Coexistence of sympatric yellow (*Cynictis penicillata*) and slender (*Galerella sanguinea*) mongoose in an urban environment

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DECLARATION

I hereby declare that this thesis is my own unaided work and that recognition has been given to the references used and assistance received. It is being submitted for the Degree of Doctor of Philosophy in the Faculty of Science at the University of the Witwatersrand. It has not been submitted for any degree or examination at any other University.

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Nadine Elizabeth Cronk

24 May 2019

ABSTRACT

Anthropogenic effects are driving extreme change in composition and structure of habitats at a global scale. Several wildlife species have been negatively impacted, yet other species are thriving in urban areas by exploiting anthropogenic habitats matching pre-existing niche preferences or modifying their biology for urban life. For species thriving in urban areas, food and shelter are potentially easily accessible and predation risk is reduced. Thus, urban areas might offer competing species similar opportunities to exploit the same resources, but the resources exploited might also be abundant enough to support large co-existing populations of these competing species. My study sought to determine the mechanisms of coexistence between the closely related and ecologically similar, yellow *Cynictis penicillata* and slender *Galerella sanguineus* mongoose. This was evaluated in two estates that varied slightly in their relative level of urbanisation, the Eco-Estate (more urbanised) and the Nature Estate (less urbanised), located in the south of Johannesburg, South Africa. I collected field data to assess diet, food selection, habitat preferences, activity patterns, and space use of each species, as well as the overlap in these biological parameters between the two species. Additionally, the home range of yellow mongoose was studied. First, scat analysis showed that: 1) insects and mammals were most abundant food item for both species in the Nature Estate and for slender mongoose in the Eco-Estate, while anthropogenic items were more prevalent than mammals for yellow mongoose in the Eco-Estate; 2) anthropogenic items were only prevalent in the more urbanised Eco-Estate; 3) scat components varied seasonally; and 4) dietary overlap was greatest in summer and lowest in winter. Second, food choice tests and carrion baited stations were used to establish food selection and feeding behaviour. I found that: 1) both species preferred meat and insects over other items, while yellow mongoose in the more urbanised estate preferred anthropogenic foods over insects; 2) yellow mongoose exhibited a shorter latency to approach and consume foods; and 3) slender mongoose were more prevalent at baited carcasses. Third, camera trap surveys established space use and activity patterns and showed that: 1) yellow mongoose were more prevalent in open habitats located near human residents, and slender mongoose were more common in covered areas further away from human residents, with spatial overlap being greater in a less urbanised estate; 2) species varied in peak active periods and overlap was greater in the more urbanised estate; and 3) complete spatio-temporal overlap was not apparent. Lastly, collaring and GPS tracking of the yellow mongoose showed that: 1) male home ranges were larger than that of females; 2) home range sizes in the less urbanised estate were larger; 3) home range sizes

varied seasonally; and 4) home range overlap with human residents was greater in the more urbanised estate. In conclusion, I showed that urbanisation can have an effect on the resource use of the yellow and slender mongoose. Both species displayed similar characteristics of diet and space use to their non-urban counterparts. They varied in their use of different resources, and while they overlapped in some aspects, they differed in others, thereby permitting their coexistence in urban areas as presumably they would in non-urban areas. However, particularly in the yellow mongoose in the Eco-Estate, the exploitation of anthropogenic resources shows that they are also responding flexibly to urbanisation, and the differential use of these resources in urban areas further aids in their coexistence.

DEDICATION

I dedicate this thesis to the loving memory of my grandfather, William Arthur Cronk, whose wisdom and brilliance will never be surpassed. Your presence in all of our lives was truly a blessing, and you will never be forgotten.

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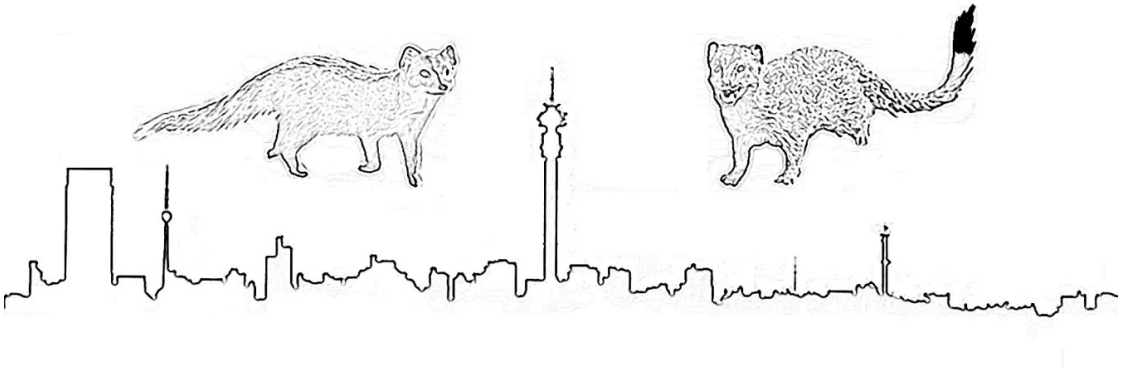

TABLE OF CONTENTS

LIST OF FIGURES

CHAPTER 1:

CHAPTER 2:

CHAPTER 3:

CHAPTER 4:

CHAPTER 5:

LIST OF TABLES

CHAPTER 2

CHAPTER 3

CHAPTER 4

CHAPTER 5

CHAPTER 6

CHAPTER ONE

General Introduction

INTRODUCTION

Urbanisation

At a global scale, severely altered environmental conditions are often the result of anthropogenic disturbances (Partecke and Gwinner, 2007), an example of which is urbanisation, the fastest growing land use type (Wong and Candolin, 2015). The term 'urbanisation' refers to the transition of a natural/rural environment to an unnatural, heavily human influenced and populated environment (Chen 2007). Currently, across the globe, there are more people residing in urban areas/cities than there are in rural areas (United Nations 2014), and there are no signs of this migration to cities abating (Pauw and Louw, 2012). In South Africa alone, the most industrialised economy in Africa, at least 60% of the population lives in urbanised areas (Turok 2012). Of the numerous negative effects of human activity on the environment, urbanisation produces the greatest rates of loss of native wildlife species and overall local extinction of wildlife (Marzluff and Rodewald, 2008; Duduś *et al.,* 2014). The development of urban environments results in a permanent change in the habitats of wildlife, leading to substantial losses in biodiversity through diminishing and fragmented natural habitats (Gould and Andelt, 2013; Šálek *et al*., 2015).

In recent years, the effects of urbanisation on biodiversity have been the focus of a number of biological investigations. These studies have aimed to understand how some animals are able to persist under the drastic changes driven by anthropogenic forces (McKinney 2002; Magle and Angeloni, 2010; Bateman and Flemming, 2012; Gould and Andelt 2013, Šálek *et al*., 2015). Urban-living wildlife show changes in their life history biology, such as in population structure and dynamics (Shochat *et al.*, 2006; Šálek *et al*., 2015), morphology (Ditchkoff *et al.,* 2006) and feeding, ranging and/or activity behaviour (Herr 2008; Gould and Andelt, 2013; Walton *et al*., 2017). These adjustments of species to human conditions and consequent adaptation has been coined as 'synurbization' (Andrzejewski *et al.,* 1978), a term most widely described for bird and mammal species colonizing urban environments (Luniak 2004; Plumer *et al*., 2014). Ultimately, the various studies of urban ecology aspire to contribute knowledge to local and global biodiversity conservation under ever changing environmental conditions (Alvey 2006; Marzluff and Rodewald, 2008; Gehrt *et al.,* 2010; Magle and Angeloni, 2010).

Despite the fact that multiple species are either locally lost or displaced as a result of urbanisation, many other species are left which survive well in urban areas by exploiting habitats matching their pre-existing niche preferences, or modifying their biology for urban life (Partecke and Gwinner, 2007; Gehrt *et al.,* 2010; Bateman and Flemming, 2012; Duduś *et al.,* 2014). It is therefore imperative to first address the issue of 'biotic homogenisation' which has rapidly increased over time (McKinney and Lockwood, 2001). Biotic homogenisation can be described as the process of widespread non-native species replacing local indigenous species (McKinney 2006; Shochat *et al.,* 2006). Due to the rise in intentional exotic species importation over time (e.g. for pet trade, cultivation; Levine and D'Antonio, 2003) as well as the accidental introduction of species (Davis 2003; Alvey 2006), introduced species face a plethora of resources and no natural predators or enemies, consequently displacing numerous natives (Wong and Candolin, 2015). Key examples of species of biotic homogenisation are generalist species such as the feral house cat *Felis catus* and the rock dove (also referred to as the feral pigeon *Columba livia*; Blair 2001; Alvey 2006; McKinney 2006; Marzluff and Rodewald, 2008).

Although urbanisation and competition from introduced non-native and invasive species reduces overall native species richness and biodiversity (McKinney 2006), some urban areas are able to attain high levels of biodiversity (Alvey 2006). This raises the concept of the 'rural-urban' gradient, which describes the change in species composition and richness and overall biodiversity along a gradient that varies in the level of urbanisation/human impact (McKinney 2002; Magura *et al.,* 2008; Šálek *et al*., 2015; Walton *et al*., 2017). Essentially, the level of biodiversity tends to increase with a decrease in the intensity/level of urbanisation (i.e. more animals in less urbanised areas; Walton *et al*., 2017). At intermediate levels (rural-urban mix), conditions start becoming favourable for numerous species, which maintain a stable level of biodiversity (McKinney 2002). With the development of suburban areas comes an increase in structural diversity, with different forms of buildings and structures, which then become sites of shelter/refugia and reproduction for species (McKinney 2002; Baker and Harris, 2007; Herr 2008; Magura *et al.*, 2008). Furthermore, favourable conditions in these areas include an easily obtainable and abundant food resources and greatly reduced predation pressure in most instances (McKinney 2002; Wong and Candolin, 2015; Cronk and Pillay, 2018). In particular, sub-urban parks and gardens have provided suitable habitats for numerous organisms (Mahan and O'Connell, 2005; Baker and Harris, 2007; Herr 2008).

It is clear that different species vary in adaptability and not all animals are able to adapt or survive urbanisation. It is for this reason that Blair (2001) categorized species according to their response to urbanisation, regarding them as urban adapters, exploiters and avoiders. Urban adapters are those that are able to use anthropogenic resources as well as natural resources (Blair 2001). Typically, these originate from the areas surrounding the new-founded urban environments (McKinney 2006). Typical urban adapters include groundhogs *Marmota monax*, skunks *Mephitis mephitis*, and also the red fox *Vulpes vulpes* (McKinney 2002). Some organisms have become entirely dependent on human resources. These are termed the urban exploiters (Blair 2001), described as species that are firstly either pre-adapted to certain urban conditions, or species that are even better adapted to intense urban conditions, therefore becoming fully reliant on human resources for survival (such as the house mouse *Mus musculus* and the Norway rat *Rattus norvegicus*, McKinney 2006; Pauw and Louw, 2012; Duduś *et al.,* 2014); these are usually not native to a region (Adams 1994). Finally, those that are generally completely reliant on natural resources are the urban avoiders, which are most sensitive to anthropogenic change (Blair, 2001; Bateman and Fleming, 2012). These include the species that are most likely to disappear first following urbanisation, and are typically the larger mammals due to human persecution, for example cougars *Puma concolor* (McKinney 2002).

Humans and urban wildlife

Urban wildlife does provide a host of benefits to people. For example, Curtin (2009) noted that exposure to wildlife has certain emotional benefits; a number of people obtain personal enjoyment out of nature through simple viewing or photographing wildlife, and a more species diverse area gives it a greater aesthetic value (DeStefano and DeGraaf, 2003; Adams 2005). However, the close association between humans and wildlife in urban areas often results in inevitable conflict (Gehrt *et al.,* 2010). Typically the urban adapters also negatively impact on humans and their lives. Urban wildlife has a long history of nuisance behaviour which comes with damage to personal property and detriment to health (through the carrying of diseases) and to human safety. For example, and prevalent worldwide, is the damage caused by house mice and house rats, through denning and feeding related issues (Conover 2002). These animals and numerous others such as racoons *Procyon lotor*, skunks (Grosenbaugh *et al.,* 2007), red foxes (Truyen *et al.,* 1998) and even white-tailed deer *Odocoileus viginianus* (Raizman *et al.,* 2013), are also carriers of multiple diseases (Hamer *et*

al., 2012) that are harmful to human health. Worldwide, there are urban environments that are host to carnivores which in itself, might impose a direct infringement on human safety. It is typically the larger carnivores that are of concern, such as cougars (Kertson *et al.,* 2011), coyotes *Canis latrans* (Murray *et al.,* 2015), grey wolves *Canis lupus* and black bears *Ursus americanus* (Bateman and Flemming, 2012), which are prevalent in urban America and Europe. Large carnivores are often eliminated from urban environments, mostly as a safety precaution for people and domesticated animals (Clark *et al.,* 1996).

Interestingly, a number of smaller carnivores thrive in urban environments globally (Riley 2006). These typically include numerous feral species and non-domesticated animals, often highly adapted and resident in urban environments, exploiting the abundant resources and safety net of the lack of apex predators (Bateman and Flemming, 2012). Most urban adapted small- to medium-sized carnivores are referred to as meso-carnivores, whose diets contain a combination of vertebrates and invertebrates (and some plant matter), and they also commonly consume anthropogenic food items (e.g. garbage, pet food, non-native plants; Buskirk *et al.,* 2003; Ditchkoff *et al.,* 2006; Herr 2008; Prigioni *et al*., 2008; Bateman and Flemming, 2012; Murray *et al*., 2015). For example, the red fox and raccoon in America and Europe respectively, are two of the most widespread and widely studied synanthropic carnivore species (i.e. urban animals) that have exhibited an extraordinary ability to exploit urban environments. Similarly, so has the stone marten *Martes foina* in Europe (Ditchkoff *et al.*, 2006; Herr 2008; Prigioni *et al*., 2008; Duduś *et al.,* 2014). Additionally, the larger coyote fares extremely well in urban areas (Murray *et al*., 2015; Poessel *et al*., 2017). Through the manipulation of newly found resources, and increased tolerance for humans (Gehrt *et al*., 2010), these species have attained high population densities and continue to thrive in urban areas (Bateman and Flemming, 2012; Plumer *et al*., 2014; Wong and Candolin 2015; Adams 2016). In urban areas, there is potential for coexistence of several meso-carnivores which otherwise may not co-occur in their natural environments. What mechanisms would allow them to coexist?

