on previous vegetation studies conducted in the secondary area of the Sasol Synfuels Operations property (Matthews 2016; Figure 1).

Correlation between variables was tested for by using a Variance inflation factor (VIF; Fox 2008). Grassland was excluded as it had a high VIF and, therefore, only retained Wetland and disturbed Grassland and Wetland as habitat variables. Survey dates (Julian day) were modelled as a species-specific random effect on detection probability (Dorazio & Royle 2005). A priori model was, therefore, defined where occupancy is affected by relative abundance of black-backed jackal (expressed as number of pictures per 1,000 camera trapping days = RAI) and livestock activity, (expressed as the percentage of days during the surveys that livestock were active/detected in the grid cell where a camera was located) while detection is affected by survey date (Julian day). In this study, specific interest was focused on small carnivore predation pressure. Therefore, estimated small carnivore species richness was used as a proxy for predation pressure, which was expressed spatially. To determine spatially explicit species richness, the number of species per camera trap station was estimated by following a species-specific parameterisation with random effects on detection and occupancy (for example, species-specific relationships with covariates).

The community occupancy model was parameterised as follows:

$$z_{ik}|w_k \sim Bernoulli(w_k \psi_k) \text{ \# State process (occurrence)}$$

$$y_{ijk}|z_{ik} \sim Bernoulli\left(z_{ik} p_{ijk}\right) \text{ \# Observation process (detection)}$$

$$\text{\# models of species heterogeneity (Eq. S1) } logit(\psi_{ik}) = lpsi_k + \beta 1_k \mathrm{BBJ}_i + \beta 2_k Livestock_i + \beta 3_k Disturbed_i + \beta 4_k Wetland_i$$

$$\# \; (Eq.S2) \; logit(p_{ijk}) = lp_k + \beta.dlp_k * Date_{ij}$$

With

$$lpsi_k \sim Normal(\mu_{lspi}, \sigma^2_{lspi})$$

$$\beta 1_i \sim Normal(u_{\beta 1}, \sigma^2_{\beta 1})$$

$$\beta 2_i \sim Normal(\mu_{\beta 2}\,, \sigma^2_{\beta 2})$$

$$\beta 3_i \sim Normal(\mu_{\beta 3}, \sigma^2_{\beta 3})$$

$$\beta 4_i \sim Normal(\mu_{\beta 4}, \sigma^2_{\beta 4})$$

$$lp_k \sim Normal(\mu_{lp}, \sigma^2_{lp})$$

$$\beta.d1_i \sim Normal(\mu_{\beta.d}, \sigma^2_{\beta.d})$$

The observed species – 11 – were augmented with species never detected (12; a Bernoulli random variable [w]) presented as part of the metacommunity studied (Kéry & Royle 2015). Z_{ik} is the true occupancy state (0 = not occupied and 1 = occupied) for a species *k* at camera site *i*; ψ_{ik} is the occupancy probability (between 0 and 1) for each species *k*; $lpsi_k$ is the logit-linear predictor intercept of the occupancy probability, indexed by species (*k*). β_1 is the coefficient for the relative abundance of black-backed jackal (expressed as number of pictures/1,000 camera trapping days), β_2 the coefficient for livestock activity (expressed as the percentage of days during the surveys that livestock were active/detected in the camp where a camera was located), β_3 is the coefficient for the percentage of disturbed vegetation in each camera grid cell and β_4 is the percentage of Wetland in each grid cell. Species specific intercepts and coefficients were drawn from Normal distributions with mean (μ_{lpsi}), and variance σ^2_{lpsi} for the community, mean ($\mu_{\beta 1}$- $\mu_{\beta 4}$) and variance ($\sigma^2_{\beta 1} - \sigma^2_{\beta 4}$) for coefficients. Similarly, γ_{ik} are the species detections (1 being detected [photographed] and 0 not detected [not photographed]) of *k* species at *i* sites; p_{ik} is the detection probabilities per species, lp_k is the logit-linear predictor intercept of the detection probability indexed by species *[k]*. $(\beta.d)$ is the effect of Julian survey date on detection probability. Species-specific detection intercepts were drawn from a Normal distribution with community mean (μ_{lp}) and variance (σ^2_{lp}) and for Julian date coefficient mean $(\mu\beta.d)$ and variance ($\sigma^2_{\beta.d}$).

The community occupancy models were implemented in a Bayesian framework (JAGS; Plummer 2003) using the R package ‘jagsUI’ version 1.4.4 (Kellner 2016). Three parallel Markov chains with 50,000 iterations were run. 10,000 were disregarded as burn-in, and remaining chains were reduced by 10 to make output manageable. Chain convergence was first assessed by visually inspecting chains and calculating the Gelman-Rubin statistic (Gelman *et al*. 2014), where values of <1.1 indicated convergence. All parameters had R values <1.1 which indicates adequate chain mixing and convergence.

Model fit was tested by calculating the Bayesian p-value (Gelman *et al.* 1996), where observed residuals are compared to residuals simulated under the model (>0.95 Bayesian p-value <0.5 indicates lack of fit).

Freeman-Tukey residuals (R) were used to calculate the Bayesian p-value:

$$R(\mathbf{y}, \boldsymbol{\theta}) = \sum (\sqrt{y} - \sqrt{E(y)})^2$$

In this equation, y represents the binary observations, $\boldsymbol{\theta}$ represents all parameters in the community occupancy model. $E(y)$ is the expected value of y, which is the product of the species, site and the species-specific detection and occupancy probabilities. The residuals are then summed over species, sites and occasions.

The model simulations resulted in a Bayesian p-value of 0.54, indicating a good model fit (Figure 2).

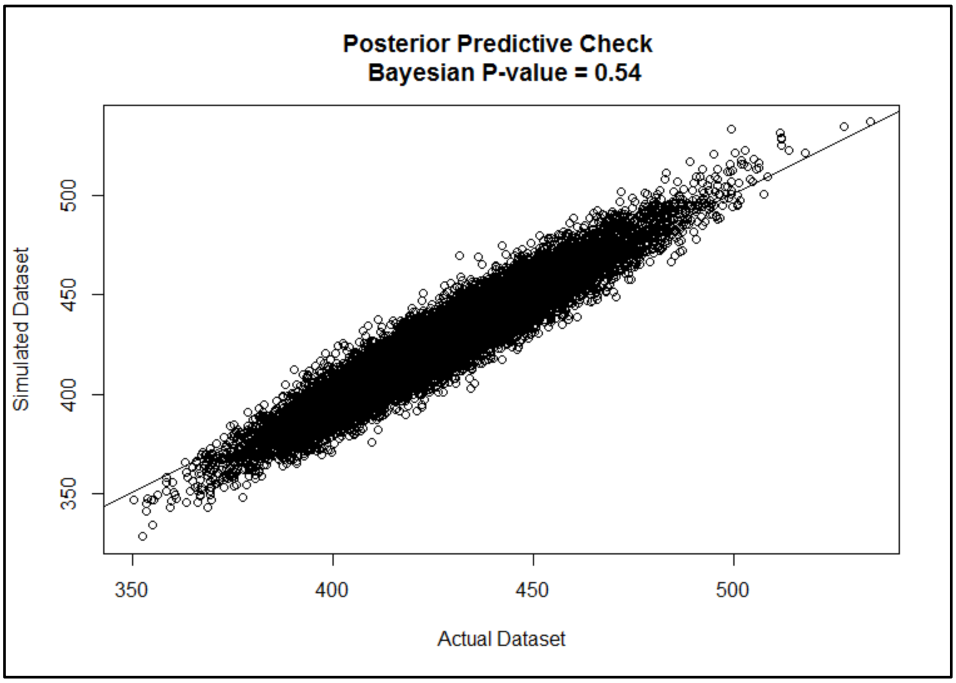

Figure 2. Model fit of actual dataset against simulated dataset.

Results are reported in mean, standard deviation and 95% Bayesian confidence intervals (95 BCI taken from the 2.5% and 97.5% percentiles of the posterior mean). Coefficients were regarded as having strong inference values if their 95 BCI values did not include 0. In addition, the number of small carnivore species per land use was estimated by summing the estimated species richness at each camera trap site, in each habitat type. Since the model output is extracted from posterior distributions, each parameter can be extracted: a mean, lower BCI and upper BCI. In the model parameterisation, each camera trap site is also regarded as a parameter, where each camera trap will have a posterior distribution for species richness. For each camera trap, the mean species richness was extracted, which is regarded as the mean expected species per camera site. Similarly, lower BCI was extracted, which was regarded as the minimum number of species per camera site, while the upper BCI would represent the maximum number of species per camera site. These values were summarised per habitat type (disturbed Grassland and Wetland, Grassland and Wetland), as well as spatially (mean, minimum and maximum species richness maps).

Species richness at each camera trap location (mean, minimum and maximum) was estimated using inverse distance weighted interpolation to create spatially explicit species richness maps (Sarmento *et al*. 2009). R v3.4.1 (R Core Team 2017) was used for all modelling, with the following R packages; raster for IWD (Hijmans 2014) and jagsUI (Kellner 2016). Model parameter estimates are only presented for the detected small carnivore species.

2.3 Results

2.3.1 Species diversity and richness

While 11 small carnivore species were detected (Table 2), results from the multispecies occupancy analysis predicted that 23 species occurred on site. This suggests 12 species were not detected during the camera trap surveys and that the small carnivore community only realised 48% of the potential species (11/23 species) that could occur on the Sasol Synfuels Operations property. Spatially, species richness was highest (for mean [7.9], minimum [1.96] and maximum [14]) in the disturbed habitats (i.e. disturbed Grass and Wetland), even though some individual camera traps located in Grassland were also allocated a high species richness (Figure 3). Upon comparing broad species richness between disturbed Grassland and Wetland, and Grassland habitats, no significant difference was found (Figure 4). Grassland did, however, have a higher variance in data, with many species being detected at individual camera trap sites (outliers; Figure 4).

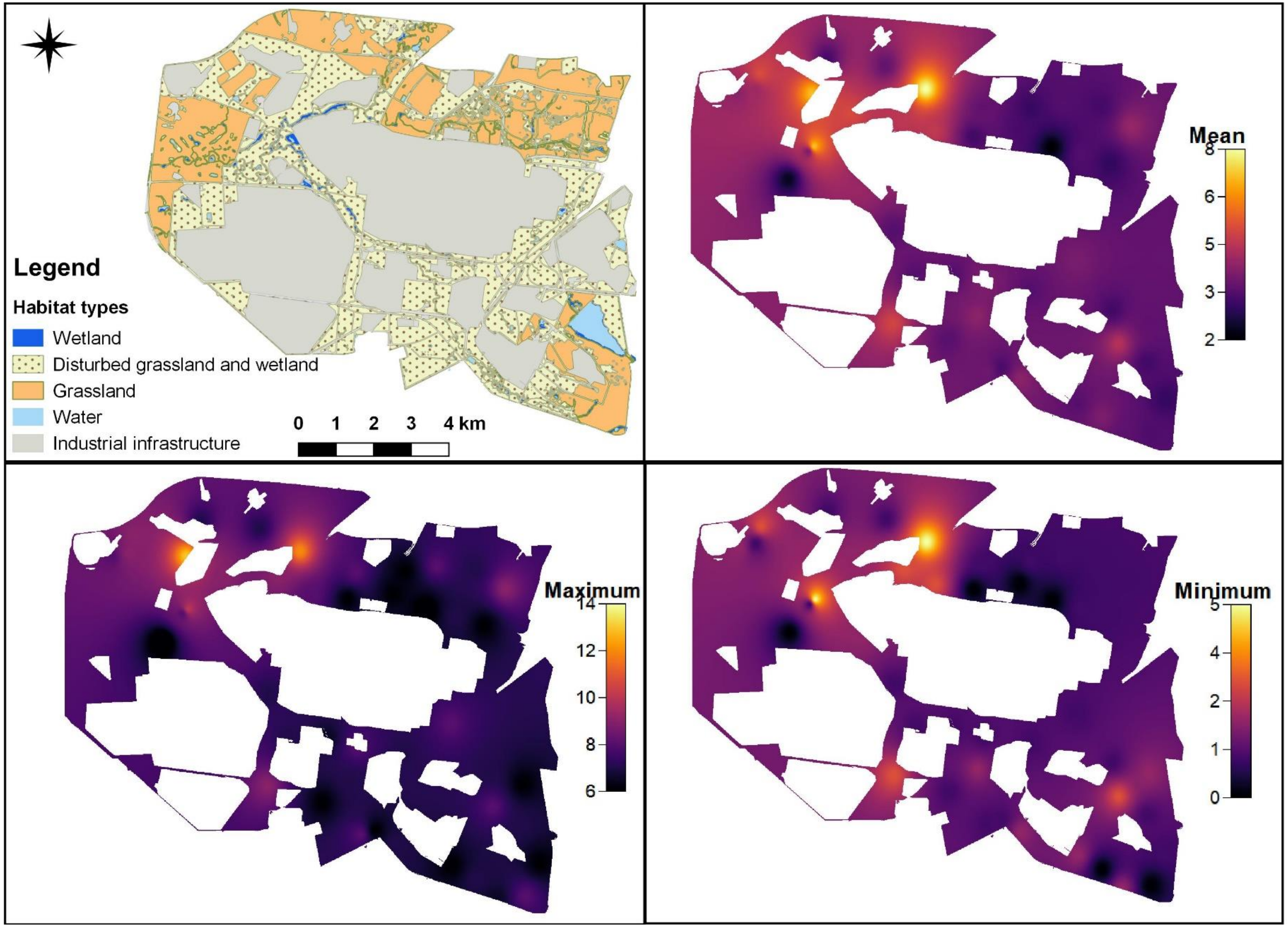
Legend
Habitat types
Wetland
Disturbed grassland and wetland
Grassland
Water
Industrial infrastructure
0 1 2 3 4 km
Mean
8
6
5
3
2
Maximum
14
12
10
8
6
Minimum
5
4
2
1
0

Figure 3. Spatial representation of the mean, maximum and minimum species richness across the study area. A map of habitat types is presented to indicate the effect of habitat on species richness.

