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# The occurrence, behaviour and public perception of rock hyraxes, Procavia capensis, in urban areas

**Naylor, Andrea Jayne**

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# The occurrence, behaviour and public perception of rock hyraxes, *Procavia capensis*, in urban areas

Andrea Jayne Naylor

A dissertation submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg in fulfilment of the requirements for the degree of Master of Science

Johannesburg, 2015

# Declaration

I declare that this dissertation is my own unaided work. It is being submitted for the degree of Master of Science in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other university.



Andrea Naylor

23/10/2015

# Abstract

With the continuous urban expansion, assessing how some species can survive in urban environments, particularly through modifying their behaviour, is becoming increasingly important. Urban wildlife can show phenotypic (e.g. behavioural) flexibility to exploit urban areas but it is also possible that they could seek refuges that match their phylogenetic niche requirements. The public's perceptions of these "urban" species may also influence their success within urban centres. Using the rock hyrax, *Procavia capensis*, in Greater Johannesburg as a model species, I assessed the flexible and niche conservative hypotheses for its occurrence in urban areas. In particular, I investigated 1) the behaviour and flight initiation distance (FID; a measure of habituation to people) of rock hyraxes in warm (February and September) and cold (June and July) months at an urban site, Meyersdal Eco Estate, south of Johannesburg; and 2) the occurrence and public perception of rock hyraxes in Greater Johannesburg. At Meyersdal Eco Estate, three colonies were identified along an approximately 2km gradient of proximity to humans, from those living in a storm-water drain and gardens to a colony situated >100m from houses. The three colonies showed differences in behavioural patterns compared to a natural population located in the Mountain Zebra National Park, Eastern Cape Province. Although behaviours such as basking, sunbathing, travelling, grooming, and vigilance did not change between the colonies, feeding behaviour was greater and FID scores were shorter in the colony closest to people, indicating greatest habituation to people compared to the colony furthest from people, which showed reduced feeding behaviour and greatest FID distance. The intermediately situated colony showed intermediate levels of feeding and FID. The behaviour of rock hyraxes was not influenced by deterrents (boa, *Boa constrictor constrictor*, dung and wild garlic, *Tulbaghia violacea*) used at Meyersdal to keep rock hyraxes away from gardens. Rock hyraxes ate a variety of plants including grasses, forbs, shrubs, trees and succulents at each of the colonies, but the colony closest to people also ate a variety of garden plants which I did not observe at the two other colonies, including two species of wild garlic, *T. violacea* and *T. simmleri*. Within Greater Johannesburg, rock hyraxes occurred in the northern and southern suburbs, and appeared to avoid densely urbanized areas. Resource selection functions suggested rock hyraxes associated with rocky outcrops potentially conforming to the niche conservatism hypothesis, although they did not select for any particular landscape feature in the Greater Johannesburg environment. The public viewed rock hyraxes more positively than anticipated, with most

suggesting that they were part of the urban biodiversity of Greater Johannesburg. In conclusion, rock hyraxes have modified their behaviour and habituated to people over surprisingly small spatial scales. Such behavioural flexibility over comparatively short distances is a novel finding. However, rocky outcrops are still important natural habitats to meet thermoregulatory and denning requirements, and are used to explore and exploit the urban environment. Because they are constrained by their thermoregulatory requirements, habitat analogues (e.g. storm water drains) might create opportunities to enter houses and gardens. Such flexible responses, which together with a tolerant public, might allow them to flourish in Johannesburg.

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# Chapter 1. General introduction

*Urbanisation and wildlife*

Urbanisation, as defined by Randa & Yunger (2006), is the "anthropogenic conversion of land into residential, commercial, and industrial uses, which leads to pronounced landscape-level changes that significantly alter the structure and function of affected ecosystems" (p 1154). Along with global climate change, urbanisation is one of the most important human-induced rapid environmental changes (HIREC) threatening global biodiversity (Coleman & Barclay 2011; Hubert et al. 2011; Maklakov et al. 2011; Sih et al. 2011; Sih 2013; Sol et al. 2013). Urbanisation comprises of several important environmental changes, including replacement and fragmentation of natural vegetation by built structures, such as buildings and roads (Dearborn & Kark 2009; Sol et al. 2013). In addition, there is replacement of natural food sources with exotics such as artificial food as well as plant and animal species not naturally found in those areas (Sol et al. 2013) and increases in anthropogenic disturbance (e.g. vehicles, human foot traffic and building construction; Marzluff & Rodewald 2008). Urbanisation alters predator communities (Sol et al. 2013), and the loss of top predators within urban environments, instead, facilitates the preponderance of mesopredators, such as domestic cats, *Felis catus*, raccoons, *Procyon lotor*, striped skunks, *Mephitis mephitis* (Crooks & Soule 1999; Gehrt & Prange 2006). Finally, pollution such as night-time lights, noise and chemicals, is more frequent in urban areas (Sol et al. 2013).

As urbanisation is a progressive process, it is sometimes difficult to define urban, suburban and peri-urban areas and, therefore, to incorporate the different extents and intensities of urbanisation, this study considers areas in Greater Johannesburg as being either natural or urban developed. As defined by Fischer et al. (2015), urban developed areas have been substantially altered for residential, recreational, commercial, or industrial use, while natural areas have either not been modified at all or minimally modified for human use including habitat remnants and restored habitats.

Urban expansion is unfortunately inevitable as the global urban population is expected to gain 2.5 billion people (from 3.9 billion in 2014 to 6.4 billion in 2050; United Nations; Department of Economic and Social Affairs; Population Division 2014). More urban areas are expected to be developed to absorb the population growth and incorporate some of the rural population (Beckmann & Berger 2003; Kark et al. 2007; Coleman & Barclay 2011;

Fontúrbel & Tarifa 2014). On top of the inevitability of urbanisation, the environmental alterations that follow are often swift and drastic and have a negative influence on surrounding habitats through altering landscapes, as evidenced by the dramatic loss of species diversity in urbanised areas (Randa & Yunger 2006; Sih et al. 2011; Coleman & Barclay 2011; Sol et al. 2013).

However, alteration of landscapes has also created new niches and resources that are novel to most wildlife species (Mccleery 2009). Although some species have been unable to utilise these new environments (Mccleery 2009; Sih et al. 2011; Sih 2013; Sol et al. 2013), many others have adjusted their population dynamics (Mccleery 2009; Dudus et al. 2014), habitat selection (Hubert et al. 2011), movements (Mccleery 2009; Dudus et al. 2014), and behaviour (Sih 2013; Sol et al. 2013) in response to urbanisation (Mccleery 2009), thereby thriving in urban habitats (Sih et al. 2011; Sih 2013; Sol et al. 2013; Dudus et al. 2014). Despite the potentially dangerous interactions with novel anthropogenic situations (e.g. permanent human presence, greater non-native predator densities (cats and dogs), roads and vehicles, noise and light pollution; Partecke et al. 2006), warmer temperatures, accessibility to illuminated areas, and an increase in anthropogenic food availability might be advantageous for urban-dwelling species (Miranda et al. 2013).

There are several examples of avian and conspicuous mammalian species persisting in urban environments. Due to most urban vertebrate studies focusing on these two groups, little is known about the other groups (Coleman & Barclay 2011), and as such, the focus for my study will be mostly on mammal examples. Some common urban dwellers include raccoons (Prange et al. 2004), coyotes, *Canis latrans* (Gehrt et al. 2011), striped skunks (Weissinger et al. 2009), European badgers, *Meles meles* (Harris 1984), white-tailed deer, *Odocoileus virginianus* (Etter et al. 2002), and a large variety of bird species (Conole & Kirkpatrick 2011). Examples of South African urban wildlife are the southern African hedgehog, *Atelerix frontalis* (Artingstall 2013), large-spotted genet, *Genetta tigrina* (Widdows & Downs 2015), and chacma baboons, *Papio ursinus* (Hoffman & O'Riain 2011). Many successful urban species are generalists and tend to be omnivorous, taking advantage of the wide variety of food resources found in urban environments (McKinney 2006; Bateman & Fleming 2012; Sol et al. 2013).

Regarding den or nest site selection, many urban species utilise urban buildings or artificial structures for dens, nests and/or resting sites. Examples include bats (Coleman & Barclay 2011), stone martens, *Martes foina*, red foxes, *Vulpes vulpes* (although red foxes

preferred residential estates; (Dudus et al. 2014), and a variety of raptors (Chace & Walsh 2006). When obtaining food, some mammal and bird species find higher food productivity in urban environments in gardens, refuse and through intentional feeding by humans. Some of these species show lower latencies to respond to novel food opportunities than non-urban individuals (Sih et al. 2011). On the other hand, when coping with human disturbances such as road traffic and buildings, red foxes, and Eurasian hedgehogs, *Erinaceus europaeus*, adjust their activity patterns to avoid or minimise contact with high human traffic, both pedestrian and vehicular (Sol et al. 2013). This ability to adjust demonstrates an adaptability of some wildlife species to urban life.

Those species that have adjusted to live in urban environments can be categorised as either urban dwellers or urban utilizers (adapted from urban exploiters and urban adapters respectively, Blair 1996; McKinney 2006) depending on the importance of developed and natural areas found in urban environments to their population dynamics (Fischer et al. 2015). Urban dwellers are those species which can persist in urbanised landscapes independent of natural areas and range from species that have viable populations in both natural and developed areas to those that rely on developed areas and its resources for survival (Shochat et al. 2006; Fischer et al. 2015). In contrast, urban utilizers are those species that can occur in urban environments as either non-breeders, such as those that make infrequent use of urban resources, or breeders that are present in developed areas due to dispersal from adjacent natural areas (Fischer et al. 2015). Alternatively, species that rarely occur in developed areas due to populations being extirpated or having self-sustaining networks in natural areas embedded in an urban matrix, are known as urban avoiders (Marzluff & Rodewald 2008; Fischer et al. 2015), which are not considered further in my study."

*Behavioural flexibility*

Phenotypic plasticity is the capacity of a genotype to produce different phenotypes in response to prevailing environmental conditions (West-Eberhard 1989; Ghalambor et al. 2010). Phenotypic plasticity differs from evolutionary (genetic) adaptation because plastic responses tend to be more rapid, facilitating quicker adjustments to environmental changes (Gross et al. 2010). Behavioural plasticity describes behavioural changes without accompanying genotypic changes (Wright et al. 2010). Some animals are able to modify their behaviour dynamically and show flexible changes rather than simply plastic responses. For

example, the African striped mouse, *Rhabdomys pumilio*, adjusts its social behaviour in response to prevailing environmental conditions, in which both sexes switch between solitary- or group-living according to which social tactic has greater fitness at a particular time (Schradin et al. 2012).

For species that survive in urban environments, behavioural flexibility/ plasticity might be the mechanism used to respond to rapidly changing conditions and thus may be an important adaptation to human-induced rapid environmental change (HIREC) (Ghalambor et al. 2010; Wright et al. 2010; Sih et al. 2011). An example of behavioural plasticity in urban-dwelling species is the acoustic signalling adjustment by birds due to an increase in human-made noise levels (Luther & Derryberry 2012; Sol et al. 2013). In urban environments, bird songs can be easily masked by human noises, which can have reproductive consequences especially for males when their song correlates to male reproductive success (Luther & Derryberry 2012). Male reed buntings, *Emberiza schoeniclus*, adjust their songs to a higher minimum frequency and at a lower rate, especially when ambient noise levels are high in order to overcome song-masking (Gross et al. 2010).

*Alternative strategies: Niche conservatism and refugia*

Even if species are unable to alter their behaviour in response to urbanisation, they can still persist in urban environments. Niche conservatism is a broad concept which explains how species tend to maintain their fundamental, niche-related, ecological traits over time (Wiens et al. 2010). A niche is defined as the collection of abiotic and biotic features in which a species can persist, so that niche conservatism relates to traits constrained by features of the niche over various time scales (Wiens et al. 2010). These traits include responses to abiotic features (e.g. temperature tolerance), exploitation of resources (e.g. diet) and interspecific interactions (e.g. cryptosis, Wiens et al. 2010). For example, snail kites, *Rostrhamus sociabilis*, feed almost exclusively on one genus, *Pomacea*, of freshwater apple snails but reject other genera of snails even though their bill morphology is adapted for extracting snails from their shells (Beissinger et al. 1994). Snail kites, however, have been shown to eat crabs, *Dilocarcinus dentatus*, in preference to other genera of snails, especially when the preferred snails are unavailable. Therefore, the bill morphology constrains them to removing flesh from shells while their neophobic behaviour constrains them to consuming

one genus of snail and a particular alternative food source highlighting niche conservatism in their diet.

*Rock hyrax, Procavia capensis*

The rock hyrax, *Procavia capensis*, is a small sized (~3-4kg), subungulate (*Mammalia: Hyracoidea*) that is widespread in southern and North Africa and the Middle East (Olds & Shoshani 1982; Kershenbaum et al. 2011), inhabiting rocky outcrops, also known as *koppies* in South Africa (Skinner & Chimimba 2005). Within these areas, it will den within rock crevices which offer a refuge of protection not only from predators but also from the midday heat (Olds & Shoshani 1982; Druce et al. 2006; Kershenbaum et al. 2011). It lives in groups of between 10-50 individuals usually consisting of a dominant, territorial male, a harem of females, and subadults, juveniles and pups of both sexes (Gerlach & Hoeck 2001; Druce et al. 2006; Koren & Geffen 2009). Males are generally heavier than females (4kg vs 3.6kg) and have thicker necks, thinner bodies and their incisors are better developed (Olds & Shoshani 1982). Peripheral males (i.e. those not holding a harem) may be loosely associated with the colony and due to the breeding season being seasonal and synchronised among the females, may have a chance to sire offspring with some of the females when the territorial male is mating with other females (Koren & Geffen 2009). The lifespan of the territorial male is suggested to be around 8 years (Hoeck 1989), and thus it may hold tenure for only a few years until it is either killed or evicted by another male, generally a peripheral male (Koren & Geffen 2009). Rock hyraxes tend to urinate and defecate in a single location (latrine or midden) which can become rather large from continued use (Skinner & Chimimba 2005) and is generally an indicator of rock hyrax colony presence (Rübsamen et al. 1982).

The synchronised breeding results in synchronous births, which is likely to function as a way to reduce predation risk through the dilution effect (Fourie 1983; Skinner & Chimimba 2005). The mating season varies according to location since it is triggered by photoperiod rather than rainfall or temperature changes (Skinner & Chimimba 2005). In the Western Cape Province, the mating season is around February whereas in the Free State and Limpopo Provinces it is around April and May respectively (Skinner & Chimimba 2005). Gestation is long, being around 230 days (~7.5 months), and thus time of parturition in the Western Cape is around September/October compared to November/December and December/January respectively in the Free State and Limpopo Provinces (Skinner &

Chimimba 2005). Females will breed once a year to once every alternate year (Barocas et al. 2011) and will give birth to an average of two to three precocial pups, but litters can be as large as six pups (Skinner & Chimimba 2005). Females will continue to be fertile for most of their lifetime (over 11 years of age) and there appears to be no reproductive senility (Skinner & Chimimba 2005).

Males are forced, due to aggressive behaviour displayed by the territorial male (Fourie 1983), to disperse as subadults or adults (around 28 months old) before or during the breeding season (Koren & Geffen 2009; Visser 2013), while females are largely philopatric and may disperse voluntarily after they mature (around 16 months old) (Visser 2013). Generally, females disperse less than 500m because they receive less resistance and are accepted into nearby colonies more easily, while males, due to confronting resistance from territorial males when dispersing, will either remain near their natal group or will disperse across distances >500m (Fourie 1983; Skinner & Chimimba 2005; Barocas et al. 2011; Visser 2013). During times of high population densities and low food abundance, rock hyraxes are capable of dispersing considerable distances (~20km) to other suitable rock areas (Visser 2013).

The thermoneutral zone of rock hyraxes is 20-30°C (McNairn & Fairall 1984), and they have labile body temperature, that can range from 33.5-40.5°C in summer and 34.5-39.5°C in winter (Brown & Downs 2006). Rock hyraxes are considered poor thermoregulators and their general activity is largely associated with the prevailing environmental conditions to improve their energy acquisition through foraging, sun basking and retreating into shade or cover (Brown & Downs 2005, 2007). Consequently, rock hyraxes are predominantly diurnal and emerge from dens around sunrise, with all members of the colony emerging between 1-3 hours after sunrise, and retire before sunset (Fourie 1983; Skinner & Chimimba 2005). Although diurnal, they have been known to forage on moonlit nights (Brown & Downs 2005).

Their diurnal activity follows a bimodal distribution generally with the greatest activity, usually foraging, occurring at two peaks during the day: early to mid-morning and late afternoon (summer months) and late morning and late afternoon or one extended period across the late morning to early afternoon (winter months, Skinner & Chimimba 2005). During these times, at least one adult (generally an old female) will assume the role of sentinel and will keep vigilance (Fourie 1983). When not feeding, they are generally inactive

and bask, adopting either a hunched or flat position (sunbathing) posture on the rocks. The behavioural postures, use of sun and shade sites and use of rock surfaces are influenced by the ambient air temperatures (Brown & Downs 2007). When the ambient air temperature is below the thermoneutral zone, heat loss to the environment becomes greater than heat production and is further aggravated by conduction to colder surfaces (such as rock surfaces), and therefore rock hyraxes will bask and have minimal body contact with rock surfaces to reduce heat loss (Brown & Downs 2007). As ambient air temperatures become warmer, rock hyraxes will increase their surface area exposed to the sun by basking flat against rocks (Brown & Downs 2007). However, when ambient air temperatures exceed the thermoneutral zone, rock hyraxes will shuttle between sun and shade locations, utilising basking postures to minimise the surface area exposed to the sun (Brown & Downs 2007) and maximise the surface area to lose heat to the cooler shaded rock surfaces (Skinner & Chimimba 2005; Brown & Downs 2007) to avoid hyperthermia (Brown & Downs 2007). As the ambient air temperature starts to drop, basking flat against the rock surfaces will assist in absorbing residual heat from these surfaces (Skinner & Chimimba 2005; Brown & Downs 2007). Thus the same behaviour can have two different outcomes influenced by the surrounding environment because the rock surfaces can be colder or warmer than the ambient temperatures due to the exposure of solar rays and heat gain.

Rock hyrax populations are known to fluctuate due to predation, droughts, and infectious diseases (Wimberger et al. 2009; Visser 2013). While there have been population explosions in Ladysmith, Kwa-Zulu Natal (KZN) Province, South Africa (Wimberger et al. 2009), there have also been major population crashes reported for the Western Cape (Visser 2013) and the Midlands of KZN (Wimberger et al. 2009). Their main predators are the Verreaux's (black) eagle, *Aquila verreauxii,* leopard, *Panthera pardus*, and the caracal, *Felis caracal*, which regulate population densities of rock hyraxes (Druce et al. 2006, Visser 2013). Due to the threat of predation away from their refuges, hyraxes forage in groups and utilise sentinels that maintain vigilance while partaking in group activities (Druce et al. 2006).

Rock hyraxes are facultative grazers, opportunistically exploiting the seasonal availability of grasses, generally during the wetter months (Fourie 1983; Skinner & Chimimba 2005). As such, they feed throughout the year on a variety of herbaceous plants, selecting phenological stages of all their plant food, with leaves from trees and shrubs comprising a major part of their diet throughout the year (Fourie 1983; Skinner & Chimimba 2005). Feeding times during warmer months occur throughout the day with peak feeding

occurring during the early morning and again in the late afternoon and ends around sunset (Skinner & Chimimba 2005). During colder months, feeding times shift to later, either becoming one session from late morning until early afternoon or two separate peaks with one in the late morning and again in the late afternoon, ending around sunset (Skinner & Chimimba 2005). Rock hyraxes will feed from around their dens and up to 50m away but when food is not available within this vicinity, they can travel as far as 500m from their dens (Olds & Shoshani 1982, Fourie 1983).

Rock hyraxes are a suitable model species to investigate whether and how wildlife adjusts to urbanisation because they occur within urban environments by utilising road culverts and holes in buildings, such as roofs, under sheds, for den sites (Olds & Shoshani 1982; Skinner & Chimimba 2005) as well as foraging in residential gardens (Kershenbaum et al. 2011; Wiid & Butler 2015). Populations living within residential areas have been known to become rather large and although the normal home range size of a territorial male is around 4800 $m^2$, these residential populations appear to co-exist in one home range, potentially due to an abundance of food sources, refuges and a shortage of natural predators. Unfortunately, due to their habits of exploiting human habitats, particularly at high populations, they can cause conflict with residential owners (Olds & Shoshani 1982; Wimberger et al. 2009, Kershenbaum et al. 2011). Thus, by investigating their behaviour in urban environments, we can gain a better understanding of how wildlife generally and rock hyraxes, in particular, exist in urban environments.

## Aims and objectives

My study aimed to 1) investigate the behaviour of rock hyraxes in an urban site, Meyersdal Eco Estate, south of Johannesburg, and 2) to investigate the occurrence and public perception of rock hyraxes in Greater Johannesburg region. For the first aim, I assessed the behavioural responses of rock hyraxes in Meyersdal Eco Estate, I recorded activity patterns in three rock hyrax colonies along a gradient of proximity to people. I also investigated their diet and habituation to people. Lastly, I assessed the efficacy of deterring rock hyraxes from homesteads for two previously used deterrents. For the second aim, I collected reported sightings by the public, from which I generated a sightings map which was assessed against environmental parameters to ascertain resources that predict rock hyrax occurrence in Greater

Johannesburg. I distributed surveys to the public and assessed responses for an overall opinion of rock hyraxes in Greater Johannesburg.

## Layout of the dissertation

Apart from the present chapter (general introduction), my dissertation comprises two experimental chapters with the corresponding predictions, and a general discussion (chapter 4). Page numbers are sequential for the entire dissertation but line numbers, figures and tables are in sequence for each chapter. There is a single reference section provided at the end of the dissertation. Due to the layout of the dissertation, there is overlapping of information between chapters.

# Chapter 2. Behaviour of rock hyraxes in an urban site

## Introduction

*Behavioural flexibility and niche conservatism in urban environments*

Whether or how animals will respond to human-induced rapid environmental change is an important question asked in animal behaviour. Behaviour is predicted to be one of the first traits to change in modified environments through flexible behavioural responses, often seen along an urban gradient (Carrete & Tella 2013; Kaiser et al. 2014). Behavioural flexibility, defined as changes in the behavioural phenotype without changes in the genotype (Thibert-Plante & Hendry 2011), may even assist animals to tolerate or even habituate to various levels of anthropogenic disturbances that occur when wildlife live in close proximity to people (Lowry et al. 2013).

Behavioural flexibility may result in animals modifying their antipredator responses to humans so that these species can prioritise other fitness enhancing behaviours, such as the exploitation of additional resources (Bateman & Fleming 2014). Along a rural-urban gradient, altered anti-predatory behaviour occurs in several small mammals, such as the eastern grey squirrel, *Sciurus carolinensis* (Bateman & Fleming 2014); Cape ground squirrel, *Xerus inauris* (Chapman et al. 2012); fox squirrel, *Sciurus niger* (Mccleery 2009); these species in urban areas showed reduced wariness to approaching humans compared to their rural counterparts.

Many urban animals, such as the American black bear, *Ursus americanus* (Beckmann & Berger 2003); wild boar, *Sus scrofa* (Podgórski et al. 2013); javelina/ collared peccary, *Pecari tajacu* (Ticer et al. 1998); European hedgehog, *Erinaceus europeaus* (Hubert et al. 2011); coyote, *Canis latrans*; red fox, *Vulpes vulpes*; opossum, *Didelphus virginianus*; racoon, *Procyon lotor* (Bateman & Fleming 2012), and numerous bird species (Sol et al. 2011) have altered their behaviour to exploit novel food resources found in urban environments. These novel foods include human refuse, orchards, roadkill, pets, livestock, pet food and other forms of human-derived food resources through supplementary feeding by people (Bateman & Fleming 2012). Food resources in urban environments appear to be abundant and constant and being able to utilise these resources may aid in the urban

colonisation success of many of these species (McKinney 2002; Anderies et al. 2007; Podgórski et al. 2013).

Behavioural flexibility may enable animals with a limited tolerance towards human activity to succeed. For example, the American black bear (Beckmann & Berger 2003), bobcats, *Lynx rufus*, coyote (Tigas et al. 2002), and wild boar (Podgórski et al. 2013), can become nocturnal in urban environments, which reduces their interaction with humans. The European hedgehog adjusts its foraging movement to avoid roads and is more active after midnight when vehicular and human disturbance is greatly reduced (Dowding et al. 2010). For some species, altering behaviour to tolerate human activity may be impossible. For example, some animals retain their diel activity niche (known as temporal niche conservatism), often because of physiological and/or morphological constraints, but can still persist in urban environments, such as owls and geckos (Wiens et al. 2010).