Interspecific competition and coexistence

To contribute to the conservation of biodiversity, it is imperative for biological investigations to gain a better understanding of the factors that determine the patterns of species diversity, one of which is interspecific competition and co-existence. Competition is

defined as a direct or indirect interaction among two or more organisms utilizing the same resources that may be limited, resulting in a decrease in the fitness of either or both involved (Holt 2001; Aschehoug and Callaway, 2015). Ultimately, competition between species can lead to a reduction of population sizes and loss of species from communities (Aschehoug and Callaway, 2015).

Intraspecific competition refers to the competition that can occur between individuals of the same species, interacting for common resources. Interspecific competition on the other hand, and the focus of my study, occurs between individuals of different species that interact over common resources (Svanbäck *et al.,* 2008). Various types of competition exist, with exploitative and interference competition being well-studied examples (Le Bourlot *et al*., 2014). Exploitative competition occurs when one species finds and utilises a limited resource which excludes the other species (Holt 2001). Interference competition can occur either indirectly or directly, whereby one species actively prevents another from accessing a resource, for example by territoriality or aggression (Adams 2005). With the potential negative consequences of competitive interactions, e.g. death, it is beneficial for species to avoid such interactions (Aschehoug and Callaway, 2015).

Coexistence is simply defined as the state at which two or more organisms/species are able to live together spatio-temporally (Karanth *et al*., 2017). For two (or more) species that maintain similar and constant population numbers, coexistence can occur only if behavioural and ecological differences exist among the species (Holt 2001; Barrientos and Virgós, 2006). This phenomenon has been referred to as the competitive exclusion principle, which maintains that complete ecological overlap among species cannot result in coexistence in any given environment (Tokeshi 2009). Niche differentiation (i.e. ecological diversification) is the consequent mechanism of coexistence (Ribeiro 2016). A 'niche' is defined as an n-dimensional hyper volume in which species are arranged according to resource requirements and abiotic conditions. The dimensions of a niche can range from spatial and temporal use (e.g. habitat use or activity time) to food use and mate resource acquisition (Prigioni *et al*., 2008; Kylafis and Loreau, 2011; Frey *et al*., 2017). The niche of a species is then further constrained by competitors, conspecifics and other biotic factors.

The niche concept emphasises that if two or more species use a particular niche dimension, they must differ in some other dimension to be able to coexist (Barrientos and Virgós, 2006; Kylafis and Loreau, 2011; Ribeiro 2016). In foundational research, MacArthur (1958) showed that various species of similar-sized, co-existing warblers (genus *Dendroica*)

fed on the same insect taxa, but just in different parts of a tree; this reduced the potential for competition and promoted coexistence. More recently, dholes *Cuon alpinus* were shown to avoid competition with nocturnal tigers *Panthera tigris* and leopards *Pantera pardu* by being primarily diurnal (Karanth *et al*., 2017); while the different feeding habits of the red fox and Eurasian badger *Meles meles* enable their coexistence in peri-urban Portugal (Ribeiro 2016). Garneau (2005) investigated the coexistence between black bears and grey wolves and concluded that although sharing the same prey (moose *Alces alces* and caribou calves *Rangifer tarandus*), they segregated temporally: black bears preyed on calves earlier in the breeding season whereas wolves did so later in the season. Cheetahs *Acinonyx jubatus* segregate spatially by hunting in less energetically profitable habitats to avoid competitive interactions with lions *Panthera leo* and spotted hyena *Crocuta crocuta* (Durant 2000). Other studies of coexistence in the sympatric canid species, the maned wolf *Chrysocyon brachyurus*, crab eating fox *Cerdocyon thous*, and the hoary fox *Lycalopex vetulu,* found that these carnivores differ in activity time in hunting for common prey (Jacomo *et al.,* 2004).

The ecology and coexistence of species has been extensively studied in natural areas, yet far less attention has been given to the coexistence of sympatric species in urban environments. Moreover, the coexistence between two closely related carnivores in an urban area, assessing diet, space and temporal use and overlap has not been addressed. As previously mentioned, urbanisation has been shown to significantly influence the biology of small urban carnivores, but at the same time, urban areas provide a surplus of easily accessible resources. Nonetheless, these urban areas might offer competing species similar opportunities to exploit the same resources, and the resources exploited might also be abundant enough to support large co-existing populations of competing species. Therefore, by investigating the ecology of urban animals in comparison to non-urban counterparts, we are able to establish how species modify aspects of their ecology in order to adapt to human-induced changes and co-exist with competing species.

Study species

General biology of the yellow mongoose

The yellow mongoose *Cynitis penicillata* (Ogilby 1833) is a member of the *Herpestidae* family and is the only species of its genus (Earlé 1981; Taylor and Meester, 1993). Yellow mongoose are endemic and widespread throughout Southern Africa (Mills and

Hess, 1997). In South Africa, they occur mostly in the Free State and North West provinces, excluding the north-eastern and southern regions of Kwa-Zulu Natal (Skinner and Chimimba, 2005; Figure 1). The yellow mongoose utilises a wide range of habitats and is usually found in open and low vegetation areas (Blaum *et al.*, 2007; Kingdon *et al.*, 2013). Shrub coverage, however, was found to be an important predictor of their habitat use (Blaum *et al*., 2007) because it provides protection against primary predators (Kingdon *et al.,* 2013), such as martial *Polemaetus bellicosus* and tawny *Aquila rapax* eagles (Blaum *et al.*, 2007). Other predators include black-backed jackal *Canis mesomelas* and large snakes such as the Cape cobra *Naja nivea* (Kingdon *et al.,* 2013*).*

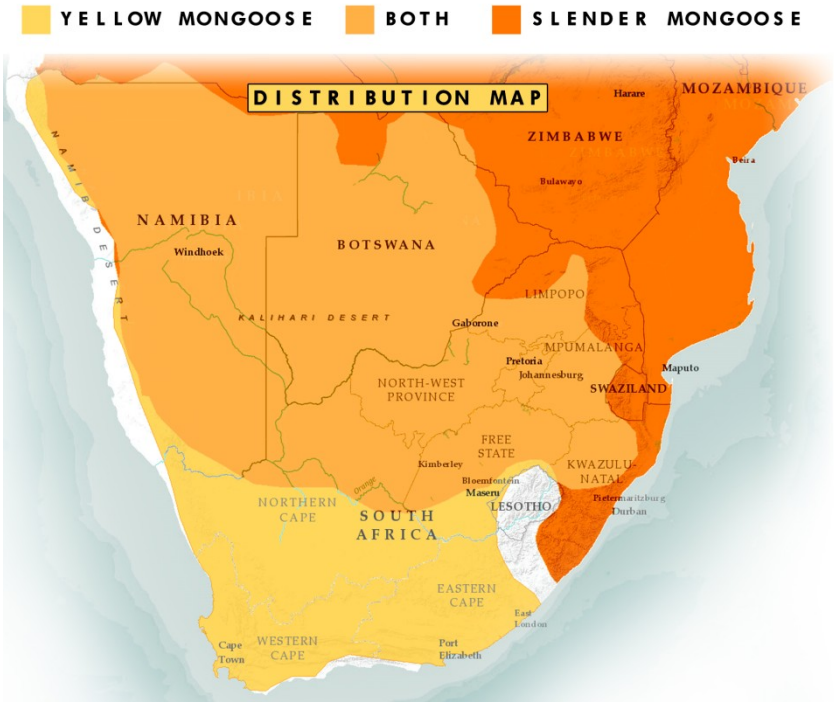

Figure 1. A composite map showing the current published distribution and overlap of the yellow and slender mongoose in southern Africa (generated using maps produced by Do Linh San *et al.*, 2015 and Do Linh San and Maddock, 2016).

Its pelage varies from greyish-tawny yellow or orange in colour, with a long, bushy tail with a white tip (Taylor and Meester, 1993; Estes 2012). It is relatively small and slight sexual size dimorphism exists: males weigh 600 g on average with a body length of ±560 mm, and females 550 g on average with a body length of ±550 mm (Skinner and Chimimba, 2005; Waterman and Roth, 2007).

Mating begins in July and females produce two litters annually (2-4 months apart; Rasa *et al.*, 1992) following a 42-57 day gestation period (Zumpt, 1976). Females produce small litters varying between 2 and 5 pups (Rasa *et al*., 1992) and the species has evolved cooperative breeding, whereby non-breeding members of a group feed and care for young (Rasa *et al.,* 2012). Weaning occurs at 8 weeks of age, followed by young accompanying adults to forage before becoming nutritionally independent (Rasa *et al.*, 1992). Both sexes reach sexual maturity around 12 months; at sexual maturity, subordinate males disperse to establish a new territory or gain admission to other colonies (Le Roux *et al.*, 2008; Estes 2012). The longevity of yellow mongoose in the wild is unknown, although they have been found to live up to 15 years in captivity.

While members of the *Herpestidae* family are found to be either highly social or solitary (Skinner and Smithers, 1990; Veron *et al.,* 2004), the yellow mongoose appears to be unusual in the family. It lives in colonies (considered family groups) of between 2 and 13 individuals on average (usually a pair, a few additional adults that have not dispersed from the natal burrow, and the young produced in the year; Balmforth 2004; Mbatyoti 2012; Kingdon *et al.,* 2013), which occupy a den, defends a territory against conspecifics, and rears young cooperatively as a group (Le Roux, 2007). However, it is a solitary forager (Le Roux, 2007), showing a spatial dichotomy in denning and foraging.

The yellow mongoose is predominantly insectivorous but also an opportunistic carnivore, feeding on smaller vertebrates and sometimes carrion (Earlé 1981; Avenant and Nel, 1992; Nel and Kok, 1999; Skinner and Chimimba, 2005). It is diurnal, and its typical daily activity commences at sunrise and ends at sunset (Earlé 1981; Skinner and Chimimba, 2005; Mbatyoti, 2012). Earlé (1981) mentioned that after emerging from dens in the morning (around 6 am), individuals first move to the groups' midden to defecate before returning to the den for a short period. Thereafter, they sunbathe for a short duration before leaving the den to forage (Earlé 1981). Few studies have considered the yellow mongoose's activity budget, with Cavallini (1993a) reporting activity to include foraging, sunbathing, travelling (in search of food), resting, digging at denning sites (presumably to open new holes), social interactions at dens before retreating, and occasional grooming.

The maximum home range size of the yellow mongoose is 250 ha (mean of 70 ha; Taylor and Meester, 1993; Le Roux, 2007; Mbatyoti 2012). Male home ranges, which substantially overlap with that of other males (Cavallini 1993a), are more than twice the size

of that of the female home ranges (Zumpt 1976; Mbatyoti 2012). In addition, these larger home ranges of males typically include the home ranges of their offspring (Le Roux, 2007) and of several females; however, females from different dens have non-overlapping home ranges which suggests territoriality among females (Cavallini 1993b). Most commonly, the yellow mongoose occupies holes excavated by other animals and have even been found to share burrows with other species, such as meerkats *Suricata suricatta* and Cape ground squirrels *Xerus inauris* (Earlé 1981; Estes 2012; Kingdon *et al.,* 2013).

General biology of the slender mongoose

The slender mongoose *Galerella sanguinea* (Rüppell 1836) is also a member of the *Herpestidae* family, but of the subgenus *Galerella* (Skinner and Chimimba, 2005; Kingdon *et al.*, 2013). It has a widespread distribution that ranges throughout all of Africa south of the Sahara (Taylor 1975; Estes 2012). In South Africa, it occurs in the northern parts of the country (Stuart and Stuart, 2001; Figure 1). The slender mongoose inhabits a wide range of environments from woodlands to the outskirts of forests (not in the forests themselves; Skinner and Chimimba, 2005) and mountain regions (Maddock and Perrin, 1993). It is commonly preyed upon by large raptors, such as the martial eagle and African hawk *Hieraaetus spilogaster*, and by large carnivores such as wild dog *Lyacaon pictus* and leopard (Kingdon *et al.*, 2013).

The pelage of the slender mongoose varies geographically, with some appearing almost black and others redder, although it is commonly grey-brown in colour (Skinner and Chimimba, 2005). Sexual size dimorphism exists in that the males are larger than the females: males weigh up to 630 g, with a body length of ±600 mm on average, and females weigh up to 460 g, with a body length of ±550 mm on average (Kingdon *et al.*, 2013). The tail is over 80% the length of the body, and varies in length measuring up to 260 mm in females and 280 mm in males, and has a characteristic black tip (Skinner and Smithers, 1990). Both males and females possess anal glands; males have been recorded to use anal gland scent marking during the mating season (Estes 2012; Kingdon *et al.*, 2013).

The breeding season for the slender mongoose in southern Africa appears to correlate with the warmer months of the year, between October and March (Kingdon *et al.*, 2013). The exact gestation period is unknown, but is assumed to last between 60 and 70 days, with females producing 2 young per litter on average (Taylor 1975; Skinner and Chimimba, 2005).

Weaning occurs at roughly 8 weeks of age (Estes 2012), and, in one study conducted in the Serengeti National Park, juveniles were recorded dispersing from 6 months old (Kingdon *et al.,* 2013). Waser *et al.* (1995) recorded the longevity in nature to be 8 years for both sexes, while in captivity some individuals may live up to 12.6 years.

The slender mongoose is predominantly solitary and the sexes only come together to mate, but may form associations with up to four other individuals using the same home range (Kingdon *et al.,* 2013); slender mongoose rarely form small groups. Its home range size is not known precisely, although Taylor (1970) estimated a home range size of 100 ha. Non-overlapping male territories (encompassed within a larger home range) have also been estimated at approximately 50 ha (Rood and Waser, 1978). Several females hold territories measuring half the size of that of male territories (± 25 ha) occurring within a males' territory, although the female territories do not overlap intrasexually (Kingdon *et al.*, 2013). The slender mongoose tends to utilise holes excavated by other animals, namely old termite mounds and aardvark *Orycteropus afer* warrens as dens (Kingdon *et al.*, 2013).