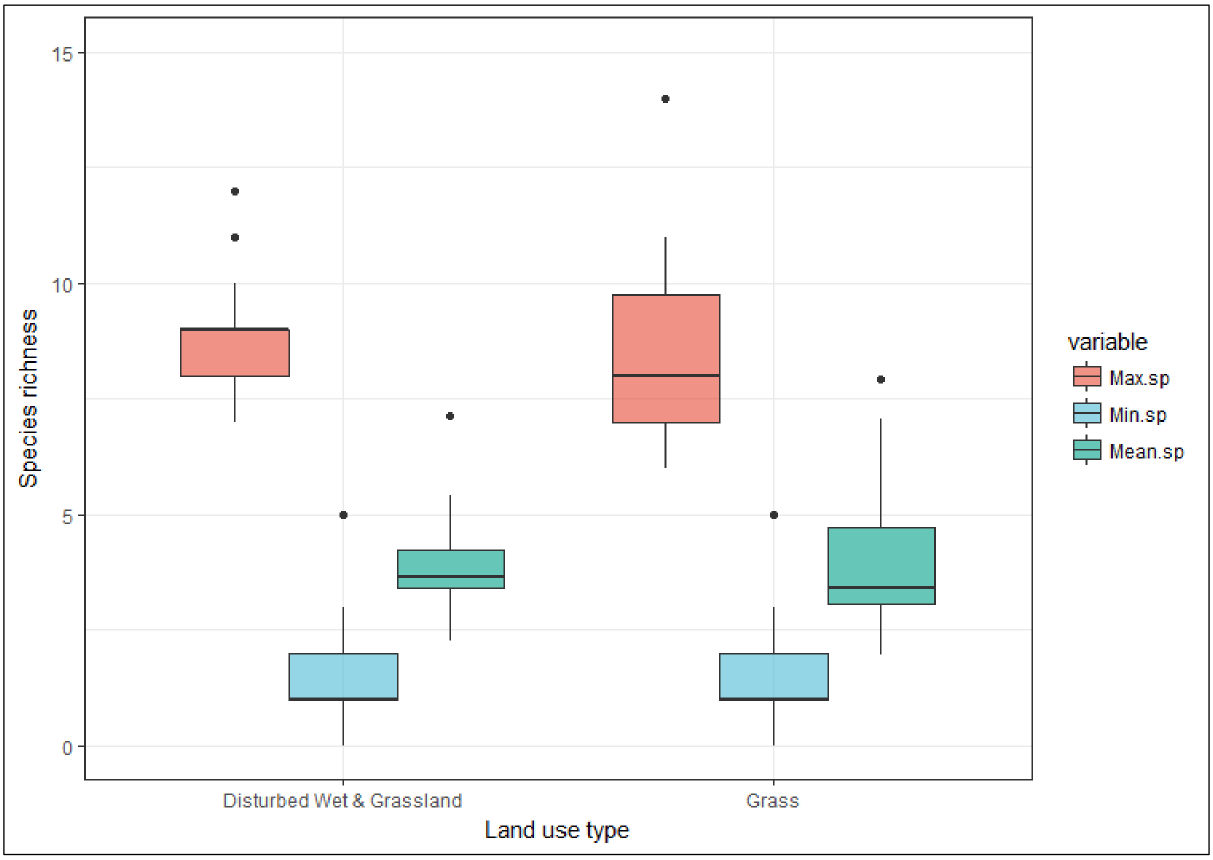

Figure 4. Comparison of species richness between disturbed Wetland and Grassland, and Grassland habitats.

Apart from successfully detecting the target species, serval, additional carnivore species were also frequently detected including black-backed jackal, slender mongoose (*Galerella sanquinea*), suricate, water mongoose (*Atilax paludinosus*), white-tailed mongoose (*Ichneumia albicauda*) and yellow mongoose (*Cynictis penicillata*). Less frequently detected small carnivore species include Cape fox, Cape clawless otter (*Aonyx capensis*), small-spotted genet (*Genetta genetta*) and large-grey mongoose. Camera trap photos of these small carnivore species are presented in Appendix B. Domestic species captured, which can also be considered as mesocarnivores include domestic cat (*Felis catus*) and dog (*Canis lupus familiaris*). A complete list of all mammal species detected during the survey can be found in Appendix C.

2.3.2 Sampling coverage

Sampling coverage across the three camera trap surveys was adequate for disturbed Grassland and Wetland, and Wetland (>0.9; Figure 5). However, Grassland was relatively undersampled (>0.8; Figure 5). Species accumulation curves indicate that across all habitat types, numerous species were detected at some camera trap sites, but incidence was low, showing that many of these species occasionally passed through these areas rather than permanently using them, particularly Grassland (Figures 6 & 7). This again suggests that Grassland assemblages were undersampled, i.e. several species present were not detected (although confidence intervals are very wide; Figures 6 & 7). In Grassland, the Shannon diversity measure (Hill number 2) is lower than the other habitats, indicating the dominance of a single species (black-backed jackal; Figures 6 & 7), which potentially explains the low detection incidence of other species in this habitat type.

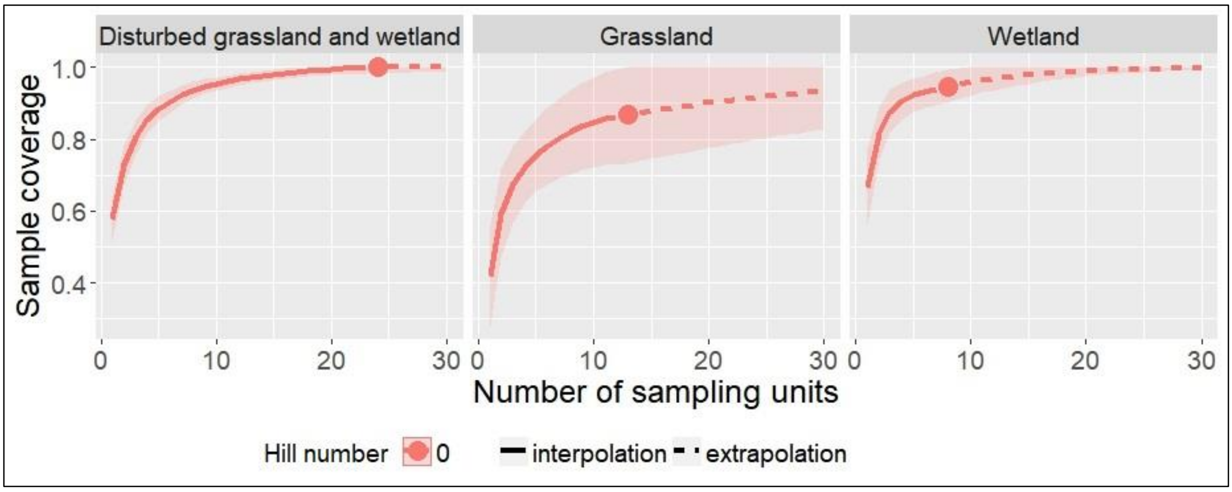

Figure 5. Relationship between sample size and sample coverage across the three habitat types.

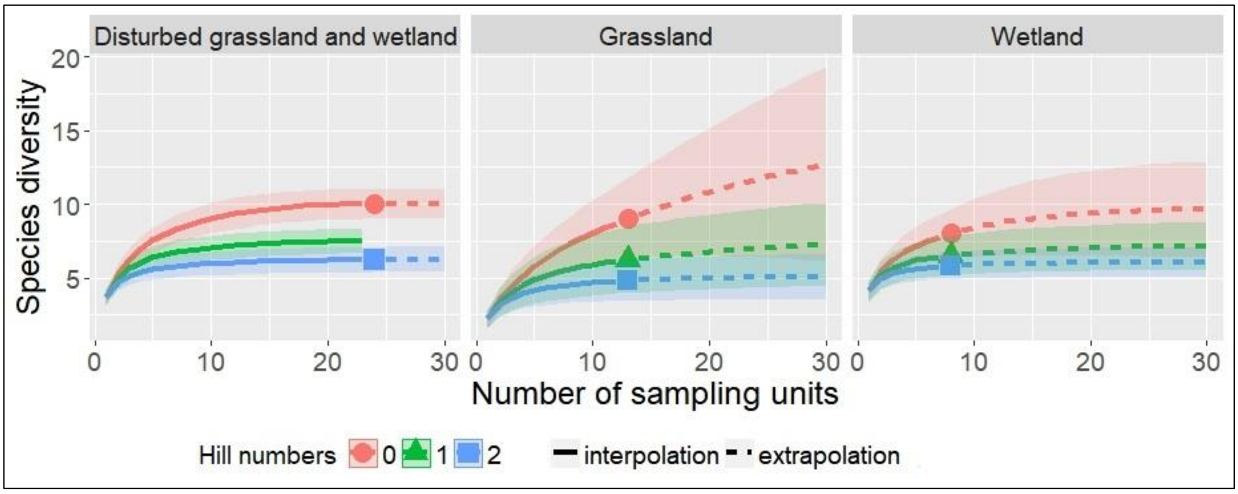

Figure 6. Response of alpha diversity metrics (Hill numbers 0, 1 and 2) to sample size.

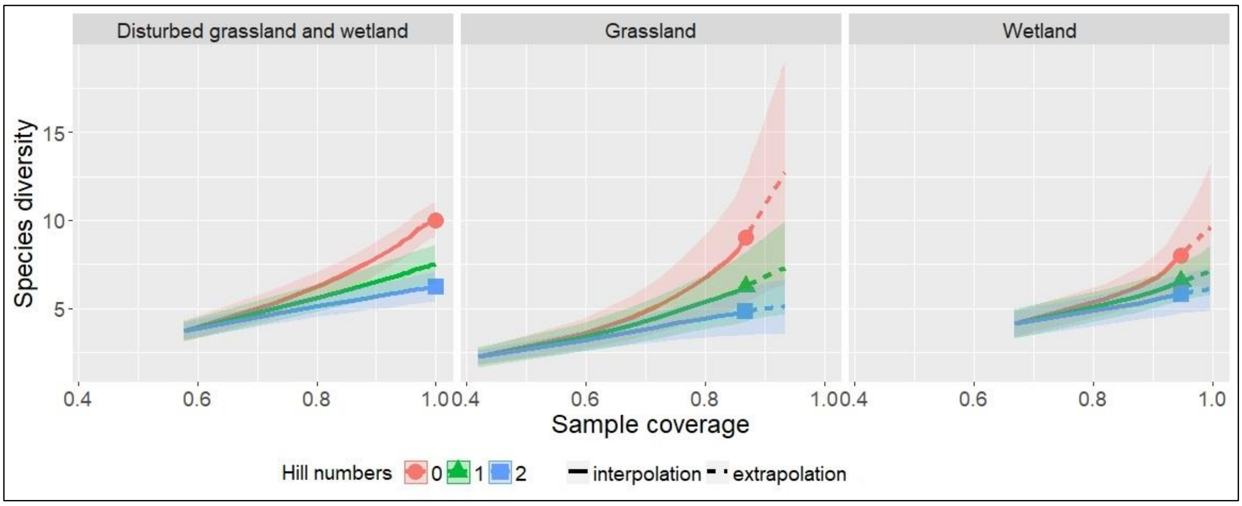

Figure 7. Response of alpha diversity metrics (Hill numbers 0, 1 and 2) to sample coverage.

2.3.3 Occupancy modelling

The mean detection probability of all small carnivores was 0.0461 (SD = 0.0890), while mean occupancy probability was 0.2175 (SD = 0.2715). However, there were large variations in detection and occupancy probabilities between individual species (Table 2 & Appendix D). Serval had the highest mean detection (0.1821, SD = 0.0124) and occupancy probabilities (0.7491, SD= 0.0967; Table 2). Small spotted genet had the second highest detection probability (0.1280, SD = 0.0528), while black-backed jackal had the second highest occupancy probability (0.4360, SD = 0.1364; Table 2).

Suricate and small-spotted genet had the lowest mean detection and occupancy probabilities, respectively.

Table 2. Mean detection and occupancy probabilities per small carnivore species.

Species	**Mean detection probability**	**Lower 95% Highest Density Interval (HDI) limit – detection**	**Upper 95% HDI limit – detection**	**Mean occupancy probability**	**Lower 95% HDI limit – occupancy**	**Upper 95% HDI limit – occupancy**
1. Serval	0.1820	0.1580	0.2060	0.7490	0.5580	0.9290
2. Black-backed jackal	0.0662	0.0438	0.0899	0.4360	0.1810	0.7080
3. Cape fox	0.0838	0.0000	0.0314	0.1990	0.0000	0.8310
4. Small spotted genet	0.1280	0.0309	0.2290	0.0237	0.0000	0.0717
5. Large grey mongoose	0.0087	0.0000	0.0337	0.1950	0.0000	0.8360
6. African clawless otter	0.0080	0.0000	0.0318	0.2540	0.0000	0.9280
7. Slender mongoose	0.0525	0.0122	0.0964	0.0878	0.0050	0.2080
8. Suricate	0.0075	0.0000	0.0250	0.3200	0.0006	0.9430
9. Water mongoose	0.0456	0.0163	0.0748	0.1680	0.0220	0.3560
10. White-tailed mongoose	0.0078	0.0000	0.0323	0.2380	0.0000	0.8970
11. Yellow mongoose	0.0393	0.0120	0.0690	0.2380	0.0404	0.5260

2.3.3.1. *Effects of different covariates on small carnivore occupancy*

Contrary to initial hypotheses, neither black-backed jackal (Figure 8) nor vegetation type (disturbed Grassland and Wetland & Wetland; Figure 9) significantly affected small carnivore occupancy, either individually or at the community level (Figures 8 & 9). Livestock had a negative effect on serval occupancy but did not affect other small carnivores individually or at the community level (Figure 8).

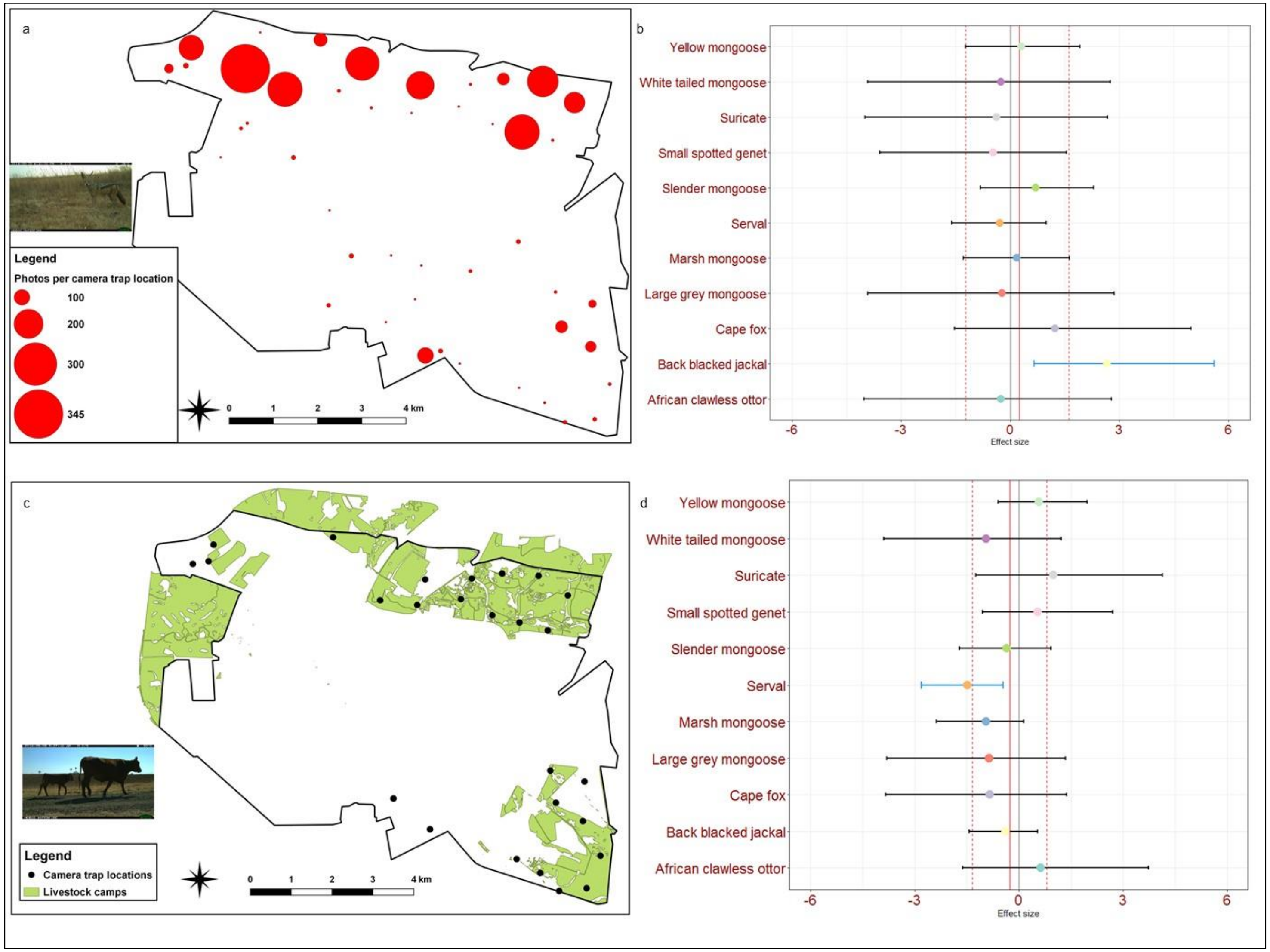

Figure 8. The effects of covariates on small carnivore occupancy. a) Number of blacked-backed jackal photos per camera trap; b) effect of black-backed jackal on small carnivore species; c) cameras located in livestock camps (livestock presence); and d) effect of livestock on small carnivore occupancy. In the plots, the grey line indicates zero effect, the red line represents the mean community response, and the dotted red line indicates the BCI for community response.