*Anti-predator behaviour in urban environments*

Anti-predator behaviours, including vigilance and avoidance behaviour, are adaptive responses to predation risk (Apfelbach et al. 2005). Urbanisation increases the contact between urban wildlife and humans and domesticated cats and dogs, which can pose a threat. Urban wildlife can either avoid areas frequented by humans and pets, occupy such urban areas, particularly in the case of less fearful individuals, or can gradually adapt to the disturbance in urban habitats (Møller 2012). When faced with a multitude of disturbances (e.g. vehicles, foot traffic, dogs on leashes), the ability to distinguish between threatening and non-threatening stimuli may influence the success of these animals, especially prey species, in urban environments (Bateman & Fleming 2014).

Prey species are frequently at risk of being eaten by native and/or introduced predators (Apfelbach et al. 2005; Hayes et al. 2006). To facilitate recognition of, and defence against predators, prey species have developed specific behaviours known as anti-predatory behaviours. These aid survival through the detection of and response to visual, auditory and chemical cues that predators produce (Apfelbach et al. 2005). Unfortunately, preventing predation can be costly and prey species naturally show trade-offs between anti-predatory behaviours and foraging and/or reproduction (Cooper et al. 2006; Hayes et al. 2006; Møller 2012; Møller et al. 2013). Vigilance is the major behavioural mechanism that facilitates

predator detection. Visual vigilance is utilised especially in habitats that lack relative concealment, which in turn permits the initiation of secondary defences, such as flight (Apfelbach et al. 2005).

Rock hyraxes are central place foragers that start and end foraging bouts from their dens (Kotler et al. 1999; Druce et al. 2006). Foraging patches closer to dens are generally more preferred than those further away because those further away have an added energy cost when retreating to a refuge or the colony from an attacking predator (Kotler et al. 1999; Druce et al. 2006). It is when feeding that rock hyraxes are generally more susceptible to predation and thus sentinels keep vigilance from a vantage point over exposed foragers and potential dangers (Kotler et al. 1999). With foraging being mainly a group activity and members generally foraging in the same direction, the effectiveness of sentinels may be enhanced (Kotler et al. 1999). Additionally, foraging in groups provides benefits such as the dilution effect and group vigilance, which may allow rock hyraxes the opportunities to exploit resources away from the central refuge (Kotler et al. 1999). However, it is possible that when out of sight of the sentinels, rock hyraxes may incorporate individual vigilance and may individually assess the risks of the disturbance, prompting evasive behaviour, if needs be.

Optimal escape theory originally described by Ydenberg & Dill (1986) predicted that prey animals should remain where they are to minimise the cost of fleeing until the point where the cost of staying exceeds the cost of fleeing (i.e. the cost of potentially being caught or killed is greater than the loss in foraging and mating opportunities as well as the energy expenditure; Stankowich & Coss 2006). This is known as the flight initiation distance (FID), defined as the distance from which an animal moves away or takes flight from an approaching threat (Ydenberg & Dill 1986; Stankowich & Coss 2006; Cooper & Frederick 2007; Engelhardt & Weladji 2011). Deciding when to flee is a crucial decision, so that FID is under strong selection, including responding to the direction of the threat (Stankowich & Blumstein 2005), starting distance of approach of a predator (Blumstein 2003), distance from refuge (Engelhardt & Weladji 2011), physical fitness of the prey animal (Stankowich & Blumstein 2005; Cooper & Frederick 2007), predator lethality (Cooper & Frederick 2007, 2010), and habitat structure (Engelhardt & Weladji 2011).

Olfaction is another major sensory mode through which predators can be detected and potentially identified (Apfelbach et al. 2005). When exposed to predator odours, many prey

species utilise behavioural defences that can facilitate avoidance of potential predators, such as altering activity patterns, decreasing non-defensive behaviours and retreating to a safe location where the threat can be monitored, or shifting habitats (Apfelbach et al. 2005). This avoidance behaviour is probably driven by the recognition of predators (Hayes et al. 2006) or that of their by-products. In particular, mammalian prey can recognise predators through the odour of sulphurous compounds in the body odour and faeces of predators (Woolhouse & Morgan 1995; Hayes et al. 2006; Kemp & Kaplan 2012).

This ability to potentially detect predators through olfaction has also been manipulated in some non-lethal methods for controlling wildlife foraging damage. Non-lethal methods for controlling wildlife foraging damage are becoming more popular as many lethal methods are considered inhumane (Atkinson & Macdonald 1994). However, these methods have not been adequately researched (Baker et al. 2005). Non-lethal control methods may offer conservation, ethical and legal advantages over lethal controls, especially in urban environments where lethal control may be inappropriate because of effects on people, livestock or pets (Woolhouse & Morgan 1995; Baker et al. 2005). There are numerous studies using predator odours to induce avoidance behaviour in controlling wildlife foraging damage. Predator odours can include the actual predator (Koivisto & Pusenius 2003), pelts of predators (Vazdarjanova et al. 2002), collars previously worn by domesticated dogs and cats (McGregor et al. 2002), and deterrents of predator urine (Sullivan & Crump 1986), faeces (Pillay et al. 2003; Hayes et al. 2006), gland secretions (Zhang et al. 2003) as well as compounds derived from these biological fluids (Woolhouse & Morgan 1995). The use of predator faeces follows the scat-avoidance hypothesis, whereby prey avoid areas containing faeces of predators (Banks et al. 2003; Hayes et al. 2006),

There are several other chemical repellents, generally plant-derived, and these are compounds from plant secondary metabolism (Fischer et al. 2013). Plant repellents can be grouped into three groups; irritants, odorous and those that cause gastrointestinal distress (Mason 1998). Sensory irritants are generally more effective deterrents to depredation than those that are odorous or substances that cause gastrointestinal distress (Mason 1998). An example of a sensory irritant is capsaicin which is a known irritant to mammals (Baker et al. 2005). Taste repellents have variable success, especially bitter substances, and have been shown to be ineffective for many herbivores (Mason 1998).

In this study, I investigated whether and how the rock hyrax, *Procavia capensis*, alters its behaviour within urban environments. These alterations may include differences in activity patterns, use of exotic food plants, use of artificial dens, and habituation to humans. Due to their location in close proximity to people and pets within residential areas, lethal control of rock hyraxes was not appropriate. Therefore, there was a need to assess the efficacy of non-lethal options on deterring rock hyraxes as part of controlling human-wildlife conflicts with rock hyraxes.

In the study area, rock hyraxes appeared to be well established, utilising rocky ridges and artificial denning sites. In pilot studies, it became apparent that the largest colonies were situated along a gradient of proximity to humans, ranging from colonies situated alongside houses to those occurring some distance away from houses. I had four aims, each with accompanying predictions.

1. My main objective was to establish the daylight activity patterns of rock hyraxes in three colonies along a gradient of proximity to humans in the Meyersdal Eco Estate, Alberton in the colder and warmer times of the year. To assess whether rock hyraxes alter their behaviour in urban environments, I compared my findings to those of a natural population in the in the Mountain Zebra National Park, Eastern Cape Province (MZNP, Fourie 1983). If the behaviours differ, it would suggest behavioural flexibility and if the behaviours did not differ, it would suggest niche conservatism of the species. Based on the biology of rock hyraxes (Chapter 1), I made three predictions. i) Basking would be the most common behaviour in the warm (February and September) and cold (June and July) months, followed by sunbathing and feeding, both of which would increase in the cold months due to lower ambient air temperatures and vegetation drying out during the winter. Vigilance would increase in the cold months, coinciding with the onset of when a resident pair of Verreaux's (black) eagles, *Aquila verreauxii*, started breeding. Travelling would increase in the cold months as food would become more scattered and males solicit matings from females in different parts of the colony. Lastly, aggressive and mating behaviour would also increase during the mating season which occurs during the cold months;

ii) Along the gradient of proximity to humans, basking and vigilance of rock hyraxes would increase and sunbathing would decrease further from people, coinciding with changes in habituation to people and raptors potentially having more effect on colonies further from humans. Feeding would also increase from colonies closest to people to those furthest away

along the gradient due to gardens providing high-quality food year round, so providing high energy resources to colonies closest to gardens. Travelling would decrease closer to people as gardens are concentrated in small areas and the distance to food is shorter than in more natural areas.

iii) Compared to a natural population studied by Fourie (1983), the colonies of rock hyraxes in Meyersdal Eco Estate would generally have lower proportions of basking/sunbathing activity due to the lower levels of predation in urban environments and comparatively more accessible resources, potentially, allowing for other behaviours to occur. The rock hyraxes in Meyersdal Eco Estate would have lower proportions of feeding and travelling as plant availability would be greater in urban environments and distances to those plants would be shorter in urban environments.

2. To investigate the diet of rock hyraxes in the three colonies during warm and cold months. I made two predictions. i) The colony situated closest to humans will increase foraging in residential gardens during the colder months but its diet will potentially remain the same as in the warmer months due to gardens generally providing high-quality vegetation year round. ii) The diet for the colonies situated further away from humans will shift from grasses to mostly trees and shrubs from warmer to colder months as the grassland vegetation in the Highveld dries out during the winter.

**3.** To investigate habituation to people by rock hyraxes from the three colonies through the measurement of flight initiation distances (FID) of individuals when a food incentive (apples) is provided or not, in the warm (February and September) and cold (June and July) months. I had two predictions. i) FIDs would be shorter in the colony situated closest to humans, indicating habituation. ii) FIDs would further decrease with the food incentive than without it, particularly in the population furthest away from people in the cold months when natural vegetation would decrease in quality and abundance.

4. To ascertain whether two deterrents, namely South American red-tailed boa, *Boa constrictor constrictor*, (boa) dung and Cape wild garlic, *Tulbaghia violacea*, (wild garlic) plants, (Andrew Jackson pers. comm.), were effective in deterring rock hyraxes from a food incentive in the warm (February and September) and cold (June and July) months. I made four predictions. i) Due to none of the colonies previously being exposed to boa faeces, all

colonies would show an increase in latency to approach a food incentive encircled by boa dung. ii) Due to the colony closest to people being exposed to wild garlic previously, which is planted in gardens at Meyersdal, this colony would have a shorter latency to approach a food incentive encircled with wild garlic than rock hyraxes from the other colonies. iii) In all colonies, the latency to approach the food incentive for both deterrents would become shorter across trials within a season as hyraxes become habituated to the deterrents. iv) In all colonies, the latency to approach the food incentive regardless of deterrent would become shorter in the cold months when the food incentive would be better than the surrounding vegetation and the deterrent is, therefore, less effective.

## Materials and methods

*General information*

Meyersdal Eco Estate (480 ha) (GPS coordinates -26.285817, 28.086946) is a private residential estate that forms part of the larger Meyersdal Nature Area (1080 ha) and is about 20km south of Johannesburg. The estate promotes the Eco Estate philosophy in which people live in harmony with nature and less than 15% of the natural area is developed. Residents have access to hiking trails, four mountain bike trails and 4x4 routes. The Estate has 12 reintroduced mammalian herbivore species (totalling approximately 300 individuals), such as eland, *Taurotragus oryx* and steenbok, *Raphicerus campestris*, and 98 bird, 28 reptile, five fish, and a large number of plants and insect species (Meyersdal Eco Estate 2014).

The Estate has concerns about the management of their rock hyrax population with some colonies occurring within the residential area of the property and residents complaining about rock hyraxes destroying their gardens, denning in their roofs as well as denning under decks; rock hyrax latrines also create an unpleasant smell. Even though the Eco Estate has a resident breeding pair of Verreaux's eagles, nesting on an artificial nesting platform, the population numbers of rock hyraxes on the property appear not to be impacted by eagle predation (Andrew Jackson, Environmental Manager, pers. comm.).

The three rock hyrax colonies selected for study were located at three sites designated as cul-de-sac (-26.290766°; 28.075817°), rubble dump (-26.271616°; 28.077996°) and boulder pile (-26.281697°; 28.092603°) (Figure 1). The selection of the colonies was based

on firstly the presence of rock hyraxes and for the following factors: 1) the sites were easily accessible; 2) the rock hyraxes were easily visible; 3) the populations appeared to be stable due to their persistence at each site (Andrew Jackson pers. comm.); 4) the sites were about 2km apart from each other which is greater than the reported dispersal distance and thus indicating that the colonies were unlikely to overlap; and 5) each site was at a different proximity to humans, so that each had different types and intensities of disturbance by people. With these factors in consideration, the colony entrances as well as the most advantageous viewing points governed at which direction the observations occurred.

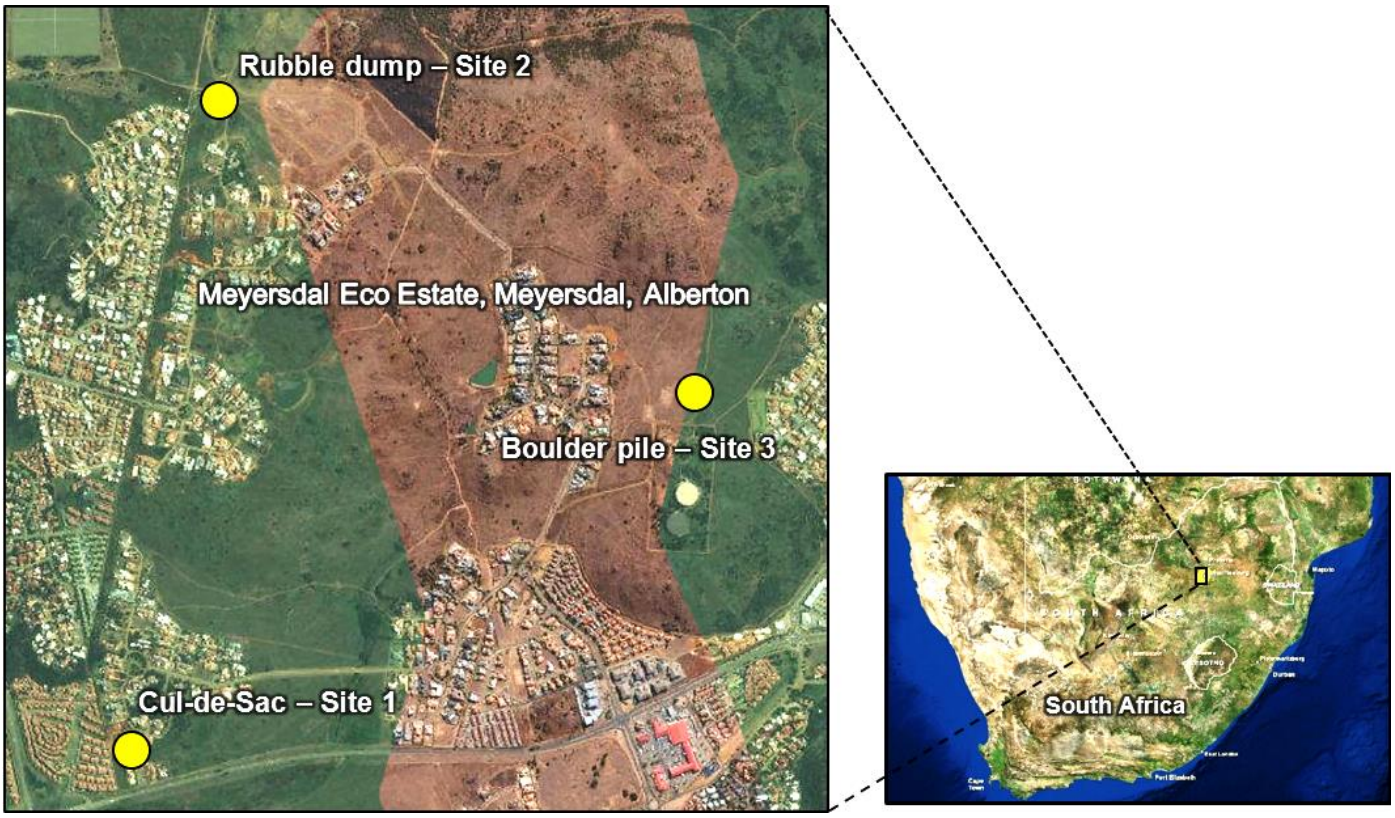



Figure 1. A map showing the locations of the three colonies under study at Meyersdal Eco Estate– cul-de-sac (-26.290766°; 28.075817°), rubble dump (-26.271616°; 28.077996°) and boulder pile (-26.281697°; 28.092603°), generated in ArcMap™10.1 (ESRI, 2012) and adapted to include site names. The dots represent the locations of each colony.

The cul-de-sac colony had the closest proximity (0m) to humans because it was located within the residential area of the estate with rock hyraxes denning within the storm water drains and houses (i.e. they were using anthropomorphic structures) in the vicinity of

the cul-de-sac. The types of disturbance for this colony comprised of one of the eco-trails passing nearby, regular traffic of residents either on foot or in vehicles, as well as pets. The rubble dump colony had an intermediate proximity (<100m) to humans as it was on the edge of the last building stands to be developed on the property. The types of disturbance at this colony comprised of rubble trucks, builders, a few residents, their vehicles, mountain bikers and potential hikers, the last two due to an eco-trail passing by the site. This site also received direct sunlight later than the other two colonies as the entrances were facing in a more southerly direction and the sun disappeared behind the surrounding hill sooner than at the other colonies. The boulder pile colony was located furthest away from people (>150m). The types of disturbance by humans at this colony involved occasional mountain bikers due to two of the eco-trails passing nearby to the den, hikers, and game viewers in passing vehicles. On weekends, the level of disturbance increased at all colonies, and also included recreational aeroplanes flying over the estate (Andrew Jackson pers. comm.).

*Climate and vegetation*

Rainfall occurs from early October to March and is between 754mm to 1185mm per annum. Temperatures range from 10°C to 32°C in summer and between -2°C and 20°C in winter, with frost being common in winter (Oosthuizen 2012). The area features rocky ridges that form the foothills of the Klipriviersberg and consists of almost entirely volcanic rock, basalt and andesite. The vegetation is a mixed wiry grassveld that experiences regular frost in winter and is part of the Bankenveld False Grassveld (Oosthuizen 2012). The rocky hills and ridges are characterised by bushveld vegetation which is generally dominated by hook thorn trees, *Senegalia caffra* and white stinkwood trees, *Celtis africana* (Oosthuizen 2012). Mountain cabbage trees, *Cussonia paniculata* and succulents, such as aloes, are also scattered around numerous hills and rocky outcrops. The veld is dominated by redgrass, *Themeda trianda*, speargrass, *Heteropogon contortus*, trident grass, *Apochaeta hispida*, *Sporobolus* species and a number of *Eragrostis* species. The majority of these grasses are perennials which form a continuous ground layer, with a growing season from September to April; thereafter it is too dry and cold for growth for most species (Oosthuizen 2012).

## Activity patterns

At each of the three colonies (cul-de-sac, rubble dump and boulder pile), I conducted scan observations of colonies, with an interscan interval of 5 min. from dawn until dusk during weekends (Friday – Sunday) or on public holidays when building construction on the estate was prohibited. This minimised observation disturbance especially in the residential areas of the estate. Observations were conducted under similar weather conditions, such that if it was raining on an observation day, the observation was postponed for another day. I conducted observations twice per warm (February and September) and cold (June and July) months for each of the colonies and sampled all the colonies within three weeks of each other per season. Observation times coincided with sunrise and sunset when rock hyraxes were visible. As such, for the warm months, observations occurred from 05:30 – 18:30 and for the cold months, observations occurred from 06:30 – 18:00. Observations were conducted at between 15-20m from the colonies. Every 5 min., I recorded the frequency of the behaviours listed in Table 1, using 10x50 binoculars. At every 15 min. interval, I counted the number of visible individuals for the colony and I recorded ambient temperatures at hourly intervals, using a standard maximum-minimum thermometer maintained in an open area for the duration of each observation day. For comparative purposes, I used techniques similar to those of Fourie (1983). To establish the occurrence of nocturnal activity, I placed a camera trap (Bushnell Trophy Cam Essential HD) facing the den at each of the colonies for one week per colony and surveyed camera trap footage for rock hyrax activity outside of the den locations between sunset and sunrise (17:45 – 07:00).

To compare behaviours over time for the three colonies sampled, I combined the frequency of each behaviour per hour for each colony for the warm and for the cold months. I generated line graphs for each behaviour per season and visualised patterns before applying statistical analyses.

I ran a generalised mixed (glmer) repeated measures effects model with colony, season and behaviour as fixed effects, frequency of behaviours as the dependent, hourly temperature and colony size as covariates, and months as a random effect, using R version 3.1.2 (R Core Team 2014), using the lme4 package (Bates et al. 2014). To obtain model convergence, I omitted aggressive behaviour from the data set. Wald $\chi 2$ test statistics, generated with type III sum of squares, are presented. I conducted Tukey post-hoc analyses

Table 1. Behaviours scored for rock hyrax, *Procavia capensis*, activity patterns adapted from Fourie (1983).

| **Behaviour** | **Behaviours termed by Brown & Downs (2005) and Fourie (1983)** | **Definition** |
|---|---|---|
| Basking | Basking hunched, basking (two of four positions) | Sitting in a hunched position with piloerection and with the head held up into the body and legs tucked underneath with the belly touching the rock surface or not. |
| Sunbathing | Basking flat, basking (two of four positions) | Lying against the rock with legs outstretched either on the belly or the side |
| Vigilance | | Sitting in a hunched position with the head held up, back against the rock, protruding through a gap in the rock or on top of the rock. Movement of potential threats is tracked by head movements |
| Travelling | Moving | Movement, such as jumping, walking, and running, from one location to another |
| Feeding | Foraging | Actively eating vegetation –mastication visible |
| Grooming | | Using teeth or scratching with hind feet to groom |
| In refuge | Refuge, Den | Not visible outside the den and/or visible within the den entrances |
| Social Behaviour: | | |
| <u>Aggressive behaviour</u> | | |
| Chasing | | Running after another individual accompanied by vocalisation, usually causing it to flee |
| <u>Amicable behaviour</u> | | |
| Allogrooming | | Grooming of another individual or being groomed by another individual |
| Sniffing | | Sniffing another individual or being sniffed by another rock hyrax in an amicable manner |
| Huddling | | Sitting in body contact with another individual |
| Heaping | | Sitting on top of another individual (usually young on adults) and usually at low temperatures |
| Playing | | Small individuals or juveniles chasing one another close to the den |

using the glht() function from the multcomp package (Hothorn et al. 2008) in R for all significant fixed effects and their interactions.

To compare my findings to those of the rock hyrax population from the MZNP (Fourie 1983), I pooled my data for the two days per season per colony because Fourie (1983) had pooled his data for summer (February - April) and winter (May - July) respectively. I combined sunbathing and basking to form a basking/sunbathing category because these had been combined by Fourie (1983). I pooled grooming, vigilance, amicable and aggressive behaviours from the three colonies at Meyersdal Eco Estate and sandbathing and in refuge from MZNP and categorised them as "other" to enable comparison with Fourie's (1983) data. I converted all pooled data into a percentage for comparison and generated stacked bar graphs for each colony (cul-de-sac, rubble dump and boulder pile) and the MZNP population for warm and cold months. I visually identified patterns since statistical comparisons with Fourie's (1983) data were not possible.

**Diet**

To establish what rock hyraxes fed on at each colony, during the behavioural activity observations, I used 10x50 binoculars to observe individuals when feeding and to identify the plants eaten. These observations lasted until the plant was identified or the individual stopped feeding and the location of the plant was identified. From these observations, I recorded plants that I could identify on site, otherwise I took cuttings of the plants to identify *ex situ* at the University of Witwatersrand with assistance from Dr Rene Reddy, manager of the C.E. Moss Herbarium. I also took photographs of the plants as additional aids for identification. I conducted observations during warm and cold months. Due to rock hyraxes moving out of sight to an enclosed area with no immediate access at the colonies closest and furthest from people, I could not make comparisons between the cold and warm months of observed plants eaten. Therefore, I could not test the predictions to compare cold and warm months. Instead, I compared the plant species consumed at each colony generally.

I identified plants to species level where possible and grouped plants according to a plant growth-form classification scheme (IUCN 2013) into graminoid (grasses), forbs (herbaceous, flowering plants), shrubs (small to medium sized woody plants), trees (large woody plants), and succulents (fleshy leaf or stemmed plants). I created an additional

category called garden plants that contained cultivated plants species found in the Meyersdal Eco Estate gardens, excluding trees. I tabulated all plants that rock hyraxes fed upon in each colony.

**Flight initiation distance (FID)**

Using the methods of Chapman et al. (2012), I measured FID, in metres, using a laser range finder (Skil 20m Laser Range Finder Xact 0530; accuracy: ± 3.0mm). To ascertain the FID of rock hyraxes in the three colonies, I randomly selected a focal individual and walked towards the individual hyrax from a starting position of about 20m away. I pointed the range finder laser on the ground just in front of the rock hyrax and recorded the distance when the rock hyrax moved away or fled from me. To remove observer bias, I conducted all observations. Ten different individuals were sampled (by focusing on different parts of the colony to avoid selecting the same individual twice) in each colony in the warm and cold months. Since the rock hyraxes were not marked, it is possible that I tested some individuals across seasons.