It is largely diurnal, although it is reported to hunt at night if it is warm under moonlight (Taylor 1975). As with the yellow mongoose, daylight activity starts and ends with the onset of sunrise and sunset (Kingdon *et al.,* 2013), and consists of bouts of resting and sunbathing and foraging. Maddock and Perrin (1993) investigated the spatio-temporal ecology of viverrids in the Vernon Crookes Nature Reserve in KwaZulu-Natal Province, South Africa, and reported that the slender mongoose in this region had an activity peak in the hour period leading up to sunset. The species also makes use of middens which are regularly visited (Estes 2012). It is a dietary generalist carnivore (Kingdon *et al.,* 2013), with a diet consisting mainly of small vertebrates and insects; the dentition and musculature of the slender mongoose also makes it well adapted to feeding on carrion (Skinner and Chimimba, 2005; Kingdon *et al.,* 2013).

Suitability of yellow mongoose and slender mongoose as study species

Since the yellow and slender mongoose co-occur sympatrically in parts of Johannesburg (South Africa), it presented me with the opportunity to pioneer an assessment of the ecology of these species in an urban environment. These species are suitable models for assessing the mechanisms of coexistence in urban areas because they are both diurnal, locally abundant, and are often easy to observe since they are not elusive and show habituation to humans. Additionally, the biology of these species is known from previous

studies on non-urban counterparts. A comparison with previous studies on non-urban counterparts will provide an indication of how these species may modify their behaviours in order to adapt to urbanisation.

Study site

The field work for this study took place within the Meyersdal Eco-Estate (26°17'10.4"S 28°05'14.7"E) and the Meyersdal Nature Estate (26°17'32.1"S 28°05'23.2"E) located in the south of Johannesburg, South Africa (Figure 2). Both the Eco and Nature Estate form part of the larger 1080 ha Meyersdal Nature Area (300 ha and 480 ha respectively) where less than 15% of the nature area of each estate area is developed for human settlement. Wildlife occurs on both estates but more frequently come into contact with human residents and residential gardens in the Eco-Estate, which is residentially built-up and interspersed with natural areas. The residential area within the Nature Estate is separated from the natural area by palisade fencing (which is permeable to mongoose; Cronk and Pillay 2018).

The area is characterized by a grassveld vegetation type and boasts a wide range of vertebrates, such as 14 game, 23 reptile and numerous bird species. The yellow and slender mongoose are the most commonly occurring small carnivores in the area (pers. obs.) Other species include porcupine *Hystrix africaeaustralis* and potential competing carnivores such as the Cape fox *Vulpes chama,* black-backed jackal *Canis mesomelas*, small-spotted genet *Genetta genetta* and feral and domestic cats *Felis catus* (Meyersdal Eco-Estate 2014; Meyersdal Nature Estate 2015). Potential predators of mongooses within these estates include black eagles *Ictinaetus malaiensis* and the black backed-jackal.

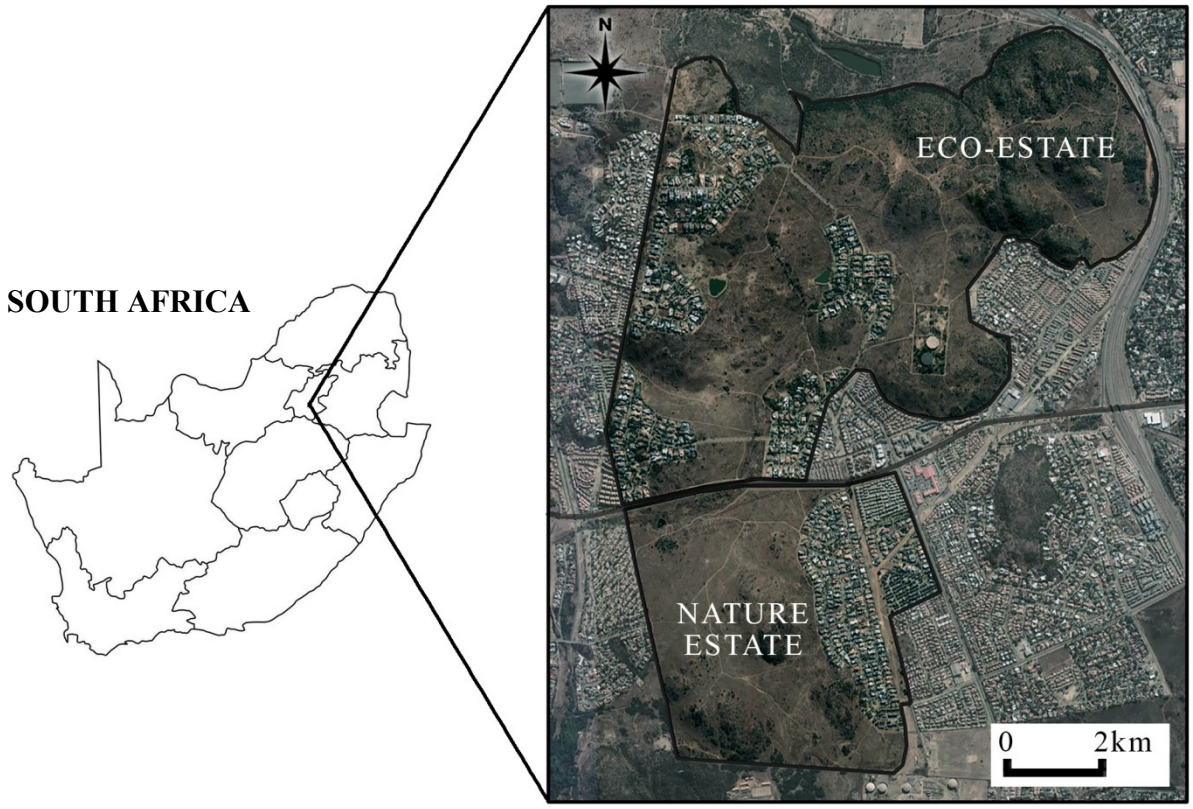

Figure 2. Meyersdal Eco-Estate and Nature Estate located on the border of the south of Johannesburg, Gauteng, South Africa (inset).

AIM AND OBJECTIVES

The overarching aim of my study concerned using the niche differentiation theory to assess the mechanisms promoting coexistence between the sympatric yellow and slender mongoose in an urban area. I hypothesized that these species are able to coexist in urban areas due to the reported species-specific differences in their biology in non-urban areas. However, should the opportunity arise to exploit additional urban resources (e.g. anthropogenic food), this would further aid coexistence. The use of two different estates with different levels of human contact (with seemingly different levels of urbanisation) also allowed for an additional level of comparison; in all subsequent data chapters comparisons were made not only between species, but between populations of the two estates too. To my knowledge, the ecology and occurrence of these species in urban areas has not previously been assessed, nor has the coexistence of two urban sympatric carnivore species in the context of diet, spatial and temporal use, as well as the overlap of the use of these resources between species.

The main objectives of this thesis were as follows:

- To investigate the diet, as well as use of anthropogenic food items, and establish dietary overlap between the yellow and slender mongoose in an urban environment through scat analysis.
- To assess the feeding behaviour of both the yellow and slender mongoose by using food preference trials and feeding stations.
- To evaluate the spatial and temporal occurrence, as well as the combined spatio-temporal co-occurrence of these mongoose species, and also specifically assessing habitat preference and activity patterns of each species.
- To assess the home range sizes and the use of human residential gardens by the yellow mongoose. Due to unforeseen constraints, I was unable to include the slender mongoose in this analysis in order to compare home range use between the species.
- In addition to assessing aspects of mongoose ecology (resource use), I further assessed the occurrence of yellow and slender mongoose in the greater Johannesburg area using a citizen sciences approach, since the extent of their occurrence and coexistence in urban Johannesburg has not previously been reported.

LAYOUT OF THESIS

This thesis comprises an introductory chapter (Chapter 1), five experimental chapters (Chapters 2-6), and a general discussion and conclusion chapter (Chapter 7). Each of the experimental chapters is written in a manuscript format for publication. Two of the experimental chapters have been published (Chapter 2 and Chapter 3), and one chapter is under revision (Chapter 4). In the dual-author work already published, I was the principal designer and executor of all experiments and was responsible for the data collection, data analysis, initial write-up, and preparation of the manuscripts for publication. My supervisor provided standard supervisory guidance throughout, and assistance with write-up for final journal submission. The PDF versions of the published Chapter 2 and Chapter 3 are inserted in this thesis. The under revision Chapter 4, and unpublished Chapters 5 and 6 are formatted similarly in manuscript format. Each chapter has its own reference list, with consequent repetition of references, and some introduction, methods and discussion material. Tables and figures are numbered sequentially within each chapter and not for the thesis as a whole. The pages for the entire thesis are numbered in sequence.

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CHAPTER TWO

Dietary overlap of two sympatric African mongoose species in an urban environment

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Dietary overlap of two sympatric African mongoose species in an urban environment

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Abstract: Urbanisation creates challenges and opportunities for wildlife. Globally, small carnivores have colonised urban spaces, but we do not know whether or how sympatric carnivores partition resources in order to co-exist. We studied the diet and degree of dietary overlap of two sympatric herpestid mongooses – yellow, *Cynictis penicillata*, and slender, *Galerella sanguinea* mongoose – in a small urban nature area in South Africa. The composition of 2600 yellow and 2000 slender mongoose scats was sampled over a year in an Eco-Estate, where wildlife have contact with humans, and a Nature Estate, where contact is reduced. We analysed the frequency of occurrence of invertebrates, mammals, birds, plants and anthropogenic items in scats. Invertebrates and mammals were most abundant for both species in the Nature Estate and for slender mongoose in the Eco-Estate, while anthropogenic items were more prevalent in yellow mongoose scats in the Eco-Estate. Both species included anthropogenic items in their diet in the Eco-Estate only. Scat components varied seasonally. In summer, invertebrates were more abundant in scats of both species, yet during the colder months, invertebrates decreased and vertebrates (more so in the slender mongoose) and anthropogenic items (more so in the yellow mongoose) increased. Dietary overlap was greatest in summer and lowest in winter. Nonetheless, the specialised slender mongoose diet and a generalist yellow mongoose diet potentially facilitates their co-existence.

Keywords: anthropogenic items; co-existence; scat analysis; slender mongoose; yellow mongoose.

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Introduction

Urbanisation creates challenges and opportunities for wildlife (McKinney 2002, Candolin and Wong 2012). Globally, carnivores have become increasingly affected by expanding urban areas and accompanying anthropogenic changes (Carnivores 2004). Yet, several carnivore species have adapted to human-dominated habitats (Newsome et al. 2010), such as the raccoon *Procyon lotor*, Linnaeus 1758 (Carnivores 2004, Garcia et al. 2012), red fox *Vulpes vulpes*, Linnaeus 1758 (Duduś et al. 2014, Young et al. 2015), stone marten *Martes foina*, Erxleben 1777 (Duduś et al. 2014), Eurasian badger *Meles meles*, Linnaeus 1758 (Bateman and Fleming 2012, Young et al. 2015) and coyote *Canis latrans*, Say 1823 (Morey et al. 2007). These animals benefit from a combination of novel shelter and food, and a reduction in predation risk (Bateman and Fleming 2012), resulting in higher population densities compared to their non-urban counterparts (Adams 2016). These benefits often attract wildlife to urban areas (Newsome et al. 2010, Bateman and Fleming 2012). What is not known is the extent and nature of resource overlap, and consequently, the level of interspecific competition among urban carnivores.

Carnivore species often share similar habitats and consequently trophic resources (Gatti et al. 2006), potentially leading to competition in sympatry. The niche differentiation theory predicts a degree of resource partitioning among species to reduce intraspecific competition and promote co-existence (Carvalho and Gomes 2004, Barrientos and Virgós 2006), especially in resource limited environments. Resource partitioning in carnivores can occur spatio-temporally and in the use of trophic resources (e.g. water sources and available prey; Gatti et al. 2006, Hayward and Slotow 2009). Moreover, the degree of dietary overlap may be influenced by specific prey availability, as well as the ability of each species to obtain/capture the prey (Hayward and Slotow 2009).

The diet of co-existing free-living carnivore species has been the focus of numerous co-existence studies (Rysavá-Nováková and Koubek 2009, Cupples et al. 2011). In contrast, no studies have considered the dietary overlap of co-existing sympatric species in urban areas, with studies focussing instead on the diets of individual

species (Morey et al. 2007, Mewada 2015). Investigating the diets of co-existing competitive urban-living species can reveal the level of resource partitioning, which may lead to competition or co-existence (Glen et al. 2011). Moreover, opportunities to scavenge from anthropogenic items (e.g. refuge) might facilitate co-existence.

We investigated the diet and dietary overlap of two co-existing herpestid species, the yellow mongoose *Cynictis penicillata*, Cuvier 1829, and the slender mongoose *Galerella sanguinea*, Rüppell 1835, in a small urban reserve (Meyersdal Nature Area) in South Africa. Both species are diurnal and have a wide distribution in southern Africa. Yet, they co-exist only over the northerly portions of their respective ranges in South Africa, including our study area (Skinner and Chimimba 2005). The diet of both species has been variously studied (e.g. by scat, stomach contents) and varies geographically. Nonetheless, the diet of the yellow mongoose (Cavallini and Nel 1995, Nel and Kok 1999, Mbatyoti 2012) has been better studied than that of the slender mongoose (San et al. 2013).

The yellow mongoose has been described as primarily insectivorous, feeding, for example, on Isoptera, Orthoptera and Coleoptera (Avenant and Nel 1992, Nel and Kok 1999). The comparatively weak temporalis and masseter muscles of yellow mongoose (compared to the slender mongoose) are suggestive of a diet of softer foods (Friscia et al. 2007, Kingdon et al. 2013), but they are also known to feed on rodents, birds, reptiles and amphibians, and eat eggs and scavenge on a variety of carrion (Skinner and Chimimba 2005). Vegetation (fruits and seeds) form a very small part of the general yellow mongoose diet (Du Toit 1980). In South Africa, yellow mongooses alter their diets seasonally depending on prey availability (e.g. rodents, Avenant and Nel 1992; insects, Nel and Kok 1999).