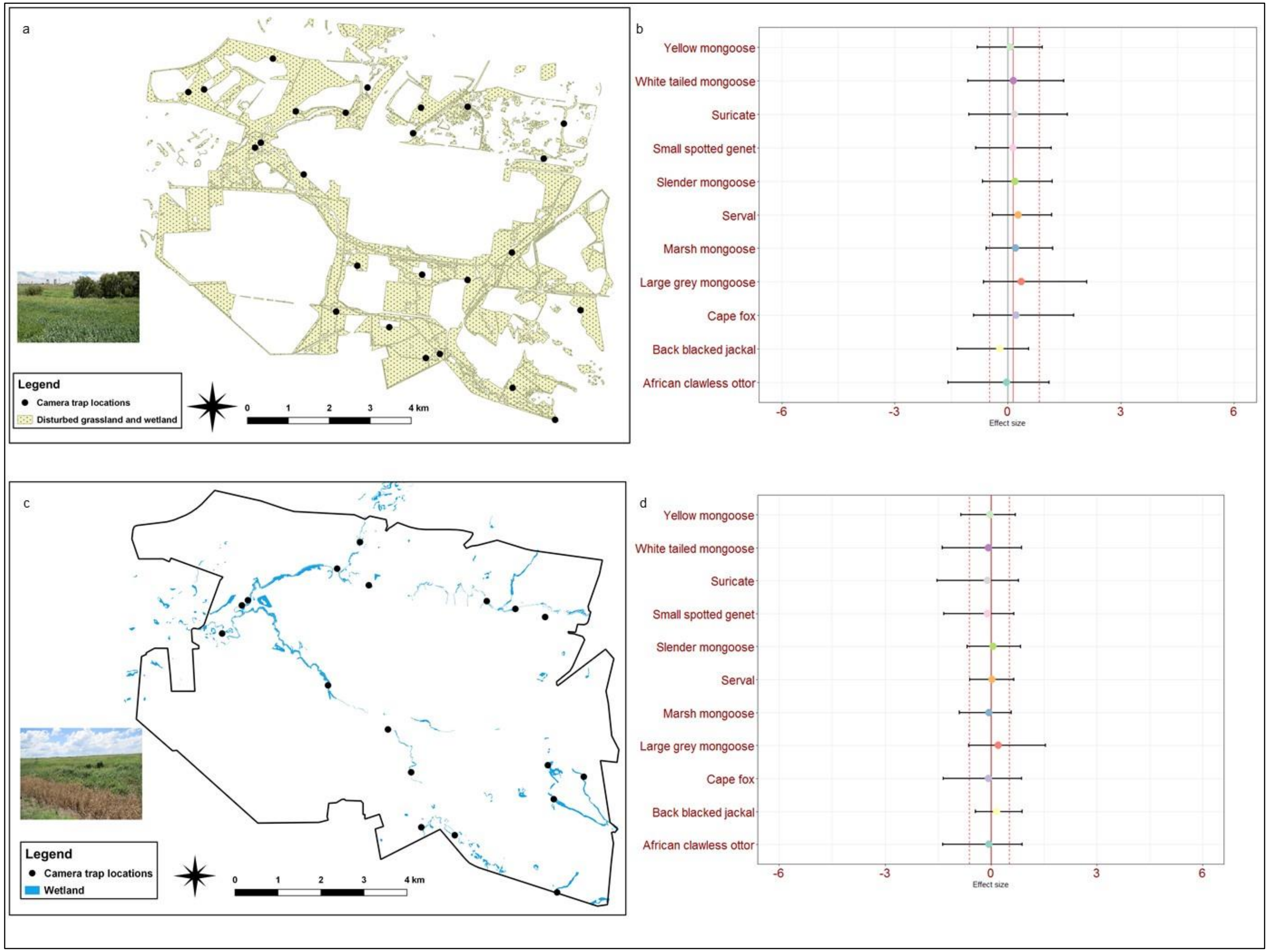

Figure 9. The effects of covariates on small carnivore occupancy. a) Cameras located in disturbed Grassland and Wetland; b) effect of disturbed habitats on small carnivore occupancy; c) cameras located in Wetland; and d) effect of Wetland on small carnivore occupancy. In the plots, the grey line indicates zero effect, the red line represents the mean community response, and the dotted red line indicates the BCI for community response.

2.4. Discussion

Out of the 23 small carnivore species that were predicted to occur within the study area, 11 were detected over the three camera trap surveys. These predicted and detected carnivore richness values compare well with those across the natural Grassland biome of South Africa (e.g., Gelderblom *et al*. 1995). This highlights the conservation importance of modified landscapes such as the Sasol Synfuels Operations property for small carnivores. Such an observation is aligned with several studies that suggest generalist carnivores tolerate and sometimes benefit from the modification of landscapes (Crooks & Soulé 1999, Gehring & Swihart 2003, Šálek *et al*. 2010). Similarly, Caruso *et al*. (2016) observed a positive correlation between the occurrence of Geoffroy's cat (*Leopardus geoffroyi*; a small carnivore) and landscape disturbance and fragmentation in Central Argentina, while Gálvez *et al*. (2018) found that güiñas/kodkods (*Leopardus guigna*; a small carnivore) can tolerate a high degree of habitat loss.

Of particular importance in terms of conservation value are the high detection and occupancy probabilities of serval, as well as the presence of large grey mongoose in the study area. Serval are declining across their range (Ramesh & Downs 2013). This is mainly attributable to the loss and degradation of their preferred wetland habitat (Thiel 2011). The IUCN Red List of Threatened Species classifies serval as Least Concern, however, in southern Africa, they are listed as Near Threatened (Thiel 2015, Ramesh *et al*. 2016). Consequently, the conservation potential of the study area for serval in southern Africa is considerable (Loock *et al*. in review). The detection of large-grey mongoose (listed as Least Concern by the IUCN Red List of Threatened Species; Do Linh San *et al*. 2016) is remarkable as the study area occurs outside of the species' known range in southern Africa (Emslie *et al*. in review), further emphasising the role that the Sasol Synfuels Operations site can play in conserving species – including vulnerable and threatened species.

Even though no meaningful differences in species richness (mean, minimum and maximum) were found between disturbed Grassland and Wetland, and Grassland habitats, the results were clouded by individual variation in species richness between camera trap locations. For example, spatially, small carnivore species richness was the highest in the disturbed Grassland and Wetland habitat types. This is in agreement with previous studies, which found that some generalist species (including carnivores) are positively influenced by disturbed habitats leading to increased species richness (Murua & Rodriguez 1989, Tellería *et al*. 1991, Austen *et al*. 2001, Caruso *et al*. 2016, Gálvez *et al*. 2018). A relatively higher small carnivore species richness may be traced to a suite of factors. Firstly, the high availability of small mammal prey biomass (up to 130 individuals per hectare in the disturbed habitats of the study area; Swanepoel & Keith 2016) is expected to attract small carnivores to disturbed habitats (Austen *et al*. 2001, Burton *et al*. 2012, Caruso *et al.* 2016). Secondly, there may be a level of ecological adaptability across the small carnivore guild (Pereira *et al*. 2012) allowing many of these species to tolerate and even thrive under conditions of human disturbance (Castillo *et al*. 2008). Thirdly, the absence of large carnivores in human-modified landscapes limits intraguild interactions such as competition and predation, which are known to influence carnivore occurrence (Crooks 2002, May *et al*. 2008, Sergio & Hiraldo 2008, Vanak *et al*. 2013). Relatively lower intraguild interactions in disturbed habitats may open them up to exploitation by small carnivores (Caruso *et al*. 2016, Gálvez *et al*. 2018), resulting in mesocarnivore release (Soulé *et al*. 1988, Ritchie & Johnson 2009, Brashares *et al*. 2010). Fourthly, a degree of vegetative cover, which is an important habitat characteristic for some small carnivore species (Caruso *et al*. 2016, Gálvez *et al*. 2018), as well as some of their small mammal prey species (Smit *et al*. 2001), is extensive in the disturbed Grassland and Wetland habitats compared to the natural Grassland habitats of the study area. Fifthly, the absence of livestock, which can be used as a proxy for relatively low stocking rates in the disturbed habitats compared to the presence of livestock – relatively high stocking rates – in the natural Grassland habitats of the livestock camps, is also expected to have a positive effect on small carnivore diversity and abundance (stocking rates have been found to be inversely proportional to small carnivore abundance; Blaum *et al*. 2009). Finally, it is likely that the large extent of disturbed habitat in the study area, 2,350.2 ha (Matthews *et al*. 2016), has the capacity to support a high number of carnivore species and territories (Lindenmayer & Fischer 2006).

In contrast with disturbed habitats, slightly lower small carnivore species richness values were recorded across most of the undisturbed habitats such as Grassland. However, certain camera trap sites located in undisturbed Grassland habitat (particularly those bordering disturbed areas) had relatively high species richness values compared to other traps in this habitat. These are areas bordering disturbed habitats, therefore, potentially falling within the territories of carnivores that spend most of their time within disturbed habitats, occasionally moving through neighbouring undisturbed areas (once again indicating the ecological plasticity of these species; Pereira *et al*. 2012). In addition, some of these camera traps were located in undisturbed Grassland where livestock were either absent or only present for limited periods of time during the surveys (i.e. relatively lower stocking rates compared to game and livestock camps), negating the associated adverse effects of livestock on small carnivore species richness and densities (Blaum *et al*. 2009). This scenario would also potentially allow for relatively greater understory cover because of reduced grazing pressure and trampling of vegetation (Smit *et al*. 2001), having a positive effect on small mammal prey densities (Keesing 1998) and, consequently, small carnivore species richness. Once again, the importance of the role of habitat characteristics on small carnivore diversity is demonstrated (Burton *et al*. 2012, Caruso *et al*. 2016, Gálvez *et al*. 2018). However, sampling coverage analyses suggest that Grassland was undersampled. Species richness extrapolation results infer that should sampling in Grassland be increased, species richness in this habitat type would be similar to, if not greater than that in the disturbed habitats. Therefore, additional small carnivore species may have been detected within the study area with greater sampling coverage in Grassland.

The detection values across small carnivore species in the study area varied and were low. As a result, there was a large uncertainty in occupancy values. It is suggested that this is attributable to the camera trap placements and height (e.g., Meek *et al*. 2015), which were selected with the primary goal of capturing serval (see Section 2.2.2, General Camera Trapping). Apart from the presence of livestock (i.e. a relatively high stocking rate compared to areas where livestock are not present; Blaum *et al*. 2009) combined with the relatively lower and less dense vegetative structure of the natural Grassland[7] (which is expected to negatively affect both small carnivore; Caruso *et al*. 2016, Gálvez *et al*. 2018; and small mammal prey occurrence; Smit *et al*. 2001), which appeared to have a negative effect on serval occupancy, none of the

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[7] Soweto Highveld Grassland (Matthews 2016).

variables (black-backed jackal, disturbed Grassland and Wetland habitat type and Wetland habitat type) affected individual small carnivore species or community occupancy.

The lack of negative effect related to the presence of black-backed jackal is surprising given that they are known to occasionally exert both lethal (predation) and sub-lethal (behavioural changes) impacts on other small carnivore species (Kamler *et al*. 2013). This lack of effect on other small carnivore species *via* intraguild interactions (including competition and predation) may be related to several scenarios (in combination or individually). Firstly, the relatively high prey (small mammal) densities in the disturbed habitats of the study area (Swanepoel & Keith 2016), are likely to limit intraspecific competition for food and the related predation, allowing for small carnivores to coexist at high abundances within the study area. Secondly, as the largest of the suite of carnivores detected, black-backed jackal presumably face greater human persecution (particularly in the surrounding semi-urban and agricultural landscapes), possibly resulting in a relatively low population density. Conversely, the lack of lethal control of this species in the study area could have resulted in densities remaining stable and preventing the migration of conspecifics into the area, i.e. social perturbation (Tuyttens & Macdonald 2000, McManus *et al*. 2015). Furthermore, the presence of domestic dogs within and around the study area potentially exposes black-backed jackals to lethal viruses (such as canine distemper and rabies), which can decimate a population (Gowtage-Sequeira *et al*. 2009, Bellan *et al*. 2012). Consequently, the black-backed jackal population present within may not be reaching densities that are high enough to influence the other small carnivore species negatively.

The presence of livestock (a proxy for a relatively high stocking rate; Blaum *et al*. 2009) combined with the low and less dense vegetative structure of natural Grassland[8] in livestock camps seemed to negatively affect the occupancy of serval, which is in accordance with what was hypothesised. A number of possible reasons for this are provided. Firstly, the presence of livestock results in a decrease in understory vegetative cover, which is already limited in the site's natural Grassland habitats[8], through grazing and trampling (Smit *et al*. 2001). As a result, the preferred habitat of small mammals, serval's main prey, is reduced resulting in a local decrease in the densities of these species (including vlei rat [*Otomys* sp.], four-striped grass mouse [*Rhabdomys dilectus*] and multimammate mouse [*Mastomys natalensis*]). A lack a small mammal prey in the livestock camps would indeed contribute to the low occupancy of serval compared to areas, such as disturbed habitats, where livestock are not present, and small mammal prey biomass is high. Secondly, the livestock camps are predominantly covered by natural Grassland – with a lack of cover for serval to rest and hunt in – with only a limited area covered by Wetland, the preferred habitat of serval. In addition, where Wetland is present in livestock camps, trampling of reed beds by livestock reduces the cover available for serval to rest in. The movement of livestock through the limited Wetland areas is also likely to disturb serval while they are resting or hunting, negatively affecting their occupancy (Blaum *et al*. 2009). As a result, serval occupancies are lower in these predominantly natural Grassland areas and greater in those – mainly disturbed Grassland and Wetland – outside of livestock camps.

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[8] Soweto Highveld Grassland (Matthews 2016).

The lack of effect of the presence of livestock on the occupancy of all carnivore species other than serval can be attributed to several reasons. Dietary studies of serval in the study area indicated that the majority of their prey are small mammals (~90%; Ravhuanzwo *et al*. 2017). Such dietary specialisation is generally not characteristic of some of the other small carnivores present in the study area, which are generalists or opportunists, making use of a large variety of food sources, including small mammals (Andersson & Erlinge 1977). Studies have found some generalist carnivores to be tolerant and even benefit from agriculture (e.g., livestock farming) because of food availability and diversity (Gehring & Swihart 2003, Šálek *et al*. 2010). For example, yellow mongooses are predominantly insectivorous (feeding on insects including termites, beetles and locusts). However, they are highly opportunistic, also preying on small mammals and amphibians for example (Kingdon & Hoffmann 2012). Such dietary flexibility allows yellow mongooses and other generalists in the study area to adapt to and occupy its various habitats, including livestock camps where the densities of insects (such as beetles) are expected to be higher because of their attraction to livestock dung (Losey & Vaughan 2006). Specialist insectivores, such as suricate, who prefer open habitats such as Grassland (Kingdon & Hoffmann 2012), would also, therefore, be present in livestock camps, rather than being deterred.