To assess the effects of a preferred food resource on the FID of the rock hyraxes, I used a food incentive (Golden Delicious apples). I placed 3 large floor tiles (400x400mm) permanently at the rubble dump colony at least a week before all FID experiments but, at the other two colonies, I placed tiles on the days of the FID experiments due to building disturbance during the weekdays and theft. Tiles were used as they were an easily sourced, flat surface of a chosen natural-looking colour (dusty brown) that was low to the ground and would allow a standardised surface for presenting an incentive food item for all experiments regardless of the location of the colonies**.** I started FID observations at these colonies 10-15 min. after rock hyraxes emerged from the dens following the placement of the tiles. I positioned tiles approximately 2-5m within the vicinity of the rock hyrax den and 2-5m from the next tile during the experiments. I cut a small apple into 0.5cm slices and diced each slice into about 1cm pieces. I placed 2-4 apple pieces in the centre of the tile and when a rock hyrax fed on the incentive, I measured FID using the same method as above. I conducted these observations on 10 different individuals at each colony in the warm and cold months.

Using Statistica v7.1 (Statsoft, Inc 2006), I ran a general linear model (GLM) with colony, season and treatment as fixed effects and the FID measurement as the dependent,

with a repeated measures (with and without incentive) design. I ran Fisher's post-hoc comparisons for all significant fixed effects and their interactions. To assess whether the experimental design itself led to a decrease in FID which would indicate habituation to the experimental procedure, I ran a simple regression for the between FID scores (with and without incentive) and trial number from 1 to 10 per colony for the warm and cold months.

**Deterrents**

I assessed the efficacy of two potential deterrents, boa dung (a predator odour) and wild garlic (an indigenous plant with a strong odour), for deterring rock hyraxes from a food incentive. I used boa dung as the colonies had not been exposed to this deterrent previously (Andrew Jackson pers. comm.).

I used fresh boa dung from Andrew Jackson and stored it in a sealable plastic bag at -18°C until the day of use, when I allowed it to thaw and moistened it with lukewarm water. I collected the wild garlic leaves 24-48 hrs before the experiments and stored them in sealable, plastic bags at 5°C until the day of experimentation when I transferred them to a cooler bag until used. I presented the deterrents on three large tiles (400x400mm). Using latex gloves, I spread each of the deterrents along the edge of the tiles to ensure the food incentive was surrounded by the deterrent. For the wild garlic, I spread the leaves along the edges ensuring that they overlapped. For the boa dung, I pulled apart pieces of the moistened dung and spread these pieces together with the juices along the tile edges. I then placed 2-4 apple pieces (prepared as in the FID methods) in the centre of each of the tiles.

I started a timer once I placed the incentive on the tile and I stopped the timer when the individual rock hyrax started eating the apple, which was the latency (in seconds) for when a hyrax approached the apple. I tested each of the deterrents separately starting with the wild garlic then the boa dung with a minimum of a week between switching deterrents. I repeated this procedure until there were measurements for ten different individuals for each colony and treatments for the warm and cold months. As a control, I measured latency (as described above) to approach the apple in the centre of the tile without the deterrents present for ten individuals per colony for the warm and cold months.

Using Statistica v7.1 (Statsoft, Inc 2006), I ran a general linear model (GLM) with colony, season and treatment as fixed effects and the latency as the dependent, with a

repeated measures (control, wild garlic, boa dung) design. I ran Fisher's post-hoc comparisons on all significant fixed effects and their interactions. I used an orthogonal polynomial decomposition for linear and quadratic components to assess whether differences in latency for the treatments between colonies and seasons were random (interaction colony × season ×treatment). To assess whether the experimental design itself led to a decrease or increase in latency which would indicate habituation or sensitisation respectively to the experimental procedure, I ran a simple regression for the between latency scores (boa dung and wild garlic) and trial number from 1 to 10 per colony for the warm and cold months.

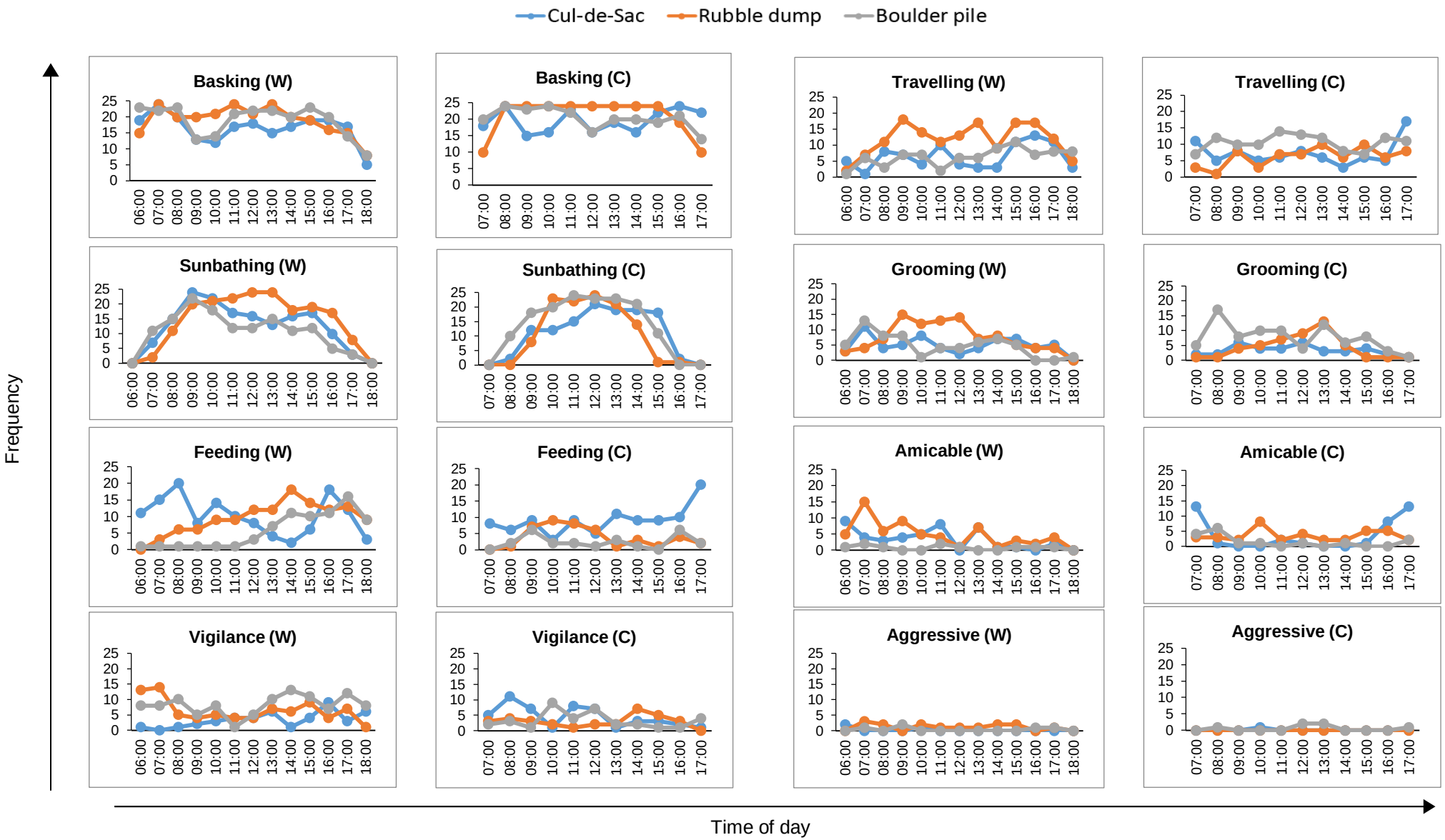
## Results

### Activity patterns

*Daylight activity patterns along gradient of human proximity at Meyersdal Eco Estate*

The comparison of behaviours over time for the three colonies sampled in the warm and cold months is shown in Figure 2. Basking had the highest frequency of all the behaviours, and frequencies remained high throughout the day for the warm and cold months. In the warm months, basking showed a bimodal pattern, peaking in the early morning and again around midday with a gradual decrease throughout the afternoon before decreasing greatly in the last 2 hours of the day. The cold months showed different patterns of basking frequency among the three colonies, fluctuating throughout the day at the cul-de-sac colony. For the rubble dump colony, basking increased during the early morning and remained high throughout the day before decreasing greatly in the last three hours of the day. The boulder pile colony showed a bimodal basking pattern, peaking in the early to mid-morning and again during the early afternoon to mid-afternoon before decreasing in the last hour of sampling (Figure 2).

Sunbathing had the second highest frequency (Figure 2). The three colonies showed similar patterns within the warm and cold months, although sunbathing frequency decreased overall during the cold months compared to the warm months. In the warm months, sunbathing showed a bimodal pattern with the first peak for the cul-de-sac and boulder pile colonies occurring around mid-morning while, at the rubble dump colony, the peak occurred later around midday. The second peak for the colonies occurred around mid-afternoon before the frequency for sunbathing decreased greatly in the last three hours of the day. In the cold months, sunbathing showed a unimodal pattern, increasing during the morning and peaking around midday before decreasing greatly until the end of the day (Figure 2).




420 Figure 2. Daylight activity patterns of rock hyrax colonies during the warm (W – February and September) and cold (C – June and July)
421 months for basking, sunbathing, feeding, grooming, travelling, vigilance, amicable, and aggressive behaviours. Blue line = cul-de-sac
422 colony, orange line = rubble dump colony, grey line = boulder pile colony.

Feeding varied for the three colonies within the warm and cold months (Figure 2). In the warm months, the rubble dump and boulder pile colonies showed a gradual increase in feeding throughout the day while the cul-de-sac colony had high frequencies of feeding during the morning that gradually decreased in the afternoon. However, feeding peaked in the late afternoon for all three colonies. In the cold months, the rubble dump and boulder pile colonies showed a peak in feeding frequency in the morning while the cul-de-sac colony had feeding fluctuations throughout the day with an increase in feeding in the afternoon, peaking in the last hour of sampling (Figure 2).

Vigilance varied throughout the day for both warm and cold months (Figure 2). The cul-de-sac colony showed a peak in vigilance in the afternoon for the warm months. The rubble dump and boulder pile colonies started with high vigilance in the morning in the warm months and the frequency fluctuated throughout the rest of the day. In the cold months, the cul-de-sac colony had a peak in the morning for the cold months, while vigilance peaked around midday for the boulder pile colony and in the afternoon for the rubble dump colony (Figure 2).

Travelling varied in the warm months for the three colonies but remained similar in the cold months (Figure 2). In the warm months, all the colonies started and ended the day with low travelling compared to the cold months. The cul-de-sac colony had a peak in the late morning and late afternoon. The boulder pile colony had a peak around mid-morning dropping at midday before steadily increasing throughout the afternoon. The rubble dump colony had the highest travelling frequency that peaked in the mid-morning, early afternoon and again in the late afternoon before decreasing in the last 2 hours of observations. In the cold months, all three colonies started and ended the day with greater travelling than in the warm months. The three colonies showed similar peaks in the morning, around midday and in the late afternoon (Figure 2).

Grooming varied for the three colonies within the warm and cold months (Figure 2). In the warm months, the cul-de-sac and boulder pile colonies showed a bimodal pattern with a peak in the early morning and in the mid-afternoon, before grooming at the boulder pile colony stopped altogether in the late afternoon. The rubble dump colony showed a unimodal pattern where grooming increased throughout the morning, peaked around mid-morning and decreased from midday through the rest of the afternoon. In the cold months, the boulder pile colony showed a bimodal pattern with peaks in the early morning and early afternoon. The rubble dump colony showed a unimodal pattern where grooming increased throughout the morning, peaked around the

early afternoon before decreasing and stopping in the late afternoon. The cul-de-sac colony had low frequencies of grooming throughout the day (Figure 2).

Amicable behaviour varied in the three colonies for the warm and cold months (Figure 2). In the warm months, the frequency was high in the first hour of the morning for the cul-de-sac and rubble dump colonies. The cul-de-sac colony showed decreased amicable behaviour thereafter while the rubble dump colony had variable peaks of amicable behaviour throughout the day. The boulder pile colony had a low frequency of amicable behaviour throughout the day. In the cold months, the cul-de-sac colony showed peaks of amicable behaviour in the early morning and late afternoon which coincided with basking. Amicable behaviour in the rubble dump colony varied throughout the day while the boulder pile colony only showed a peak in the morning (Figure 2).

Aggressive behaviour was low throughout the day for both the warm and cold months for all three colonies (Figure 2).

*Behavioural comparisons along a gradient of human proximity*

Comparisons of basking, sunbathing, feeding, vigilance, travelling, grooming and amicable behaviours made using the glmer() function with a repeated measures design indicated that colony (Wald $\chi^2_2 = 15.162$, $p < 0.001$), behaviour (Wald $\chi^2_6 = 289.649$, $p < 0.001$), colony size (Wald $\chi^2_1 = 54.290$, $p < 0.001$), colony × behaviour (Wald $\chi^2_{12} = 101.494$, $p < 0.001$), season × behaviour (Wald $\chi^2_6 = 72.387$, $p < 0.001$), and colony × season × behaviour (Wald $\chi^2_{12} = 77.151$, $p < 0.001$) were significant predictors of behaviour. Season (Wald $\chi^2_1 = 1.142$, $p = 0.285$), minimum temperature (Wald $\chi^2_1 = 0.350$, $p = 0.554$), and colony × season (Wald $\chi^2_2 = 1.918$, $p = 0.383$) were not significant predictors.

Temperature was not a significant covariate. In support, similar ambient temperatures were recorded in the three sites for the warm months: 10-25°C for the cul-de-sac colony; 14-31°C for the rubble dump colony; and 12-33°C for the boulder pile colony. For the cold months, the temperatures ranged between 1-17°C for the cul-de-sac colony, 8-22°C for the rubble dump colony, and 1-20°C for the boulder pile colony. The MZNP population experience ambient temperatures between 3-30°C for the warm months and -4-24°C in the cold months.

The Tukey post-hoc tests revealed that basking was the most common behaviour (Figure 3). Sunbathing had the second highest level of occurrence and showed similar levels of occurrence to travelling. Travelling also showed similar levels of occurrence to grooming. Feeding showed similar levels to vigilance and amicable behaviour (Figure 3).

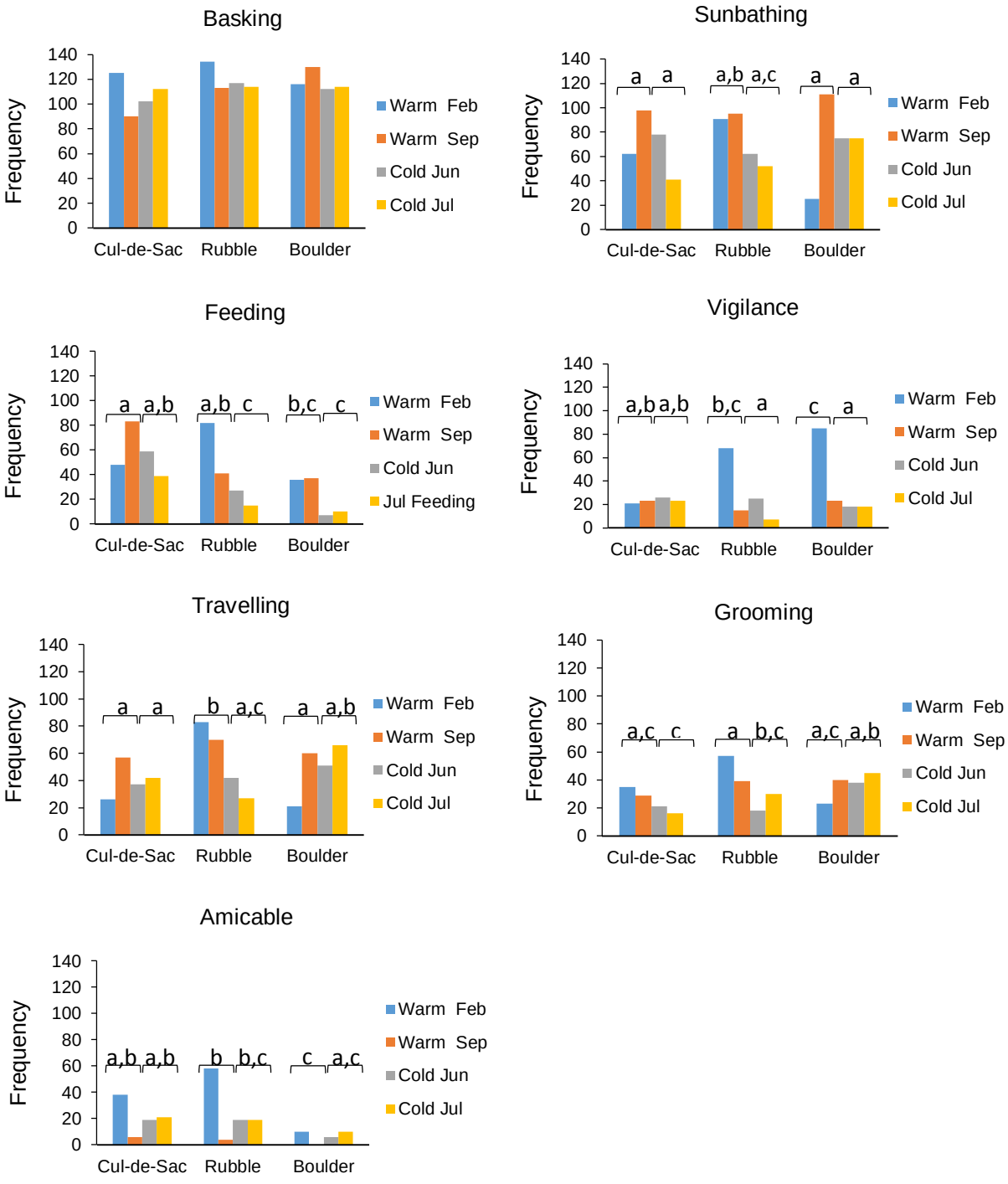


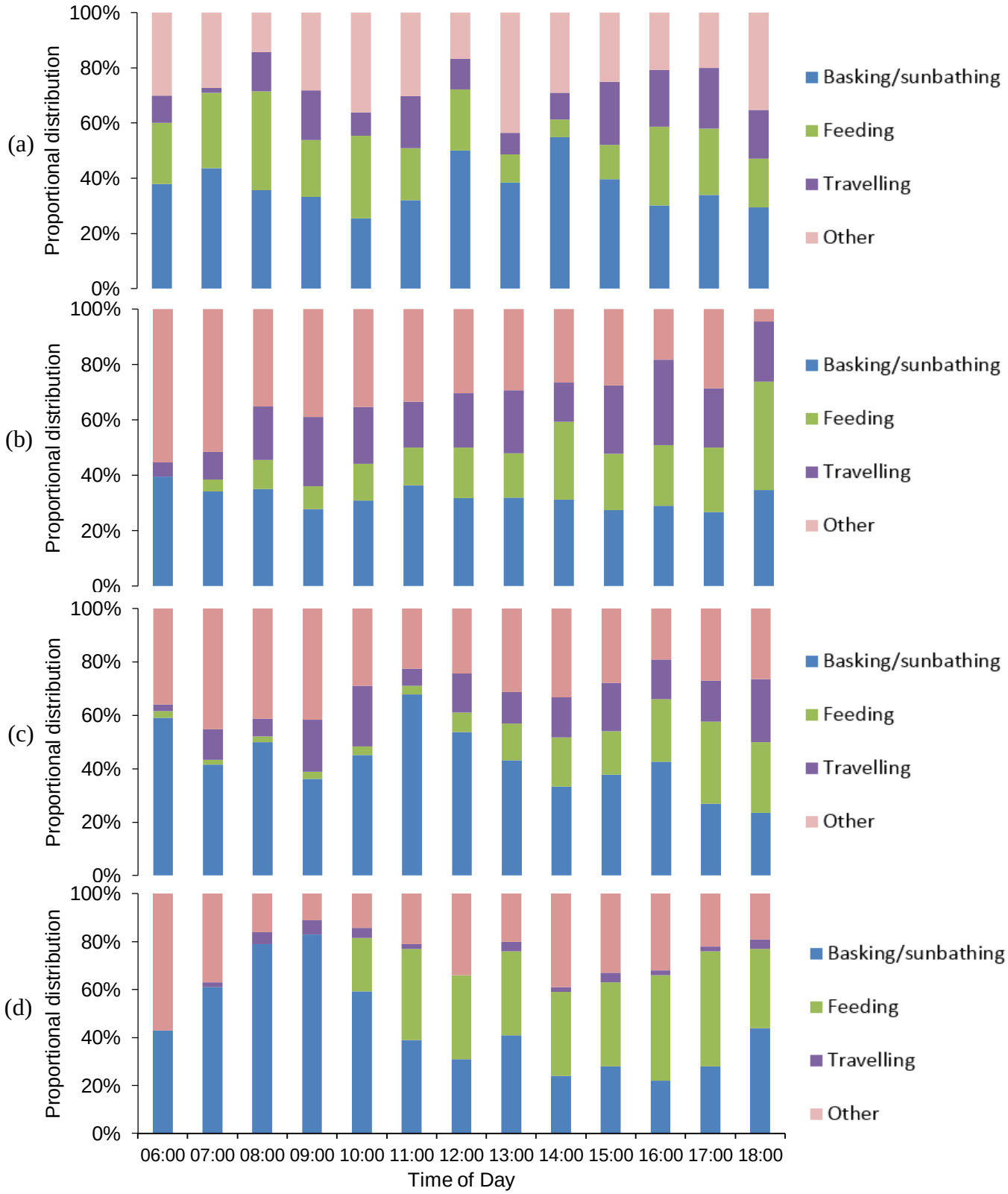

Figure 3. Frequency of rock hyrax basking, sunbathing, travelling, feeding, grooming, vigilance and amicable behaviour for all three colonies (cul-de-sac, rubble dump and boulder pile) for the warm (February and September) and cold (June and July) months. Significantly different post-hoc interactions are represented by different alphabets.

Due to the complexity of the colony × season × behaviour interaction, I chose to present only two-way interactions for colony × behaviour and season × behaviour in Figure 3. For the colony × behaviour interaction, basking had the highest level of occurrence for all three colonies while amicable behaviours were lowest at the boulder pile colony (Figure 3). There were no significant differences among the three colonies in levels of basking, sunbathing, travelling, grooming, and vigilance (Figure 3). Feeding showed similar levels of occurrence between the cul-de-sac and rubble dump colonies and was greater than feeding at the boulder pile colony. Amicable behaviours also showed similar levels of occurrence between the cul-de-sac and rubble dump colonies and both were greater than the boulder pile colony (Figure 3). Within the cul-de-sac colony, feeding had similar levels of occurrence to sunbathing and travelling but travelling was lower than sunbathing. Vigilance, grooming and amicable behaviours had the lowest levels of occurrence at this colony. Within the boulder pile colony, the levels of occurrence for feeding was lower than sunbathing, travelling, vigilance and grooming but had higher levels of occurrence than amicable behaviours. The rubble dump colony had an intermediate behavioural response to both the other colonies with travelling having similar levels of occurrence to sunbathing and feeding but feeding had lower levels of occurrence than sunbathing. Grooming, vigilance and amicable behaviours had the lowest levels of occurrence at this colony.