The slender mongoose is a generalist carnivore (Smithers 1983, Friscia et al. 2007). Compared to yellow mongoose, the dentition and facial musculature of the slender mongoose makes it well adapted for slicing through tougher foods and carrion (Skinner and Chimimba 2005, Kingdon et al. 2013). However, there is some discrepancy in the literature about its diet, with some authors suggesting a predominantly vertebrate diet (e.g. striped mouse, *Rhabdomys pumilio*, Sparrman 1784 and grooved-toothed mouse, *Pelomys fallax*, Peters 1852; Taylor 1975, Rood and Waser 1978), and others suggesting a predominantly invertebrate diet (e.g. Isoptera and Orthoptera; Smithers 1971). The discrepancy may be due to differences in geographic location of study sites, and potentially seasonal variation in prey availability (Nel and Kok 1999). Vegetation (wild fruits and seeds) also form a very small part of the slender mongoose diet (Smithers 1983).

Our study site, the Meyersdal Nature Area (details below), is divided into two parts: an Eco-Estate where wildlife utilise household gardens and corridors between houses, and a Nature Estate, where houses are separated from wildlife by fences, reducing contact with humans and homes. We investigated the contents of scats of yellow and slender mongoose over 13 consecutive months in both estates. From the undigested remains, we identified the broad and specific food categories and their frequency of occurrence, for both species, to ascertain the principal food items consumed. We specifically ascertained whether the diet of both species consisted of anthropogenic items.

Our predictions were: (1) The scat contents of the yellow and slender mongoose will contain insects and small vertebrate prey, reflecting the diets of their non-urban counterparts (Skinner and Smithers 1990, Kingdon et al. 2013). (2) The scats of both species will contain anthropogenic contents (e.g. plastic; found in various urban species; Murray et al. 2015), particularly in the Eco-Estate where there is greater contact with people. (3) Seasonally, we expected a higher occurrence of invertebrate remains during summer than in the winter, as well as a resultant increase in anthropogenic items and vertebrate prey during the colder periods, when invertebrate availability decreases (Davies et al. 2015). (4) We expected a large degree of overlap in diets as seen in the non-urban individuals of both species (Smithers 1983, Nel and Kok 1999). However, in accordance with the niche theory (Carvalho and Gomes 2004), we also expected a variation in the frequency and type of components in scats between the species.

Materials and methods

Study site

Field work took place within the Meyersdal Eco-Estate (26°17′10.4″S 28°05′14.7″E) and Nature Estate (26°17′32.1″S 28°05′23.2″E), which are separated by a double lane tarred main road, located in south of Johannesburg, South Africa. The Eco-Estate is slightly larger (480 ha) than the Nature Estate (300 ha) with less than 15% of the natural area of each estate developed for human settlement. The Eco-Estate consists of residences interspersed among the areas used by wildlife, whereas in the Nature Estate, one half of the estate is built up housing, and the other (greater) half is a fenced off nature area. The Eco-Estate also consists of several hiking, biking and game drive trails, as well as a camping site, located in the nature area of the estate where human residents frequently come into contact with the wildlife.

Meyersdal is characterised by a grassveld vegetation type, and houses a wide range of vertebrates, such as 14 large mammal herbivore species, various reptile and numerous bird species. Other species occurring in much lower numbers include porcupine *Hystrix africaeaustralis*, Peters 1852 and carnivores, such as the Cape fox *Vulpes chama*, Smith 1833, black-backed jackal *Canis mesomelas*, Schreber 1775, spotted genet *Genetta genetta*, Linnaeus 1758, serval *Leptailurus serval*, Schreber 1776 and feral and domestic cats *Felis catus*, Linnaeus 1758. Potential predators of mongooses within these estates include black eagles *Ictinaetus malaiensis*, Temminck 1822 and the black-backed jackal.

Collection of mongoose scat

Both the Meyersdal Eco- and Nature estates were scouted for possible scat collection sites. Both mongoose species make use of latrines/middens, where individuals of a small group defecate, which is typically near denning sites (i.e. for territorial marking; Skinner and Smithers 1990). Yellow mongoose middens are typically very large (Cavallini 1995) and are larger than those of slender mongoose (per obs.), which also aided in species differentiation. Yellow mongoose dens and middens were easier to locate and sample, so sampling for this species started 3 months earlier than for slender mongoose. There were a limited number of slender mongoose den sites and consequently middens; however, through direct observation as well as camera trap data, we identified additional samples belonging to slender mongoose. Scat sample collection took place once a month from March 2015 (yellow mongoose) and June 2015 (slender mongoose) to March 2016 (both species).

A total of 10 sites where scat occurred were selected per species per estate (40 sites in total). Once a month, 10 scats were randomly sampled at each site. Because yellow mongoose dens were easily identifiable, all yellow mongoose scats were collected from middens. We confirmed that scat belonged to slender mongoose through direct observation of scat deposits, as well as an examination of location (some near slender mongoose dens and baited feeding sites; Cronk and Pillay 2018), size (longer than that of yellow mongoose), composition and/or shape of scats (Chame 2003, Dawson et al. 2007). To avoid pseudo-replication of samples collected in previous months at a site, and to ensure that samples reflected the diet of the mongooses at that time of sampling (month), we collected only fresh scat samples (based on odour and appearance). The collection of fresh samples also ensured that faecal contents had not succumbed to weathering and decomposition, resulting in loss of contents. Scats were collected using latex gloves and placed in individual paper bags labelled with the appropriate information, namely sample number, species, location and date.

Scat analysis

Scat samples were transported to and air dried for 2 h at the University of the Witwatersrand. Each scat sample was soaked in warm water for an hour to loosen the contents. Samples were subsequently washed and filtrated through a mesh sieve (0.5×0.5 mm), and the components teased apart using blunt forceps and a needle to separate all undigested materials. Undigested materials were kept and air-dried in glass Petri dishes, and then sorted into various broad categories, hereafter referred to as "prey category".

Insect and other chitin fragments were categorised as invertebrates, hair categorised as mammals, and feathers as birds. Bone fragments contained in samples with hair or feathers were classified as mammals and birds, respectively. Both mongoose species are known to feed on reptiles and amphibians (Smithers 1993, Nel and Kok 1999, Kingdon et al. 2013), but these were not identifiable in scats. Grass, leaves, seeds or fruits were categorised as plant material. Anthropogenic elements, such as fruits (not growing naturally) or fragments of various garbage materials such as plastics, rubber and aluminium foil, were categorised as anthropogenic (Gatti 2006, Widdows 2015). A subsample of 400 scat samples per species (200 per species per estate) were further analysed, and invertebrates, mammalian and avian prey taxa were identified to appropriate taxonomic levels (order, family or species) using reference materials, and with the assistance of relevant specialists at the University of the Witwatersrand.

The presence and absence of each broad food category were recorded by estate, species and season in Microsoft Excel® (Microsoft Corporation, 2007). Multiple methods exist for the analysis of animal scat to ascertain general diet. We used two methods, i.e. frequency of occurrence and numerical frequency for each food category (Ackerman et al. 1984, Dawson et al. 2007), both based on presence-absence data, to minimise the individual bias of using only one analysis. The protocol used enabled comparison with other dietary studies on both the yellow and slender mongoose. Frequency of occurrence of each food category was calculated by dividing the total frequency of a food category by the total number of scats analysed, and expressed as a percentage. The numerical frequency was expressed as the percentage of occurrence of a food

category divided by the total number of occurrences of all food categories (Mewada 2015).

Plant material, such as grasses and leaves, does not form part of the yellow or slender mongoose diet (Cronk and Pillay 2018), and may have been present in scat samples due to indirect ingestion when feeding on insects (Cavallini and Nel 1990, Avenant and Nel 1992); hence, plant material was not included in calculating numerical frequency, so as to avoid biasing the analyses. However, for frequency of occurrence, the other categories are not influenced by the inclusion of plant material, as frequency of occurrence takes into account the entire sample collection number and not the number of occurrences of other categories. Excluding plant material in the calculation of numerical frequency also allowed us to assess whether, in comparison to frequency of occurrence, the relative importance of other food items would change.

Using the frequency of occurrence and numerical frequency, we ranked the relative importance of each food item to assess which categories formed the predominant part of the diet (Corbett 1989). The frequency of occurrence method showed that plant material was overrepresented as the second most 'important' category in the diet of the yellow and slender mongoose. Therefore, as grass and leaves do not form part of the mongoose diet, numerical frequency (where plant material was excluded from all calculations) was statistically analysed.

Data analysis

All statistical analyses were done using R Statistical Software (www.r-project.org, R version 3.3.0). A general linear model (GLM), with a binomial distribution and logit-link function (R packages used: car, AICcmodavg, lem4), was used to compare the numerical frequency of occurrence of each food item between the two species as well as between the two estates. Season was added as a fixed variable. Sampling periods were divided into four seasons according to South Africa's weather patterns: winter (June–August), spring (September–November), summer (December–February) and autumn (March–May). The model comprised first-order effects and interaction effects of the following variables: Species, Estate, Season and Content (the different food categories) as fixed effects, and numerical frequency as the dependant variable. To ascertain dietary overlap between yellow and slender mongoose in each estate as well as whether dietary overlap varied over seasons, we used Pianka's index (Pianka 1974) of dietary overlap.

Several diet analysis studies have used the frequency of occurrence method in conjunction with other quantitative methods (e.g. %volume, %total mass or %biomass), yet a vast majority have used frequency of occurrence alone to provide a simple comparison of diet or assessment of dietary overlap between species (Paltridge 2002, Vieira and Port 2007, Cupples et al. 2011). While concerns have been raised about the frequency of occurrence analysis, biases also exist for quantitative methods, such as sensitivity to changes in the structure of undigested remains, or changes in the surface/volume ratio in food (prey) of different sizes (Ciucci et al. 1996, Zabala and Zuberogoitia 2003). Therefore, we decided to determine whether our prey category rank order results (using frequency of occurrence) would differ compared to the published data of both frequency of occurrence and volumetric measures.

We conducted a literature search of diet studies for yellow and slender mongoose, involving both frequency of occurrence and percentage volume methods. We then ran a Spearman rank correlation analysis for the frequency of occurrence and percentage volume on these published data. A strong positive correlation between the results of the two methods occurred in three studies ($Rs = 0.70$ – Maddock and Perrin 1993, $Rs = 1.0$ – Nel and Kok 1999, $Rs = 1.0$ – Martinoli et al. 2006) and a negative correlation in the other studies ($Rs = -0.2$ – Maddock 1988). These results showed that there is good agreement between frequency and percentage volume scores. The results of some studies have also shown that despite different methods used (which included frequency of occurrences compared to various other quantitative measures), the ranking of main prey categories remained the same (Kruuk and Parish 1981, Delibes et al. 1984, Ciucci et al. 1996, Borkowski et al. 2011). Therefore, we established the rank orders of the main prey categories in these studies and assessed how these rank orders changed when frequency of occurrence was compared to percentage volume.

Ethical approval

All applicable international, national and/or institutional guidelines for the care and use of animals were followed; ethics clearance was received (clearance number: 2015/06/22/A) from the Animal Screening and Ethics Committee of the University of the Witwatersrand.

Results

A total of 4600 scat samples were collected from 40 sites located in the Eco- and Nature estates from March 2015

Table 1: Number of occurrences (N), frequency of occurrence (%O) and numerical frequency of occurrence (%N) for each food category contained in the scat (n = 4600) collected for yellow mongoose and slender mongoose within the Meyersdal Eco- and Nature Estate, South Africa.

Food category	Eco-Estate						Nature Estate					
	Yellow mongoose (n = 1300)			Slender mongoose (n = 1000)			Yellow mongoose (n = 1300)			Slender mongoose (n = 1000)		
	N	%O	%N	N	%O	%N	N	%O	%N	N	%O	%N
Plant material	731	56.23	[a]	331	33.10	[a]	530	40.77	[a]	383	38.30	[a]
Invertebrates	943	72.54	65.62	401	40.10	44.61	1066	82	78.50	453	45.30	52.80
Mammals	186	14.31	12.94	326	32.60	36.26	229	17.62	16.86	286	28.60	33.33
Birds	48	3.69	3.34	78	7.8	8.68	63	4.85	4.64	119	11.90	13.87
Anthropogenic	260	20.00	18.09	94	9.4	10.46	0	–	–	0	–	–

[a]Numerical frequency for plant material was excluded to prevent over-representation of its importance in mongoose diet, thereby not affecting the importance of other categories. –, No data obtained for this category.

to March 2016, representing 1300 yellow mongoose scats from 10 sites per estate (2600 in total) and 1000 slender mongoose scats from 10 sites per estate (2000 in total). The scats of both species contained a combination of all listed food categories with the exception that no anthropogenic items were contained in scats of both species in the Nature Estate (Table 1). The results of a GLM indicated that Content had a significant effect on the numerical frequency of occurrence of different food categories whereas Estate, Species and Season were not significant predictors of numerical frequency of occurrence (Table 2). Species × Content, Estate × Content and Season × Content were significant predictors of numerical frequency of occurrence. The three-way interaction between Estate × Species × Content approached significance. None of the other statistical interactions were significant predictors of numerical frequency (Table 2).

Table 2: Outcomes of a general linear model analysing the predictors of frequency of occurrence and numerical frequency of occurrence of various food categories in the scats of yellow mongoose and slender mongoose within the Meyersdal Eco-Estate and Nature Estate.

Effects and interactions	Numerical frequency		
	χ^2	*d.f.*	p-Value
Estate	0.02	1	0.881
Species	2.65	1	0.104
Season	0.52	3	0.914
Content	**837.60**	**3**	**<0.001**
Estate × Species	1.88	1	0.170
Estate × Season	0.27	3	0.967
Estate × Content	**81.12**	**3**	**<0.001**
Species × Season	0.81	3	0.847
Species × Content	**111.16**	**3**	**<0.001**
Season × Content	**69.81**	**9**	**<0.001**
Estate × Species × Season	0.68	6	0.995
Estate × Species × Content	2.42	3	0.489
Estate × Season × Content	1.41	12	0.998
Species × Season × Content	1.63	9	0.996
Estate × Species × Season × Content	0.55	9	1.000

Test statistics in bold indicate significant predictors of occurrence.

Invertebrates were the most frequent components of scats of both species in both estates (Table 1). The yellow mongoose scat contained a higher percentage of invertebrates than the slender mongoose in the Eco- (59.50%) and Nature (69.27%) estates (Figure 1). In both methods, invertebrates were most prominent in the diet of both species (Table 3). Prey taxon identification (Table 4) revealed that Isoptera (termites) was the most commonly occurring in yellow mongoose scat in both the Eco-Estate (70.1%) and Nature Estate (74.8%), followed by Orthoptera (grasshoppers and crickets; 53.5% and 57.9%, respectively) and Coleoptera (beetles; 46.5% and 45.3%, respectively). In contrast, for the slender mongoose in both estates, Coleoptera was the most frequent prey taxon (84.8% in the Eco-Estate and 86.2% in the Nature Estate), followed by Isoptera (45.2% and 43.1%, respectively) and Orthoptera (39.2% and 41.3%, respectively; Table 4). Scat samples of both species in both estates contained Lepidoptera (butterflies/moths and caterpillars) fragments in 26%–39% frequency of occurrence, and Diptera (flies) comprised <10%.