Finally, some of the caveats to the study design are discussed. The most significant caveat was the camera trap placements, which were optimised for serval. As a result, detection probabilities for species occurring in the same habitat types and using the same roads and natural pathways as serval (for example, black-backed jackal) would have been higher than those for species that do not commonly use such areas (such as large grey mongoose and suricate). This also resulted in the under-sampling of

Grassland habitat, which potentially resulted in the non-detection of additional rare small carnivore species within the study area. Furthermore, the camera traps may have been erected too high from the ground (50 cm) to detect some of the smaller species (such as slender and yellow mongoose) on every occasion that they travelled past a trap, particularly when passing directly in front of or under a camera. It is suggested that such a bias towards serval might have negatively affected the detection probabilities of the small carnivore species. This observation is consistent with the findings of previous studies, which indicate that camera trap placement and height may affect the detection probabilities of certain species (e.g., Kelly & Holub 2008, Kelly 2008, Burton *et al*. 2012). Additional caveats include the lack of access to certain restricted zones within the study area and the limited number of camera traps available (34). These caveats also had an adverse effect on sample coverage across the study area.

2.5 Conclusion

The degradation of natural habitats related to the modification of landscapes by humans has and continues to result in varying levels of biodiversity loss. While the negative impacts of such disturbances have received much research focus, the potential conservation value of modified landscapes (such as industrial sites) is relatively unknown. The absence of large apex predators in these areas has opened them up to smaller carnivores, many of which have a high capacity to adapt to and flourish in the disturbed habitats, taking advantage of the often-abundant small mammal prey.

Data from three camera trap surveys conducted between August 2014 and July 2015 was used to determine small carnivore occupancy and detection probabilities, as well as species richness across the highly industrialised Sasol Synfuels Operations property in Secunda. 11 small carnivore species were detected within this modified landscape, including serval (near threatened and currently in decline in southern Africa as a result of habitat loss and persecution; Ramesh *et al*. 2016) and large-grey mongoose (outside of its known range; Do Linh San *et al*. 2016). Spatially, small carnivore species richness was the highest in the disturbed Grassland and Wetland habitat types, which may be attributable to: i) abundant small mammal prey related to extensive understory vegetative cover; ii) considerable vegetative cover for hunting, nesting and escaping threats; and iii) limited human (persecution) and livestock (disturbance) activity in these areas. Conversely, natural Grassland had a marginally lower species richness value, which is suspected to be related to the presence of livestock, lack of vegetative cover and low small mammal prey densities. However, Grassland was relatively undersampled, and extrapolation of species richness values indicates that with greater sampling coverage these values will increase, potentially being higher than those in disturbed areas.

Small carnivore detection values were, in general, varied and low, resulting in large uncertainties in occupancy probabilities. It is suspected that this is due to the camera trap surveys being tailored specifically to capture serval. Out of all the site-specific variables modelled, the only significant effect observed was the adverse impact of livestock presence on serval occupancy. This may indicate habitat specialisation of serval, whereas the other small carnivores may be more adaptable to the presence of livestock and the conditions in their camps (predominantly Grassland). The lack of effect of black-backed jackal on the other small carnivore species may indicate that the densities of this canid are not high enough on the site to cause any considerable intraguild effects.

Clearly, modified landscapes such as the Sasol Synfuels Operations property have a role to play in biodiversity (including small carnivores) conservation. These areas may function as refugia in highly degraded and fragmented landscapes. As we move into the Anthropocene (Tucker *et al*. 2018) and sixth mass extinction (Ceballos *et al*. 2015), the outlook for many fauna, especially carnivores, is becoming increasingly dismal. Therefore, the value of modified landscapes in conserving these species and limiting biodiversity loss cannot be overlooked. More studies and biodiversity assessments on these areas, as well as the adaptability of species, communities and ecosystems found within them, are, therefore, necessary.

CHAPTER 3: A STUDY ON THE FEEDING BEHAVIOUR OF SMALL MAMMALS ON AN INDUSTRIAL SITE USING THE GIVING-UP DENSITY FRAMEWORK

3.1 Introduction

The current rate of landscape modification related to industrial development is greater than ever before (Laurance *et al*. 2015). Major impacts of such development include habitat degradation and fragmentation, pollution, soil erosion and the introduction of alien invasive species (e.g., Foley *et al*. 2005). These impacts result in large-scale biodiversity loss (e.g., Pauchard *et al*. 2006, Snep *et al*. 2011), including indigenous species declines and local extinctions (Pimm & Raven 2000). Large mammals, especially large carnivores, are the most severely affected and first to experience declines because of food (decrease in prey abundance) and habitat requirements, as well as human intolerance (Ripple *et al*. 2014). The decrease or absence of larger apex species minimises the related threat of intraguild competition and predation on small carnivores, allowing densities of these species to increase (e.g., mesopredator release; Ritchie & Johnson 2009). Under such conditions, it is possible for small carnivores to dominate industrial landscapes (see Chapter 2), affecting local predation processes.

Predation is one of the major forces that shape natural communities (Shochat *et al*. 2006). An increase in small carnivore numbers on an industrial site is expected to aggravate predation pressures on their small mammal prey. This will affect small mammals both directly (through predation) and indirectly (through the costs of behavioural changes or risk effects; e.g., Creel & Christianson 2008). Several meta-analyses have shown that prey population sizes and reproductive success can be directly suppressed by predation (top-down control) (Salo *et al.* 2010). Naïve prey populations are particularly susceptible to limitation by both native and introduced predators (e.g., Kavanagh 1988, Johnson 2006, Salo *et al.* 2007, Kovacs *et al*. 2012). Furthermore, Salo *et al.* (2010) found that under reduced predator densities, there was a positive and significant 1.7-fold effect on prey populations, indicating that most vertebrate predators seem to limit prey populations. Consequently, elevated rates of predation (hyperpredation) attributable to the irruption of small carnivores may result in small mammal declines (Smith & Quin 1996). Such declines can destabilise ecosystems and lead to local extinctions of prey, decreasing diversity (Prugh *et al.* 2009, Ritchie & Johnson 2009). However, for those small mammal species that thrive in disturbed conditions, densities may be so high that predation rates are unable to keep up with population increases, with prey escaping top-down regulation, i.e. prey hyperabundance (Fischer *et al*. 2012). In such a situation, the indirect effects of predation may be more apparent. For example, increased predator abundance and richness is likely to exacerbate the landscape of fear for small mammal prey (Mahlaba *et al*. 2017). In a landscape of fear, antipredator behavioural responses or risk effects are more apparent. These include changes in: i) habitat use (Creel *et al*. 2005); ii) vigilance (Childress & Lung 2003); iii) foraging (Lima & Bednekoff 1999); iv) aggregation (Boesch 1991); v) movement patterns (Fortin *et al*. 2005); and vi) sensitivity to environmental conditions (Winnie *et al*. 2006). In terms of foraging costs, an amplified landscape of fear should cause prey to sacrifice food for safety (Matassa & Trussell 2011).

The optimisation of foraging time is essential for any forager to compete and survive effectively, particularly under the risk of predation (Mahlaba *et al*. 2017). Foraging describes the process when an animal looks for food, defining where and what it chooses to consume (Bedoya-Perez *et al*. 2013). The giving-up density (GUD) framework is an experimental and mathematical approach used to quantitatively determine the foraging decisions of an animal in the wild based on patch characteristics. The framework is dependent on the existence of food patches as a depletable food source that foragers use differently to maximise fitness. Simply put, GUD is the amount of food left in a patch by foragers, indicating the apparent cost of foraging at that patch, such that a lower GUD reflects a lower net cost (Bedoya-Perez *et al*. 2013). Although initially developed to determine perceived predation risk while foraging, i.e. assuming that prey species will eat less when predation pressures are higher (Brown 1988, Brown *et al*. 1988, Kotler & Brown 1988), the framework has since been used to investigate other constituents of foraging behaviour.

Practically, the most common method of GUD framework implementation is to mix food with an inedible substrate in a replacement patch, leading to the search cost being directly proportional to the amount of food harvested. The amount of food remaining (GUD) is an indication of the composite costs associated with that type of food and the surrounding area – such as predation (Bedoya-Perez *et al*. 2013). Foragers can assess the risk of predation while foraging via indirect signs (e.g., foraging habitat, weather and light levels) or direct signs (such as predator urine) (Orrock 2004), facilitating a foraging decision.

In this study, I aimed to investigate perceived predation risk in an ecosystem where mesopredator release and habitat disturbance co-occurred. In disturbed habitats, it is not uncommon for highly adaptable plant and animal species (indigenous and alien) to flourish (Wood *et al*. 2003, Batty 2005). Regarding small mammals, disturbed landscapes can be highly productive (Williams *et al*. 2018), providing preferred structurally complex habitats with closed understories (Foster & Gaines 1991, Den Ouden & Smit 1997). For example, multimammate mice are considered pioneer species, responding well to disturbance, usually being the first small mammal species to colonise and then dominate areas in the early stages of regeneration after a disturbance event (Ferreira & van Aarde 1996). Landscape modification may result in the extent of disturbed habitat increasing significantly, providing the ideal conditions and resources necessary to sustain elevated densities of small mammals (McKinney 2006). Greater small mammal densities should, in theory, lead to increased local predator (such as small carnivores, and raptors) diversities and abundances (predator proliferation; Prugh *et al*. 2009).

A GUD framework was applied to investigate the extent to which predation pressure influences the predation risk of small mammals and if habitat type neutralises predation pressure. It was predicted that areas with relatively high small carnivore richness (a proxy for high predation pressure) would reduce small mammal foraging activity and increase their GUDs compared to those in areas with a relatively lower predation pressure. Additionally, it was predicted that in disturbed habitats with structurally complex vegetation (understory cover and height) foraging activity will be greater than in those with simpler and shorter vegetation, resulting in lower GUDs.

3.2 Methods

3.2.1 Study area

The study was conducted in the secondary area of the Sasol Synfuels Operations property situated alongside the town of Secunda (26° 33’S, 29° 10’E), Mpumalanga

(Figure 1). Approximately 3,000 ha in size (total size of the property is 8,445 ha), this is the land that surrounds the Sasol Synfuels plant (Matthews 2016). The secondary area is situated on the Highveld plateau at ~1,590 m above sea level, and its landscape is a mix of gentle and moderate undulations. This previously disturbed area supports a variety of short to medium-high, dense, tufted grasses. This Grassland vegetation is interrupted by scattered small Wetlands (man-made and natural), narrow stream alluvia (part of the upper catchment of the Waterval River), and occasional ridges or rocky outcrops (Matthews 2016). Mean annual precipitation of this summer rainfall (October to March) area is 772 mm (Burger 2013). The climate is cool-temperate with thermic continentality – high extremes between maximum summer and minimum winter temperatures, frost is common, and there are large thermic diurnal differences (Mucina & Rutherford 2006).

Initial mapping of the site classifies the property's landcover as follows: i) 4,042.7 ha (48%) transformed; ii) 2,350.2 ha (28%) degraded; iii) 1,920 ha (23%) untransformed; and iv) 132 ha (2%) water. Of the untransformed areas, 245.4 ha (3%) is classified as Wetland and 1,674.6 ha (20%) as dry land (Grassland) (Matthews 2016). The study area is located within the ecologically sensitive Soweto Highveld Grassland vegetation unit (classified as a vulnerable ecosystem; SANBI 2011), which is part of the Mesic Highveld Grassland Bioregion of the Grassland Biome (Mucina & Rutherford 2006). Broad plant communities of Soweto Highveld Grassland occurring in the secondary area include:

- *Themeda triandra – Cymbopogon pospischilii* relatively unspoiled grassland;
- *Setaria nigrirostris – Eragrostis plana* relatively unspoiled moist grassland;
- *Hyparrhenia tamba – Verbena bonariensis* relatively disturbed tall grassland;

- *Schkuhria pinnata* – *Aristida bipartita* disturbed grassland; and
- *Bidens pilosa* – *Cosmos bipinnatus*[9] transformed disturbed flats and floodplains (Matthews 2016).

The indigenous common reed dominates the area's Wetlands. Scattered amongst the site's vegetation is various industrial infrastructure including roads, process water dams, ash heaps and powerline pylons. The Sasol Synfuels Operations property is surrounded by urban and semi-urban settlements, as well as agricultural land. As a National Keypoint[10], the property is highly secure, with strict access control measures in place. Consequently, there is minimal human activity in the secondary area.

3.2.2 Giving-up density experiment

Four sites were selected for the GUD experiment, two high-predation and two low-predation sites (Figure 10a). Two prerequisites were required for these sites to be selected. Firstly, all had to have a mosaic of three vegetation treatments (high ≥1 m, medium ≤0,5 m and low ≤0,3 m cover; Figures 11, 12 & 13). Secondly, the high-predation sites needed to be in an area of high small carnivore species richness, while the low-predation sites needed to be in an area of lower small carnivore species richness. High- and low-predation sites were, as a result, classified according to estimated spatially explicit species richness (i.e. small carnivore species richness was used as a proxy for predation pressure; see Section 2.2.3.2; Figures 3 & 10).

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[9] Naturalised alien invasive plant species (Bromilow 2010).
[10] A site of national strategic importance.

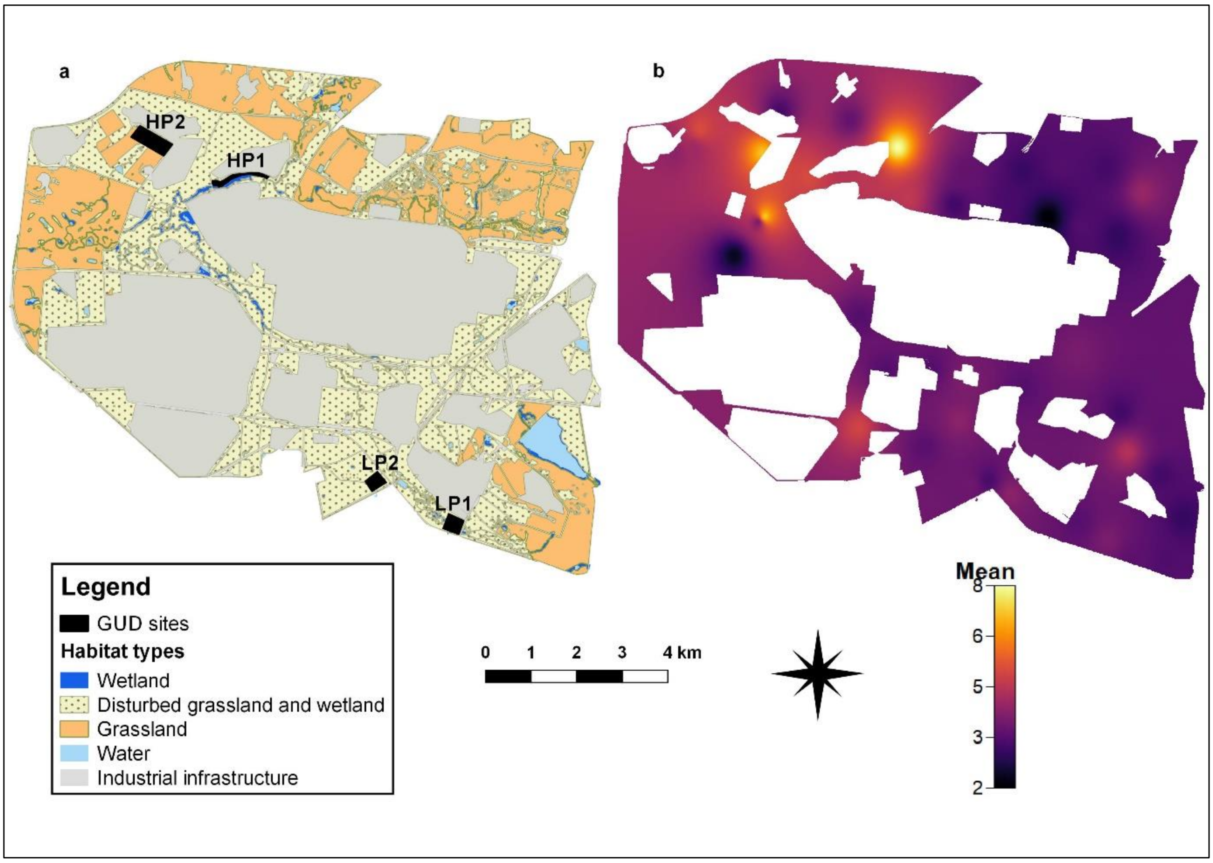

Figure 10. a) Map showing the Sasol Synfuels Operations property and the GUD site (high- [HP] and low-predation [LP]) locations in its secondary area; and b) map showing the mean small carnivore species richness across the study area.