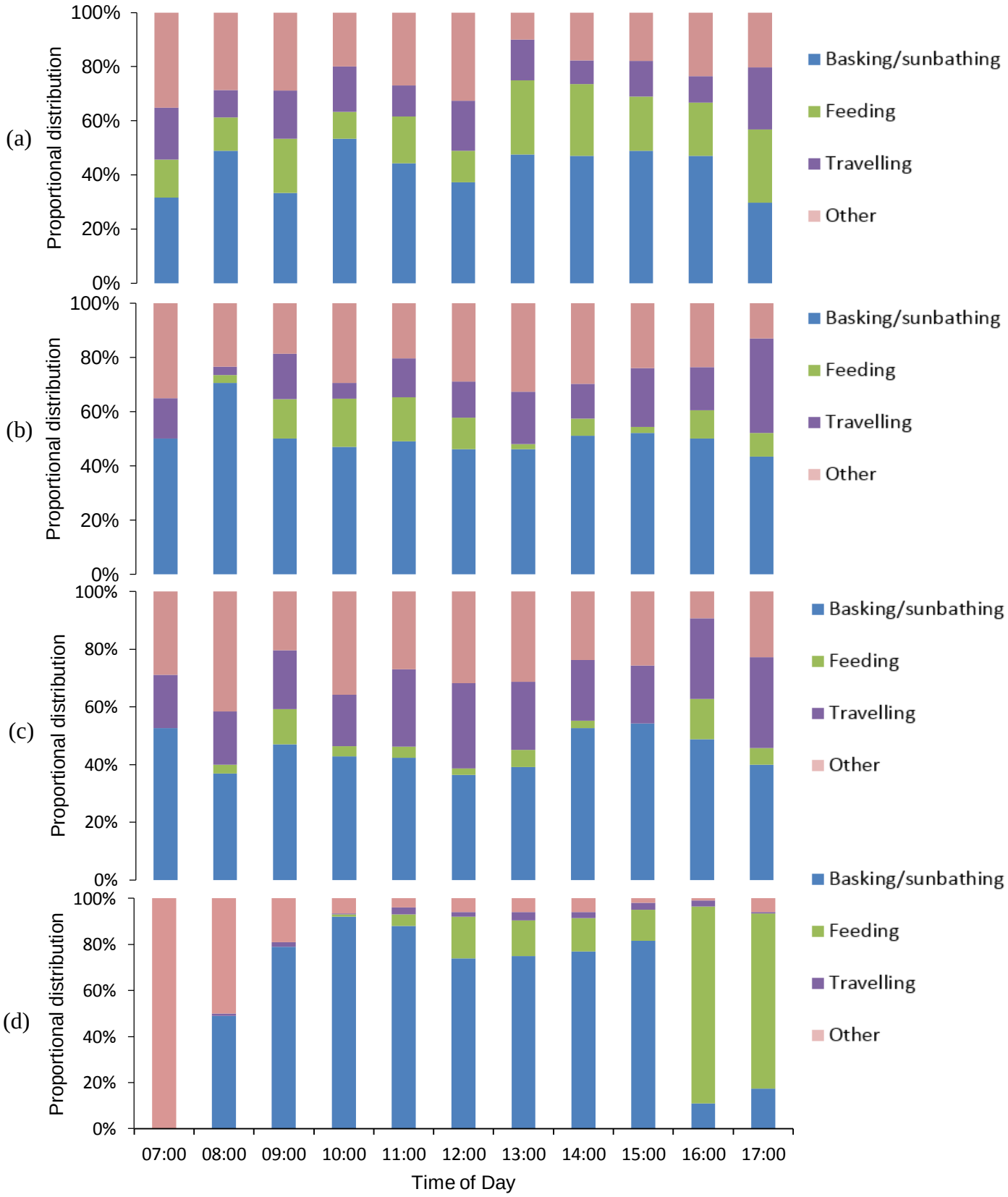
For the season × behaviour interaction, basking had the highest levels of occurrence while amicable behaviours had the lowest levels of occurrence for the warm and cold months (Figure 3). There were no differences in each of the levels of occurrence for basking, sunbathing, travelling and grooming in the warm and cold months (Figure 3). Vigilance, feeding and amicable behaviours had higher levels of occurrence in the warm months than in the cold months (Figure 3). Within both the warm and cold months, sunbathing occurred more frequently than the remainder of the behaviours. Within the warm months, feeding and travelling had similar levels of occurrence, which were higher than the similar levels of occurrence between grooming and vigilance. Amicable behaviour had the lowest levels of occurrence. Within the cold months, travelling had higher levels of occurrence than grooming, feeding and vigilance which were similar in their levels of occurrence. Although amicable behaviours had lower levels of occurrence than the remainder of the behaviours, it showed similar levels of occurrence to vigilance.

*Comparison with MZNP*

During the warm months (Figure 4), the colonies differed in their basking/sunbathing activity whereby the MZNP population had a peak in basking/sunbathing proportions in the early morning while the boulder pile colony had a peak in the later morning with the cul-de-sac and rubble dump colonies showing no definite peaks in proportions throughout the day. Feeding had




528 Figure 4. Proportion of basking/sunbathing, feeding, travelling and other behaviours during
529 daylight hours for rock hyrax colonies in the warm (February and September) months for boulder
530 pile (a), rubble dump (b), cul-de-sac (c) and MZNP for summer (February - April) (d, after Fourie
531 1983).




532 Figure 5. Proportion of basking/sunbathing, feeding, travelling and other behaviours during
533 daylight hours for rock hyrax colonies in the cold (June and July) months for boulder pile (a),
534 rubble dump (b), cul-de-sac (c) and MZNP for winter (May-July) (d, after Fourie 1983).

similar frequencies among the three colonies and the MZNP population, although feeding at the three colonies occurred throughout the day while feeding at the MZNP population was greater from late morning throughout the afternoon. Travelling was high at the three colonies compared to the MZNP population which had low proportions of travelling. Proportions of other behaviours were higher at the three colonies compared to the MZNP population and occurred throughout the day for the three colonies and the MZNP population (Figure 4).

During the cold months (Figure 5), the MZNP population had high basking/sunbathing proportions from mid-morning until mid-afternoon where basking proportions were low in the late afternoon. Basking/sunbathing proportions were similar for the three colonies throughout the day and basking/sunbathing proportions were generally higher at the MZNP population. Feeding proportions were low for the early afternoon for the MZNP population but increased to very high proportions in the late afternoon while feeding occurred throughout most of the day at the three colonies. Travelling at the MZNP population as well as at the three colonies occurred throughout most of the day. However, these proportions were lowest at the MZNP population. Proportions of other behaviours were lowest at the MZNP population being only high in the morning before decreasing to low proportions for the rest of the day compared to the three colonies in my study where the proportions of other behaviours were relatively high throughout the day (Figure 5).

*Nocturnal activity*

Rock hyraxes from the cul-de-sac colony were active up to 1.5 hours after sunset but this activity occurred irregularly. Rock hyraxes from the cul-de-sac and rubble dump colonies showed later nocturnal activity on one occurrence and on the same evening between 00:00 – 00:30. Apart from these instances, I found no other evidence of rock hyrax activity after sunset and before sunrise at each of the colonies.

**Diet**

The observed plants species eaten by rock hyraxes at the three colonies is shown in Table 2. I observed rock hyraxes feeding on a variety of plant growth-forms. At the cul-de-sac colony, they fed on a greater variety of plants especially in the forb and garden plant categories and was the only colony that fed on garden plants. Rock hyraxes at the rubble dump colony fed on plants from most categories except plants from the garden plants category. Rock hyraxes from the boulder pile colony fed on the least variety of plants and I observed rock hyraxes eating more plants from tree growth-form than did the other colonies.

567 Table 2. Observations of the plant species eaten by rock hyraxes at each of the three colonies (cul-de-sac, rubble dump and boulder pile). Plant
568 species are grouped under plant growth-forms for comparison.

| Plant life form | Cul-de-sac | | Rubble dump | | Boulder pile | |
|---|---|---|---|---|---|---|
| | Common name | Scientific name | Common name | Scientific name | Common name | Scientific name |
| Graminoid | Common turpentine grass | *Cymbopogon excavatus* | | | Common turpentine grass | *Cymbopogon excavatus* |
| | Common thatching/ blue grass | *Hyparrhenia hirta* | | | Common thatching/ blue grass | *Hyparrhenia hirta* |
| | | | Kikuyu grass | *Pennisetum clandestinum* | | |
| | | | Pampas grass | *Cortaderia selloana* | | |
| Forb | Black-jack | *Bidens pilosa* | Black-jack | *Bidens pilosa* | Black-jack | *Bidens pilosa* |
| | Khakibush | *Tagetes minuta* | Khakibush | *Tagetes minuta* | Khakibush | *Tagetes minuta* |
| | Thorn apple | *Datura stramonium* | Thorn apple | *Datura stramonium* | | |
| | Prostrate sandmat | *Euphorbia prostrata* | Prostrate sandmat | *Euphorbia prostrata* | | |
| | Horseweed/ butterweed/ fleabane | *Conyza spp.* | | | | |
| | Forest inkberry | *Phytolacca octandra* | | | | |
| Shrub | | | Cape gooseberry | *Physalis peruviana* | | |
| Tree | | | Mountain/ Highveld cabbage tree | *Cussonia paniculata* | Mountain/ Highveld cabbage tree | *Cussonia paniculata* |
| | Karee | *Searsia lancea* | Karee | *Searsia lancea* | Karee | *Searsia lancea* |
| | | | | | Wild peach | *Kiggelaria africana* |
| Succulent | Spotted aloe | *Aloe greatheadii* | Spotted aloe | *Aloe greatheadii* | Spotted aloe | *Aloe greatheadii* |
| | Tree aloe | *Aloe barberae* | | | | |
| Garden plants | Agapanthus / Lily of the Nile | *Agapanthus praecox* | | | | |
| | Cape wild garlic (green) | *Tulbaghia violacea* | | | | |
| | Sweet wild garlic (grey-green) | *Tulbaghia simmleri* | | | | |
| | Spider plant/ airplane plant/ hen-and-chicken | *Chlorophytum comosum variegatum* | | | | |
| | Cape honeysuckle | *Tecoma capensis* | | | | |

569

**Flight Initiation Distance (FID)**

I measured flight initiation distance (FID) with and without the provision of apple. Colony ($F_{2, 108} = 12.21$; $p < 0.001$) and treatment ($F_{1, 108} = 23.28$; $p < 0.001$) were significant predictors of FID. Fisher's post-hoc comparisons showed that FID values increased along the gradient of human proximity from closest to people, the cul-de-sac colony, to furthest from people, the boulder pile colony (Figure 6). The FID values for treatments were higher for the treatment without apple and decreased for the treatment with apple present. The boulder pile colony had the largest decrease in FID measurement between the two treatments during the cold months (Figure 6). Season ($F_{1, 108} = 0.04$; $p = 0.838$), colony × season ($F_{2, 108} = 0.26$; $p = 0.773$), colony × treatment ($F_{2, 108} = 1.88$; $p = 0.158$), season × treatment ($F_{1, 108} = 2.66$; $p = 0.106$), and colony × season × treatment ($F_{2, 108} = 0.25$; $p = 0.793$) were not significant predictors of FID.

I ran a simple regression to test for habituation to the experimental setup. There was no evidence of habituation in each colony and season (Table 3) except for the rubble dump colony during the warm months for FID without apple ($R^2 = 0.55$, $F_{1, 8} = 9.76$, $p = 0.014$) (Table 3). This indicates that rock hyraxes mostly did not become accustomed to repeated testing.

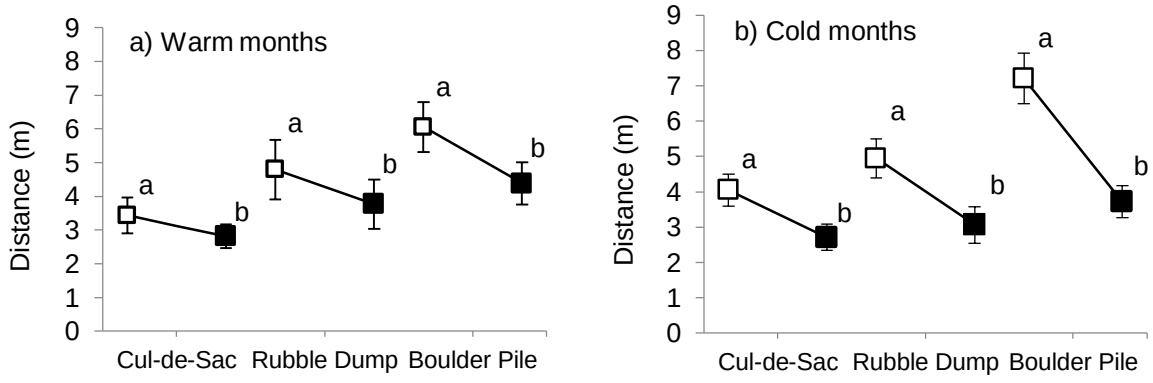



Figure 6. FID (m) recorded for rock hyraxes in treatments without apple present (open squares) and with apple present (closed squares) at the three colonies (cul-de-sac, rubble dump and boulder pile) in a) warm (February and September) and b) cold (June and July) months. Values are given as mean (±SE) metres. Points with the same alphabet in each season are not significantly different (Fisher's post-hoc comparisons).

Table 3. Results of a simple regression between FID scores (with and without apple) in trials 1 to 10 per colony per season for the three colonies (cul-de-sac, rubble dump and boulder pile). Bold values indicate significant correlation.

| Colony | Season | Treatment | Statistics |
|---|---|---|---|
| Cul-de-sac | Warm months | Without apple | $R^2$ = 0.02, $F_{1, 8}$= 0.13, $p$ = 0.727 |
| Cul-de-sac | Warm months | With apple | $R^2$ = 0.03, $F_{1, 8}$= 0.23, $p$ = 0.647 |
| Cul-de-sac | Cold months | Without apple | $R^2$ = 0.02, $F_{1, 8}$= 0.13, $p$ = 0.730 |
| Cul-de-sac | Cold months | With apple | $R^2$ = 0.30, $F_{1, 8}$= 3.46, $p$ = 0.100 |
| Rubble dump | Warm months | Without apple | **$R^2$ = 0.55, $F_{1, 8}$= 9.76, $p$ = 0.014** |
| Rubble dump | Warm months | With apple | $R^2$ = 0.09, $F_{1, 8}$= 0.76, $p$ = 0.409 |
| Rubble dump | Cold months | Without apple | $R^2$ = 0.00, $F_{1, 8}$= 0.01, $p$ = 0.928 |
| Rubble dump | Cold months | With apple | $R^2$ = 0.17, $F_{1, 8}$= 1.61, $p$ = 0.239 |
| Boulder pile | Warm months | Without apple | $R^2$ = 0.02, $F_{1, 8}$= 0.12, $p$ = 0.737 |
| Boulder pile | Warm months | With apple | $R^2$ = 0.01, $F_{1, 8}$= 0.11, $p$ = 0.750 |
| Boulder pile | Cold months | Without apple | $R^2$ = 0.00, $F_{1, 8}$= 0.01, $p$ = 0.910 |
| Boulder pile | Cold months | With apple | $R^2$ = 0.16, $F_{1, 8}$= 1.49, $p$ = 0.257 |

**Deterrents**

The three treatments (garlic chives, boa dung, and control) made it possible to investigate the efficacy of potential deterrents versus the motivation to overcome potentially dangerous stimuli with the reward of access to resources (i.e. apple). Colony ($F_{2, 162}$= 28.78; $p < 0.001$), treatment ($F_{2, 162}$ = 9.36; $p < 0.001$), colony × season ($F_{2, 162}$ = 32.83; $p < 0.001$), colony × treatment ($F_{4, 162}$ = 8.09; $p < 0.001$), and colony × season × treatment ($F_{4, 162}$ = 6.83; $p < 0.001$) were significant predictors for the latency to approach the apple. Season ($F_{1, 162}$ = 0.99; p = 0.321) and season × treatment ($F_{2, 162}$ = 2.95; p = 0.055) were not.

Fisher's post-hoc comparisons revealed that regardless of the treatment, latency was shortest for the rubble dump colony and longest for the boulder pile colony (furthest away from people). Latency for treatment was longest for the boa dung than that for the wild garlic and control (Figure 7).

For the colony × season interaction (Figure 7), latency was shortest at the rubble dump colony for the cold months and at the cul-de-sac colony for the warm months and latency was longest at the cul-de-sac colony in the cold months and the boulder pile colony in the warm months (Figure 7).

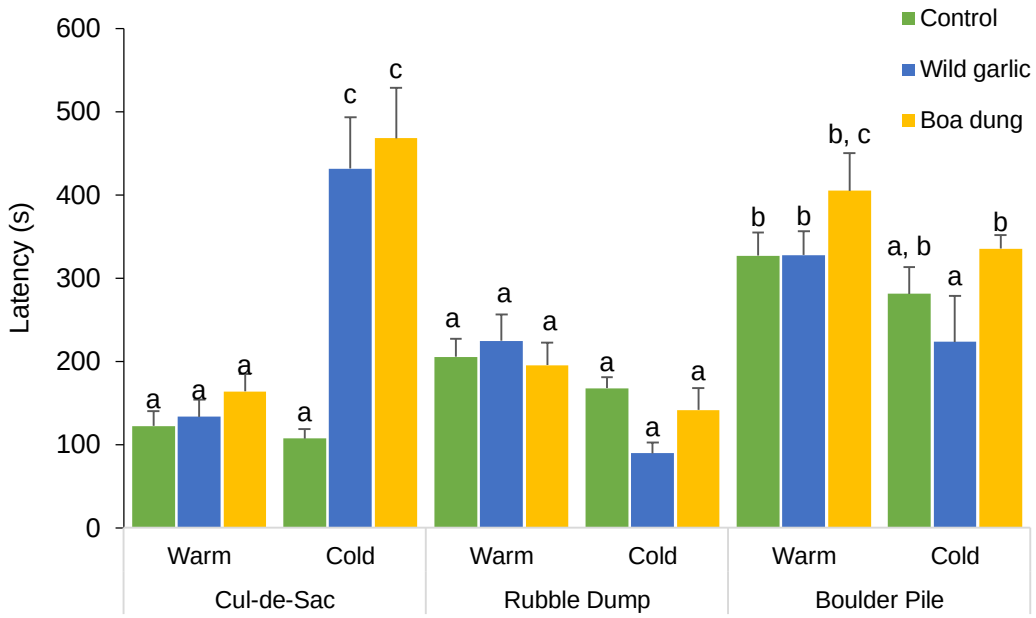



Figure 7. Latency (s) for rock hyraxes to approach three treatments (control, wild garlic and boa dung) in the warm (February and September) and cold (June and July) months at the three colonies along the gradient of human proximity (cul-de-sac, rubble dump and boulder pile). Values are given as mean (±SE) seconds. Bars with the same alphabets are not significantly different (Fisher's post-hoc comparisons).

For colony x treatment (Figure 7), the cul-de-sac colony showed the shortest latency for the control treatment and longest latency for the boa dung treatment. The rubble dump showed similar latencies for all treatments while the boulder pile colony showed equally short latencies for the wild garlic and control treatments and longest latency for boa dung treatment. For the control treatment, the cul-de-sac colony had the shortest latency while the boulder pile colony had the longest. For both the wild garlic and boa dung treatments, the rubble dump colony had the shortest latency while both the boulder pile and cul-de-sac colonies had the longest latencies (Figure 7).

For the colony × season × treatment interaction, polynomial contrasts were significant for the linear component ($t = -2.86$, $p = 0.005$) but not for the quadratic component ($t = -0.65$, $p = 0.516$), indicating a general linear increase in latency from the control treatment to the boa dung treatment in the warm months to those in the cold months along a gradient of human proximity from the cul-de-sac colony to the boulder pile colony.

A simple regression between latency and trial number (1-10) was run to test for habituation or sensitisation and showed that there was no correlation in each colony and season (Table 4) except for weak correlation between the latency and trial number for the

681 boulder pile colony during the cold months for the boa dung treatment and the cul-de-sac
682 colony during the cold months for the control treatment (Table 4). This indicates that,
683 generally, rock hyraxes did not become accustomed or sensitised to repeated testing.

684

685 Table 4. Results of a simple regression between latency scores for treatment in trials 1 to 10
686 per colony per season for the three colonies (cul-de-sac, rubble dump and boulder pile). Bold
687 values indicate significant correlation.

| Colony | Season | Treatment | Statistics |
|---|---|---|---|
| Cul-de-sac | Warm months | Control | $R^2$ = 0.00, $F_{1, 8}$= 0.03, $p$ = 0.862 |
| Cul-de-sac | Warm months | Wild garlic | $R^2$ = 0.02, $F_{1, 8}$= 0.20, $p$ = 0.670 |
| Cul-de-sac | Warm months | Boa dung | $R^2$ = 0.00, $F_{1, 8}$= 0.01, $p$ = 0.929 |
| Cul-de-sac | Cold months | Control | **$R^2$ = 0.48, $F_{1, 8}$= 7.30, $p$ = 0.027** |
| Cul-de-sac | Cold months | Wild garlic | $R^2$ = 0.00, $F_{1, 8}$= 0.00, $p$ = 0.971 |
| Cul-de-sac | Cold months | Boa dung | $R^2$ = 0.03, $F_{1, 8}$= 0.29, $p$ = 0.605 |
| Rubble dump | Warm months | Control | $R^2$ = 0.02, $F_{1, 8}$= 0.14, $p$ = 0.714 |
| Rubble dump | Warm months | Wild garlic | $R^2$ = 0.26, $F_{1, 8}$= 2.81, $p$ = 0.132 |
| Rubble dump | Warm months | Boa dung | $R^2$ = 0.11, $F_{1, 8}$= 0.99, $p$ = 0.349 |
| Rubble dump | Cold months | Control | $R^2$ = 0.19, $F_{1, 8}$= 1.85, $p$ = 0.211 |
| Rubble dump | Cold months | Wild garlic | $R^2$ = 0.00, $F_{1, 8}$= 0.00, $p$ = 0.954 |
| Rubble dump | Cold months | Boa dung | $R^2$ = 0.15, $F_{1, 8}$= 1.37, $p$ = 0.276 |
| Boulder pile | Warm months | Control | $R^2$ = 0.07, $F_{1, 8}$= 0.59, $p$ = 0.465 |
| Boulder pile | Warm months | Wild garlic | $R^2$ = 0.17, $F_{1, 8}$= 1.63, $p$ = 0.237 |
| Boulder pile | Warm months | Boa dung | $R^2$ = 0.00, $F_{1, 8}$= 0.02, $p$ = 0.881 |
| Boulder pile | Cold months | Control | $R^2$ = 0.02, $F_{1, 8}$= 0.16, $p$ = 0.702 |
| Boulder pile | Cold months | Wild garlic | $R^2$ = 0.02, $F_{1, 8}$= 0.16, $p$ = 0.699 |
| Boulder pile | Cold months | Boa dung | **$R^2$ = 0.42, $F_{1, 8}$= 5.70, $p$ = 0.044** |

688

Table 5. The outcome of the predictions for the four aims of this study.

| Prediction number | Prediction description | Met or not met |
|---|---|---|
| Aim 1. To establish the daylight activity patterns of rock hyraxes in three colonies along a gradient of proximity to humans in the Meyersdal Eco Estate, Alberton in the colder and warmer times of the year and to compare my findings to those of a natural population in the in the Mountain Zebra National Park, Eastern Cape Province (Fourie 1983). | | |
| i) | Basking would be the most common behaviour in the warm and cold months | Yes |
| | Sunbathing would be the second most common behaviour | Yes |
| | Feeding would be the third most common behaviour | No |
| | Sunbathing and feeding would increase in the cold months | No |
| | Vigilance would increase in the cold months | No |
| | Travelling would increase in the cold months | No |
| | Aggressive and mating behaviour would increase in the cold months | No |
| ii) | Basking would increase further from people | No |
| | Vigilance would increase further from people | No |
| | Sunbathing would decrease further from people | No |
| | Feeding would increase further from people | No |
| | Travelling would decrease closer to people | No |
| iii) | Compared to a natural population studied by Fourie (1983): | |
| | Colonies in Meyersdal Eco Estate would generally have lower proportions of basking/sunbathing activity | Yes |
| | The rock hyraxes in Meyersdal Eco Estate would have lower proportions of feeding | Yes |
| | The rock hyraxes in Meyersdal Eco Estate would have lower proportions of travelling | No |

| | | |
|---|---|---|
| Aim 2. To establish the diet of rock hyraxes in the three colonies during warm and cold months | | |
| i) | Foraging in residential gardens would increase for colony situated closest to people in the cold months but diet would remain similar to warm months. | No |
| ii) | Diet will shift from grasses in the warmer months to mostly trees and shrubs in the colder months at the colonies further from people | No |
| Aim 3. To investigate habituation to people by rock hyraxes from the three colonies through the measurement of flight initiation distances (FID) of individuals when a food incentive (apples) is provided or not, in the warm (February and September) and cold (June and July) months | | |
| i) | FIDs would be shorter in the colony situated closest to humans, indicating habituation. | Yes |
| ii) | FIDs would further decrease with the food incentive than without it, particularly in the population furthest away from people in the cold months | Yes |
| Aim 4. To ascertain whether two deterrents, namely South American red-tailed boa, *Boa constrictor constrictor*, dung and Cape wild garlic, *Tulbaghia violacea*, plants (Andrew Jackson pers. comm.), were effective in deterring rock hyraxes from a food incentive in the warm (February and September) and cold (June and July) months | | |
| i) | All colonies would show an increase in latency to approach a food incentive encircled by boa dung | Partially |
| ii) | Colony closest to people would have a shorter latency to approach a food incentive encircled with wild garlic than rock hyraxes from the other colonies. | No |
| iii) | In all colonies, the latency to approach the food incentive for both deterrents would become shorter across trials within a season | No |
| iv) | In all colonies, the latency to approach the food incentive regardless of deterrent would become shorter in the cold months | Partially |

# Discussion

## Activity patterns

The aim of my study was to assess whether the activity patterns of rock hyraxes differed along a gradient of proximity to humans in warm and cold months, and differed between an urban and non-urban population (Table 5). Rock hyraxes were predominantly inactive with basking and sunbathing being the most frequently observed behaviours. The high frequencies of basking and sunbathing are consistent with other studies that suggest rock hyraxes spend a large part of their activity period being inactive ( >90%, Sale 1970; Fourie 1983). Basking and sunbathing did not increase along the gradient of proximity to people, nor did sunbathing increase in the cold months, as predicted, and instead remained similar between the colonies and between warm and cold months. The expression of these behaviours is influenced by the interaction between the body temperature of rock hyraxes, ambient air temperatures and, the thermoneutral zone (20 – 30°C) of rock hyraxes (McNairn & Fairall 1984), indicating their thermoregulatory importance (Brown & Downs 2007). These behaviours were first thought to be used to "rewarm" rock hyraxes following shallow nocturnal hypothermia, so that other activities, such as feeding and mating, could take place (Taylor & Sale 1969; Sale 1970). However, Brown & Downs (2007) suggest that through the use of solar radiation, basking instead assists rock hyraxes in conserving energy to maintain core body temperature than to endogenously create heat for body temperature maintenance. Thus, under similar environmental conditions, rock hyraxes may display similar frequencies of basking and sunbathing as these behaviours reflect the internal and external thermal environment experienced by rock hyraxes.