Mammalian prey was an important food source for both species (Figure 1; Table 3). Overall, mammal prey occurred more frequently in the slender mongoose than the yellow mongoose scat but only significantly more than the yellow in the Eco-Estate (Figure 1). Taxon identification revealed that both species in both estates consumed small mammals (mice and rat species, such as *Rhabdomys pumilio* and *Otomys irroratus*, Brants 1827) most commonly

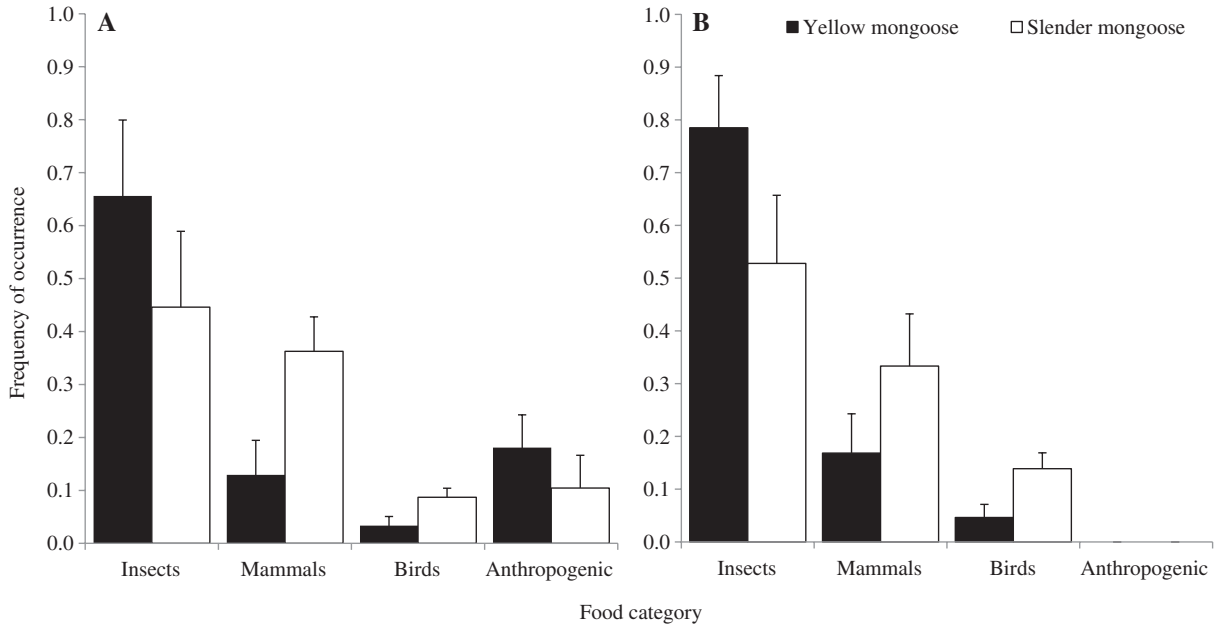

Figure 1: The numerical frequency of occurrence of each food category in the diet of the yellow mongoose and slender mongoose in the Meyersdal (A) Eco-Estate and (B) Nature Estate, South Africa.
Bars denote proportions generated through a general linear effects model for each of the food items consumed; error bars denote 95% confidence limits.

Table 3: The rank of each food category (with 1 being the highest ranking and 6 being the lowest) for the two methods (frequency of occurrence %O, and numerical frequency of occurrence %N) of analysis for yellow mongoose and slender mongoose in the Meyersdal Eco-Estate and Nature Estate.

Prey category	Eco-Estate				Nature Estate			
	Yellow mongoose		Slender mongoose		Yellow mongoose		Slender mongoose	
	%O	%N	%O	%N	%O	%N	%O	%N
Plants	2	[a]	2	[a]	2	[a]	2	[a]
Invertebrates	1	1	1	1	1	1	1	1
Mammals	4	3	3	2	3	2	3	2
Birds	5	4	5	4	4	3	4	3
Anthropogenic	3	2	4	3	–	–	–	–

[a]Numerical frequency for plant material was excluded to prevent over-representation of its importance in mongoose diet, thereby not affecting the importance of other categories.

(>75%) and only the slender mongoose in the Eco-Estate consumed carrion (7.3%; eight samples contained red hartebeest *Alcelaphus buselaphus caama*, Geoffroy Saint-Hilaire 1803 hair from carcases made available by estate environmental management). Rock hyrax *Procavia capensis*, Pallas 1766 hair samples occurred in low quantities in scats of both species in the Nature Estate (6.5% in yellow mongoose, and 13.6% in slender mongoose), but only in slender mongoose scat in the Eco-Estate (11.6%; Table 4); this might have been consumed as carrion.

Table 4: Prey taxa identified to appropriate taxonomic levels (order, family or species) having >5% numerical frequency of occurrence within each major food category in the scat of yellow mongoose and slender mongoose in the Eco-Estate and Nature Estate.

Taxa	Eco-Estate				Nature Estate			
	Yellow mongoose		Slender mongoose		Yellow mongoose		Slender mongoose	
	n	%	n	%	n	%	n	%
Insecta	127		93		159		109	
Coleoptera	59	46.5	79	84.9	72	45.3	94	86.2
Isoptera	89	70.1	42	45.2	119	74.8	47	43.1
Lepidoptera	49	38.6	30	32.3	57	35.9	29	26.6
Orthoptera	68	53.5	37	39.2	92	57.9	45	41.3
Diptera	2	1.57	9	9.68	1	0.63	7	6.42
Unidentified	11	8.7	7	7.5	14	8.8	6	5.5
Mammalia	23		69		31		66	
Rodents	19	82.6	53	76.8	26	83.9	56	84.9
Procaviidae	0	–	8	11.6	2	6.5	9	13.6
Carrion	0	–	5	7.3	0	–	0	–
Unidentified	4	17.4	3	4.4	3	9.7	1	1.5
Aves	7		20		10		28	
Burhinidae	0	–	1	5.0	1	10.0	4	14.3
Columbidae	6	85.7	14	70.0	7	70.0	15	53.6
Malaconotidae	0	–	2	10.0	1	10.0	4	14.3
Passeridae	1	14.3	3	15.0	2	20.0	5	17.9

Bird remains were least represented in the yellow mongoose and second last to anthropogenic items for the slender mongoose (Figure 1). Bird remnants were significantly less frequent in scats in both estates, with the exception of

anthropogenic items in the Nature Estate (0%; Figure 1). Slender mongoose scat contained more bird remnants than the yellow mongoose in both estates (Figure 1). The yellow mongoose in the Eco-Estate consumed a fewer variety of taxa (Table 4), while both species in both estates consumed Columbidae (doves and pigeons) more frequently (>55% frequency of occurrence) than other taxa such as Passeridae (sparrows; 14%–20%), Burhinidae (spotted thick knee; <15%) and Malaconotidae (bushshrikes; <15%).

Interestingly, anthropogenic items were absent in the scat of both species in the Nature Estate (Table 1), whereas in the Eco-Estate, anthropogenic items occurred in yellow (16%) and slender mongoose (9%; Table 1; Figure 1) scats. Anthropogenic items were significantly more frequent than feathers in the yellow mongoose scat (Figure 1) and ranked second to invertebrates in the yellow mongoose diet, whereas it was not different from birds, and ranked third for slender mongoose (Table 3). Plant material occurred in 48.5% and 35.5% (Table 1) of the scat collected for yellow and slender mongoose, respectively, comprising grass fragments, although a few (n = 12) yellow mongoose scat collected from two sites in the Eco-Estate during winter contained seeds and fruit of the invasive sticky nightshade *Solanum sisymbriifolium*.

When comparing rank order of the main food categories in our study with previous studies, we excluded the anthropogenic item category as no other published studies included this category. Similar to three of the four studies, we found a consistent ranking in our study (in both estates) for insects, mammals and birds according to frequency of occurrence (study A, B and C; Table 5). In a fourth study (D), the ranking of birds was fourth after reptiles, although birds still occurred less frequently than insects and mammals, as in our study. A comparison between the ranks according to frequency of occurrence and percentage volume showed consistent ranking in three of the four studies with insects first, while in a fourth study, insect ranked was first in the frequency of occurrence and last in the percentage volume (Table 5). The Nel and Kok (1999) study showed that the volume rank of mammals changed from second to third and birds from third to fifth (whereas mammals was second and birds third in our study when we excluded anthropogenic items) – hence the rank order still remained the same for the categories as in our study. Analyses of the studies by Martinoli et al. (2006) and Maddock and Perrin (1993) showed that the ranking remained the same according to both methods used and were consistent with our study. The Maddock (1988) study showed the most variation in rank order: the insect rank changed from first according to frequency of occurrence and fourth with percentage volume. The volume rank of mammal remains changed from second to first, and comparable to our study, birds changed from fourth to third and were still ranked after mammals. The Maddock (1998) study was the only one where the different methods used produced divergent rankings of the main food category (insects); however, Maddock (1998) reports that the estimation of mass/volume greatly underestimated the mass of the Orthoptera group, which in our study proved to be an important group of insects consumed.

Seasonality

In order to evaluate seasonal variation in food use, we plotted the monthly numerical frequency of occurrence of each food category for both species, in both estates (Figure 2). Invertebrate remains were significantly more frequent than all other food categories during spring, summer and autumn, but, in winter, it was only significantly greater than birds. A general trend can be seen where the presence of invertebrates (which occurred in

Table 5: A comparison of the frequency of occurrence (%O) rank order of remains in scats of yellow mongoose and slender mongoose in the Meyersdal Eco-Estate and Nature Estate with that of other studies using frequency of occurrence (%O) and percentage volume (%V).

Food Category	Eco-Estate		Nature Estate		Study A[a]		Study B[b]		Study C[c]		Study D[d]	
	Yellow mongoose	Slender mongoose	Yellow mongoose	Slender mongoose								
	%O	%O	%O	%O	%O	%V	%O	%V	%O	%V	%O	%V
Insects	1	1	1	1	1	1	1	1	1	1	**1**	**4**
Mammals	3	2	2	2	**2**	**3**	2	2	2	2	**2**	**1**
Birds	4	4	3	3	**3**	**5**	3	3	–	–	**4**	**3**
Amphibians	–	–	–	–	**5**	**2**	–	–	–	–	–	–
Reptiles	–	–	–	–	4	4	–	–	–	–	**3**	**2**
Anthropogenic	2	3	–	–	–	–	–	–	–	–	–	–

Values in bold indicate rank changes. [a]Nel and Kok 1999 – yellow mongoose; [b]Martinoli et al. 2006; [c]Maddock and Perrin 1993; [d]Maddock 1988.

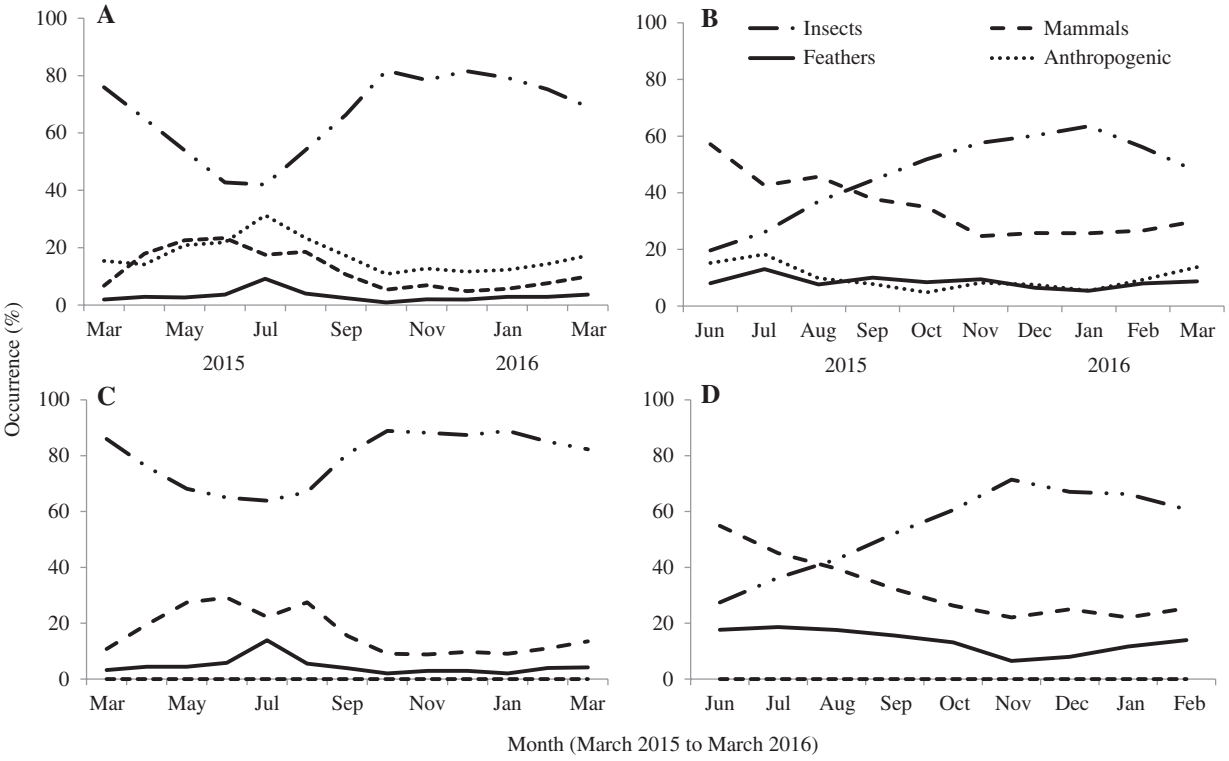

Figure 2: Monthly numerical frequency of occurrence (%) showing seasonal variation in food use for (A) yellow mongoose and (B) slender mongoose in the Eco-Estate, and for the (C) yellow and (D) slender mongoose in the Nature Estate from March 2015 (yellow mongoose) and June 2015 (slender mongoose) to March 2016.

both species) was greater during warmer months of spring and summer compared to the colder months of autumn and winter. In contrast, hair, feathers and anthropogenic items were more frequent, although not significant, in the colder months than in the warmer months (Figure 2).