Figure 11. High vegetation treatment. Dominated by the common reed, cosmos and black-jack.

Figure 12. Medium vegetation treatment. Dominated by grasses, forbs and invasives.

Figure 13. Low vegetation treatment. Dominated by grasses and forbs.

3.2.2.1 *Pilot study*

The experiment was calibrated prior to its initiation by means of a pilot study. Different feeds including peanuts, sorghum, linseed, pumpkin seed, sunflower seed and almonds were mixed with 1,5 litres of local sieved sand in round plastic trays 3,5 cm deep and 35 cm in diameter (Figure 14). These feeding trays[11] were put out in the study area from 21 to 26 January 2016 to determine which feed would be the most efficient for the research. During the pilot study, small mammal activity was highest at the trays containing sunflower seed. Therefore, this feed was selected for the remainder of the experiment. Rodent feeding activity at the trays was confirmed by placing Reconyx™ Hyperfire™ HC600 camera traps (black flash) at each of the trays (Figures 14 & 15).

Figure 12. Plastic tray with sieved sand and feed mix, and Reconyx™ Hyperfire™ HC600 camera trap.

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[11] From now on also referred to as artificial feeding stations.

Figure 13. Multimammate mouse at an artificial feeding station during the pilot studies.

3.2.2.2 *Giving-up density experiment implementation*

At the centre of each vegetation treatment (in the high- and low-predation sites), three pairs of plastic feeding trays (35 x 35 x 3,5 cm) were placed in a triangular pattern (Figure 16), with a distance of approximately 10 m between each pair and a distance of ~1 m between the two trays in a pair (Mohr *et al.* 2003). An artificial canopy was erected over one tray in each pair. The canopies were constructed using wooden poles, sackcloth and wire 30 cm above the ground (Figure 17). The hypothesis behind the erection of the canopies was that the additional cover provided would exclude avian predators and result in lower GUDs at the respective feeding stations (in all vegetation treatments at all sites). The short distance between the two trays ensured that the surrounding conditions (for example, environment, vegetation/cover, food availability, rodent density and weather conditions) were similar for both trays in a pair. Camera traps (36) were placed at one tray in each pair, with placement alternating between those with an artificial canopy and those without. The cameras were used to identify small mammal species foraging at the artificial feeding stations.

The feeding trays (72 in total) were put out from 4 to 6 May (early winter) and 8 to 10 June (mid-winter) 2016 or 6 days/432 combined GUD nights and 720 GUDs (Table 3). 1,5 litres of substrate (local sieved sand) was mixed with 50 sunflower seeds and placed in the feeding trays at sunrise. Feeding trays were then checked for signs of foraging before sunset in order to obtain data for diurnal small mammal species. If signs of foraging were detected, the contents of the relevant trays were then emptied into plastic bags that were marked with the respective tray's number (for example, high-predation site 1 high-vegetation site1 – H1H1). The contents of these bags were sieved later that morning and the remaining sunflower seeds counted to determine the GUD. Once emptied for processing, feeding trays were refilled with the substrate-seed mix and left overnight. The feeding trays were then rechecked the following morning before sunrise to obtain data for nocturnal species, and the above sieving and counting process repeated to determine the GUDs.

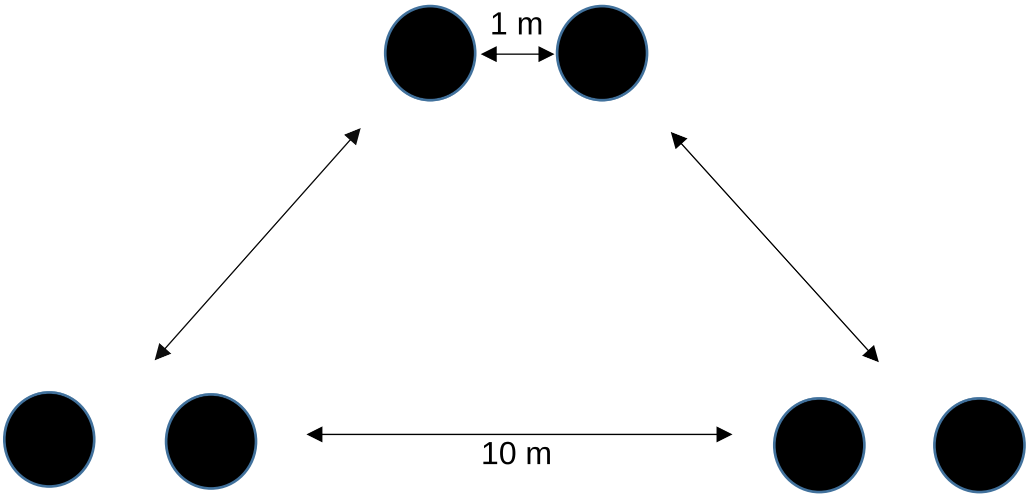

Figure 14. Artificial feeding station layout within vegetation treatments.

Figure 15. Feeding station with artificial canopy.

Table 3. GUD effort per survey.

GUD survey	Dates	GUD days	Total GUDs
Early winter	4 – 6 May 2016	3	360
Mid-winter	8 – 10 June 2016	3	360

3.2.3 Statistical analyses

Generalised linear mixed model (GLMM) were used to examine response in the levels of GUDs to different predation pressures (high and low) and vegetative treatments (high, medium and low cover; Figures 10, 11, 12 & 13). At first, a global model was constructed and fitted to a generalised linear mixed-effects model with a negative binomial distribution. This was used to assess if there was overdispersal in the data. The negative binomial dispersion parameter was estimated as $\alpha = 2.3953$ (SE = 0.4679), which suggests data were overdispersed (Poisson distribution $\alpha = 0$). We, therefore, fitted GUD to a negative binomial distribution using the glmmADMB package for R (R Core Team 2017, Skaug *et al*. 2012). For the GUD GLMMs, only the GUDs from artificial feeding stations that registered any feeding activity (for example, none of the feeding stations within any of the low vegetation treatments registered any feeding activity, i.e. the mean GUD was 50) were included, as well as one variable as a fixed effect, i.e. vegetative treatment. This was done because small mammal trapping studies within the study area failed to detect any significant small mammal populations in the areas with no feeding activity (e.g., areas covered with short grasses and forbs; Swanepoel and Keith 2016). For all models, site (*pred.rep*) was included as a random variable. Sites were classified as being under either a high- or low-predation pressure, based on the species richness of the study area (Figure 10), i.e. if the site is located where there is a relatively high estimated small carnivore species richness, then predation pressure is also assumed to be high. The opposite is true for sites located where a low species richness was estimated.

11 generalised linear mixed models (GLMM) were then constructed based on the following biological hypotheses. Firstly (model 1), I hypothesised that vegetation height (which translates to available cover, i.e. high, medium or low) would influence GUDs, with individuals expected to consume more food at sites with a greater vegetative cover (Kotler & Blaustein 1995, Keesing 1998, Colman *et al*. 2014). Secondly (model 2), I hypothesised that predation pressure (high or low) would influence GUDs, with individuals expected to consume more food at sites with low predation pressure. In this model, small carnivore species richness was used as a proxy for predation pressure. Thirdly (model 3), it was hypothesised that the combination of predation pressure and vegetation height (cover) would influence GUDs. For example, sites with a low predation pressure and high or medium vegetation height were expected to have lower GUDs than those with a high predation pressure and low vegetation height. Fourthly (model 4), I hypothesised that GUDs would be influenced by differences in

feeding behaviour and activity patterns of nocturnal or diurnal small mammals and small carnivores, respectively. Fifthly (model 5), it was hypothesised that the feeding trays with artificial canopies would have lower GUDs than those without artificial cover. Sixthly (model 6), I hypothesised that GUDs would be lower at sites with a combination of natural (vegetative) and artificial cover than those with only natural cover. Seventhly (model 7), it was hypothesised that the additional cover provided by artificial canopies would enhance the amount of food consumed by both diurnal and nocturnal small mammal species (i.e. GUDs at covered sites would be lower during the day and night). Eighthly (model 8), I hypothesised that the feeding behaviour of both diurnal and nocturnal small mammal species would be positively correlated with vegetation height (natural cover), resulting in lower GUDs at sites with more vegetative cover (medium and high vegetation treatments). Ninthly (model 9), it was hypothesised that GUDs would differ temporally between the two surveys (early and mid-winter), with GUDs being lower in mid-winter as natural food supplies decrease and metabolic requirements of small mammals increase. Tenthly (model 10), I hypothesised that the availability of natural cover (vegetation height) together with diurnal or nocturnal feeding behaviour and the timing of the survey (i.e. early or mid-winter) would influence GUDs. Lastly (model 11), it was hypothesised that temporal differences between the two surveys would influence the feeding behaviour of diurnal and nocturnal species. The greater difference between day- and night time temperatures in mid- compared to early winter may result in the metabolic requirements of nocturnal species being greater than that of diurnal species. Consequently, the GUDs of nocturnal species would be lower than those of diurnal species.

The full model is, therefore, represented by the following formula:

GUD ~ Vegetation height (cover) + Predation pressure + Predation pressure: Vegetation height + Day or Night + Artificial cover + Artificial cover : Vegetation height + Artificial cover : Day or Night + Day or Night : Vegetation Height : Survey time (early or mid-winter) + Day or Night : Survey Time

The models were then ranked using AICc and estimated model weights for each variable. To determine variable importance, AICc weights were summed for each variable in a model. The most parsimonious model was then used to calculate predicted estimates for activity and GUDs (using the predict command in the AICcmodavg package; Mazerolle & Mazerolle 2016). Treatments with beta estimates (β) and 95% Confidence Intervals that did not include 0 were considered to be significantly different from the reference category.

3.3 Results

3.3.1 Small mammal trapping

Small mammal trapping has been conducted biannually on the site in summer and winter since 2014. Species composition in terms of biomass was dominated by two species, multimammate mouse (*Mastomys* sp.) and four-striped grass mouse (*Rhabdomys* sp.), comprising 45 and 50% of captures respectively. Trapping results indicated biomass values (kg.ha^{-1}) of 1.75 for four-striped grass mouse and 1.32 for multimammate mouse in 2016 (Swanepoel *et al*. 2017). Other species were captured less frequently. These include: climbing mouse (*Dendromus* sp.), pygmy mouse (*Mus minutoides*), vlei rat (*Otomys* sp.), musk shrew (*Crocidura* sp.) and single-striped grass mouse (*Lemniscomys rosalia*); Swanepoel *et al*. 2017).

During GUD experiment implementation, the results of the small mammal trapping surveys were reaffirmed by camera trap photos from the artificial feeding stations, with multimammate mouse (nocturnal; Figure 15) and four-striped grass mouse (diurnal; Figure 18) being captured most frequently. Of the small mammal photographs captured by the camera traps during GUD implementation, 62.2% were of multimammate mouse, 33.6% of four-striped grass mouse, 2.5% vlei rat and 1.7% of musk shrew.

Figure 16. Camera trap photo of a four-striped grass mouse at an artificial feeding station.

3.3.2 Giving-up densities

Model results showed little support for several main variables or the interaction of variables on the GUDs (Table 4; Figure 19). The most significant variables seem to be *daynight* (ω = 1; Table 4; Figure 19) and *survey* (ω = 0.91; Table 4; Figure 20), suggesting that these two variables had the greatest influence on the variation in GUDs. GUD's in May (β = 0.1933, SE = 0.0695, p = 0.0054) were significantly higher than those for June (Figure 21), while evening GUD's (PM; $\beta = 0.3311$, SE = 0.0693, p = 0.000) were higher than those measured in the mornings (AM; Figure 21). These results indicate a difference in feeding behaviour between the two survey periods and between nocturnal (primarily multimammate mouse) and diurnal (primarily four-striped grass mouse) small mammal species.

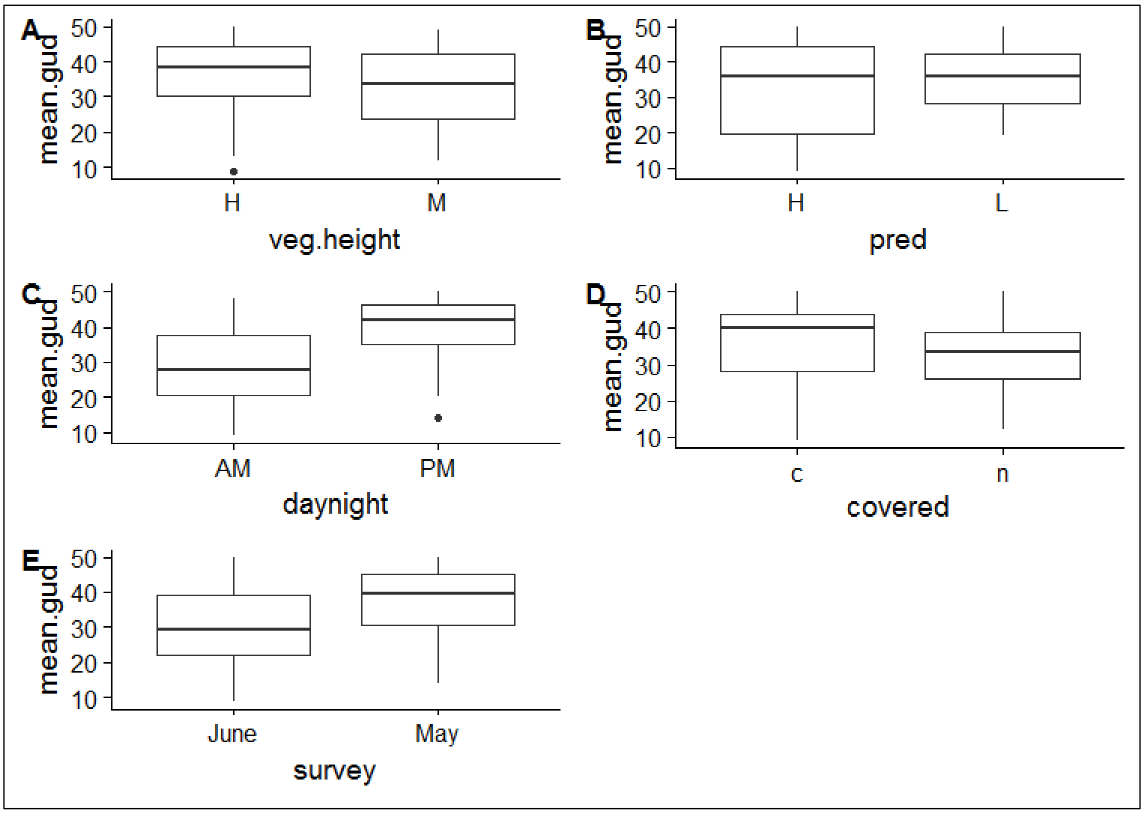

Figure 17. Main effect models fitted to GUD data: A (model 1, vegetation height – high [H] and medium [M]), B (model 2, predation pressure – high [H] and low [L]), C (model 4, day [PM] or night [AM]), D (model 5, artificial cover – covered [c] and not covered [n]), E (model 9, survey).