I did not distinguish between basking and sunbathing in the sun and the shade, yet the selection of microclimates is important in thermoregulation along with orientation to incidental solar radiation (Brown & Downs 2007). Although thermoregulation has been extensively researched (Taylor & Sale 1969; Sale 1970; Bartholomew & Rainy 1971; Rübsamen et al. 1982; McNairn & Fairall 1984; Brown & Downs 2005, 2006, 2007; Downs et al. 2013), the pattern of these behaviours have not, such that dividing basking and sunbathing further into sun and shade locations may provide additional information as to whether rock hyraxes differ in their use of these behaviours along the gradient of proximity to people between seasons.

Amicable and aggressive behaviours were lower than expected with aggressive behaviours hardly present. Amicable, especially huddling and heaping, behaviours occurred mostly in juvenile rock hyraxes. Huddling and heaping are suggested to aid in thermoregulation in rock hyraxes, especially at low ambient temperatures (Sale 1970), although Downs et al. (2013) found that huddling (at least at night) did not affect core body temperature regulation. Fourie (1983) found very few occurrences of huddling and no heaping and suggested that pelt properties of rock hyraxes may reduce conductance in temperate habitats compared to rock hyraxes occurring in the tropics studied by Sale (1970).

Grooming was common and was similar in all colonies and seasons, indicating similar behavioural priorities. Grooming can be associated with basking (Olds & Shoshani 1982) and is apparently used at high temperatures with saliva and panting to help prevent overheating (Olds & Shoshani 1982). In addition, rock hyraxes are host to a variety of ecto- and endoparasites (Fourie 1983), and grooming along with dust-rolling may aid rock hyraxes in controlling ectoparasites (Skinner & Chimimba 2005).

Rock hyrax vigilance was difficult to identify during scan samples because it resembled the basking posture. Sentinels also keep vigilance during group basking and feeding (Hoeck 1975; Kotler et al. 1999; Fanson et al. 2011), and these may have been overlooked during scan sampling. Having sentinels reduces the need for personal vigilance in other group members, which can then focus on other fitness-enhancing behaviours, such as feeding and mating (Ridley et al. 2013). These behaviours generally cease when an alarm call is given, causing group members to flee to safety from where they can keep vigil (Kotler et al. 1999; Ridley et al. 2013, pers. obs.). Most rock hyrax vigilance occurred after a disturbance event and thus the similar levels in vigilance for the three colonies may reflect similar disturbance event occurrences. Studies on vigilance between species in rural and urban localities have found varying outcomes, with vigilance decreasing in urban localities for Cape ground squirrels (Chapman et al. 2012), and fox squirrels (Mccleery 2009), while vigilance either remained unchanged or increased in woodchucks, *Marmota monax* (Watson 2009; Lehrer et al. 2012), Eastern grey squirrels (Partan et al. 2010), and yellow-bellied marmots, *Marmota flaviventris* (Li et al. 2011). Vigilance behaviour in the three colonies would need to be compared to vigilance behaviour from non-urban colonies, which was not conducted by Fourie (1983), to establish whether vigilance has decreased or remained similar between urban and rural localities.

Vigilance was lower in the cold months which was unexpected as a resident pair of Verreaux's eagles had bred and were incubating eggs and feeding hatchlings during the cold month observations (Andrew Jackson pers. comm.). At this time, predation pressure should have been greater when the eagles would be required to bring food to the newly hatched chick and rock hyraxes are considered the main prey items for Verreaux's eagles (Davies 1994; Barry & Mundy 2002; Symes & Kruger 2012). However, I only observed the eagles flying near the rock hyrax colony intermediate to people as the artificial nest was located closer to this colony. These observations occurred twice in total and invoked an alarm call alerting the rock hyraxes to the presence of the eagles along with vigilance until the eagles had moved out of sight. This suggests that predation attempts were generally low at the colonies.

The two active behaviours observed were feeding, and travelling and because travelling is associated with many behaviours, it tended to be more frequent than feeding. Travelling was similar in the three colonies and between the warm and cold months. Rock hyraxes are known to shuttle between sun and shade locations when basking and sunbathing (Fourie 1983; Brown & Downs 2006). Shuttling between hot and cool locations has been documented in the Cape ground squirrel (Bennett et al. 1984; Fick et al. 2009), and degu *Octodon degus* (Bozinovic et al. 2000) and is used to regulate body temperature under thermal stress (Fick et al. 2009). Rock hyraxes travel to feeding locations around the den site (Fourie 1983). Rock hyraxes also travel away from the den during the cold months when food at the den location is scarce and of potentially low quality (Brown & Downs 2005, pers. obs.). Travelling was much more frequent than feeding during the cold months at the colony furthest from people where I observed rock hyraxes travelling to an enclosed area away from the den location throughout the day. Travelling can also be associated to vigilance because when rock hyraxes are alarmed, they are often observed fleeing to the safety of the den (Sale 1965; Fourie 1983; Kotler et al. 1999).

Feeding did not increase in the cold months and instead was lower in all colonies. Rock hyraxes have been found to have greater feeding frequencies in the warm months, with basking being more prominent in the cold months (Brown & Downs 2005). Rock hyraxes are selective feeders with regards to the phenological stages of plants and generally select the plant parts most advantageous to them during each season (Skinner & Chimimba 2005). As such, in the cold months, rock hyraxes may incorporate plant parts that were not utilised in the warm months (e.g. highly fibrous food) into their diet. The digestion of more fibrous food

takes longer to acquire sufficient energy for optimal metabolism and in these situations, animals need to either spend large portions of their day foraging or gain energy through other means (Ashby 1972; Veloso & Bozinovic 1993). As rock hyraxes fed less frequently in the cold months than in the warm months in my study, they may have augmented the reduced foraging with basking and inactivity to lower their energy costs.

Feeding has been found to generally decrease in urban environments because the availability of high quality food at a constant rate enables animals to meet their energy requirements by utilising less food than they would in non-urban environments, as seen in the American black bear, *Ursus americanus* (Beckmann & Berger 2003). However, feeding was generally more frequent at the colony closest to people (cul-de-sac). According to Sale (1965), feeding occurs in rock hyraxes in two forms, casual feeding, which is short and usually consists of an individual feeding near the den, and group feeding, which is longer, generally causing peaks in feeding activity, and usually consists of feeding at a central location. In the cold months, especially, casual feeding was reduced due to the low-quality food items surrounding the den location and group feeding generally involved travelling to suitable feeding location. Rock hyraxes closest to people were observed feeding at relatively higher frequencies throughout the day in both the warm and cold months. This altered feeding activity may have been the result of the constant food items available from gardens that were in close proximity to the den location, supporting casual feeding throughout the day during both the warm and cold months and reducing travelling to reach adequate feeding locations further away.

Rock hyraxes at the three colonies were relatively active throughout the day compared to the non-urban rock hyrax population from MZNP which showed a unimodal activity in the afternoons during summer and later in winter. Changes in diel activity have been also been observed in the synurbic Eastern grey squirrel (Parker et al. 2014). Feeding overall was similar in the warm months between the MZNP population and the three colonies, suggesting that both environments had similar levels of food resources available to meet energy requirements. Feeding in the cold months was more intense at the MZNP population in the late afternoon than at the three colonies in my study where feeding occurred throughout the day. The intense feeding period in the MZNP population is indicative of group feeding while the feeding throughout the day by the three colonies is indicative of increased casual feeding. This increase in casual feeding may reflect the increased feeding opportunities in urban areas, particularly in gardens along with lower predation risk in urban environments, facilitating

more frequent activity throughout the day (McKinney 2002; Luniak 2004). Basking/sunbathing was greater in the cold months in the MZNP population, but basking did not increase in the three Meyersdal colonies but remained lower than that of the MZNP population during both the warm and cold months. These reduced basking proportions may be the result of minimal variation in ambient temperature and temperatures around the thermoneutral zone because rock hyraxes would focus less on maintaining a stable body temperature through basking, allowing for the increase in activity observed throughout the day in the three colonies compared to the MZNP population. Additionally, lower predation risk in urban environments may also allow for increased activity (McKinney 2002; Shochat et al. 2006; Møller 2012).

In addition to the diurnal activity patterns, I surveyed camera trap footage to examine nocturnal activity since some diurnal animals alter their diel activity in urban environments (Tigas et al. 2002; Beckmann & Berger 2003; Dowding et al. 2010; Podgórski et al. 2013). Rock hyraxes, however, showed little nocturnal activity, suggesting that they are diurnal, potentially due to the energy costs to maintain body temperature at night because daytime behaviour appears to utilize solar radiation as an energy saving mechanism.

**Diet**

The objective of investigating the diet of rock hyraxes was not achieved (Table 5). However, rock hyraxes fed on a variety of plant types such as grasses, forbs, shrubs, succulents and trees (Sale 1965; Olds & Shoshani 1982; Fourie 1983; Fanson et al. 2011). They are known to select phenological stages of these plants that are most advantageous during a season, for example preferring young leaves over older leaves but when food is limited, especially in the cold months, rock hyraxes will eat older leaves if available (Hoeck 1975; Olds & Shoshani 1982). Such flexibility in feeding behaviour is also seen in the European rabbit, *Oryctolagus cuniculus* (Bakker et al. 2005).

Rock hyraxes at the two colonies further away from people fed on the vegetation surrounding the den sites, which consisted of various forbs, and grasses that were of high quality during the warm months (pers. obs.). However, in the cold months, the vegetation that the rock hyraxes fed on was of low quality, comprising of dry grass mostly. During this period, I observed rock hyraxes feeding on trees which were further away from the den (pers. obs.).

Rock hyraxes in all colonies fed on similar plants to those from the MZNP, including *Hyparrhenia hirta* (common thatching/ blue grass), *Searsia lancea* (Karee tree), *Aloe* spp (aloes), *Tagetes minuta* (khakibush) and *Conyza* spp (horseweed/ butterweed/ fleabane). *Cussonia paniculata* (mountain/ highveld cabbage tree) was one of 10 plants forming the majority of the diet at the MZNP population (Fourie 1983) and, in my study, was observed to be fed on at the rubble dump and boulder pile colonies where the trees were growing naturally. This tree did not occur at the cul-de-sac site.

Many of the plant species eaten by the rock hyraxes at Meyersdal Eco Estate were either not native to South Africa or were cultivated by people. According to Oosthuizen (2012), Meyersdal Eco Estate was previously used as a dumping ground for garden refuse and some of the plants eaten by rock hyraxes were invasive plants that grow in disturbed areas, such as black-jack *Bidens pilosa* (Foxcroft et al. 2008), thorn apple *Datura stramonium* (Nel et al. 2004; Foxcroft et al. 2008), prostrate sandmat *Euphorbia prostrata* (Vosse et al. 2008), forest inkberry *Phytolacca octandra* (Nel et al. 2004) and Cape gooseberry *Physalis peruviana* (Nel et al. 2004). The residential areas of the estate also contained cultivated gardens, consisting of plants that may be native to South Africa but were planted for aesthetic reasons. I observed rock hyraxes from the colony closest to people feeding on these cultivated garden plants, such as agapanthus *Agapanthus praecox* (Norton 2004), Cape wild garlic *Tulbaghia violacea* (Harris 2004), sweet wild garlic *Tulbaghia simmleri* (Norton 2013), hen-and-chicken *Chlorophytum comosum variegatum* (van Jaarsveld 2012), and Cape honeysuckle *Tecoma capensis* (Mutshinyalo 2008).

Sale (1965) observed rock hyraxes in Kenya feeding on a type of poisonous pokeweed, the African soapberry, *Phytolacca dodecandra*. Similarly, rock hyraxes from the colony closest to people were observed feeding on another pokeweed, the forest inkberry, *Phytolacca octandra*. Sale (1965) suggested that rock hyraxes might not be susceptible to poisonous plants potentially due to the efficient functioning of their hindgut.

**Flight initiation distance (FID)**

As predicted (Table 5), FIDs (a measurement of habituation) increased along the gradient of proximity to humans, with rock hyraxes closest to people having the shortest average FID than those from the other colonies. FID also became shorter when a food incentive was introduced and this decrease was greatest for the colony furthest from people in

the cold months. FID can be influenced by the distance to refuge (Dill M. & Houtman 1989; Bonenfant & Kramer 1995; Stankowich & Blumstein 2005), starting distance of approach (Blumstein 2003), and size of threat (Stankowich & Blumstein 2005). In my study, I conducted all measurements at the den locations from a set starting distance of around 20m, and to avoid pseudoreplication of individuals, I took each new measurement at a different location at the colony. Past experience with the threat (Stankowich & Blumstein 2005) and threat lethality (Cooper & Frederick 2010) are also factors that affect FID. However, it is expected that wildlife that occurs closest to people would have increased encounter rates with people (Stankowich 2008; Cooper & Frederick 2010; Møller et al. 2013). If the encounters are non-lethal humans, FIDs would potentially be shorter to an approaching person.

As found in other studies investigating FIDs along an urban gradient (Møller 2008, 2009; Mccleery 2009; Chapman et al. 2012; Grolle et al. 2014), the FIDs measured along a gradient of human proximity reflect a pattern of increasing FID the further away the rock hyraxes were from people. Two hypotheses can explain the difference in FID along a gradient of varying intensities in human activity: the habituation hypothesis and the risk-allocation hypothesis. Habituation is the decrease of response due to repeated and/or prolonged exposure to a non-lethal stimulus, and as such regular non-lethal human disturbances can lead to habituation (Sirot 2010). The risk-allocation hypothesis predicts that animals will adjust their antipredator responses under temporal variation in perceived risk situations (Lima & Bednekoff 1999). As the outcomes of these hypotheses are not independent, a combination of these processes may influence FID under different human activity intensities (Sirot 2010). Wildlife closer to people would thus experience greater interactions with people and thereby habituate to the high intensity of non-threatening human activity occurring around them (Stankowich & Blumstein 2005). Thus, rock hyraxes closest to people appear to be more tolerant of human disturbance by perceiving approaching humans as less of a risk than colonies occurring further from people.

Rock hyraxes were more tolerant of an approaching person when a food incentive was presented, resulting in a shorter FID. The optimal escape theory predicts that individuals should flee when the benefits of fleeing outweigh the benefits of staying (Ydenberg & Dill 1986; Cooper & Frederick 2007). This is based on the risk posed by the predator as well as the cost of fleeing that results in the loss of benefits, such as feeding (Bateman & Fleming 2014). Thus, individuals should adjust their FID according to the benefits that augment their fitness (Engelhardt & Weladji 2011), suggesting that the food incentive might potentially

provide an added fitness benefit to rock hyraxes that influenced their risk assessment. In this instance, rock hyraxes adjusted their FID to gain the benefits of eating the apple, allowing a closer approach and supporting the optimal escape theory.

**Deterrent efficacy**

This objective was partially achieved (Table 5) and found that the latency for the control treatment (no deterrent on the presentation tile) increased along the gradient of proximity to people, with latencies in the colony furthest from people being longer than the latencies for most of the treatments in the colonies closer to people. This latency for the control possibly reflects neophobia (the aversion to approach novel food or objects, (Kimball et al. 2009; Sol et al. 2011). The colony closest to people was, therefore generally less neophobic, as occurs in urbanised species (Sol et al. 2011). Although all three colonies occurred within an urban environment, the colonies further from people were probably least exposed to novel stimuli as often as the colony closest to people.

The presentation of the wild garlic was a visual and vapour (i.e. a repellent not applied directly to the food) repellent (Kimball et al. 2009), which proved to be ineffective at deterring rock hyraxes from the food incentive. The wild garlic was not associated to any negative consequences and relied solely on visual and olfactory cues to deter the rock hyraxes. These types of repellents generally rely on a neophobic mechanism which can be subjected to habituation as these repellents act on the animal's fear of unknown consequences and without negative consequences the cues may not be avoided for prolonged periods (Kimball et al. 2009; Kimball & Taylor 2010). Plant-based repellents need to be associated with an aversive visual, olfactory, or taste cue, or even a combination to be effective against herbivores (Kimball & Taylor 2010). Rock hyraxes may have therefore habituated to the presentation of the wild garlic and food incentive and thereafter ate both the food incentive and the wild garlic during the warm and cold months.

The presentation of the boa dung was a visual and vapour animal-product repellent (Kimball et al. 2009) and produced higher latencies to approach the tile in the colonies closest and furthest from people than wild garlic. The life history, ecology and evolutionary history may influence the response of prey species to predator odours. Older individuals may differ in their response to predators when compared to their younger counterparts and habitat and season may elicit different responses for a specific species (Hayes et al. 2006). At all the colonies, I found older individuals initially approaching the tiles during the experiments

before younger individuals followed (pers. obs.). Latency to approach was predicted to become shorter in the cold months and this was true for the colonies intermediate and furthest away from people but was not true for the colony closest to people. This prediction was based on the theory that in the cold months when food resources are of low quality and/or scarce, the food incentive would be more profitable and thus individuals would risk more to acquire the food incentive (Brown & Kotler 2004). Rock hyraxes are known to take on this risk in the cold months (Brown & Downs 2005) as seen in the colonies intermediate and furthest from people. The colony closest to people had long latencies for the wild garlic and boa dung deterrents in the cold months, although this could also be because the food sources near this colony were not as depleted and/or of low quality as at the other colonies and thus the timing of the experiment may have occurred after rock hyraxes had become satiated or the food incentive was not as profitable as the surrounding vegetation. I predicted that the colony closest to people would have the shortest deterrent latency overall due to exposure of this colony to potentially more risk situations than the other colonies. However, the latency was shortest at the colony intermediate to people and longest at the colony furthest from people. This may relate to the high latency experienced in the cold months by the colony closest to people due to the potentially better alternative food sources in the surrounding gardens.

As sulphurous compounds are common in most carnivorous predator odours, avoidance by herbivores may be innate and generalised. However, it is also possible that the intensity of prey response to predator odours may be influenced by co-evolution of both the prey and predator species with prey species potentially being better able to recognise the predator odour of a specific predator (Woolhouse & Morgan 1995; Hayes et al. 2006; Russell & Banks 2007). However, the boa dung was ineffective at deterring rock hyraxes from feeding on the food incentive. This is not uncommon because some prey species are known not to respond to predator faecal odours (Apfelbach et al. 2005; Hayes et al. 2006). Alternatively, extinction of the avoidance behaviour may have occurred when the repellent does not cause pain or malaise and the food is highly desired (Kimball et al. 2009).

A potential reason for the non-response may be because of the method of spreading the boa dung around the tile edge. It has been suggested that the presentation of the odour should have been in a manner that was useful for the determination of the predator's behaviour or in the way it would be encountered in nature as a single bowel motion by the predator (Hayes et al. 2006). However, it has also been suggested that snake faeces may be an unreliable cue to indicate predator presence due to the infrequency with which they defecate

(Hayes et al. 2006). Another possibility is that the odour concentration may have been too weak to achieve an optimal odour concentration required to achieve a repellent effect (Apfelbach et al. 2005). An additional possibility could be that the boa snake was not recognised as a predator due to the lack of co-evolution or a mismatch of predator and prey (Apfelbach et al. 2005; Hayes et al. 2006). However, it has been proposed that even if predator odours provide cues as to the predator density and influence feeding decisions, once the decision to forage is made, the predator odour does not influence feeding consumption (Kimball et al. 2009).

Finally, deterrents or repellents have varying efficacies depending on the species they are used against. Some deterrents that work on mammals do not work for birds (Kimball & Taylor 2010), while some deterrents that work for some mammal species are not effective on other mammalian species (Apfelbach et al. 2005). For example, anal gland secretions from the least weasel, *Mustela nivalis*, were effective at deterring the field vole, *Microtus agrestis*, but not at deterring the wood mouse, *Apodemus sylvaticus* (Apfelbach et al. 2005).

## Conclusion

My study is the first to consider the behavioural activity patterns of urban-occurring rock hyraxes. However, there are other urban rock hyrax studies (see (Brown & Downs 2005, 2006, 2007; Wiid & Butler 2015). Most other studies on rock hyraxes have focused on thermoregulation and the associated behaviours (Sale 1965, 1970; Louw et al. 1972; Rübsamen et al. 1982; McNairn & Fairall 1984), especially in winter (Brown & Downs 2005, 2006, 2007; Downs et al. 2013), or casual behavioural observations (Fourie 1983). I found that rock hyrax activity differed to a rural population, indicating potential responses to urbanisation in reduced basking/sunbathing activity (inactivity) and more frequent feeding. Rock hyrax activity may show similarities under similar environments but even within an urban setting, feeding behaviour and habituation to people varied across short spatial scales. In addition, the odour deterrents used were ineffective in deterring rock hyraxes from a preferred food source and alternative deterrents, including an indigenous predator species' odour, should be considered in future to assess whether predator odour response is inherent or is acquired in the rock hyrax.

# Chapter 3. Occurrence and public opinion in Greater Johannesburg

## Introduction

With the rapid expansion of urban areas, it is becoming increasingly important to better understand the effects of urbanisation on the occurrence and habitat use of urban wildlife species (Chace & Walsh 2006). Species that utilise a variety of habitats are considered habitat generalists while those that utilise a particular habitat are considered habitat specialists (Mennechez & Clergeau 2006). Generalists tend to be more successful in urban environments while specialists tend to be less successful and either avoid urban disturbance or move into areas within the urban environment where disturbance is reduced or absent (Sih et al. 2011; Dudus et al. 2014). Establishing the occurrence of species and the habitats used within urban environments can highlight important areas of interest or concern with regards to the relevant species and can aid in the development of management and/or conservation plans for those species by wildlife managers (Dudus et al. 2014).

The persistence of species may be dependent on whether species have a wide enough tolerance to include or acclimatise to new environmental conditions or modified habitats, typical of behaviourally plastic species (Sol et al. 2013). In urban environments, behaviourally flexible species can utilise alternative (i.e. anthropogenic) resources when natural resources are inaccessible or not available. For example, the stone marten, *Martes foina*, utilises attics and roof spaces of inhabited buildings as den locations, but it prefers natural den locations, such as dense vegetation, trees, underground burrows or brushwood piles, when they are within easy reach (Herr et al. 2010). A South African example is the large-spotted genet, *Genetta tigrina*, which a generalist small carnivore that is known to occur in some urban areas (Widdows & Downs 2015). For most of the year, large-spotted genet will mostly utilise natural food resources, but in winter when natural food sources become scarce, they may use anthropogenic food resources to supplement their diet (Widdows & Downs 2015).

On the other hand, some urban dwelling animals show ecological niche conservatism where the fundamental ecological niche of a species changes through time, but adaptations to the new environments are slower than the rate of change (González-Oreja 2011). These species would need to find suitable habitats in urban areas or face extinction (Wiens et al. 2010). Through this concept, species would then theoretically seek out habitats within urban

environments that resemble habitats to which they are adapted to historically or from previous experience (Wiens et al. 2010). For example, the Florida manatee, *Trichechus manatus latirostris*, has a limited tolerance to cold, so water temperature is the main factor determining its distribution, and in winter it seeks out thermal refuges such as natural thermal springs providing warmer water temperatures to avoid hypothermia (Laist & Reynolds 2005). However, the manatee's winter distribution has expanded more northward (i.e. to areas previously avoided) where the thermal discharges from power plants provide similar water temperatures to those found in thermal springs (Laist & Reynolds 2005). These ecologically similar habitats would serve as refugia in a changing urban landscape (Keppel et al. 2012).