Food categories were also ranked according to season for both species per estate to establish the seasonal importance of each category (Supplementary Material, Table OR1). Invertebrates remained the main food item for both species in both estates in summer, spring and autumn, but during winter, slender mongoose scat contained more mammal remains followed by invertebrates. Anthropogenic items were the second most important category for the yellow mongoose in the Eco-Estate throughout the year, whereas this varied between third (summer, autumn and winter) and fourth (spring) rank for the slender mongoose.

Dietary overlap

Pianka's index of dietary overlap showed a strong overlap between the general diet composition of the yellow and the slender mongoose in both the Eco-Estate (0.843) and Nature Estate (0.895). Seasonally, dietary overlap was less apparent in winter and greater in summer in both estates. Dietary overlap was also slightly greater between the yellow and slender mongoose within the Nature Estate compared to the Eco-Estate (Table 6). In analysing the overlap for dietary food categories (Table 7), the greatest overlap occurred within the mammal category, overlap being greater in the Nature Estate (0.997) compared to the Eco-Estate (0.985). This was followed by the avian category where overlap was also greater in the Nature Estate (0.873) compared to the Eco-Estate (0.741). The lowest overlap occurred within the Invertebrate category, where once again overlap was greater in the Nature Estate (0.846) compared to the Eco-Estate (0.691).

Table 6: Pianka's index of overall and seasonal dietary overlap between the yellow mongoose and slender mongoose within both the Meyersdal Eco-Estate and Nature Estate.

Time period	Eco-Estate	Nature Estate
Overall	0.868	0.929
Winter	0.807	0.848
Spring	0.889	0.949
Summer	0.943	0.963
Autumn	0.914	0.936

Table 7: Pianka's index of dietary overlap within major food categories between the yellow and slender mongoose in both the Meyersdal Eco-Estate and Nature Estate.

Food category	Eco-Estate	Nature Estate
Invertebrates	0.691	0.846
Mammals	0.985	0.997
Birds	0.741	0.873

Discussion

We studied the diet and dietary overlap of co-existing yellow and slender mongoose in a small urban reserve in South Africa. The contents of both the yellow and slender mongoose scat in the Meyersdal Nature Area consisted of invertebrates, vertebrates, some occurrences of anthropogenic items and plant material, which supports the generalist diets of both species (Kingdon et al. 2013). Invertebrates contributed the greatest proportion to the diet, as reported in other studies of yellow and slender mongoose (Avenant and Nel 1992, Nel and Kok 1999). Invertebrates occurred more frequently in yellow mongoose than slender mongoose scats in both estates, but the occurrence was greater in the Nature Estate than the Eco-Estate. Specific prey taxa consumed was similar to that found in non-urban populations of both species (Smithers 1971, Lynch 1979, Nel and Kok 1999). However, Isoptera was most common in the yellow mongoose and Coleoptera most common in the slender mongoose in both estates, indicating that slender mongoose are more likely to consume hard bodied insects (e.g. beetles).

Mammals contributed more than twice as much to the slender mongoose (28%) than the yellow mongoose (12%) scat in the Eco-Estate and to a lesser extent, but still greater (26%) than the yellow mongoose (15%), in the Nature Estate. Mammals constitute an important part of the diet of both species (Smithers 1971, Nel and Kok 1999). However, the frequency of occurrence of mammal remains in yellow mongoose scat was lower in our study compared to several other studies, ranging from 21% (Nel and Kok 1999) to 28% (Cavallini and Nel 1995) and as high as 48% (also through scat analysis; MacDonald and Nel 1986). For slender mongoose, mammals constituted 25% of the diet (Smithers 1971), which concur with our study, although Smithers (1983) reported values of up to 40%. Importantly, we observed slender mongooses in the Eco-Estate feeding on carcasses of mammals (e.g. hyrax, small- to medium-sized antelope, and black wildebeest; Cronk and Pillay 2018). Frequency of occurrence equates hair samples equally regardless of prey size (van Dijk et al. 2007), and hence this method may have overrepresented the importance of mammal prey in the slender mongoose diet. The subsample analysed showed the slender mongoose in the Eco-Estate indeed consumed carcasses, due to the presence of red hartebeest hair. Nonetheless, the greatest occurrence of hair was from small mammals in both yellow and slender mongoose scats. This is consistent with previous studies which reported that both species feed on small mammal prey (Kingdon et al. 2013). The occurrence of rocky hyrax hair, with the greatest frequency in the slender mongoose, may also be as a result of carrion feeding.

One disadvantage of assessing the contribution of anthropogenic items in scats is that only indigestible/non-edible items are identified, and any other items that are easily digested, such as bread, fruits/vegetables (not occurring naturally) and processed meats, are often not detected (Balestrieri et al. 2011, Allen et al. 2016). We could only identify garbage (e.g. plastic) and chicken egg shells in the scat, which were subsequently classified as part of the anthropogenic category; these items alone contributed 16.40% of the yellow and 8.13% of the slender mongoose scat. Reasons for these differences could be because yellow mongooses (1) occur more frequently and closer to human residences, and/or (2) are less elusive and more habituated to people in the estate in comparison to the slender mongoose (per obs.). As a result of there being numerous other (completely digestible) food to which these mongooses may have access, we suggest that the occurrence of anthropogenic items in their diet may be underrepresented in this study. Nonetheless, we assume that the relative importance of anthropogenic items in the yellow mongoose diet would still remain greater than that of the slender mongoose, for reasons discussed earlier.

Other components featured less prominently in both species. Bird remains were the least frequent animal matter of both mongoose species. Similarly, Smithers (1971) reported a low number of birds in the diets of slender (8%) and yellow (2%) mongoose. The greater frequency of birds in the slender mongoose diet may be related to its ability to climb trees and catch birds (Estes 2012). Several studies of both species reported low occurrences (~1% to 10%) of Arachnida, Amphibia and Reptilia (Smithers 1971, Lynch 1979, Rautenbach 1982, Nel and Kok 1999). We found even less (0– < 1%) of these components, being similar to other studies (Du Toit 1980, Earle 1981, MacDonald and Nel 1986). Grass and sand in the scat of both species might have been due to incidental consumption during ingestion of other food. *Solanum sisymbriifolium* fruit in yellow mongoose scats during winter suggests that this fruit is consumed during times of low availability of other foods.

In assessing the efficacy of using frequency of occurrence in our study, our comparisons with the available literature on yellow and slender mongoose showed that in most cases, the rank order of insect, mammal and bird remains were consistent with ours, regardless of whether the frequency of occurrence or percentage volume methods were used. The inconsistency with ranking in one study (Maddock 1998) affected only the rank of insects, but consistent rank order was still evident for mammal and bird remains. We chose the widely used frequency of occurrence method to compare the diets of two mongoose species and to calculate dietary overlap. Nonetheless, as concerns have been raised for different methods of analysis, it is highly beneficial to use two or more methods in conjunction in diet studies to provide a viable assessment of diet.

In conclusion, our study provides the first data for the diet of co-existing small carnivores in an urban environment. Our results show two levels (and interpretations) of dietary overlap between the mongoose species studied. (1) Pianka's index (Pianka 1974) showed that dietary overlap, using the broad categories of scat components, was high (>0.8). This index varied seasonally, being greater in summer when food is abundant and reduced in winter with the species exploiting different resources (anthropogenic vs. mammals), with some seasonal variation. (2) Despite the overlap in major food categories, the species differed in the taxa consumed, with yellow mongoose consuming softer bodied insects more frequently than slender mongoose, and slender mongoose consumed a wider variety of mammal prey compared to the yellow mongoose. At a finer scale of individual components, it is apparent that the species differ in the relative frequency and timing of individual components in scats, showing partitioning of resources in the Meyersdal estates. In particular, the frequency of scat contents revealed a less generalist slender mongoose diet and a more generalist yellow mongoose diet, facilitating co-existence. An important caveat to this interpretation is the method of diet assessment because scat analysis might overinflate occurrences of different food items. For example, Lynch (1979) and Shepard et al. (1983) reported mammals having 9% occurrence in stomach contents and 75% occurrence in scats of yellow mongoose. Future studies should consider the feeding behaviour of urban-living yellow and slender mongoose species to assess the conclusions reached here.

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Supplementary material

Online Resource

Table OR1. Numerical frequency and rank of each prey category contained in the scat collected per season for the yellow mongoose and slender mongoose within the Meyersdal Eco- and Nature Estate.

Eco-Estate

Season	Yellow Mongoose								Slender mongoose							
	Invertebrates		Mammals		Birds		Anthropogenic		Invertebrates		Mammals		Birds		Anthropogenic	
	%N	R	%N	R	%N	R	%N	R	%N	R	%N	R	%N	R	%N	R
Winter	46.24	**1**	20.97	**3**	5.91	**4**	26.88	**2**	26.96	**2**	48.59	**1**	9.27	**4**	14.73	**3**
Spring	75.32	**1**	8.23	**3**	1.90	**4**	14.56	**2**	51.16	**1**	32.56	**2**	9.30	**3**	6.98	**4**
Summer	78.66	**1**	6.05	**3**	2.55	**4**	12.74	**2**	59.92	**1**	26.03	**2**	6.61	**4**	7.44	**3**
Autumn	69.09	**1**	10.00	**3**	3.64	**4**	17.27	**2**	47.50	**1**	30.00	**2**	8.75	**4**	13.75	**3**

Nature Estate

Season	Yellow Mongoose								Slender mongoose							
	Invertebrates		Mammals		Birds		Anthropogenic		Invertebrates		Mammals		Birds		Anthropogenic	
	%N	R	%N	R	%N	R	%N	R	%N	R	%N	R	%N	R	%N	R
Winter	65.28	**1**	26.41	**2**	8.31	**3**	-	**-**	35.25	**2**	46.78	**1**	17.97	**3**	-	**-**
Spring	85.86	**1**	11.18	**2**	2.96	**3**	-	**-**	60.91	**1**	27.16	**2**	11.93	**3**	-	**-**
Summer	87.09	**1**	9.93	**3**	2.98	**3**	-	**-**	64.75	**1**	24.18	**2**	11.07	**3**	-	**-**
Autumn	82.29	**1**	13.54	**2**	4.17	**3**	-	**-**	56.58	**1**	30.26	**2**	13.16	**3**	-	**-**

- = no data obtained for this category

CHAPTER THREE

Food choice and feeding on carrion in two African mongoose species in an urban environment

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ORIGINAL PAPER

Food choice and feeding on carrion in two African mongoose species in an urban environment

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Abstract

Urbanisation negatively affects many species, yet small carnivores may flourish in urban spaces because of accessible resources and a reduction of predators. Food choices of urban carnivores might be influenced by the availability and abundance of anthropogenic food resources and the co-existence of competing species. We studied the food selection and feeding on carrion of the yellow mongoose (*Cynictis penicillata*) and slender mongoose (*Galerella sanguinea*) in a small urban reserve in South Africa. In cafeteria-style food choice tests, both species preferred meat and insects over bread, dog kibble, chicken eggs, and plants; however, yellow mongoose in a more urbanised area preferred bread to insects. Yellow mongoose had a shorter latency to approach and consume provided food compared to slender mongoose. At carrion-baited stations, slender mongoose were more prevalent at carcasses and displayed aggression and competitive exclusion of yellow mongoose. Slender mongoose fed more on carcasses during the colder months than warmer months when they fed on available insects around and on carcasses. The greater consumption of anthropogenic items by yellow mongoose and the preference by slender mongoose for feeding on carcasses provide evidence of possible resource partitioning, which may aid in the co-existence of these sympatric herpestids in urban areas.

Keywords Co-existence · Food choice · Slender mongoose · Urbanisation · Yellow mongoose

Introduction

Urbanisation influences the ecological and behavioural traits of many organisms, creating new challenges, while also providing novel opportunities (Wong and Candolin, 2015; Reher et al. 2016). Synurbanisation describes how wildlife overcomes the challenges and adapts and thrives in urban areas (Luniak 2004; Plumer et al. 2014), and furthermore, how the success of urban species is promoted by an increase in tolerance and even an affinity for human habitats (Gehrt et al. 2010). One of the negative effects of urbanisation is the reduction in species' home range sizes, and as a result, several small carnivores often persist in urban green spaces (Mahan and O'Connell 2005); these are referred to as synanthropic species (Bateman & Flemming, 2012), which include the red fox (*Vulpes vulpes*, Duduś et al. 2014), raccoon (*Procyon lotor*, Ditchkoff et al. 2006), and coyote (*Canis latrans*, Murray et al. 2015). With expanding urbanisation, this continuing adaptation results in co-existing species with potentially overlapping resource requirements.

In nature, animals are often faced with various ecological challenges and successfully responding to these challenges increases the chance of survival and subsequently reproduction (Drakeley et al. 2015; Wong and Candolin 2015). A particular challenge is locating resources that are often unpredictable in their availability and abundance. When foraging, for example, animals are faced with the need to avoid risks, while still acquiring the necessary resources (Raffa et al. 2002; Verdolin 2006; Stephens 2008). This foraging process is therefore regulated by a sequence of decisions/choices in order to meet functional nutritional requirements and maximise fitness (Verdolin 2006). In contrast, the abundant and banal availability of resources in urban environments and a tolerance for humans (Gehrt et al. 2010), as well as a reduction in natural predator occurrence (Reher et al. 2016), may influence food choices of wildlife in urban areas. It has been reported that several mesocarnivores and avian species, such as the Florida

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scrub-jay (*Aphelocoma coerulescens*), can dramatically alter their diet in urban areas, and this also makes them more efficient foragers than their rural counterparts (Ditchkoff et al. 2006).