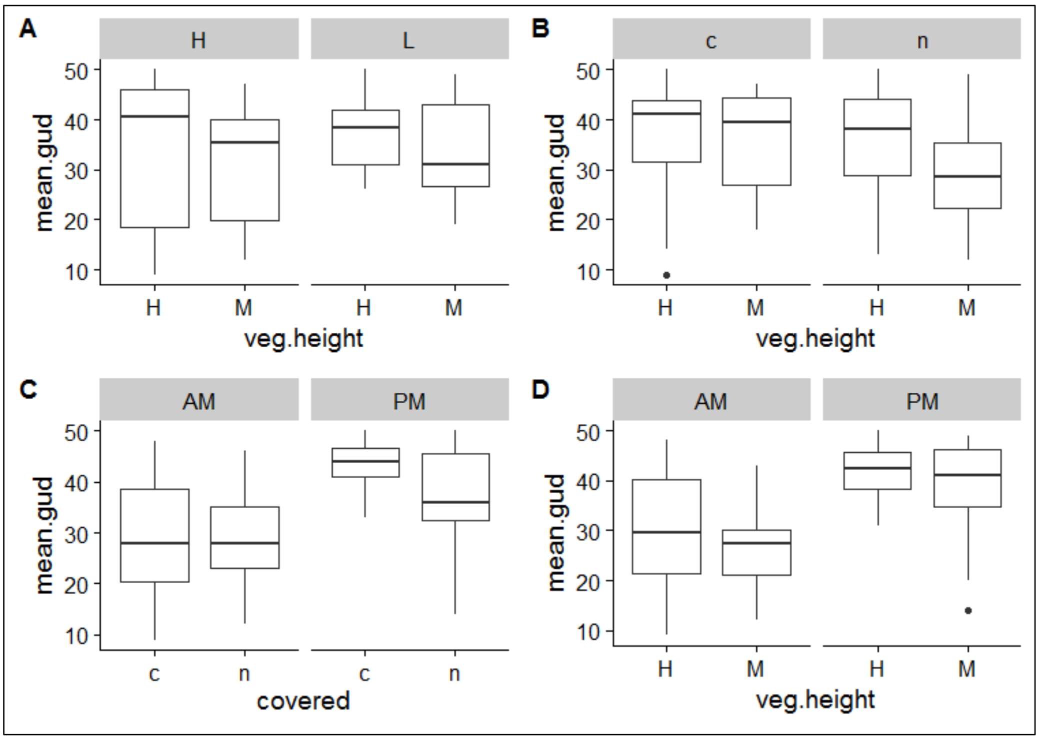

Figure 18. Interaction models fitted to GUDS: A (model 3; predation pressure – high [H] and low [L] – and vegetation height – high [H] and medium [M]), B (model 6; artificial canopy – covered [c] and not covered [n] – and vegetation height – high [H] and medium [M]), C (model 7; night [AM] or day [PM] and artificial canopy – covered [c] and not covered [n]) and D (model 8; night [AM] or day [PM] and vegetation height – high [H] and medium [M]).

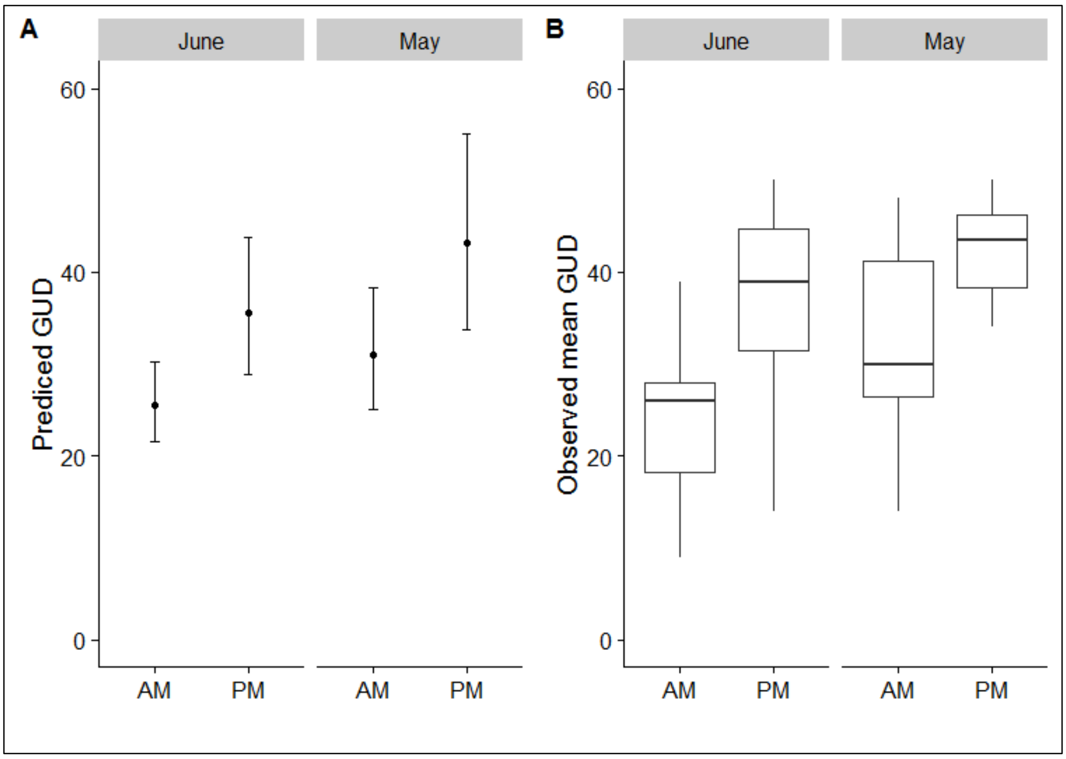

Figure 19. Plots of the: A) predicted; and B) observed small mammal GUDs (mean, upper and lower quartiles) across the four sites (three vegetative treatments per site) of this study averaged over three morning (AM – representing nocturnal GUDs) and evening (PM – representing diurnal GUDs) sampling sessions in early (May) and mid-winter (June) in 2016.

Table 4. Summary of model outputs and weights, as well as the rank of the variables' effects on GUDs (in isolation and when interacting).

		Variable/s													
Model	**Intercept**	**Veg.height**	**Pred.**	**Pred: veg.height**	**Daynight**	**Covered**	**Covered: veg.height**	**Covered: daynight**	**Daynight: veg.height**	**Survey**	**df**	**logLik**	**AICc**	**Delta**	**Weight**
Mod11	3.24				***					**	5	-218.525	448.161	0	0.488
Mod10	3.3	+			***					**	6	-217.431	448.447	0.286	0.423
Mod4	3.348				+						4	-222.272	453.271	5.11	0.038
Mod7	3.345				+	+		+			6	-219.9	453.385	5.224	0.036
Mod8	3.403	+			+				+		6	-220.826	455.237	7.076	0.014
Mod9	3.415									+	4	-228.262	465.251	17.09	0
Mod1	3.591	+									4	-230.09	468.907	20.746	0
Mod5	3.579					+					4	-230.334	469.395	21.243	0
Mod2	3.459		+								4	-230.757	470.241	22.08	0
Mod6	3.597	+				+	+				6	-228.683	470.951	22.79	0
Mod3	3.527	+	+	+							6	-229.804	473.193	25.032	0
	No. of models	5	2	1	5	3	1	1	1	3					
	Importance	0.44	0	0	1	0.04	0	0.04	0.01	0.91					

Key: "+" represents a positive but not significant effect; "**" represents a significant effect; and "***" represents a highly significant effect.

3.4 Discussion

Daynight and *survey* period were found to have significant effects on small mammal GUD's in the study area. Neither predation pressure (aligned with the findings of Mohr *et al*. 2003) or vegetation treatment (high or medium cover) significantly affected the GUDs.

The lower GUDs left by the nocturnal small mammals (predominantly multimammate mice) compared with diurnal species (mainly four-striped grass mice) suggest that nocturnal species experience lower predation pressures. This is interesting since serval diet studies at the study area (Ravhuanzwo *et al*. 2017; Figure 22) indicated relatively higher predation on multimammate mice, which is expected to have resulted in relatively higher nocturnal GUDs. Furthermore, small mammal trapping results suggested a higher density of diurnal species (four-striped grass mouse) in the study area (Swanepoel & Keith 2016), which I would expect to lead to greater interspecific competition for resources and, consequently, lower GUDs. It may be the case that multimammate mice are more active during the hours of the night when there is relatively little predator activity (Figure 23), decreasing the potential risk of predation and allowing more foraging time. However, their greater frequency in serval diet relative to four-striped grass mouse discounts this (Figure 22; Ravhuanzwo *et al*. 2017). So, it is unlikely that peaks in multimammate mice foraging activity correspond with troughs in serval activity. The effect of a landscape of fear on the foraging behaviour of multimammate mice may not be as strong as it is on four-striped grass mice. In such a situation, multimammate mice would be willing to forage under predation pressures where four-striped grass mouse activity would be limited, resulting in lower GUDs. A greater risk taken by multimammate mice would also explain why they are preyed on more than four-striped grass mouse by serval (Figure 22). Conversely, four-striped grass mice may be active during the hours of the day when there is more diurnal predator activity relative to nocturnal predator activity (Figure 23), resulting in a more considerable perceived risk of predation (landscape of fear), which is expected to decrease foraging time leading to higher GUDs. This hypothesis is supported by camera trap data collected during GUD implementation, which indicates that multimammate mice were more active at feeding stations than four-striped grass mice (62.2 and 33.6% of captures respectively).

Alternative hypotheses include, firstly, that relatively lower predator activity levels during the night may have lowered the risk of predation for nocturnal species (such as multimammate mice). However, an analysis of predator activity on the site using camera trap survey results (Chapter 2) indicates that this is not the case (Figure 23). Conversely, the analysis shows that the two most abundant predators in the study area, serval and black-backed jackal, are mostly active between sunset and sunrise. These two species are, however, still active during periods of the daytime together with many other crepuscular and diurnal predators (including small carnivores, birds of prey and snakes; Figure 23). The result may be a higher perceived risk of predation, creating a landscape of fear with a stronger influence, limiting the foraging behaviour of diurnal small mammals, thereby leading to higher GUDs. Whether or not this observation holds true for the study area is debatable, as previous studies have found that the impacts of multiple predators are usually not additive because of compensatory prey defences and predator competition, which results in interference (Sih *et al*. 1998, Schmitz 2007). Finally, there is possibly a difference in metabolic demands between diurnal and nocturnal species attributable to day and night temperature differences. Studies have found that small mammals increase their food intake when exposed to colder temperatures (Speakman 2003). Since the average body weights of the most abundant nocturnal (multimammate mouse; 36.4 g) and diurnal (four-striped grass mouse; 43.1 g) are similar (Kingdon & Hoffmann 2012), metabolic rates should be comparable in the same conditions. Therefore, nocturnal species, which are exposed to colder temperatures than diurnal species, are expected to consume more food resulting in lower GUDs.

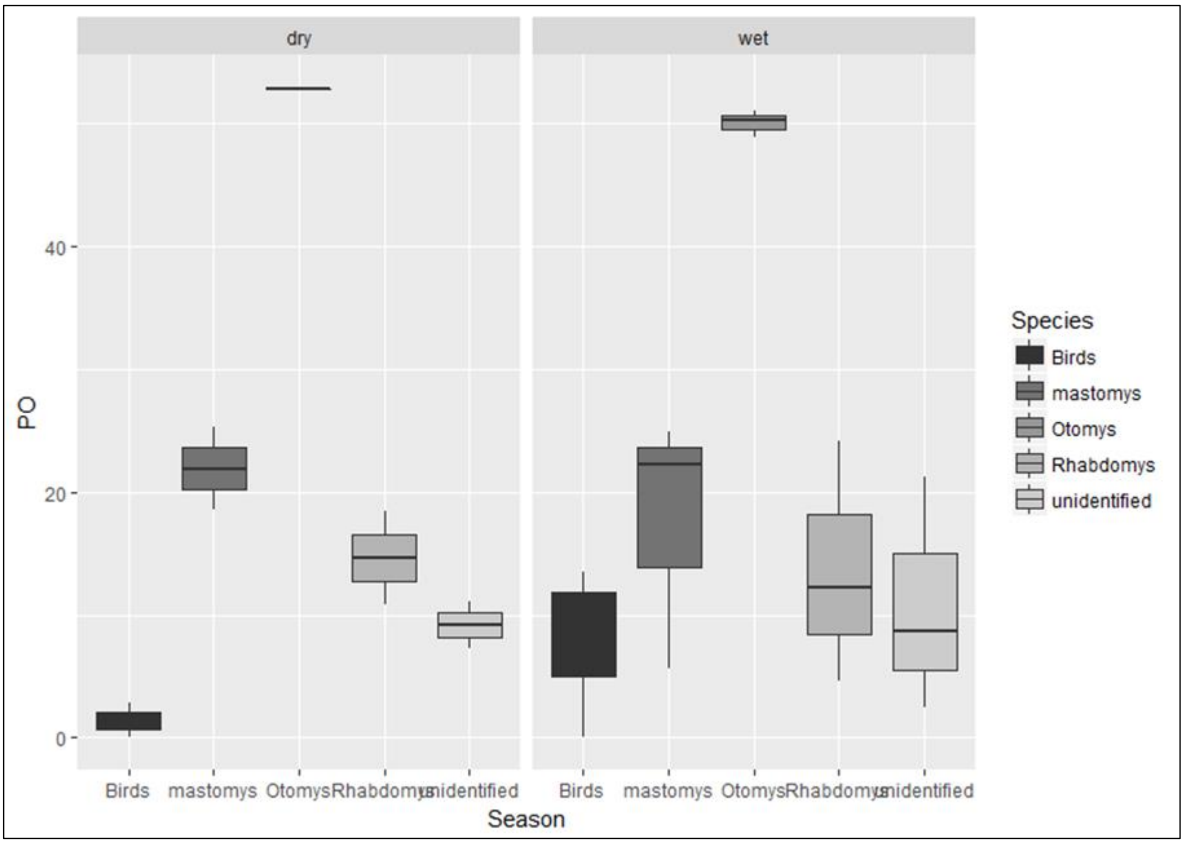

Figure 20. Diet of serval in the study area during the dry and wet seasons (Ravhuanzwo *et al*. 2017).