Møller (2012) defined refuges as habitats or locations temporarily or permanently used by prey species to reduce or eliminate predation risk. Used in an urban context, refuges can be habitats or locations that animal species can use, temporarily or permanently, to reduce or avoid anthropogenic disturbances that they may be unable to overcome. Thus, when suitable natural habitats are available within urban environments, animals that cannot utilise anthropogenic resources or cannot tolerate anthropogenic disturbances can find refuge in those habitats and may still be able to persist within urban environments. For example, the southern African hedgehog, *Atelerix frontalis*, which was common in Greater Johannesburg historically, but now due to habitat fragmentation caused by urbanisation, is forced into rocky outcrop refuges (Artingstall 2013).

Wildlife managers also have to manage the persistence of species in urban environments, especially when the spread of development increases the interactions between wildlife and people (Hill et al. 2007; McDonald et al. 2012). Sometimes the interactions between wildlife and people can lead to conflict, with these animals becoming tagged as pests or vermin because they pose a threat to human health or wellbeing (Young 2006). In addition, many invasive species are considered pests due to their threat to the indigenous biodiversity, such as the cane toad, *Rhinella marina* (Saunders et al. 2010; Phillips & Suarez 2012) and European red fox, *Vulpes vulpes* (Saunders et al. 1995), in Australia and the grey squirrel, *Sciurus carolinensis*, in Britain (Barr et al. 2002). Sometimes indigenous species also become pests through their natural behaviours that conflict with human interests. For example, by utilising roof spaces and attics, the stone marten is regarded as a pest for its production of noise, odours and stains from faecal deposits and urine, and damage to roof insulation (Herr et al. 2010). Another example is the European badger, *Meles meles*, which causes extensive damage to buildings during sett

construction, to gardens when digging during foraging, and killing chickens on poultry farms (Symes 1989). Even though the European badger is regarded as a pest by some, it is legally protected and is not listed as a pest under legislation (Symes 1989; Ward et al. 2008). Pest management is difficult under these circumstances because those negatively affected want the species considered pests while others show a sort of fondness for the wildlife in urban environments (Herr et al. 2010).

Incorporating the public in studies of urban ecosystems is becoming more important for urban ecology and wildlife management to better assess the need for pest management and conservation for indigenous urban wildlife (LaBonte et al. 2013). This may in turn reflect the overall success of species in urban environments because many problematic species occur at high population density and are thus not welcome in the areas where their occurrence conflicts with humans (McKinney 2002; Bjerke & Østdahl 2004; Hill et al. 2007; McDonald et al. 2012).

In this study, I aimed to ascertain the occurrence of rock hyraxes, *Procavia capensis,* within Greater Johannesburg and to assess how the public perceives rock hyraxes. For this study, I used reported sightings data from the public and data collected from FreeMe rehabilitation centre, located in the north of Johannesburg. Using a distribution map generated from the reported sightings and Resource Selection Function analyses (a method to model species use of resources at a local and wider scale), I predicted that rock hyraxes would mostly favour areas with or in close proximity to rocky outcrops, reflecting their ecological predisposition to den in rock crevices and bask/sunbathe on rocks (Chapter 2). From public surveys, I predicted that the public would regard rock hyraxes mostly as pests.

## Materials and methods

The study area incorporated the City of Johannesburg, various suburbs from the Ekurhuleni region in the East Rand Region and various suburbs from the Mogale City municipality in the West Rand region (see Figure 1). This area was referred to as the Greater Johannesburg for the purpose of my study. Within this area are numerous nature reserves and parks as well as private estates incorporating rocky outcrops (SANBI & Department of Environmental Affairs 2007; City of Johannesburg 2009). Rock hyraxes inhabit rocky outcrops (Olds & Shoshani 1982; Skinner & Chimimba 2005) and as such can and do occur within the study area. Home owners within Greater Johannesburg have also reported

problems caused by rock hyraxes on their properties, such as destruction of gardens and homes through foraging and location of den sites respectively, as well as aggressive behaviour (e.g. growling) towards humans and pets (this study; public opinion).

**Occurrence**

I collected rock hyrax occurrence data from public sightings and from the database of FreeMe Wildlife Rehabilitation Centre (FreeMe). FreeMe is located in Paulshof, Johannesburg (-26.02995°, 28.03972°) and receives wild animals in various health states from the public, SPCA, veterinarians and employees of parks and protected areas. When an animal is brought to the rehabilitation centre, information such as the date of arrival at the centre, contact details of the collector, suburb where the animal was found, and reason for admittance are recorded. These data are then added to FreeMe's database for each species. From the public sightings and FreeMe database, I obtained data for the date of sighting, location (street address or GPS coordinates) and the number of individual rock hyraxes, which were categorised into the following ranges: 0-5. 6-10, 11-20, 21-30, 31-40, 41-50, or >50.

To solicit occurrence data from the public from February 2014 until December 2014, I created posters (Appendix 1) and distributed them to FreeMe, local vets and community boards at shopping centres in various areas where rock hyraxes potentially occur within Greater Johannesburg. The posters contained information about the rock hyrax, a picture for identification, and information and contact details for reporting sightings. I created a Facebook page (https://www.facebook.com/watdassies) which contained the same information as the posters. I shared it with other public pages on Facebook and this allowed the public to report sightings on the page or through an e-mail address provided. I recorded the sightings data from the public and FreeMe database in an MS excel spreadsheet and converted locations into GPS coordinates (decimal degrees).

I generated an occurrence map in ArcMap™10.1 (ESRI 2012) for rock hyraxes in Greater Johannesburg using all the GPS coordinates that were either provided by the public or generated from street addresses and other descriptive information provided by the public. In this map, I incorporated the border of Greater Johannesburg using the polygon drawing tool and I exported the map as a .jpeg file.

## Resource Selection Functions (RSF)

Animal populations require useable biotic and abiotic resources for survival and reproduction (Manly et al. 2002). The selection of these resources by organisms has become of interest in various studies to understand the governing factors of distribution and abundance of species to characterise and predict how species use space and resources to meet the requirements for survival (Manly et al. 2002; McLoughlin et al. 2010; Robertson 2013). The Resource Selection Function (RSF) is a useful tool to estimate the relative probability of use of a resource unit or feature by an organism through comparing the amount of used resource units to the amount of available resource units in the specified environment (Boyce 2006; Koper & Manseau 2010; McLoughlin et al. 2010). RSFs can show which resources are more likely to be used within a defined area.

Selection of resources by animals is a hierarchical process, making it scale dependent; this means that selection of resources by organisms may differ at different spatial scales, as described by Johnson (1980). This hierarchical process includes resource selection in the organism's or population's broad geographic range (first order selection), to resource selection within the home range of the broad geographic range (second order selection), to resource selection of habitat components within the home range (third order selection), to resource selection of specific resource units (e.g. food items, available within the habitat and feeding site; fourth order selection). Habitat or food selection studies are the most common in resource selection, although selecting the appropriate scale is important to answer various resource selection questions, and multiscale studies are becoming increasingly popular (Manly et al. 2002).

The two most common sampling designs in RSFs are: 1) used/ unused design where the function is estimated by sampling units for the presence or absence of organisms; and 2) use/ availability design where the function is estimated by sampling units for the use of available resource units by a sample of individuals in a population (presence/ available). Items, points or shapes in space are the types of units being used and their associating predictors may be any number of categorical (e.g. vegetation type) or continuous (e.g. distance to feature) variables or modifying covariates (McLoughlin et al. 2010). For both the sampling designs, the most used statistical model is a binomial generalized linear model (GLM) which is usually a logistic regression. In the case of the use/availability design, the logistic regression is used as an estimating function and not for statistical inference (Boyce et al. 2002).

RSFs can provide a tool with which to potentially predict where rock hyraxes may be more likely to occur within the Greater Johannesburg boundary by assessing the relative probability of rock hyraxes associating with environmental features, both anthropogenic and natural. For my study, I used a first order selection spatial scale as rock hyrax sightings occurred across a large area containing various habitat features between sightings and because individual rock hyraxes were not identified to model smaller spatial scales (Thomas & Taylor 2006). The first order scale allowed me to make inferences about the resource use of the rock hyrax population in Greater Johannesburg. I used a use/availability design because I knew the presence of rock hyraxes through sightings with certainty, indicating use of features at that specific point. I could not assess unused sites through observation sightings (Manly et al. 2002; Boyce et al. 2002) with certainty, so available features were assessed through generation of random points within the broad study area. These random points represented features available to the rock hyrax population within the study area (Manly et al. 2002; Boyce et al. 2002; Thomas & Taylor 2006). I selected units based on the occurrence data and environmental characteristics to establish whether occurrence was random or associated with specific features.

From the occurrence data collected between February 2014 and December 2014, I used 40 occurrence points, hereafter known as rock hyrax locations, after excluding duplicates and occurrences within 1km of each other to ensure each point represented a different colony. I ran an RSF analysis with an assessment of natural and anthropogenic environmental features. The natural features included vegetation, soil, ridges, water, and natural areas. The anthropogenic features included roads and areas of human land-use (e.g. residential areas, retail areas, commercial areas, industrial areas).

I used the vegetation map produced by Mucina & Rutherford (2006), available from PlantZAfrica (www.plantzafrica.com/vegetation/vegmain.htm). The SOTER-based soils parameter estimates for southern Africa (version 1.0, Batjes 2004) were used for the soil characteristics and were obtained from ISRIC World Soil Information website (www.isric.org). Feature maps were obtained from SANBI Biodiversity GIS (www.bgis.sanbi.org) for the Gauteng Critical Biodiversity Areas found in the "Gauteng Conservation plan v3.3" file, the Mogale City, City of Johannesburg and Ekurhuleni areas (GDARD 2011), and Geofabrik (www.geofabrik.de) for "South Africa (including Lesotho) OpenStreetMap (OSM)" file (© OpenStreetMap contributors 2015). Ridges maps were obtained from GDARD (GDARD 2013).

I added the rock hyrax locations to a blank ArcGIS map. I then exported the XY data as a shape file and added the data as a layer to the map. All shape files I used were projected to WGS_1984_World_Mercator coordinate system to incorporate the linear unit of metres (m) when measuring distances.

Features within the "Landuse" and "Natural" shape files, found in the "South Africa (including Lesotho) OSM" file, needed to be separated using the Editor feature. For each desired feature layer, I removed other feature types from the attribute table to leave the chosen feature type for the layer.

I separated the "Landuse" and "Natural" shape files into the following feature attribute types: residential areas, cemeteries, recreational grounds, pitches (sporting pitches and sporting grounds), industrial areas, commercial areas, retail areas, landfill sites, mining sites, forests, parks, and water. I added the remaining ridges, roads and water shape files, to the map and grouped the layers into one of five features: areas of human land-use, natural areas, ridges, roads and water.

Ridges consisted of untransformed ridges (including rocky outcrops associated with ridges) and transformed ridges (ridge areas transformed for urban use, mining, cultivation and/or that are degraded) obtained from GDARD. Areas of human land-use consisted of residential areas, cemeteries, retail areas, commercial areas, industrial areas, landfill sites, mining sites, recreational grounds, pitches (sporting pitches and sporting grounds), and forests from the separated "Landuse" and "Natural" shape files. Natural areas consisted of protected areas (areas that have legal protection under legislation), threatened areas (land-based, priority areas for biodiversity plans), ecological support areas (natural, near-natural, degraded or heavily modified areas required to be maintained in an ecological functional state for critical biodiversity areas (CBA) and protected areas), and critical biodiversity areas (CBA, natural or near-natural features that need to be maintained in an appropriate condition) from SANBI Biodiversity GIS (http://bgis.sanbi.org) as well as forests, parks, pitches (sporting pitches and sporting grounds), and recreational grounds. Roads consisted of the roads shape file from the "South Africa (including Lesotho) OSM" file (http://www.geofabrik.de). Water consisted of rivers and wetlands from SANBI Biodiversity GIS (http://bgis.sanbi.org), and water from the separated natural shape files, rivers and waterways from the South Africa (including Lesotho) OSM" file (http://www.geofabrik.de).

In ArcMap™10.1 (ESRI 2012), I used the Intersect Tool under the Geoprocessing menu and ran an intersect analysis using vegetation and soil features (categorical variables), which calculated where rock hyrax locations overlapped with each feature layer and recorded the attribute type for each point in a new layer. For the other features, I used the Near Tool under the Proximity in the Analysis Tools Feature in the ArcToolbox and ran a proximity analysis on each of the following features: areas of human land-use; natural areas; ridges, roads; and water features, against the rock hyrax locations. This analysis measures the straight-line distance of each rock hyrax location to the specified environmental feature.

As mentioned, RSFs require data in the form of either presence/absence or presence/available to assess the probability of use or avoidance of resources. To determine the available resources, I generated random points within the Greater Johannesburg boundary at a 1:5 ratio of actual: random. I selected this ratio as rock hyraxes are territorial, den-dwelling, group-living animals and are not likely to travel far from the den location, unless dispersing (Fourie 1983; Skinner & Chimimba 2005; Visser 2013). As such, the 1:5 ratio provided an appropriate representation of availability of each environmental feature (Koper & Manseau 2010; Baasch et al. 2010). I ran intersect and proximity analyses on the 200 random points as described earlier. I exported attribute tables for all intersect and proximity analyses and converted them to .csv files for analyses.

I counted the categorical features from the intersect analysis and converted them into percentages of the used (40 points) rock hyrax locations, and available (200 randomly generated points) rock hyrax locations for vegetation and soil types. I generated stacked column bar graphs from the percentages.

I converted the collected proximity distances from metres to kilometres and calculated mean, standard deviation and standard error for both the used rock hyrax location and available rock hyrax location data for each feature measured. Using R version 3.1.2 (R Core Team 2014), I conducted randomization tests between the actual rock hyrax and available data for each feature with 50 000 iterations in a pairwise fashion to analyse whether observed locations were likely to occur by chance. This resulted in the generation of a p-value for each feature between the used and available data.

I used a logistic regression to investigate whether resources from the categorical features and the proximity distances showed selection or avoidance by the rock hyraxes. I sorted the soil and vegetation categories alphabetically and allocated each category a letter

starting from "A". I binned proximity distances into categorical groups as follows: A: 0 – 0.5km; B: 0.5 – 1km; C: 1 – 1.5km; D: 1.5 – 2km; E: 2 – 5km; F: 5 – 10km; G: 10 – 15km; H: 15 – 20km; I: >20km. I selected these distances because rock hyraxes are not likely to move large distances from the resources used, unless dispersing. I ran a generalised repeated effects linear model (glm) with a binomial function containing a default logit link in R version 3.1.2 (R Core Team 2014) and this yielded a Wald $\chi^2$ test result. Lastly, I calculated the log-odds ratios, as a type of post-hoc, for each proximity feature, and produced 95% confidence intervals, which were used to generate scatter-plot graphs. Log-odds ratios (adapted from Scott et al. 2006) are the odds of rock hyraxes occurring at a location and were calculated for each feature to describe how likely it would be for rock hyraxes to occur at various distance categories for those features. I generated the model using R version 3.1.2 (R Core Team 2014) which used the first category of a feature as a reference (i.e. 0 – 0.5km). This reference category is equal to zero selection, meaning that at this category rock hyraxes are found at this feature. All other categories and their 95% confidence intervals were compared to this reference category. For each feature, log odds ratios with values above 0 implied that rock hyraxes were more likely to occur at or select this category compared to the reference category and were relative to other categories in that feature. Log odds ratios with values below 0 indicated that rock hyraxes were less likely to occur at or select this category than the reference category and were also relative to the other categories for that feature. Any categories with confidence intervals that overlapped with 0 meant that rock hyraxes did not differ in their selection of the feature in that category; overlapping confidence intervals also implied no difference between the categories being compared.

**Public Opinion**

I created a survey on Surveymonkey.com to obtain opinions from the public about rock hyraxes in urban environments anonymously. The surveys were accessible from June 2014 and closed in November 2014. I distributed the survey link electronically via the Facebook page (www.facebook.com/watdassies) in order to target the public within the borders of the Greater Johannesburg area. I also distributed the survey electronically to residents of Meyersdal Eco Estate and Cedar Hills Private Estate. I specifically targeted these estates for the survey because both estates fall within the Greater Johannesburg area, with Meyersdal Eco Estate in the south and Cedar Hills Private Estate in the north. Both estates had rock hyraxes on their estate properties. However, from pilot studies, residents had

opposing views regarding their rock hyrax population. Residents at Meyersdal Eco Estate, the location of my behavioural studies (Chapter 2), felt that the rock hyrax population on the estate was becoming problematic while residents at Cedar Hills Private Estate did not view the rock hyrax population in the nature reserve on the estate as a problem. Thus, I decided to assess whether these views were unanimous for all residents on each of the estates.

The survey (Appendix 2) consisted of seven multiple choice questions (MCQs) for Greater Johannesburg residents and an additional eighth question for the estate residents. I sought to establish from the questions whether and where rock hyraxes occurred in Greater Johannesburg, as well as the opinion of the public regarding rock hyraxes, and whether problems associated with rock hyraxes linked to this opinion. The common seven questions included 1) whether rock hyraxes had been seen in Johannesburg, 2) their geographic location in Johannesburg, 3) the number of rock hyraxes seen, 4) the opinion of the respondent regarding rock hyraxes, 5) whether rock hyraxes had caused damage, 6) the type of damage caused, and 7) the response of the participant to the damage. I provided a comment box listed as "Other" in the multiple choice answers for certain questions to allow for other viewpoints if the multiple choice answers provided were not sufficient. For the estate surveys, the additional (non-compulsory) question asked for a unit number to check for duplicate responses and so I could assess whether negative opinions were linked to colonies associating close to that unit.

Because the responses for questions 4-7 were the most diverse, I conducted statistical analyses for only these questions. I ran a generalised repeated effects linear model (glm) using R version 3.1.2 (R Core Team 2014) on multiple choice responses, in which location and response for each MCQ were fixed effects and frequency of responses was the dependent factor. Wald $\chi^2$ test statistics, generated with type III sum of squares, are presented. I conducted Tukey post-hoc analyses using the glht() function from the multcomp package (Hothorn et al. 2008) in R for all significant fixed effects and their interactions.

## Results

### Occurrence

From the ten posters distributed to community boards and veterinarian clinics within Greater Johannesburg, the Facebook page, the e-mail address provided from the posters and

the Facebook page and the reports from the FreeMe database, there were a total of 79 reported sightings. Of these reported sightings, 23 were from the Facebook page, 14 were e-mailed and 36 were from the FreeMe database.

Rock hyraxes occurred in the northern and south-eastern areas of Greater Johannesburg (Figure 1). There was an absence of reported sightings between the two areas along the intensely developed area across central Johannesburg (Figure 1).

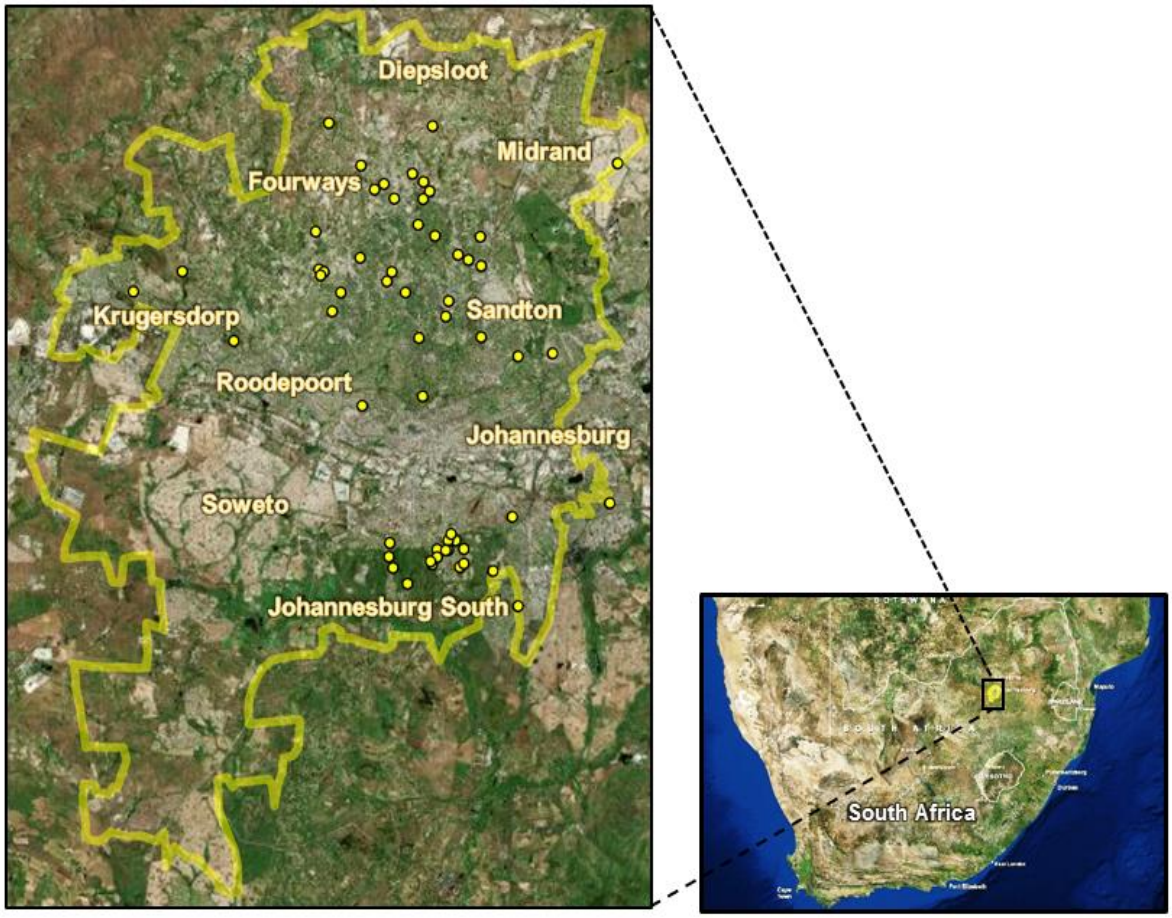



Figure 1. Occurrence map of rock hyrax location sightings reported by the public generated in ArcMap™10.1 (ESRI 2012) and adapted to include area names. The dots represent the public reported occurrence locations of rock hyraxes and the boundary line.

**Resource Selection Functions (RSFs)**

For the vegetation features (Figure 2), the Wald $\chi^2$ from the logistic regression revealed several significant predictors, with rock hyraxes more likely to be sighted in Egoli

Granite Grassland (Wald $\chi^2_9 = -4.96$, $p < 0.001$) and less likely to be sighted in Carltonville Dolomite Grassland (Wald $\chi^2_9 = -3.07$, $p = 0.002$), Soweto Highveld Grassland (Wald $\chi^2_9 = -4.55$, $p < 0.001$), and Tsakane Clay Grassland (Wald $\chi^2_9 = -3.18$, $p = 0.001$). Andesite Mountain Bushveld (Wald $\chi^2_9 = 0.258$, $p = 0.796$) and Gold Reef Mountain Bushveld (Wald $\chi^2_9 = -1.35$, $p = 0.177$) were neither selected nor avoided by rock hyraxes. Locations used by rock hyraxes did not intersect with the available Eastern Temperate Freshwater Wetlands (Wald $\chi^2_9 = -0.01$, $p = 0.991$), Gauteng Shale Mountain Bushveld (Wald $\chi^2_9 = -0.01$, $p = 0.994$), and Rand Highveld Grassland (Wald $\chi^2_9 = -0.01$, $p = 0.994$) found in the Greater Johannesburg area (Figure 2).

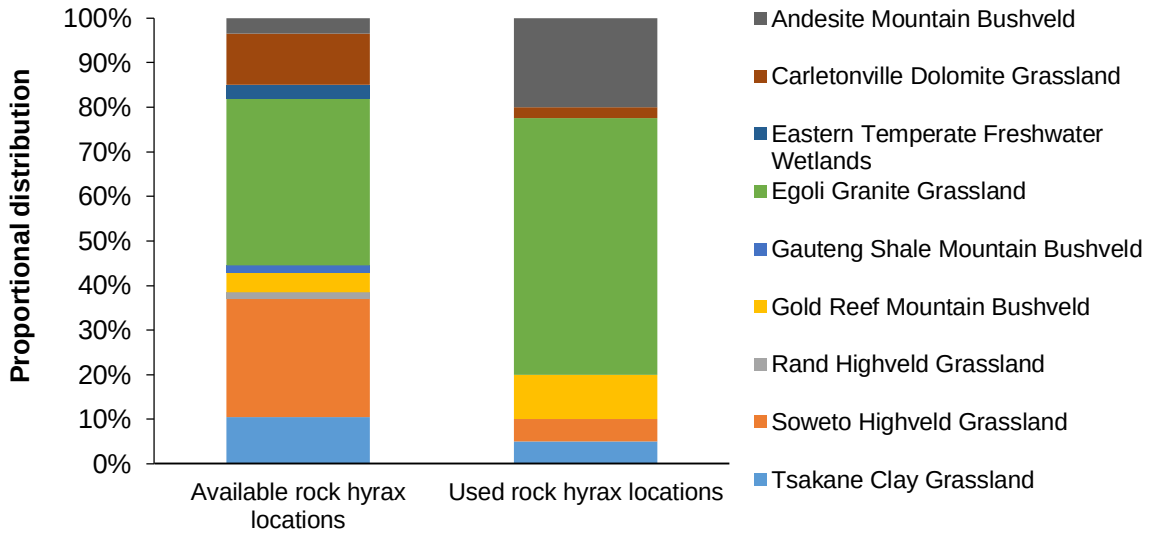



Figure 2. The percentage vegetation cover for available (200 randomly generated points) rock hyrax locations compared with location used by rock hyraxes (40 points).