Small mammal carnivores are able to thrive in urban areas due to their small size and their generalist diets (which incorporates plants, living and dead animals, and human garbage), yet little is known about the mechanisms of co-existence in co-occurring sympatric carnivores in these urban habitats. Co-existence theory postulates that should species overlap in a particular niche dimension, they must differ in another dimension (Kylafis and Loreau, 2011). For example, Garneau (2005) investigated the co-existence between black bears (*Ursus americanus*) and grey wolves (*Canis lupus*) and concluded that although they shared the same prey (i.e. moose, *Alces alces*), they segregated along a temporal scale: black bears preyed on calves earlier in the breeding season, whereas wolves did so later in the breeding season. Should species occurring in urban areas overlap in one or more niche requirement (e.g. spatio-temporal use, refuge, diet), they might differ in another, such as the extent to which they make use of anthropogenic resources. McKinney (2006) refers to species relying largely on natural resources, yet still integrating anthropogenic resources into their ecology, as "urban adapters," and those relying principally on anthropogenic resources, as "urban exploiters." It is not known how the availability and use of these anthropogenic resources affect competition between co-occurring species, be it urban adapters or exploiters. However, urban areas usually provide a more consistently abundant and predictable supply of food for wildlife (Gehrt et al. 2010; Tryjanowski et al. 2015; Bilá et al. 2016), which may promote species co-existence synanthropically.

We investigated the food choice of two co-existing herpestid mongoose species, yellow (*Cynictis penicillata*) and slender (*Galerella sanguinea*), in a small urban reserve (Meyersdal Nature Area) in South Africa. Both species are widely distributed in southern Africa, co-existing over large portions of their ranges (Skinner and Chimimba, 2005). These diurnal species reportedly forage alone, but sometimes also occur in conspecific pairs (Le Roux et al., 2008; Graw and Manser 2016). The yellow mongoose is classified primarily as insectivorous (Nel and Kok 1999), and the slender mongoose is classified as a generalist carnivore (Do Linh San and Maddock, 2016). The diet of both consists largely of invertebrate prey (mainly Isoptera and Coleoptera species) and small vertebrate prey (to a greater extent in the slender mongoose; Du Toit 1980; Smithers 1983; Hoffmann and Taylor, 2013). Based on remnants found in scats and stomach contents and few eye witness accounts, occasional carrion feeding has also been reported in both species (Stuart 1981; Avenant and Nel 1992; Kingdon et al. 2013).

In a descriptive account of carrion feeding, slender mongoose in their natural environment dug beneath a giraffe (*Giraffa camelopardalis*) carcass to feed on the pupating fly larvae in the ground: three individuals fed solitarily for continuous bouts of up to an hour exclusively on fly maggots and not on the carcass itself and then no longer visited the carcass once maggots were depleted (Vaughan 1976). There is no clear description of the carrion feeding behaviour (e.g. times of feeding, feeding durations, mechanism of feeding) observed over a period of time for both species. The ability to exploit carrion as a resource, or the lack thereof, may be a result of differences in the species' skull and dentition (Friscia et al. 2007).

The Meyersdal Nature Area is divided into two parts: an eco-estate, where wildlife utilise household gardens and corridors between houses, and a nature estate, where houses are separated from wildlife by fences, reducing contact with humans and homes. In both parts, we investigated the food choice of the yellow and slender mongoose by using cafeteria-style food choice tests, which included meat, insects, and various other anthropogenic items, to assess their food preferences, and we specifically ascertained whether both species showed a preference for anthropogenic food items. Furthermore, using camera traps, we observed feeding at carcass-baited stations over a 6-month period to establish and compare the feeding behaviour of both species in an urban environment.

We made four predictions. 1. Yellow mongoose would show a greater preference for insects and slender mongoose would show a greater preference for meat. 2. Yellow mongoose would exhibit a shorter latency to approach and consume presented foods compared to the slender mongoose, as the yellow mongoose are bolder (unpublished data). 3. The latency to approach and consume food would be shorter in both mongoose species in the eco-estate compared to the nature estate, where wildlife have reduced contact with residents and are therefore more reluctant to approach novel objects (Chapman et al. 2012). 4. We expected that the slender mongoose would frequent carrion-baited stations more than the yellow mongoose, because they have previously been recorded to do so (Vaughan 1976), as well as reported to be better adapted to feed on carcasses (Friscia et al. 2007). Should yellow mongoose visit any of the carcasses, we expected that they would feed on developing fly larvae/pupae around and beneath the carcass, rather than the carcass itself, because they reportedly feed on softer foods (Taylor and Meester 1993; Friscia et al. 2007). .

Materials and methods

Study site

The study was conducted from July 2015 to March 2016 in two ecological estates in the south of Johannesburg, South Africa. Both estates enclosed a grassveld habitat, dominated

by thatch grass (*Hyparrhenia hirta*) and red grass (*Themeda triandra*), with numerous mammal game species as well as less frequently occurring small carnivores, such as serval (*Leptailurus serval*), jackal (*Canis mesomelas*), and Cape fox (*Vulpes chama*). Yellow and slender mongoose are the most abundant carnivores in both estates and from observations; the yellow mongoose is more prevalent than slender mongoose. The residential area in the Meyersdal eco-estate (26° 17′ 10.4″ S 28° 05′ 14.7″ E; 480 ha) is scattered within the nature area where animals frequently come into contact with people. The nature estate is smaller (26° 17′ 32.1″ S 28° 05′ 23.2″ E; 300 ha), where the nature area is separated from the residents by palisade fencing, yet it is still accessible to occasional hikers and cyclists.

Food choice

Food choice was investigated using cafeteria-style feeding experiments with six choices: deli meat off-cuts, meal worms (*Tenebrio molitor*), white bread, dry dog food pellets (Bob Martin™ kibble), a raw chicken egg (shelled), and surrounding vegetation (as a control). These food items were chosen to enable us to standardise the testing protocol by using easily available food that also represented the range and variety of the diet of both mongoose species (including anthropogenic items with which they are likely to come into contact). Feeding stations were placed on both estates and comprised of six (12-cm diameter) clear plastic bowls that were pinned down to the ground with long nails to prevent bowls from being removed or blown away by wind. Each bowl contained one food choice in small, equal quantities (by volume using a tablespoon), so as to avoid having quantity affecting the measurement of preference (Krebs 1989). Bowls were spaced 30 cm apart in a linear sequence and were randomised by food type order at each trial.

A Bushnell Essential trophy camera trap triggered by a motion sensor was placed 1-2 m away from the bowls with the entire cafeteria set-up in view to video-record feeding by mongoose at the station. Stations were checked 4 h after being set out, and the video footage inspected to confirm whether a mongoose fed at the station. If the video footage revealed a yellow or slender mongoose took part in the food choice test, the station was moved approximately 300 m to another site to avoid re-sampling the same individual. This continued until a total of 10 trials per species per estate were recorded ($n = 40$) at different sites within the estates.

From the video footage, we noted the following for each species per trial: (1) the latency to approach the first feeding bowl, which was defined as the time from when the mongoose came into camera view to when it had its head or nose over a bowl; (2) the latency to consume the first food which was defined as the time from when the mongoose came into camera view to when it started feeding on the first food; (3) the food type first consumed; (4) the food types ignored; (5) sequence of food visited; (6) sequence of food consumed; and (7) total time spent at the feeding station. In the analysis, the order of consumption and visits to food types were scored by allocating the highest score to the first food type chosen, indicating a greater preference, and the lowest score to the last choice made (i.e. first = 6 and sixth = 1). Any foods not visited or not consumed were given a score of 0. The cumulative scores (the sum of the scores for each food type) for the order of bait consumed over the 10 trials for each species in each estate were also calculated to establish the food preferences of each species in each estate. Foods with the highest cumulative scores were considered to be more preferred than foods with low cumulative scores.

Carrion-baited stations

Carrion-baited stations were opportunistically set up based on the mortality of any animals in the estates. These carcasses were provided and placed out by environmental management at sites where mongoose were observed. From July to December 2015, a total of nine different carcass stations were placed in the eco-estate only. Because of the opportunistic nature of these deaths, two carcasses were provided in winter and seven in spring/summer. Carcasses comprised of two (one adult and one young) reedbuck (*Redunca arundinum*), two adult blesbuck (*Damaliscus pygargus phillipsi*), three adult red hartebeest (*Alcelaphus buselaphus*), a cane rat (*Thryonomys swinderianus*), and a black wildebeest (*Connochaetes gnou*). No carcasses were available in the nature estate. Naturally occurring animal mortalities could have occurred in the nature estate, but since none were observed or recorded, we could not compare carrion feeding between estates.

Bushnell Essential trophy camera traps were placed 1–2 m from the carcasses with the entire carcass in view, and the following was retrieved from the video-recordings: mongoose species present; number of mongoose individuals present; the food eaten (meat or insects present); feeding behaviour when visible (e.g. tearing, slicing, chewing meat off carcass); interspecific (between yellow and slender mongoose)/or intraspecific interactions; and date and time; ambient temperature of the surrounding environment. The duration of each feeding bout for each mongoose present was also recorded. A feeding bout was defined as an uninterrupted interval of feeding at a carcass; departure of a mongoose after feeding on the carcass was noted as the termination of the feeding bout.

Data analysis

All data were recorded and figures generated using Microsoft Excel® (Microsoft Corporation, 2007) and

Statistica (www.statistica.io, version 7.0), and statistical analyses were conducted using R Statistical Software (www.r-project.org, R version 3.3.0). A two-way ANOVA was used to analyse differences between species and between estates in the latency to approach and the latency to consume the first bait in the food choice trials. The order in which food was visited and the order in which food was consumed were analysed (in two separate models) using a general linear model (GLM), with a binomial distribution and logit-link function (R packages used: car, lme4, lsmeans). The models comprised of first order effects and interaction effects between the following variables: estate, species and food type, and either the score for order of consumption or score for order of visitation of food types as the dependant variables. Tukey (HSD) post hoc tests were used to obtain pair-wise comparisons of levels for significant categorical predictors of data ($n = 166$ different levels per model). A two-way ANOVA was used to analyse differences between species and between estates in the total time spent at the feeding station. Both species were present and feeding at only one carcass. Therefore, data from that feeding station was described and also analysed using a *t* test comparing feeding duration between yellow and slender mongoose. For the remainder of all feeding stations, where only slender mongoose occurred, feeding behaviour and patterns of feeding behaviour were described qualitatively for slender mongoose.

Results

Food choice

A total of 40 bait choice tests at 40 different sites were conducted. Latency to approach the feeding station was significantly affected by estate ($F_{1,36} = 13.23$, $p < 0.001$) and species ($F_{1,36} = 18.00$, $p < 0.001$), but not the interaction between the two ($F_{1,36} = 0.13$, $p = 0.718$). Estate ($F_{1,36} = 7.09$, $p = 0.011$) and species ($F_{1,36} = 6.48$, $p = 0.015$) were also significant predictors of latency to consume the first food type, and the estate ∗ species interaction was again not a significant predictor ($F_{1,36} = 0.03$, $p = 0.860$). Latency to approach and consume the first food type was shorter in the eco-estate compare to the nature estate, and the yellow mongoose had a shorter latency both to approach and consume the first food in both estates in comparison to the slender mongoose (Fig. 1). Both species in the nature estate took longer to approach feeding stations than those in the eco-estate and also appeared to be more vigilant of the surrounding area when feeding (pers. obs.).

The order of food visited was different to the order of food consumed, because individuals of both species visited a bowl without feeding, and then moved onto another bowl before commencing feeding. The GLM indicated that estate ($\chi^2_1 = 0.00$, $p = 1.00$), species ($\chi^2_1 = 0.00$, $p = 1.00$), food type ($\chi^2_5 = 48.46$, $p = 0.062$), and all interactions between them were not significant predictors of the order of food visited in both estates ($p > 0.05$). There was no significant difference in order of food consumed between estates ($\chi^2_1 = 3.12$, $p = 0.08$) or between species ($\chi^2_1 = 3.12$, $p = 0.08$).

Food type ($\chi^2_5 = 3488.13$, $p < 0.001$) and the interactions between estate ∗ food type ($\chi^2_5 = 34.92$, $p < 0.001$), species ∗ food type ($\chi^2_5 = 28.84$, $p < 0.001$), and estate ∗ species ∗ food type ($\chi^2_5 = 17.43$, $p = 0.004$) were significant predictors of the order of food consumed. Post hoc tests revealed that most (93.4%) of the pair-wise comparisons for the order of food consumed were significant ($p < 0.05$). In all trials, for both species in both estates, the order of bait consumed revealed a preference for meat, followed by mealworms, bread, dog kibble, and egg, except for the yellow mongoose in the eco-estate which showed a second highest score for bread followed by mealworms (Fig. 2). The total time spent at the station was significantly affected by estate ($F_{1,36} = 11.71$, $p = 0.002$) but not by species ($F_{1,36} = 2.88$, $p = 0.098$) or the estate ∗ species interaction ($F_{1,36} = 0.32$, $p = 0.574$). Time spent at the station was greater in the eco-estate compared to the nature estate for both species (Fig. 3).

Carrion-baited stations

Slender mongoose were most common at the nine carcass-baited stations, with only a few occurrences of yellow mongoose feeding recorded at one carcass (i.e. the adult reedbuck). Furthermore, in the remaining eight carcasses, yellow mongoose were recorded walking in view of the camera at the carcasses on 19 occasions, but none stopped to feed, regardless of slender mongoose presence ($n = 12$) or absence ($n = 7$).