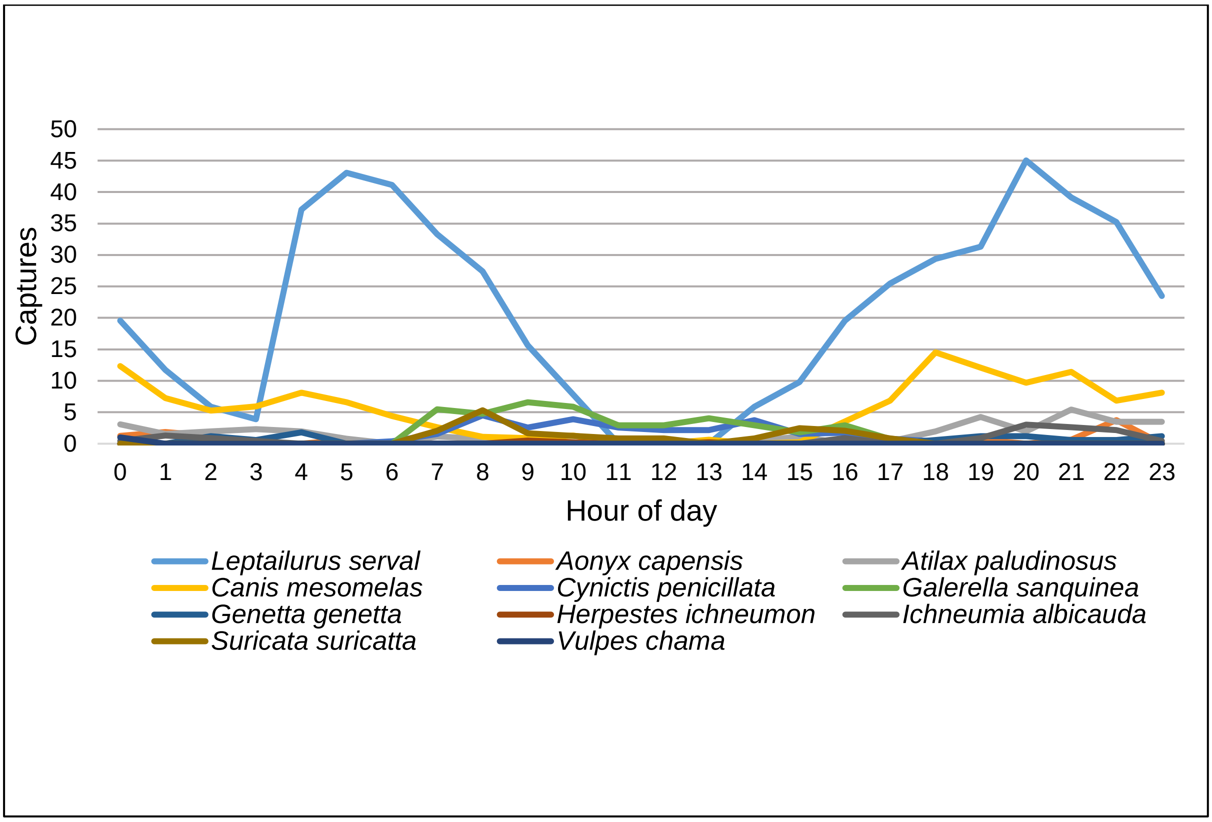

Figure 21. Activity patterns (based on camera trap detections; Chapter 2) of small carnivores detected in the study area.

Differences in the mean GUDs between early (May) and mid-winter (June; *survey*) may be attributable to a relative decrease in the availability of natural food resources by mid-winter, resulting in greater competition for that (sunflower seed) which was available during GUD experiment implementation. Furthermore, the colder temperatures in mid-winter may have resulted in an increase in small mammal metabolic requirements, causing individuals to consume more food (Speakman 2003). Apart from a decrease in food resources by mid-winter, the location of the site in a summer rainfall region means that water resources would also be limited, more so by midwinter. A reduced supply of water and other resources may have resulted in an increase in intra- and interspecific competition between and the subsequent the dispersal of predators (particularly generalist species). Reduced predator abundances in the study area could have led to a decline in predation pressure and perceived risk, allowing small mammals to allocate more time to foraging and contributing to lower GUDs in mid-winter. Nevertheless, a comparison of camera trap captures of carnivores in the study during autumn and winter (Chapter 2) does not support this, with differences in captures of the most abundant species (serval and black-backed jackal) between these periods being insignificant (Figure 24). Indeed, serval were detected more frequently in winter than in autumn, but the difference is not significant.

Contrary to the hypotheses, I observed that small mammal GUDs in the study area were not significantly influenced by vegetation treatment (cover) or predation pressure. Based on the GUD data obtained from the different vegetation treatments in the high- and low-predation pressure sites, small mammal foraging activity was shown to be similar: i) in high and medium vegetation treatments; and ii) under high- and low-predation pressures.

The lack of understory cover in the low vegetation treatment meant that the apparent risk of predation at these sites (from both small carnivores and avian predators) was amplified. It is likely that the risk presented by this exposure (together with the absence of a suitable microclimate) far outweighed benefits of foraging in this treatment, even where artificial canopies had been erected. So, in landscapes where humans have removed understory vegetation (through clearing, mowing, fire or the introduction of livestock), it is expected that small mammal activity will be minimal if not completely absent (Keesing 1998).

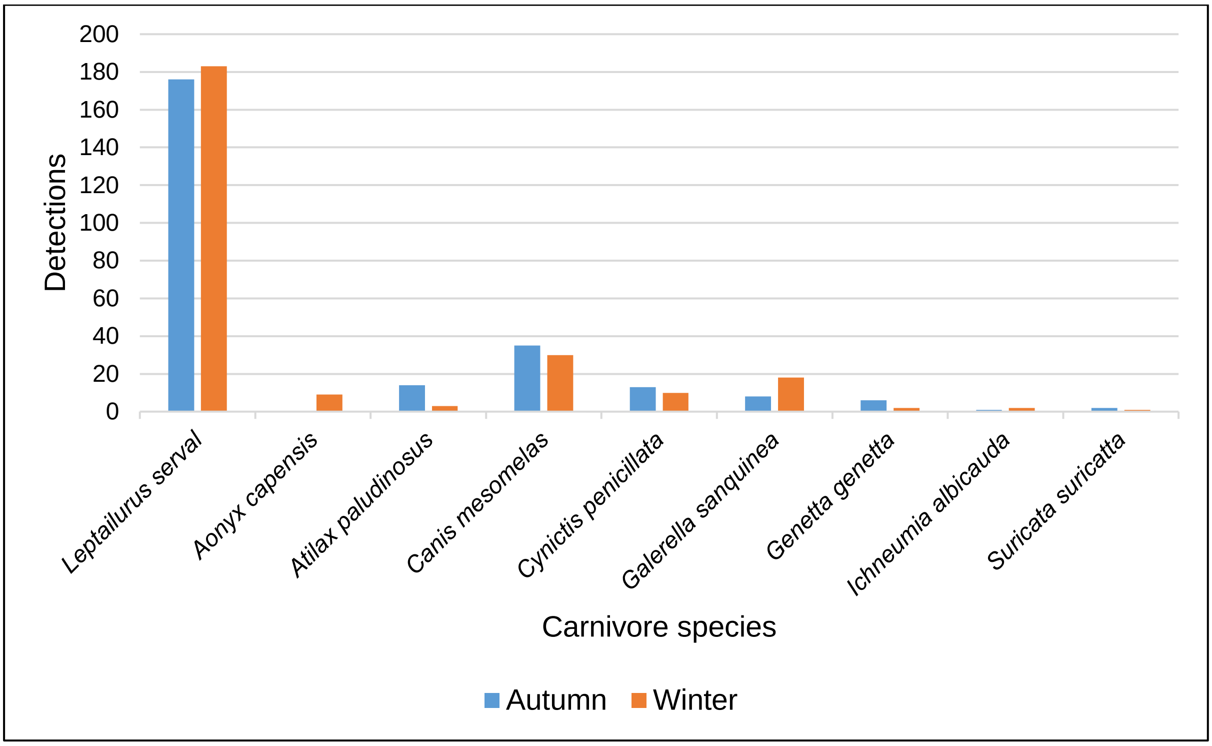

Figure 22. Comparison of number of small carnivore camera trap detections in the study area during the autumn and winter surveys (Chapter 2; *Herpestes ichneumon* and *Vulpes chama* are excluded as both were only detected once, during the autumn survey).

Regarding the similar GUDs in the high and medium vegetation treatments, although the heights of these treatments differed, the understory cover was structurally complex in both. In some instances, understory cover was more complex in the medium treatment. This is indicated by the slightly lower mean GUDs, but these differences are largely insignificant. The closed understories of the high and medium treatments provided the ideal conditions for small mammals (such as decreased predation risk and abundant food; Hansson 1978, Kotler & Blaustein 1995) minimising the potential effects of a landscape of fear and resulting in low GUDs (sometimes as low as zero).

The ideal habitat provided by the closed understories in the high and medium vegetation treatments may support high densities of small mammals, resulting in heightened competition for food resources. This competition may have contributed to the relatively low GUDs and outweighed the effects of predation risk in these treatments. Further factors associated with closed understories that may have contributed to the GUDs in these treatments include: i) the potential exclusion of certain predators (such as owls); ii) early warnings of approaching small carnivores through the sound of movement in the thick vegetation; and iii) easy access to nearby cover in the event of a predator attacking.

Contrary to the prediction, differences between mean GUDs under high- and low-predation pressures were insignificant. Apart from the abovementioned factors related to predation (and cover), additional potential reasons are outlined below. Prey specialisation by predators (such as serval favouring vlei rat; Figure 22) may lead to decreased predation pressures on and less competition with other potential prey species (such as multimammate mouse), resulting in more time available for foraging. In addition, the landscape of fear created in the areas of high-predation pressure may have had minimal impacts on certain small mammal prey species (such as multimammate mouse and four-striped grass mouse). Several hypotheses may explain this. Firstly, a number of studies suggest that fearfulness and mortality due to predation are lower in developed areas – a phenomenon known as predation relaxation (Gering & Blair 1999, Shochat *et al.* 2006, Stracey 2011). Secondly, with the relatively high abundance of small mammal predators in the study area, there must be a hyperabundance of prey or the per capita prey consumption must be extremely low to explain the lack of observed response to predation pressure (Fischer *et al.* 2012). This hypothesis is supported by the high small mammal densities recorded on the Sasol Synfuels Operations property by Swanepoel and Keith (2016). The competition for resources related to such high densities, for example, may mask the effects of predation pressure on small mammal foraging behaviour (Mohr *et al*. 2003).

Thirdly, predators in the study area may be targeting more vulnerable prey species (prey specialisation; Roth & Lima 2003) that are less adapted to the disturbed habitats on the industrial site (such as serval targeting vlei rat), allowing more adapted species (such as multimammate mice) to escape predation (lower predation pressure) and reducing competition for resources, allowing them to spend more time foraging. Only 2.5% of camera trap captures at the feeding stations were of vlei rat, while 62.2% were of multimammate mouse, suggesting a stronger effect of predation/landscape of fear on the former, and a more relaxed feeding behaviour of the latter. Fourthly, the predators on the industrialised site may have already eradicated most of the small mammal prey species that were vulnerable to predation (such as vlei rat), leaving higher densities of species more adapted to predators, further masking the effects of predation pressure (Shochat 2004). Finally, a high carnivore species richness may not necessarily result in increased predation pressure. Conversely, the impacts of multiple predators are usually not additive because of compensatory prey defences and predator competition, leading to interference (Sih *et al.* 1998, Schmitz 2007). This type of interference may have led to similar predation pressures over the high- and low-predation sites, accounting for the similar mean GUDs.

3.6 Conclusion

The feeding behaviour of small mammals is expected to be influenced by perceived predation pressure (landscape of fear) and habitat characteristics. Habitat disturbances related to the modification of landscapes often result in a change in plant and animal community structure. In many instances, certain species of small mammal can thrive in these disturbed habitats, reaching densities that attract high abundances and diversities of predators, such as small carnivores. Using the GUD framework, an attempted was made to measure the effects of varying predation pressures on small mammal foraging behaviour on the highly industrialised Sasol Synfuels Operations property in Secunda.

The findings of the study indicated interspecies (multimammate and four-striped grass mice) differences in foraging behaviour under similar predation pressures and habitat conditions. Interestingly, GUDs between high- and low-predation areas did not differ significantly, highlighting the lack of effect of this variable, even in habitats where small carnivore detection and occupancy probabilities, as well as species richness, were relatively high. Small mammal trapping surveys across the study area found high densities of four-striped grass mouse (highest; diurnal) and multimammate mice (second highest; nocturnal) in the high and medium vegetation treatments of the study. It is suspected that the GUD results are strongly aligned with these high densities (and the competition associated with them), masking the effects of a landscape of fear in a high-predation area on small mammal foraging behaviour.

Unexpectedly, GUDs for nocturnal species (predominantly multimammate mouse) were lower than those for diurnal species (mainly four-striped grass mouse), highlighting that small mammal density is not the primary factor influencing GUDs in this disturbed environment. It is unclear what the exact reasons for this are, but they may include differences in diurnal and nocturnal predator activity and interspecies differences in foraging behaviour and metabolic requirements. GUDs also differed between surveys, with values being lower in mid- compared to early winter. This may be attributable to a decreased availability of natural food sources, as well as greater metabolic requirements in the colder conditions.

Ultimately, the results of my study highlight the ecological adaptability of some small mammal species (in this case multimammate mouse and four-striped grass mouse). Provided that certain habitat conditions are met (such as understory cover and food), these species can thrive in disturbed environments under varying predation pressures. There are still many questions surrounding the ecological processes and dynamics of small mammal species and their predators within modified landscapes. With many of these areas being easily accessible, researchers are presented with ecological laboratories where further long-term studies based on these questions should be implemented.

CHAPTER 4: CONCLUSION

Studies related to the conservation value of human-modified landscapes – including industrial sites – are few and far between compared to those focusing on the biodiversity loss observed in these areas. In some cases, changes in habitat structure and species assemblages may lead to conditions where highly adaptable species are able to thrive. Such species include small carnivores, which have the capacity to adapt disturbed habitats that provide suitable conditions such as cover and food (e.g., small mammals), as well as being devoid of larger carnivore species – as a consequence of persecutions or habitat restrictions. A rise in the density and diversity of small carnivores may, however, result in negative effects on their prey – including small mammals – because of the increased predation pressure and the associated landscape of fear.

During this research project, the occupancy and diversity of small carnivores across the various habitats (disturbed Grassland and Wetland, Grassland and Wetland) of the secondary area of the highly disturbed Sasol Synfuels Operations property in Secunda, Mpumalanga were studied using data collected via three camera trap surveys conducted between August 2014 and July 2015. The results of this study were then used as a proxy for predation pressure across the research area, the effects of which on small mammal feeding behaviour in different vegetation treatments (high, medium and low cover), were measured using the GUD framework.

11 small carnivore species were detected within the study area (including serval) with species richness and occupancy being highest in disturbed Grassland and Wetland and marginally lower in Grassland. It is expected that these results are attributable to

abundant small mammal prey, dense vegetative cover, limited disturbance by livestock (relatively low stocking rate) and minimal encounters with humans in the disturbed habitats, and disturbance by livestock (relatively high stocking rate), lack of vegetative cover, low small mammal prey densities and more frequent encounters with humans in the Grassland habitats.

The results of the GUD study indicated differences in foraging behaviour between the site's dominant nocturnal – multimammate mouse; lower GUDs – and diurnal – four-striped grass mouse; higher GUDs – small mammal species under similar perceived predation pressures and habitat conditions. Reasons for this are not entirely clear but may include differences in foraging behaviours and metabolic requirements, as well as temporal variations in predator activity between day and night. There was minimal significant difference between GUDs recorded at high- and low-predation areas, with the variable having a limited effect on small mammal foraging behaviour in high and medium vegetation treatments in both. It is suspected that this is linked to the high densities of small mammals present in these vegetation treatments, which result in increased inter- and intraspecies competition for food resources, negating the expected impacts of a landscape of fear on foraging behaviour, at least in the case of the two dominant species.

The results of this study provide evidence supporting the argument that human-modified landscapes such as the Sasol Synfuels Operations site have a role to play in the conservation of biodiversity – including endangered species. However, this observation should not be misinterpreted as supporting the deliberate disturbance of unspoilt natural habitats but rather promoting studies on the potential of already transformed landscapes in biodiversity conservation instead of simply writing them off as lost. Many of the species thriving in these areas – such as small carnivores and small mammals – are able to adapt to highly disturbed environments, even in the face of many threats (such as predation) provided that certain habitat characteristics are met. The accessibility of many such areas provides an excellent opportunity to study the ecological processes and dynamics of human-modified landscapes, allowing for long-term research to be conducted and informed conservation management decisions to be made.