For the soil feature (Figure 3), there were several significant effects, with rock hyraxes more likely to be sighted on Albic plinthosols (Wald $\chi^2_4 = -4.79$, $p < 0.001$) and less likely to be sighted on Rhodic lixisols (Wald $\chi^2_4 = -6.70$, $p < 0.001$). Lithic leptosols (Wald $\chi^2_4 = -0.78$, $p = 0.435$) were neither selected nor avoided by rock hyraxes. Locations used rock hyraxes did not intersect with the available Rhodic acrisols (Wald $\chi^2_4 = -0.01$, $p = 0.989$) found in the Greater Johannesburg area (Figure 3).

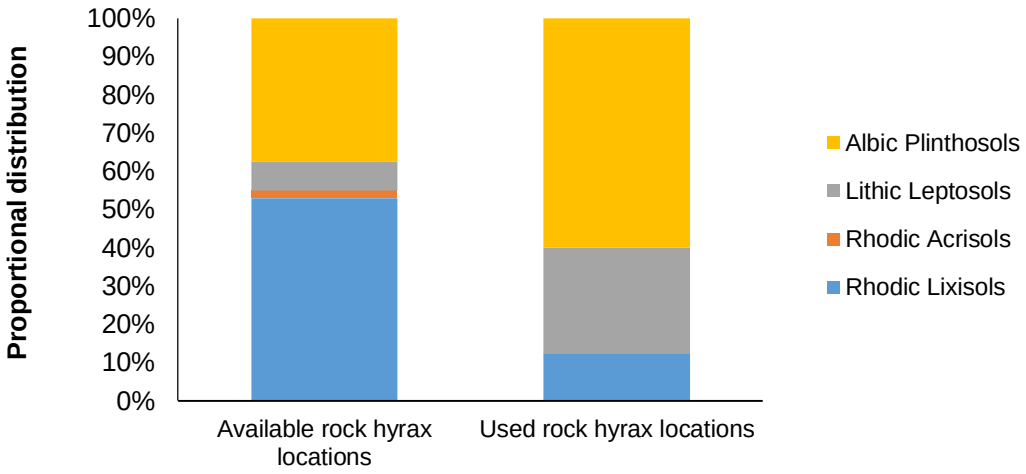



Figure 3. The percentage of soil types for available (200 randomly generated points) rock hyrax locations compared with locations used by rock hyraxes (40 points).

All locations, both used rock hyraxes locations and available (200 randomly generated points) rock hyrax locations, were on average less than 6km away from any of the features (Figure 4). However, locations used by rock hyraxes were closer to all features than those locations available to rock hyraxes, except the water feature where both sets of locations were at a similar distance. For all locations, rock hyraxes could be found closer to roads and natural areas than any of the other features.

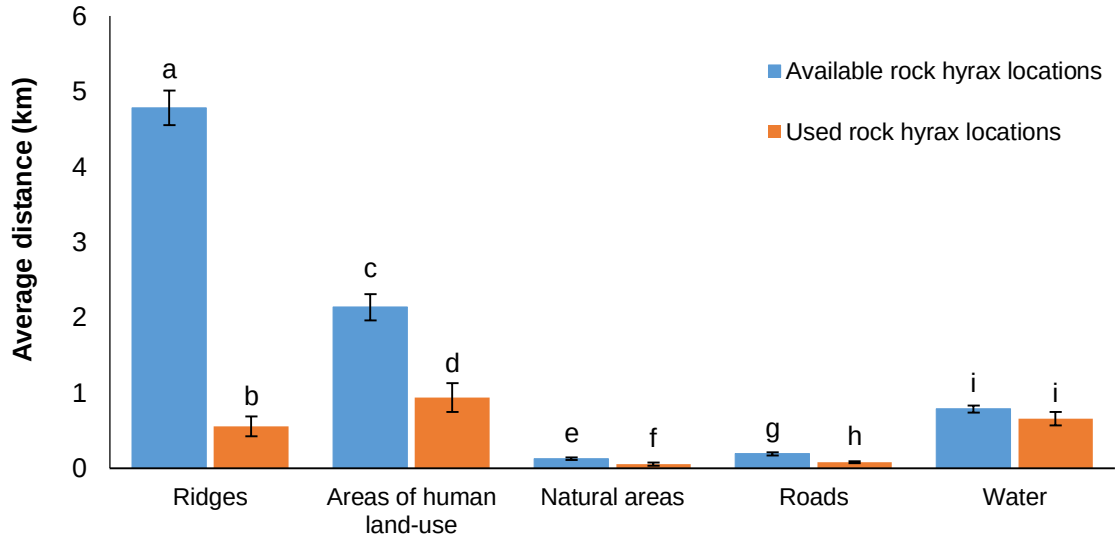



Figure 4. The mean (+SE) proximity to ridges, areas of human land-use, natural areas, roads and water for available (200 randomly generated points) rock hyrax locations and locations used by rock hyraxes (40 points). Different alphabets denote significant differences between the proximities for each feature at $p < 0.0001$ obtained from permutations test for each feature.

Randomization tests showed that the proximity between locations used and available rock hyrax locations were not random for the following features: ridges ($p < 0.001$), areas of human land-use ($p < 0.001$), natural areas ($p = 0.026$) and roads ($p = 0.004$), while proximity to water ($p = 0.120$) was random between used and available rock hyrax locations.

The Wald $\chi^2$ from the logistic regression for the distance categories showed that each feature assessed significantly influenced the rock hyrax use of that feature (Table 1). Rock hyraxes were more likely to be sighted within the following distance categories: A-E for ridges, A-F for areas of human land-use, A for natural areas, A for roads, and A-D for water.

Table 1. Results of a logistic regression for distance categories of the used and available rock hyrax locations. Significant distance categories are indicated in bold.

| Feature: Distance Category | | Wald Statistic | Feature: Distance Category | | Wald Statistic |
|---|---|---|---|---|---|
| Ridges | | | Roads | | |
| A: | 0 - <0.5km | **$\chi^2_6 = -5.25$; $p < 0.001$** | A: | 0 - <0.5km | **$\chi^2_5 = -8.57$; $p < 0.001$** |
| B: | 0.5 - <1km | **$\chi^2_6 = -4.06$; $p < 0.001$** | B: | 0.5 - <1km | $\chi^2_5 = -0.02$; $p = 0.987$ |
| C: | 1 - <1.5km | **$\chi^2_6 = -3.31$; $p < 0.001$** | C: | 1 - <1.5km | $\chi^2_5 = -0.01$; $p = 0.993$ |
| D: | 1.5 - <2km | **$\chi^2_6 = -2.08$; $p = 0.038$** | D: | 1.5 - <2km | $\chi^2_5 = -0.01$; $p = 0.995$ |
| E: | 2 - <5km | **$\chi^2_6 = -4.28$; $p < 0.001$** | E: | 2 - <5km | $\chi^2_5 = -0.00$; $p = 0.996$ |
| F: | 5 - <10km | $\chi^2_6 = -0.02$; $p = 0.987$ | | | |
| Areas of human land-use | | | Water | | |
| A: | 0 - <0.5km | **$\chi^2_7 = -4.27$; $p < 0.001$** | A: | 0 - <0.5km | **$\chi^2_5 = -5.49$; $p < 0.001$** |
| B: | 0.5 - <1km | **$\chi^2_7 = -2.68$; $p = 0.007$** | B: | 0.5 - <1km | **$\chi^2_5 = -5.46$; $p < 0.001$** |
| C: | 1 - <1.5km | **$\chi^2_7 = -2.81$; $p = 0.005$** | C: | 1 - <1.5km | **$\chi^2_5 = -4.11$; $p < 0.001$** |
| D: | 1.5 - <2km | **$\chi^2_7 = -3.31$; $p < 0.001$** | D: | 1.5 - <2km | **$\chi^2_5 = -2.29$; $p = 0.022$** |
| E: | 2 - <5km | **$\chi^2_7 = -4.54$; $p < 0.001$** | E: | 2 - <5km | $\chi^2_5 = -1.82$; $p = 0.069$ |
| F: | 5 - <10km | **$\chi^2_7 = -3.02$; $p = 0.003$** | | | |
| G: | 10 - <15km | $\chi^2_7 = -0.01$; $p = 0.989$ | | | |
| Natural areas | | | | | |
| A: | 0 - <0.5km | **$\chi^2_5 = -9.01$; $p < 0.001$** | | | |
| B: | 0.5 - <1km | $\chi^2_5 = -1.82$; $p = 0.069$ | | | |
| C: | 1 - <1.5km | $\chi^2_5 = -0.01$; $p = 0.992$ | | | |
| D: | 1.5 - <2km | $\chi^2_5 = -0.01$; $p = 0.992$ | | | |
| E: | 2 - <5km | $\chi^2_5 = -0.01$; $p = 0.992$ | | | |

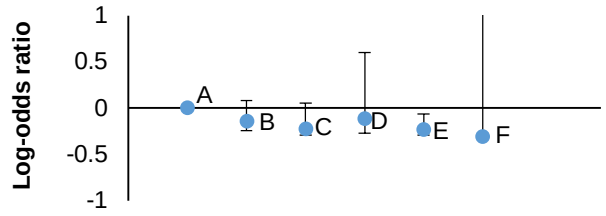
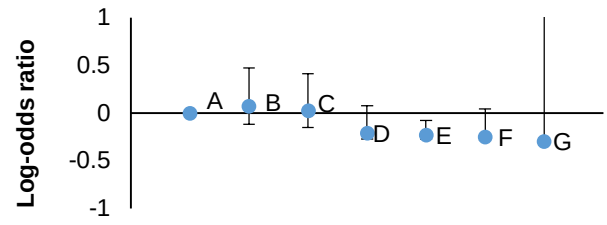
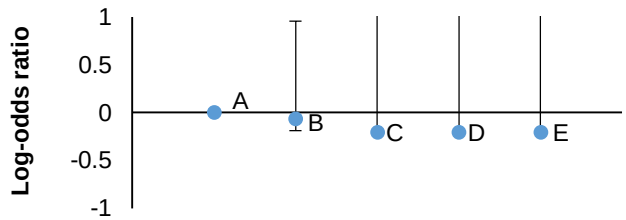
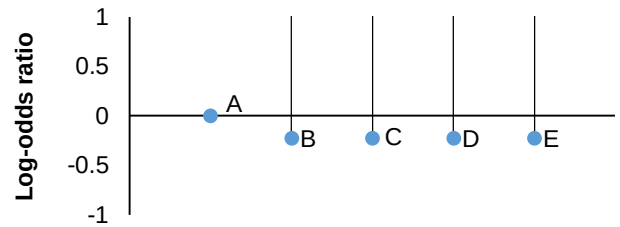
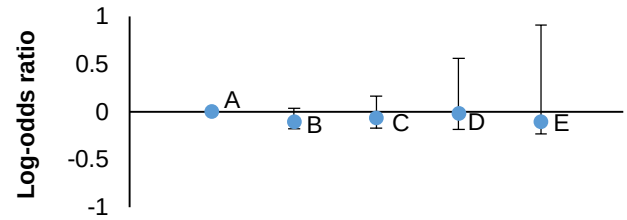
The distance categories were calculated estimates for each feature (Figure 5). Category A represented the reference category (=0) for all features and was the closest distance from each feature (i.e. 0- 0.5km). Although the 95% confidence intervals for category E, 2 - <5km, did not overlap the 0 category for ridges (Figure 5a) and areas of human land-use (Figure 5b), they did overlap with the other categories, indicating that rock hyraxes did not differ in their selection of those categories. Overall, rock hyraxes did not select for any feature at a particular distance category (e.g. natural areas, roads and water also had all categories cross over the 0 category).

Rock hyraxes were sighted (Figure 5) no further than 10km from ridges, 15km from areas of human land-use, 5km from natural areas, 5km from roads and 5km from water. For ridges (Figure 5a), the probability of sighting rock hyraxes started decreasing after 0.5km before it increased from 1.5 - <2km and decreased thereafter. The probability of sighting rock hyraxes increased between 0 - <1.5km of areas of human land-use (Figure 5b) and thereafter decreased from 1.5 - <15km. For natural areas (Figure 5c) and roads (Figure 5d), the probability of sighting rock hyraxes started decreasing from 0.5km of each feature. For water (Figure 5e), the probability of sighting rock hyraxes started decreasing after 0.5km before it increased from 1 - <2km and decreased thereafter.

**Public opinion**

I received a total of 93 responses from the surveys. 25 responses came from Meyersdal Eco Estate, 30 from Greater Johannesburg and 38 from Cedar Hills Private Estate. Question 1 asked whether rock hyraxes had been sighted in Greater Johannesburg. All (100%) of the Meyersdal Eco Estate respondents, 77% of Greater Johannesburg respondents, and 87% of Cedar Hills Private Estate respondents reporting that they had seen rock hyraxes in Johannesburg.

Question 2 asked where rock hyraxes had been sighted apart from the estates. The majority of sightings were from suburbs in the south of Johannesburg such as Meyersdal in Alberton, Glenvista, Bassonia, Mulbarton, and Linmeyer. A few sightings were from suburbs in the north of Johannesburg, such as Boskruin and Randpark Ridge in Randburg, Woodmead, and Glenferness in Midrand. The majority of sightings occurred in nature reserves within these

| A<br>0 - <0.5km | B<br>0.5 - <1km | C<br>1 - <1.5km | D<br>1.5 - <2km | E<br>2 - <5km | F<br>5 - <10km | G<br>10 - <15km | H<br>15 - <20km | I<br>≥ 20km |
|---|---|---|---|---|---|---|---|---|
| a)  | | | | | | | | Ridges<br>Rock hyraxes can be sighted at any distance between 0 - <10km of ridges. The probability of sighting rock hyraxes was more likely at 0 – <0.5km and 1.5 – <2km from ridges. |
| b)  | | | | | | | | Areas of human land-use<br>Rock hyraxes can be sighted at any distance between 0 - <15km of areas of human land-use. The probability of sighting rock hyraxes was more likely 0 – <1.5km from areas of human land-use. |
| c)  | | | | | | | | Natural areas<br>Rock hyraxes can be sighted no further than 5km from a natural feature. The probability of sighting rock hyraxes is more likely 0 – <0.5km from natural features. |
| d)  | | | | | | | | Roads<br>Rock hyraxes can be sighted less than 5km from roads. The probability of sighting rock hyraxes was more likely at 0 – <0.5km from a road. |
| e)  | | | | | | | | Water<br>Rock hyraxes can be sighted less than 5km from water. The probability of sighting rock hyraxes was more likely at less than 2km from water. |
| A<br>0 - <0.5km | B<br>0.5 - <1km | C<br>1 - <1.5km | D<br>1.5 - <2km | E<br>2 - <5km | F<br>5 - <10km | G<br>10 - <15km | H<br>15 - <20km | I<br>≥ 20km |

411 Figure 5. Log-odds ratio for distance from ridges, areas of human land-use, natural areas,
412 roads, and water features (±95% confidence intervals) by rock hyraxes. The letters are the
413 categories into which distances were binned. Categories H and I are not depicted because
414 none of the distances to the features occurred in these categories. Category A is the reference
415 category for each feature. A summary of the key findings for each of the feature is given in
416 the last column.

areas, namely Klipriviersberg Municipal Nature Reserve (MNR), Boschkop MNR, Lone Hill MNR, Rietfontein Ridge MNR, Norscot Koppies Kingfisher Nature Reserve and Fourways Gardens Nature Reserve and a few from other protected areas such as Kloofendal MNR and Walter Sisulu National Botanical Gardens (Appendix 3).

Question 3 asked about the numbers of rock hyraxes sighted. Respondents from Cedar Hills Private Estate and Greater Johannesburg reported mostly between 1-5 individuals followed by groups of between 11-30 individuals and groups between 11-20 individuals respectively. Respondents from Meyersdal Eco Estate reported groups of up to 30 individuals. The largest group sighted by respondents from Meyersdal Eco Estate and Greater Johannesburg was greater than 50 individuals while the largest group sighted by respondents from Cedar Hills Private Estate was between 30-40 individuals.

I ran the generalised repeated effects linear model for the MCQs 4 - 7 regarding the opinion of the public towards rock hyraxes and about damage caused by rock hyraxes. Location (Wald $\chi^2_2 = 9.71$, $p < 0.001$), response (Wald $\chi^2_3 = 36.69$, $p = 0.008$) and location × response (Wald $\chi^2_6 = 17.52$, $p = 0.008$) were significant predictors of the public's opinion regarding rock hyraxes. Tukey post-hoc tests showed that respondents considered rock hyraxes as part of the biodiversity in Johannesburg (Figure 6). However, Meyersdal Eco Estate and Cedar Hills Private Estate respondents did not share similar views, with Meyersdal Eco Estate respondents contending that rock hyraxes were pests compared to Cedar Hills Private Estate respondents. In contrast, Cedar Hills Private Estate respondents mentioned that were part of the Johannesburg biodiversity than Meyersdal Eco Estate respondents. Greater Johannesburg respondents had similar opinions to respondents on both estates, by indicating that rock hyraxes were sometimes pests but mostly part of the biodiversity of Greater Johannesburg (Figure 6).

Location (Wald $\chi^2_2 = 12.84$, $p = 0.002$), response (Wald $\chi^2_1 = 15.83$, $p < 0.001$), and location × response (Wald $\chi^2_2 = 13.25$, $p = 0.001$) were significant predictors of whether rock hyraxes had caused damage to a respondent's person or property. Tukey post-hoc tests showed the majority of respondents had not experienced damage by rock hyraxes. However, Meyersdal Eco Estate respondents had experienced more damage by rock hyraxes than Cedar Hills Private Estate respondents, who mostly reported that they had not experienced rock hyrax damage. Greater Johannesburg respondents mostly did not experience damage by rock hyraxes (Figure 6).

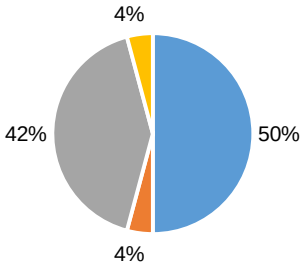
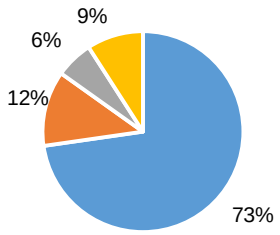
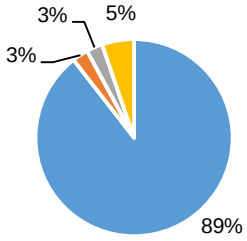
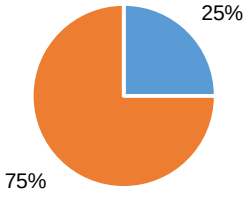
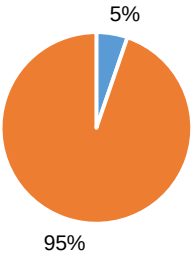
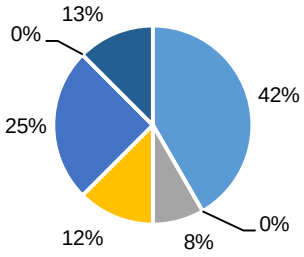
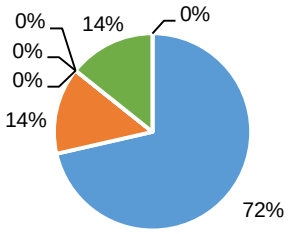
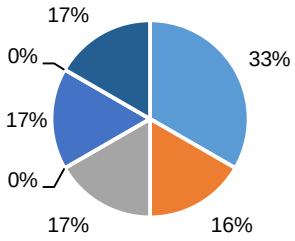
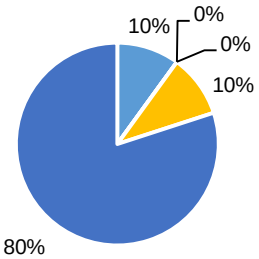
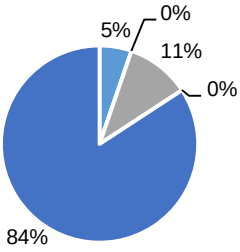
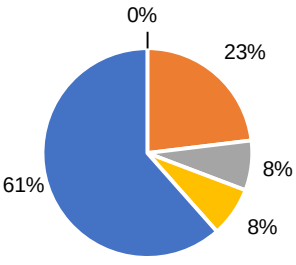
| Meyersdal Eco Estate | Greater Johannesburg | Cedar Hills Private Estate | Legends for each question |
|---|---|---|---|
| 4) What is your opinion regarding rock hyraxes in Johannesburg? | | | |
|  |  |  | They are part of the biodiversity, even in Johannesburg<br>They are part of the biodiversity, but not in Johannesburg<br>They are pests<br>They are cute and cuddly |
| 5) Have rock hyraxes caused damage to you or your property? | | | |
|  |  |  | Yes<br>No |
| 6) If so, what type of damage did rock hyraxes cause? | | | |
|  |  |  | Destroyed my garden<br>Made a den in my roof<br>Middens in my roof<br>Middens under my deck<br>Middens in my garden<br>Caused harm to me or someone I know<br>Displayed aggressive behaviour |
| 7) How did you respond to the damage caused by rock hyraxes? | | | |
|  |  |  | I do not wish to disclose any information<br>Shot or put out poison for rock hyraxes<br>Had the rock hyraxes removed from my property<br>Moved house<br>I have done nothing |

Figure 6. Percentages of responses to multiple choice questions 4 – 7 for the three survey locations – Meyersdal Eco Estate, Greater Johannesburg, and Cedar Hills Private Estate. The data for questions 1 – 3 are described in text.

Location (Wald $\chi^2_2 = 0.91$, $p = 0.636$), response (Wald $\chi^2_6 = 0.64$, $p = 0.996$) and location × response (Wald $\chi^2_{12} = 0.83$, $p = 1.000$) were not significant predictors of the type of damage caused by rock hyraxes (Figure 6). This implied that the rock hyraxes differ in the types of damage caused in each of the locations. Meyersdal Eco estate respondents reported middens-related, garden-related and aggression-related damages. Greater Johannesburg respondents reported mostly garden-related damages. Cedar Hills Private Estate respondents reported garden-related, roof-related and aggression-related damages.

Response (Wald $\chi^2_2 = 13.67$, $p = 0.008$) was a significant predictor of the public's response to damage caused by rock hyraxes. Location (Wald $\chi^2_2 = 0.00$, $p = 1.000$) and location × response (Wald $\chi^2_8 = 0.43$, $p = 1.000$) were not significant predictors. Tukey post-hoc tests showed that respondents preferred to do nothing in response to the rock hyraxes causing damage versus having them removed and performing an act they did not wish to disclose. However, there was no clear indication for any choice when selecting from the other options (Figure 6).

I summarised the open-ended responses from the "Other" option for the questions regarding the opinion of rock hyraxes by respondents, the types of damage caused by rock hyraxes, and the response of respondents to rock hyrax damage. Overall, respondents stated that rock hyraxes are part of nature but can be pests across the region due to their "offensive" behaviour and potentially high population numbers. They mentioned that rock hyraxes were known to inflict damage to property, although mostly in the winter months, are a nuisance with regards to their vocalisations and middens, attacked small pets and were reportedly aggressive towards small children.

In Meyersdal Eco Estate, 67% of respondents highlighted the aggressive behaviour of rock hyraxes towards small domestic pets. Although respondents from Cedar Hills Private Estate and Greater Johannesburg also reported this aggressive behaviour, these were two isolated cases from both locations. Cedar Hills Private Estate respondents mostly reported not having a problem with rock hyraxes on the estate coupled with isolated incidences of foraging damage and aggression to people/pests, while the respondents from Greater Johannesburg had very few comments such as rock hyraxes showing aggressive behaviour and causing some damage to garden plants.

In response to rock hyrax damage, 78% of Meyersdal Eco Estate respondents reported household management using various methods to prevent access of rock hyraxes onto their

properties. 43% of those respondents used pet dogs, especially larger breeds, to deter rock hyraxes and another 43% used physical barriers to bar access. In one isolated case, a respondent had used snake skin and dung to deter rock hyraxes, which were both unsuccessful. Cedar Hills Private Estate and Greater Johannesburg respondents provided no further comments regarding rock hyrax damage other than those provided in the MCQ (Questions 7).