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APPENDIXES

Appendix A: Detections and photos per small carnivore species

Table A 1. Detections and photos per carnivore species during each survey.

	Detections				**Photos**			
Small carnivore species	**Summer 2014**	**Autumn 2015**	**Winter 2015**	**Total**	**Summer 2014**	**Autumn 2015**	**Winter 2015**	**Total**
African clawless otter	0	1	9	10	0	5	24	29
Black-backed jackal	65	35	30	130	363	213	112	688
Cape fox	0	1	0	1	0	1	0	1
Large-grey mongoose	0	1	0	1	0	1	0	1
Serval	152	176	183	511	1,110	1,005	1,706	3,821
Slender mongoose	15	8	18	41	88	46	67	201
Small spotted genet	1	6	2	9	2	17	6	25
Suricate	15	2	1	18	88	36	42	166
Water mongoose	21	14	3	38	96	95	7	198
White-tailed mongoose	10	1	2	13	64	1	6	71
Yellow mongoose	5	13	10	28	34	112	58	204

Appendix B: Camera trap photos of all species detected

Figure B 1. Camera trap photo of serval on the Sasol Synfuels Operations property.

Figure B 2. Camera trap photos of other carnivore species captured on the Sasol Synfuels Property in Secunda: a) *Genetta genetta*; b) *Herpestes ichneumon*; c) *Aonyx capensis*; d) *Galerella sanquinea*; e) *Suricata suricatta*; f) *Atilax paludinosus*; g) *Ichneumia albicauda*; h) *Cynictis penicillata*; i) *Canis mesomelas*; and j) *Vulpes chama*.

Appendix C: Species detected during camera trap surveys

Table C1. List of species detected during camera trap surveys.

Common name	Species	Status
Carnivores	**13**	
African clawless otter	*Aonxy capensis*	Near threatened
Water mongoose	*Atilax paludinosus*	Least concern
Black-backed jackal	*Canis mesomelas*	Least concern
Yellow mongoose	*Cynictis penicillata*	Least concern
Slender mongoose	*Galerella sanquinea*	Least concern
Small-spotted genet	*Genetta genetta*	Least concern
Large-grey mongoose	*Herpestes ichneumon*	Least concern
White-tailed mongoose	*Ichneumia albicauda*	Least concern
Serval	*Leptailurus serval*	Least concern
Suricate	*Suricata suricatta*	Least concern
Cape fox	*Vulpes chama*	Least concern
Domestic cat	*Felis catus*	NA
Domestic dog	*Canis lupus familiaris*	NA
Herbivores/omnivores	**12**	
Blesbok	*Damaliscus pygargus phillipsi*	Least concern
Bush pig	*Potamochoerus larvatus*	Least concern
Grey duiker	*Sylvicapra grimmia*	Least concern
Eland	*Taurotragus oryx*	Least concern
Gemsbok	*Oryx gazella*	Least concern
Red hartebeest	*Alcelaphus buselaphus caama*	Least concern
Springbok	*Antidorcas marsupialis*	Least concern
Waterbuck	*Kobus ellipsiprymnus*	Least concern
Southern reedbuck	*Redunca arundinum*	Least concern
Mountain reedbuck	*Redunca fulvorufula*	Least concern
Black wildebeest	*Connochaetes gnou*	Least concern
Plains zebra	*Equus quagga*	Least concern
South African hedgehog	*Atelerix frontalis*	Least concern
Porcupine	*Hystrix africaeaustralis*	Least concern
Scrub hare	*Lepus saxatilis*	Least concern

Appendix D: Small carnivore detection and occupancy probabilities

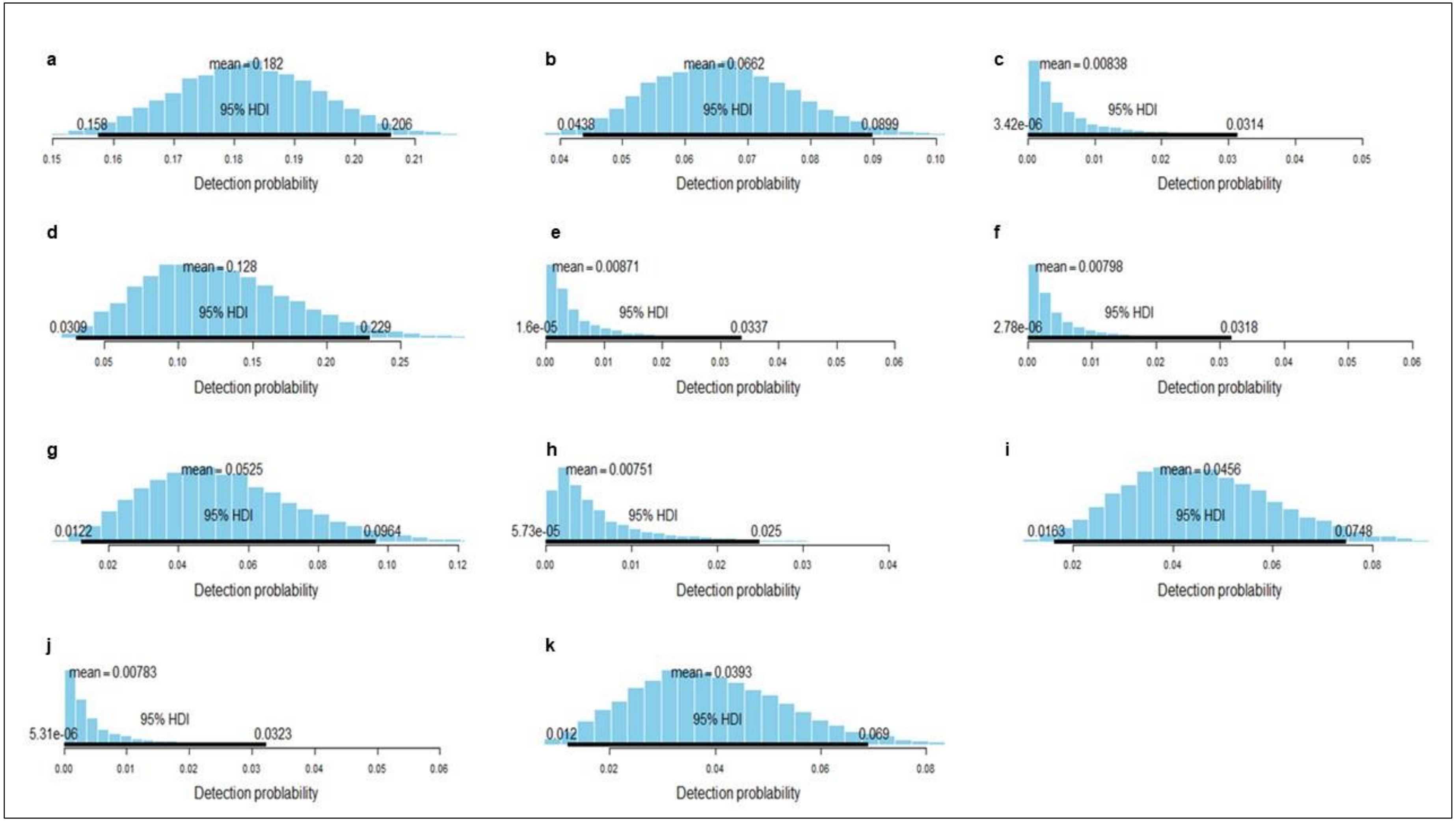

Figure D 1. Detection probabilities of: a) serval; b) black-backed jackal; c) Cape fox; d) small spotted genet; e) large grey mongoose; f) African clawless otter; g) slender mongoose; h) suricate; i) water mongoose; j) white-tailed mongoose; and k) yellow mongoose.

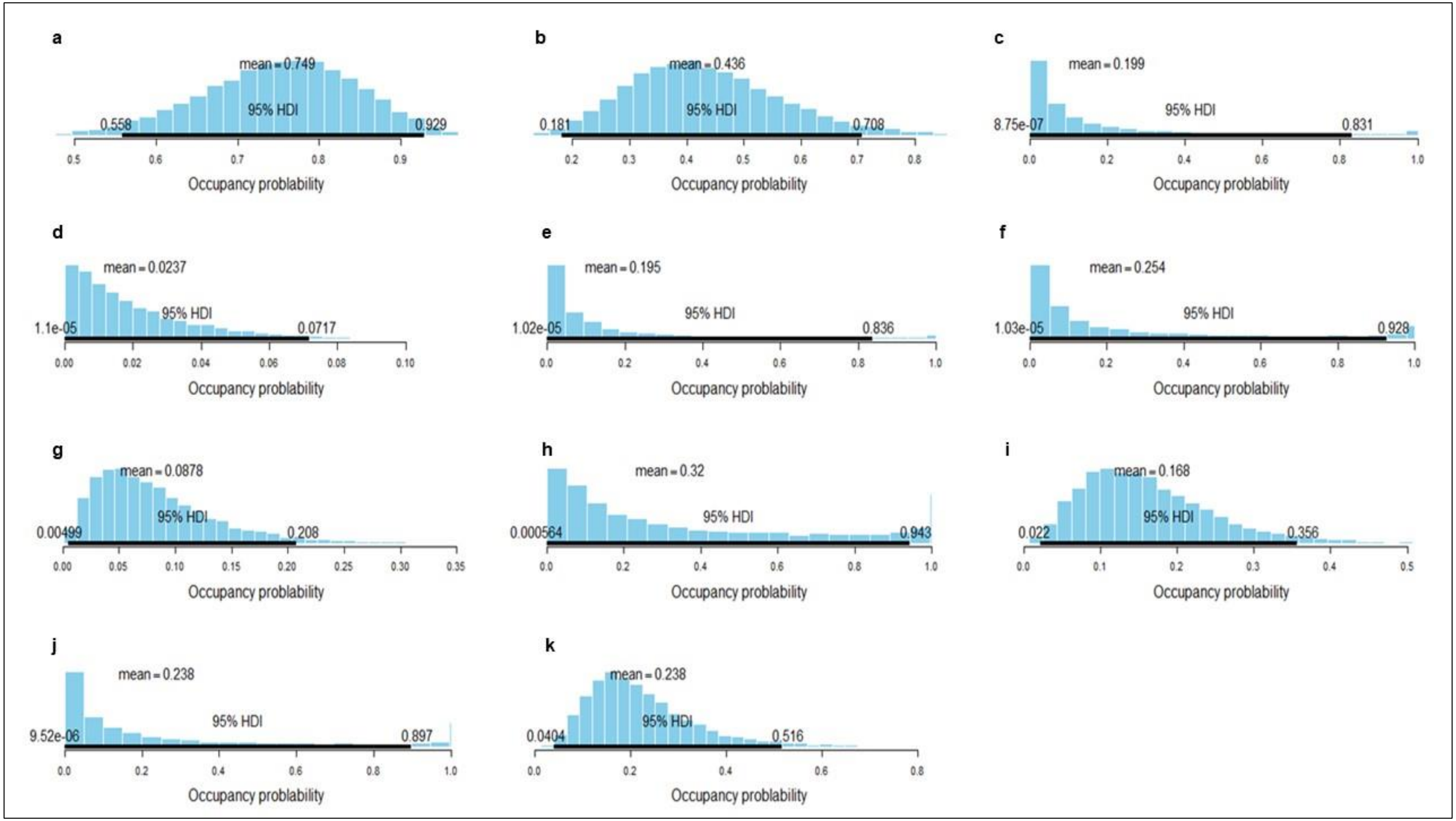

Figure D 2. Occupancy probabilities of: a) serval; b) black-backed jackal; c) Cape fox; d) small spotted genet; e) large grey mongoose; f) African clawless otter; g) slender mongoose; h) suricate; i) water mongoose; j) white-tailed mongoose; and k) yellow mongoose.

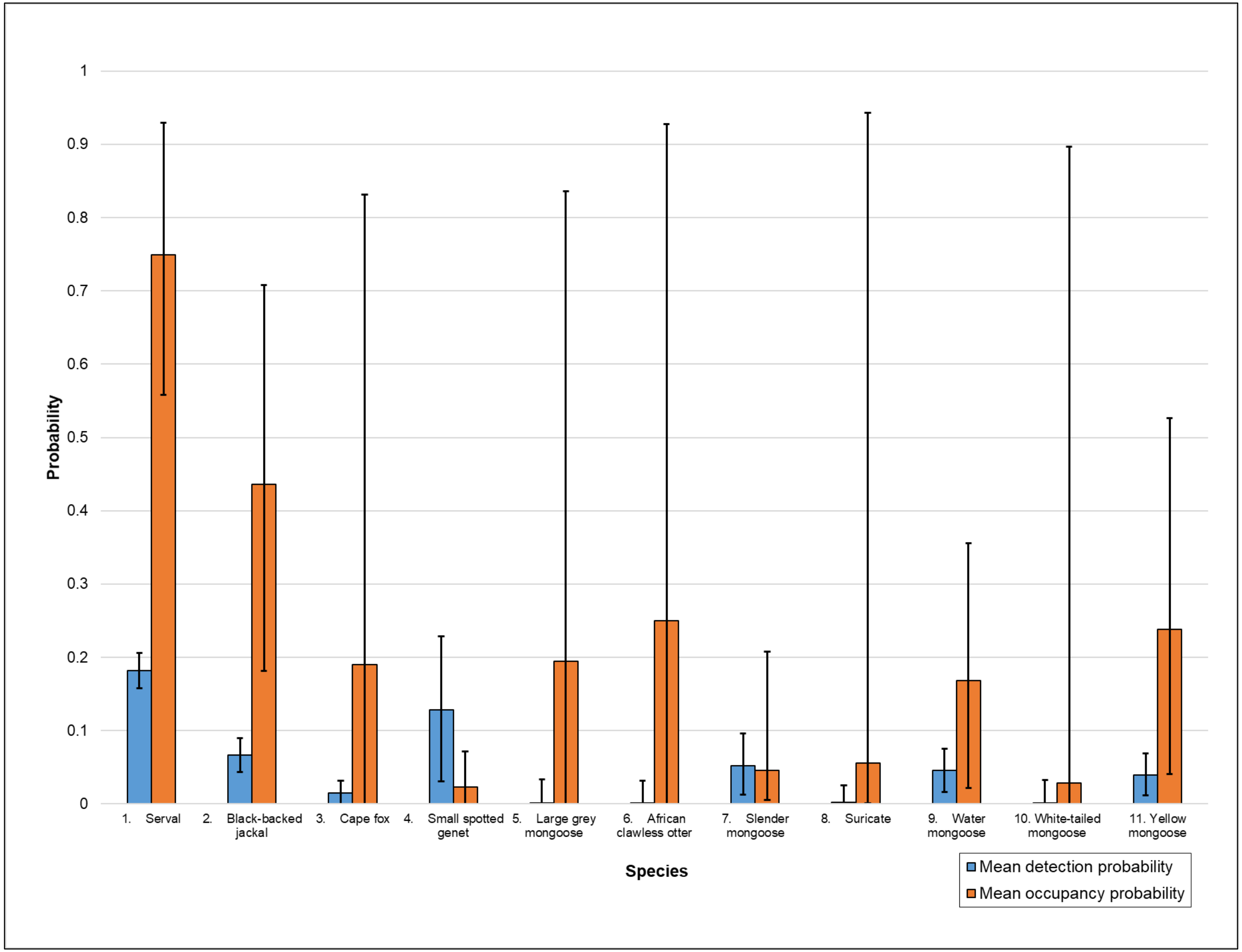

Figure D 3. Plot of small carnivore mean detection and occupancy probabilities.