## Discussion

### Occurrence in Greater Johannesburg

Whether an animal species uses urban habitats depends on the availability of resources in these habitats (Boyce & Mcdonald 1999) as well as the ability of these species to utilise these resources through morphological, physiological and/ or behavioural adaptations (Francis & Chadwick 2012). Rocky outcrops occur within the Greater Johannesburg boundaries and while most of the surrounding habitat has been developed, these outcrops tend to remain untouched due to the difficulty in developing these habitats (Jellinek et al. 2004). Due to their occurrence on rocky outcrops, I predicted that rock hyraxes would favour areas with rocky outcrops, which was partially supported in my study.

Reported sightings highlighted that rock hyraxes were occurring in the north and south of Greater Johannesburg but not in the intensely urbanised city centres. Most of the reports associated rock hyraxes with municipal nature reserves containing rocky outcrops, while other reports associated rock hyraxes to residential areas located near these reserves. The reports from residential areas also described rock hyraxes utilising urban features such as driveways, roofs and walls for basking.

The vegetation feature analysis indicated that rock hyraxes in the north of Greater Johannesburg were selecting for Egoli Granite Grassland vegetation which is characteristic of this area (Bredenkamp et al. 2006). Rock hyraxes were also found to occur in the Gold Reef Mountain Bushveld, along the west-east-trending ridge from Krugersdorp in the west to Bedfordview in the east (van Staden et al. 2013), and in the Andesite Mountain Bushveld, along the Klipriviersberg ridge in the south (Cousins et al. 2014). The Egoli Granite Grassland has been highly developed for residential, industrial and commercial land use, with approximately 61% of this vegetation having been irreversibly transformed and only 0.02% protected in the Glen Austin Bird Sanctuary, Melville Koppies Nature Reserve, Ruimsig

Nature Reserve and the Waler Sisulu Botanical Gardens (Bredenkamp et al. 2006). This could suggest that rock hyraxes in these areas may be isolated to fragments of rocky outcrops and/or utilising urban areas, such as residential areas, retail areas, parks, sports pitches, located nearby.

The soil feature analysis found that rock hyraxes were selecting for plinthosol-based soils and were also occurring on leptosol-based soils. Plinthosol-based soils are associated with savannah habitats in southern Africa while leptosol-based soils are generally associated with rocky areas (IUSS Working Group WRB 2014). These soils suggest that rock hyraxes are associating with both grassland and rocky habitats. However, with most of the grassland habitat having been developed for residential, industrial and commercial land use it is quite likely that the soils associating with the grassland habitat may fall under these developed features. Thus, rock hyraxes occurring on these soil types may be associating to these urban features such as residential areas, retail areas, parks, sports pitches, located nearby.

The proximity feature analysis showed that rock hyraxes were not selecting for any particular feature at any distance and suggests a generalist use of features within Greater Johannesburg. However, since this is the first study, to my knowledge, to assess the potential resource selection of rock hyraxes in an urban environment, future studies should investigate a broader scale using a nation-wide assessment of rock hyrax habitat use or even a finer-scale assessment of individual colony habitat use. These studies may better assess whether this generalist use of urban habitats is reflective of rock hyraxes at all spatial scales, including urban, peri-urban and rural areas.

Rock hyraxes were neither selecting nor avoiding any particular proximate feature but were more often associated with rocky outcrops and urbanised areas. Rock hyraxes have been reported to utilise buildings and storm water drains as den sites and also forage on garden plants in residential areas (see Chapter 2). The reports of rock hyraxes in association with known rocky outcrop locations within Greater Johannesburg indicate they are favouring these areas. This association could suggest that rock hyraxes may be ecologically constrained to features of rocky outcrops (i.e. niche conservative choice) since basking on rocks is important to meet their thermoregulatory requirements (Chapter 2, Brown & Downs 2007). This further suggests that rocky outcrops may be habitat refugia for rock hyraxes and they may initially require rocky outcrops from which to exploit surrounding urban areas containing

various gardens, illustrating their behavioural flexibility in foraging activity and food choice and potential denning structures (Chapter 2).

**Public Opinion**

The presence of wildlife in urban environments can be perceived positively by human residents and generally negative and positive perceptions are influenced by direct interactions between people and wildlife (König 2008; Dowle & Deane 2009). In my survey results, most of the respondents regarded rock hyraxes as part of the urban biodiversity of Greater Johannesburg. Although this was surprising, there were respondents that felt that rock hyraxes were pests. These sentiments tended to be linked with damage to garden plants by foraging rock hyraxes which may have been aggravated through denning in roofs and under decks, the deposition of odorous middens containing faecal deposits and urine in these locations, as well as aggressive behaviour towards domestic pets.

Many human-wildlife conflict studies demonstrate that the public may tolerate some aspects of human-wildlife co-existence, but when wildlife activities cause economic loss or threaten safety of humans and pets, views of these wildlife species tend to be more negative and may result in support for more stringent control measures (Hill et al. 2007; Dowle & Deane 2009). For example, the public opinions regarding brushtail, *Trichosurus vulpecula*, and ring-tailed, *Pseudocheirus peregrinus*, possums in urban environments were influenced mainly by their presence of possums in ceiling cavities linked to negative attitudes while those people not experiencing this activity provided more positive opinions (Hill et al. 2007).

The use of non-lethal deterrents is becoming more important in urban environments with an increase in the reported use of predator odours and other deterrent mechanisms (Woolhouse & Morgan 1995). One respondent from Meyersdal Eco Estate mentioned using snake skin and dung to potentially deter rock hyraxes from their property, which were unsuccessful. In Chapter 2, I assessed the efficacy of snake dung on deterring rock hyraxes from a food incentive, and I also found that the snake dung was ineffective. One suggested reason for the inefficacy of this deterrent was that it was not associated with negative consequences, resulting in rapid habituation to the stimulus (Kimball et al. 2009).

Surprisingly, I received a small number of responses of $n < 50$ per survey location. This low rate could reflect a lack of experience, familiarity, and interest in rock hyraxes by the public in Greater Johannesburg, as suggested for surveys of moose, *Alces alces*, in

Connecticut, USA (LaBonte et al. 2013). Another reason for the low response numbers could be the method of survey distribution and awareness since I had passively distributed the surveys online and actively but indirectly by e-mail through estate managers. Estate managers also indirectly relayed survey follow-ups and I posted passive reminders regarding the survey online. Perhaps a self-administered questionnaire with an active distribution may have yielded greater numbers, particularly in areas where rock hyraxes have been suggested to occur, where surveys could be delivered to a random sample pool of households per area with a suggested date of collection (Bjurlin & Cypher 2005; Hill et al. 2007)or set numbers of surveys could be actively conducted at public centres such as malls, markets (McDonald et al. 2012).

Additionally, my survey targeted a subset of the affluent public in Johannesburg and, therefore, the opinions may not reflect those of residents of all communities in the area. This may have been due to the distribution of the surveys electronically over the internet as there are various racial and socioeconomic groups that may not have consistent access to the internet and could not and/or did not participate in the survey (Payne & Barnfather 2012). Again, this suggests that the distribution method may need adjusting or should consist of multiple formats in order to reach various communities within the study area.

## Conclusion

Rock hyraxes were present in urban areas, mainly in the south and north of Greater Johannesburg, but avoided densely populated human areas in central Johannesburg. However, rock hyraxes may have been relocated from other sites to some of these areas they currently occupied, potentially resulting in inconsistencies in the data. Nonetheless, they have adapted to these sites, indicating that suitable habitats were available there or these sites represented areas that were occupied by rock hyraxes historically. Future studies could incorporate available relocation information to not only assess habitat suitability of the sites but also to assess how it influences rock hyrax habitat selection and persistence.

Rock hyraxes showed no particular preference for urban features but vegetation and soil analyses as well as reports from the public surveys associated them in areas with known rocky outcrops. This association appears to be phylogenetically constrained, with rocky outcrops being habitat refugia and basking sites from which rock hyraxes make forays into

610 gardens and buildings. In urban areas, rock hyraxes are accepted as part of the biodiversity
611 and although rock hyraxes were considered pests when they cause damage, there was no
612 strong opinion towards removing rock hyraxes from urban environments. This assessment of
613 public opinion towards wildlife, especially urban wildlife, is becoming a useful tool with
614 which to understand and implement attitudes of the public into current and future
615 management plans, particularly in the case of human-wildlife conflict mitigation (LaBonte et
616 al. 2013). These opinions would assist in better understanding the interaction between rock
617 hyraxes and humans because the outcome, positive or negative, of this interaction could be
618 influential in the overall establishment of rock hyraxes in urban environments.

# Chapter 4. General Discussion

Wildlife has been suggested to occur in urban environments either because they can flexibly adjust their behaviour mainly (Lowry et al. 2013) or because they are constrained to occupy urban areas that match their natural habitat, reflecting niche conservatism (Wiens et al. 2010). My study has shown that rock hyraxes, *Procavia capensis*, occurring in urban environments are expressing both niche conservatism as well as behavioural flexibility.

Animal species show niche conservatism when they are constrained by niche-related, ecological traits through time and these constraints influence the use of environments by those species (Wiens et al. 2010). Due to their use of behaviour for maintaining body temperature, rock hyraxes appear to be constrained to microhabitats within their environment from which to meet their thermoregulatory demands, usually through basking, sunbathing and shuttling between exposed and shady areas (Brown & Downs 2007). Rocky outcrops provide crevices and impervious surfaces which assist rock hyraxes to meet these thermoregulatory and energy demands. Rock crevices form not only dens but are important refuges from potential aerial predators (e.g. Verreaux's eagle, *Aquila verreauxii*) as well as from external ambient air temperatures that fall outside their thermal neutral zone (Brown & Downs 2007). Impervious rock surfaces provide a platform on which basking and sunbathing can occur. As a result of their thermal requirements, rock hyraxes are diurnal to maximise the utilisation of solar radiation (Fourie 1983; Brown & Downs 2007). Rock hyraxes are thus physiologically, behaviourally and ecologically constrained to rocky outcrops. In support, my assessment of resources used (RSF; Chapter 3) showed that rock hyraxes were associating with areas containing rocky outcrops.

Behavioural flexibility is a mechanism that apparently enables animal species to adjust their behaviours to change, as occurs during urbanisation (Kaiser et al. 2014). Adjustments to diel activity (Beckmann & Berger 2003), antipredator responses (Bateman & Fleming 2014) and foraging behaviour (Adams et al. 2013) are a few of the common behaviourally flexible traits used by wildlife species to adjust to urban environments. For example, the common brushtail possum, *Trichosurus vulpecula*, relies on both natural food in forest fragments but also supplements its diet with highly nutritious and energy-rich plants found in residential gardens (Adams et al. 2013). Their behavioural flexibility to exploit novel food, in addition to utilising novel den sites (e.g. wood piles, roofs, chimneys), have enabled common brushtail possums to invade New Zealand, although they still require

considerable natural vegetation in their suburban environments (Adams et al. 2013). Rock hyraxes showed behavioural flexibility by demonstrating an ability to habituate and adjust their perceived risk, according to their proximity to people (Chapter 2). This habituation to perceived risk of humans enables them to exploit urban environments where they appear to gain benefits, such as food from gardens and potential den locations near these food sources. Rock hyraxes also increased their foraging activity due to a reduction in perceived risk as well as in their ability to utilise anthropogenic food resources in residential gardens, containing both indigenous and exotic plants (Chapters 2 and 3). Urban gardens provided a variety of food items throughout the year and are maintained in winter through artificial watering (McKinney 2002; Lowry et al. 2013). As rock hyraxes are opportunistically selective feeders (Skinner & Chimimba 2005), gardens would offer a greater abundance of advantageous phenological plant stages (e.g. flowers, young leaves, fruit) throughout the year. Due to reduced predation risk associated with some gardens, rock hyraxes would feed more frequently throughout the day and especially so when in close proximity to gardens.

Similar to the common brushtail possum, rock hyraxes appear to require natural remnant rocky areas within urban environments from which to exploit human dwellings, such as gardens. These natural remnant habitats are important as they show little evidence of novelty or human impact (Lundholm & Richardson 2010). However, in some cases, human impacted areas may produce habitats that have natural analogues that can be ecologically analogous to natural habitats, for example, stone walls would resemble natural cliffs (Lundholm & Richardson 2010). Thus, these analogues are not too dissimilar to the natural habitat (Lundholm & Richardson 2010), and species utilise these habitat analogues by responding to natural habitat cues (Wong & Candolin 2015). For example, rock doves, *Columba livia*, and peregrine falcons, *Falco peregrinus*, are adapted to cliff-like rocky areas and utilise de-vegetated concrete edifices in urban environments (McKinney 2002; Lundholm & Richardson 2010).

In my study, the cul-de-sac colony in Meyersdal Eco Estate used a storm water drain, which is presumably a habitat analogue for a rocky outcrop. The use of storm water drains as habitat analogues might have been achieved by two types of movement: colony shifts and/or dispersal. Rock hyrax colonies might have moved from a rocky outcrop to the storm water drain during travelling within their home range to gain better access to resources, such as food, and resulting in the establishment of the new den sites. However, this type of movement is not documented in the literature. Alternatively, dispersal, which is usually done by subadult

and adult male rock hyraxes (Koren & Geffen 2009; Visser 2013), may be restricted by urban fences, walls, roads and buildings (Fitzgibbon et al. 2011). Thus, if no suitable rocky outcrops are available during dispersal, males dispersing may find and utilise suitable habitat analogues. Rock hyraxes would thus find rocky outcrop analogues in the surrounding urban areas, such as storm water drains (in my study) and holes in roofs and under buildings that mimic rock crevices, and tarmac, pavement, driveways, roof tiles and walls (reported in Chapter 3) that mimic impervious rock surfaces.

Animals in urban environments can be classified as an urban dweller or an urban utilizer according to the importance of developed and natural areas to their population dynamics (Fischer et al. 2015). Urban dwellers tend to be commensal species that can thrive in developed areas through the extensive use and dependence on anthropogenic resources and appear not to require considerable vegetation for shelter and food (McKinney 2006; Shochat et al. 2006; Fischer et al. 2015). Urban utilizers tend to be indigenous species that can occur in developed areas and can utilise natural and anthropogenic resources, although not as extensively as urban dwellers, in urban environments (McKinney 2006; Bateman & Fleming 2012; Conole 2014; Fischer et al. 2015). Urban utilizers can either make use of developed areas for non-breeding purposes such as foraging or may use developed areas to breed following dispersal from adjacent natural areas (Fischer et al. 2015) thus they tend to have a close affinity to habitat remnants of their natural habitat and these remnants are generally the source of emerging urban adapted species (Conole 2014). Thus, unlike urban dwellers, urban utilizers require considerable vegetation for shelter and/or food and are able to utilise both indigenous and non-indigenous plant species, commonly found in and around suburbs, particularly residential gardens (McKinney 2006; Fischer et al. 2015). Therefore, rock hyraxes can be considered urban utilizers as they utilize both natural rocky outcrops and feed in residential gardens.

The utilisation of residential gardens has been known to lead to human-wildlife conflicts when urban wildlife cause damage to plants (Dowle & Deane 2009). Additionally, human-wildlife conflicts can also occur due to damage to property and/or other nuisance factors, such as malodorous odours (Hill et al. 2007). These human-wildlife conflicts can influence the opinion of people towards the animals (Hill et al. 2007). Rock hyraxes are known to cause foraging damage and have other negative effects and although rock hyraxes were accepted as part of the urban biodiversity (Chapter 3), increased conflicts with people may change this opinion to a more negative one. Such conflicts are likely to be exacerbated

under growing urban populations of rock hyraxes, which might lead to lethal retaliation by people and ultimately influence the persistence of urban rock hyraxes.

Rocky outcrops may, therefore, provide a springboard from which rock hyraxes can exploit the surrounding urban landscape and the occurrence of urban/suburban gardens in close proximity may aid this exploitation. Habitat analogues, when available and necessary, together with gardens may further facilitate exploration and exploitation of surrounding urban features. Therefore, it appears that the preservation of rocky outcrops is required for the preservation of urban rock hyraxes.

## Future studies

My study suggests several avenues for further research. One important consideration is why certain rocky outcrops do not support rock hyrax colonies when the potential food sources are available in close proximity. For those rocky outcrops that do support rock hyrax colonies, their movement out of rocky outcrops and their exploitation of habitat analogues may require information about what causes rock hyraxes to move from phylogenetically constrained niches (rocks) to urban dwellings. A potential hypothesis would be that living in urban dwellings is risk averse, offers thermoregulatory advantages (e.g. warm tarmacs) and short travel distances to high energy-yielding food. Nonetheless, the colony furthest away from people at Meyersdal Eco Estate did not exploit urban gardens or denning sites. This colony also showed moderate habituation to people, indicating that reduced contact with people can potentially lessen conflicts, yet the conditions leading to the formation of such colonies is not known. Perhaps future studies can consider assessing relocation of rock hyraxes by humans as a way of forming such colonies. Some potential hypotheses worth testing are intra-specific competition and localised adaptation.

The mitigation of rock hyrax-human conflict may require studies of alternative deterrents and their efficacy to deter rock hyraxes from properties of homeowners because the two tested deterrents (boa dung, wild garlic) were not effective. This could assist homeowners in reducing the foraging damage of gardens by urban rock hyraxes and may maintain the positive attitude towards rock hyraxes in Greater Johannesburg. However, even this existing positive attitude might be a consequence of the unexpectedly low rate of return

in my public surveys from a small sub-set of Johannesburg residents. Future studies must generate a more inclusive public opinion data set.

## Conclusion

I investigated the behaviour of rock hyraxes in an urban site, Meyersdal Eco Estate, and investigated the occurrence and public perception of rock hyraxes in Greater Johannesburg. I showed that rock hyraxes have modified their behaviour and habituated to people and, surprisingly, such changes occurred over small spatial scales. Such behavioural flexibility over comparatively short distances is a novel finding. However, rocky outcrops are still important natural habitats from which rock hyraxes can explore and exploit the urban environment. Because they are constrained by their thermoregulatory requirements, habitat analogues are important in urban environments and rock hyraxes show the flexibility to be able to utilise these analogues when available. Such flexibility, which together with a tolerant public, might allow them to flourish in Johannesburg.

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# Appendices

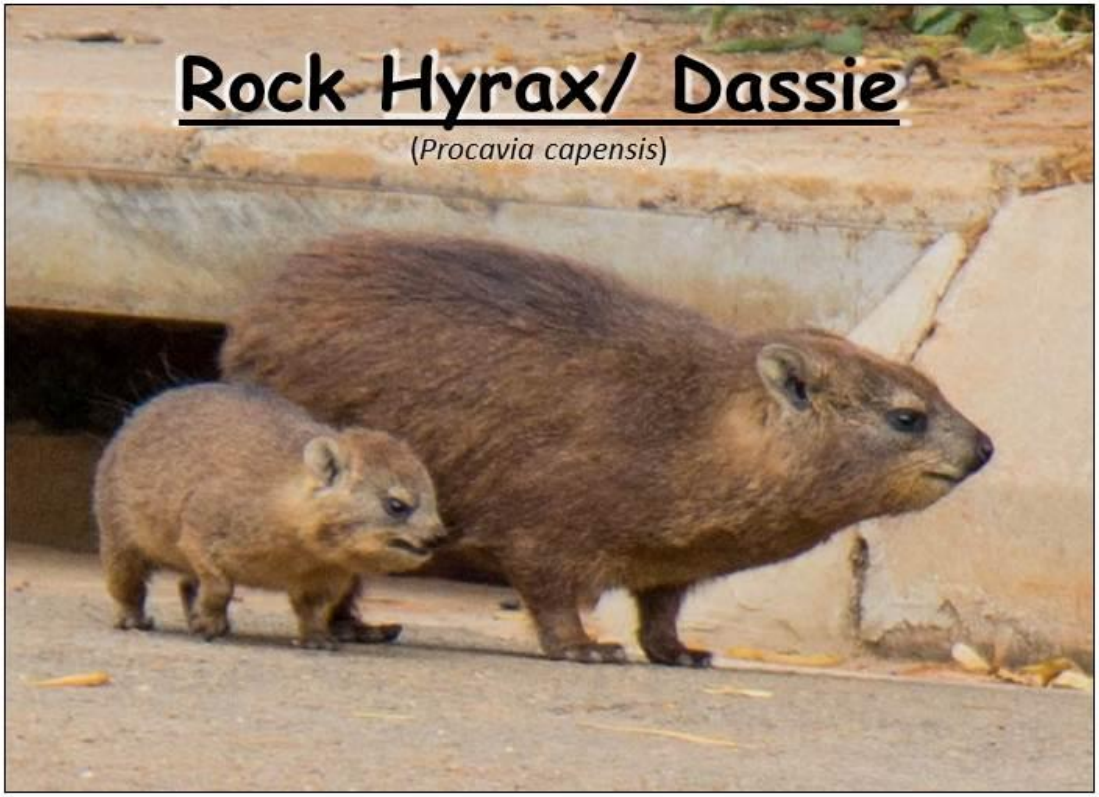
Appendix 1. Posters created and distributed to solicit occurrence data from the public

**REPORT YOUR DASSIE SIGHTINGS** to the **WAT Dassies project**.

We are investigating where dassies occur in **Johannesburg**.

Tell us **the date** when you saw it, **the location** (street address/ GPS co-ordinates), **the habitat** – koppie, grassland, drain, etc; and **how many** you saw at that sighting (1-5; 6-10; 11-20; 21-30; 31-40; 41-50; or >50).

Send it to: watdassies@gmail.com




WAT Dassies
Where Are The Dassies?

These **group-living** animals are found mostly in areas near **rocky outcrops/ koppies** in Johannesburg although they have been seen by **storm drains**. They are **diurnal/day** animals and can be seen **basking** hunched or **sunbathing** stretched out in the sun. They eat a **variety of plants** from grasses to tree leaves. If you want to find out more, like our **Facebook page** at https://www.facebook.com/watdassies and send us a message. Let us know of the dassies near you!

UNIVERSITY OF THE WITWATERSRAND JOHANNESBURG

Appendix 2. Survey consisting of seven multiple questions for Greater Johannesburg residents and the unit number question for Estate residents only.

For Estate Residents only

Unit No: _____

## Public Opinion on the Greater Johannesburg Rock Hyrax (Dassie)

* compulsory question

***1. Consent to participate:**

**- I confirm that I have read and understand the Participant Information Sheet**
**- I have had the opportunity to ask questions and had them answered**
**- I understand that all personal information will remain confidential and that all efforts will be made to ensure I cannot be identified**
**- I agree that data gathered in this study may be stored anonymously and securely, and may be used for future research**
**- I understand that my participation is voluntary and I am free to withdraw my participation BEFORE submission and that once submitted I have given final consent to take part in the study**

○ I have read and understood the details of the research and give my consent for my participation in the survey

***2. Have you seen dassies in Johannesburg?**

○ Yes

○ No

**3. If you have seen dassies in Johannesburg, where have you seen dassies? Please provide GPS co-ordinates or an address.**

**4. When you saw the dassies in Johannesburg, how many at one sighting did you see?**

○ 1-5 dassie(s)

○ 5-10 dassies

○ 10-20 dassies

○ 20-30 dassies

○ 30-40 dassies

- ○ 40-50 dassies
- ○ 50+ dassies

***5. What is your opinion of dassies?**

- ☐ They are part of the biodiversity, but not in Johannesburg.
- ☐ They are cute and cuddly.
- ☐ They are pests.
- ☐ They are part of the biodiversity even in Johannesburg.
- ☐ Other (please specify)

**6. Have they caused damage to property or person?**

- ○ Yes
- ○ No

**7. If yes, what types of damage have they caused?**

- ☐ Destroyed my garden
- ☐ Made a den in my roof.
- ☐ Middens (their toilet) in my roof
- ☐ Middens under my deck
- ☐ Middens in my garden
- ☐ Caused harm to (i.e. attacked) my person or someone I know (Please explain below)
- ☐ Displayed aggressive behaviour - growled and chased me or someone I know away
- ☐ Other (please specify) or provide further explanation on above options

**8. If dassies have caused damage, how have you tried to handle and/or fix the situation?**

- [ ] I not wish to disclose any information
- [ ] Relocated the dassies yourself
- [ ] Put out poison
- [ ] Shot the dassies
- [ ] Called pest management to take care of the dassie problem
- [ ] Moved house
- [ ] Called a wildlife organisation (e.g. FreeMe) to remove the dassies
- [ ] Ignored the dassies
- [ ] I don't see dassies as a problem
- [ ] Other (please specify)

Done

Powered by **SurveyMonkey**

Check out our sample surveys and create your own now!

Appendix 3. Map showing the areas of rock hyrax occurrence from survey responses