Feeding behaviour: yellow vs. slender mongoose

Individuals of the two species fed at the adult reedbuck carcass over 16 days in July 2015 (mid-winter) when ambient temperatures ranged between 0 and 12 °C. There were considerably more occurrences of feeding by slender ($n = 94$) than yellow mongoose ($n = 13$; Table 1). There were a total of 13 recorded yellow mongoose feeding bouts; of these, there was only one occurrence of more than one yellow mongoose simultaneously present ($n = 2$; where one sunbathed while the other fed). There were no occurrences of more than one individual feeding simultaneously. On five occasions, both species were present and feeding at the same time, and on four of these occasions ($n = 4$), aggressive vocalisations and lunging from the slender mongoose resulted in the yellow mongoose running away; the fifth occurrence resulted in concurrent

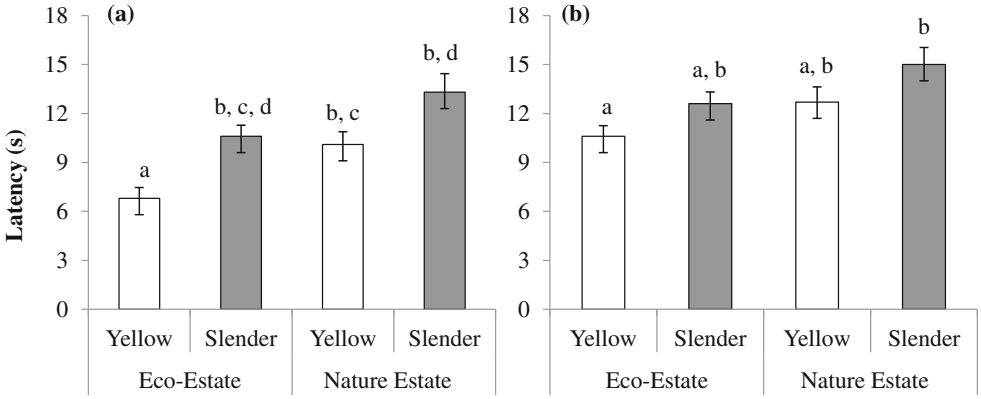

Fig. 1 Mean (± SE) latency to approach the first bowl (**a**) and latency to consume the first food type (**b**) for yellow and slender mongoose in the eco-estate and nature estate. The same alphabet letters above bars denote groups that are not significantly different

feeding with no interaction ($n = 1$). A further two occurrences resulted in the termination of feeding by the yellow mongoose when a slender mongoose arrived at the carcass after a yellow mongoose was already there, and the yellow mongoose ran away. The behaviour exhibited by yellow mongoose around the carcass was vigilance (temporary halting to walking towards carcass/feeding on carcass, standing up on hind legs, and examining/scanning of the surrounding environment) when approaching the carcass and when feeding.

Of the slender mongoose feeding, there was only one occasion ($n = 1$) where a maximum of five slender mongoose were present at the carcass at the same time. However, individuals interchangeably engaged in feeding and sunbathing, and only a maximum of four individuals fed simultaneously. Of the remaining 93 feeding bouts, there were 56 (59.6%) occurrences of solitary feeding, 29 (30.9%) occurrences of two individuals, and eight (8.5%) occurrences of three individuals feeding simultaneously. Of these, there were 11 intraspecific interactions (between slender mongoose), which only occurred during the feeding bouts of two to three individuals present, all of which were characterised by aggressive vocalisation and no physical contact, and ended in continuing of concurrent feeding.

The slender mongoose occurred at the reedbuck carcass earlier in the morning and later in the evening compared to the yellow mongoose (Table 1), and the duration of feeding was significantly greater in the slender compared to the yellow mongoose ($t_{95} = -10.506$, $p < 0.001$; Table 1). The slender mongoose fed exclusively on meat by primarily tearing and ripping off pieces of meat, whereas the yellow mongoose were observed gnawing at the carcass, chewing off small pieces of meat. In contrast to Vaughan (1976), there were no instances of digging next to/beneath carcasses.

Feeding behaviour of the slender mongoose

The slender mongoose frequented the various carcasses daily, and while there was a bias in the sampling period for warmer versus colder months, there appeared to be differences in their feeding behaviour relating to the changes in temperature (Table 2). At each carcass, individuals engaged in feeding at approximately the same time every day (Table 2). However, ambient temperature appeared to influence the start and termination times: higher temperature was associated with in an earlier start and later termination of feeding and lower temperature with a later start and earlier termination of feeding. The maximum duration of a single feeding bout occurred at the first carcass (reedbuck 1) and decreased in subsequent carcasses. However, mean feeding duration (i.e. average of all feeding bout durations at a single carcass) was greatest at the second carcass, blesbuck 1.

The first carcass, reedbuck 1, was placed out in the field from 15th July 2015, when temperatures were the lowest in this study, dropping to < 1 °C. Mongoose fed primarily (100%) on meat from the carcass itself by means of gripping and tearing off pieces (with visible jerking of the body). It was

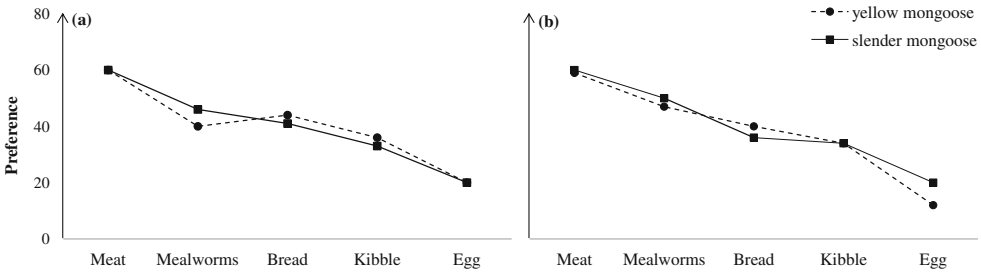

Fig. 2 Order of food preference, using cumulative score for each food type, of yellow and slender mongoose in the eco-estate (**a**) and nature estate (**b**)

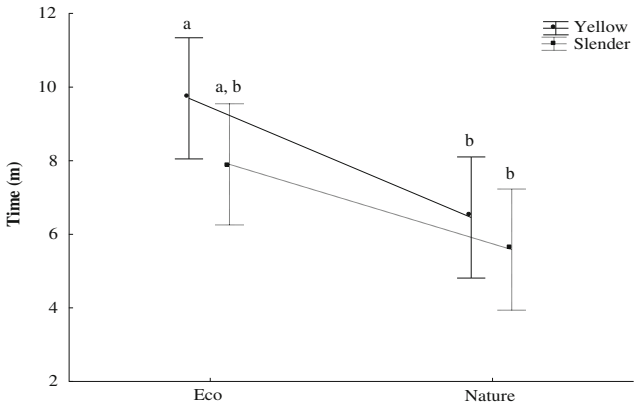

Fig. 3 Mean (± SE) time spent at feeding stations for yellow and slender mongoose in the eco-estate and nature estates. The same alphabet letters above bars denote groups that are not significantly different

assumed that as temperatures increased, the availability of invertebrate prey (flies/insects) would have increased. This was confirmed by video footage of subsequent carcasses being covered in flies and developing maggots shortly after they were placed in the field.

When temperatures increased, there was a shift from predominantly feeding on meat, to feeding on the insects present (on, around, and beneath the carcass; Table 2). The second carcass (blesbuck 1) was placed in the field at the start of spring when temperatures gradually increased. At subsequent carcasses, slender mongoose fed primarily on the insects present (98–100% of all feeding bouts) and rarely fed on the carcass (> 2% of all feeding bouts of all feeding bouts). This was not the case for the cane rat and reedbuck 2 carcasses, where, despite temperatures reaching a maximum of 32 °C, mongoose returned to feeding predominantly on the carcass itself

Table 1 Comparison of feeding behaviour of yellow and slender mongoose feeding at a reedbuck carcass in the eco-estate from 15 to 30 July 2015

Data recorded	Yellow	Slender
No. of feeding bouts	13	94
Max no. present	2	5
Max no. feeding	1	4
Aggressive intraspecific interactions	0	11
Aggressive interspecific interactions	4	4
Earliest feeding	10 h43	06 h56
Latest feeding	16 h50	16 h57
Minimum duration (min)	0.150	3.717
Maximum duration (min)	37.07	269.93
Mean duration ± SE (min)	14.8 ± 3.2	86.5 ± 6.0
Main mechanism of feeding	Chewing	Tearing

(88–94% of all feeding bouts) and considerably less on insects present (5–11%).

The minimum number of mongoose feeding at all carcasses was one, and the maximum number of concurrent feeding individuals was four individuals (Table 2). On multiple occasions ($n = 137$), at eight of the nine carcasses, several slender mongoose individuals fed at the same time, with few aggressive interactions. The majority of aggressive interactions occurred at the first (reedbuck 1, $n = 11$) and second carcass (blesbuck 1, $n = 7$; Table 2), which is also where the majority of individuals fed simultaneously.

Discussion

We investigated the food choice and feeding on carrion in yellow and slender mongoose in a small urban reserve. Both the yellow and slender mongoose in the Meyersdal Nature Area preferred meat and insects (*T. molitor*) with the exception that the yellow mongoose in the eco-estate appeared to favour bread over the insects. Animals dwelling closer to humans and therefore in closer proximity to anthropogenic foods are more likely to exhibit a marked increase in the consumption of anthropogenic food (Ditchkoff et al. 2006). Therefore, reasons for the yellow mongoose in the eco-estate favouring bread second in food choice trials and similarly having a greater cumulative score for dog kibble compared to the slender mongoose and compared to both species in the nature estate may be because they occur more frequently and closer to the human residences and have previously encountered these foods.

The ability of animals to incorporate anthropogenic items in their diet increases their dietary diversity, which is beneficial because it gives them access to readily available food items (Contesse et al. 2004; McKinney 2006), which is especially opportune during winter, when natural food sources are not readily available (Luniak 2004; Murray et al. 2015). Previous studies have shown that animals in urban areas frequently consume anthropogenic items, which has also been found in both mongoose species in the eco-estate (Cronk and Pillay, unpublished data). This is due to ease of access, relative abundance, high energy, and ease of digestion of anthropogenic foods (Wong and Candolin 2015; Reher et al., 2016), resulting in foraging costs being potentially reduced (Murray et al. 2015). For example, anthropogenic items make up the main component of the urban red fox diet (Contesse et al. 2004; Duduś et al. 2014; Plumer et al. 2014). In the USA, several urban mesocarnivores feed on pet food and at bird feeders filled with seeds that are left out by human residents (Theimer et al. 2015). Similarly, Murray et al. (2015) showed that anthropogenic items such as garbage, crabapples (*Malus* sp.), and birdseed largely contributed to the diet of coyotes in urban Canada.

Table 2 Summary of results of slender mongoose feeding at nine different carcasses in 5 months in the Meyersdal eco-estate

	Reedbuck 1 15/7/15	Blesbuck 1 2/8/15	Red hartebeest 1 7/9/15	Red hartebeest 2 9/9/15	Blesbuck 2 23/9/15	Red hartebeest 3 2/10/15	Cane rat 27/10/15	Reedbuck 2 27/10/15	Black wildebeest 19/11/15
Recording duration (days)	16	15	17	17	19	11	9	7	12
No. feeding bouts	94	64	56	29	75	25	35	17	34
Earliest feeding time	06 h50	06 h36	06 h05	06 h11	05 h49	07 h59	06 h38	06 h03	06 h15
Latest feeding time	16 h57	17 h49	18 h13	17 h47	17 h26	17 h09	16 h01	16 h45	17 h24
Mean (range) feeding duration (min)	86.5 (3.7–269.9)	95.6 (2.0–214.4)	47.0 (3.4–199.9)	21.8 (0.5–101.8)	56.3 (1.2–189.8)	36.5 (7.5–115.1)	26.1 (4.6–61.3)	9.5 (1.1–18.1)	42.3 (2.0–93.0)
Min, Max no. individuals feeding	1, 4	1, 3	1, 3	1, 1	1, 3	1, 2	1, 2	1, 1	1, 2
Meat feeding %	100	32.8	1.8	0	1.3	0	88.6	94.1	0
Insect feeding %	0	67.2	98.2	100	98.7	100	11.4	5.9	100
No. aggressive interactions	11	7	0	1	0	0	2	0	1
Min temperature (°C)	0.6	8.9	12.2	12.2	15	18.9	12.8	12.8	17.2
Max temperature (°C)	23.3	25	28.9	28.9	31.1	31.1	32.2	32.2	32.8

The double vertical line differentiates austral winter (left of line) when temperatures were lowest and austral spring (right of line) leading into summer when temperatures were gradually increased

As expected, the bolder yellow mongoose had a shorter latency to approach and consume the first food encountered in both estates compared to less bold slender mongoose, particularly in the eco-estate. In the eco-estate, both yellow and slender mongoose come into contact more frequently with humans and anthropogenic items and therefore are possibly more habituated to people and appeared less vigilant when approaching the novel feeding stations. In contrast, both yellow and slender mongoose in the nature estate had a longer latency to approach and consume the first food, showing more vigilance when approaching the feeding station. The total time spent feeding at the stations was also greater in the eco-estate (more so in the yellow than slender mongoose) compared to the nature estate. Both species spent more time feeding in the eco-estate and appeared less vigilant compared to both species in the nature estate.

Some studies have suggested that animals in urban environments exhibit a relatively high disturbance tolerance (i.e. exhibit a bolder temperament), thereby willing to take more risks when experiencing novel objects (Chapman et al. 2012; Lowry et al. 2013). It has also been suggested that animals in urban areas display a level of tameness and tolerance towards humans (Luniak 2004). Several avian species in urban areas are less wary compared to rural counterparts; for example, male song sparrows (*Melospiza melodia*) in urban areas were more territorial and bolder in comparison to their rural counterparts (Evans et al. 2010). In our study, both mongoose species were the most abundant carnivores/predators in both estates, with others, such as black-backed jackal, rarely occurring. Thus, human presence may be one of the few threats experienced by both species. The greater exposure to humans in the eco-estate may have resulted in habituation to people in both species, which may be associated with increased boldness.

Foraging decisions are based on trade-offs between the costs (in this case predation/threat risk by humans) and the benefits (food intake/energetic gain from the food types provided; Raffa et al. 2002; Verdolin 2006; Stephens 2008). While the increased vigilance and time spent being vigilant as seen in the slender mongoose in the eco-estate and by both species in the nature estate might mitigate any potential threat, it does conversely reduce time spent feeding and therefore the feeding rates (defined as the amount of food consumed per unit of time; Drakeley et al. 2015). It is possible then that the yellow mongoose in the eco-estate had an increased feeding rate (spent less time being vigilant and more time feeding). Whether differences in feeding rates alter fitness in these mongoose is unknown at present.

Previous studies have not considered whether carrion is a regular food source for the yellow and slender mongoose. Because carcasses provide an abundance of resources (Rathbun et al. 2005), it was expected that mongoose would feed on carcasses in a small urban reserve,

particularly when larger competing carnivores are absent. As predicted, slender mongoose predominantly fed on/at carcasses, and only few incidences of feeding yellow mongoose occurred, possibly due to slender mongoose being morphologically better adapted to feeding on the carcass itself (Friscia et al., 2007; Kingdon et al. 2013), and the yellow mongoose exploiting other resources, such as soft bodied prey, instead.

The general behaviour exhibited by the yellow mongoose was more vigilance while feeding, and the majority of their feeding bouts at the one carcass were terminated by the appearance or interaction of a slender mongoose. The lack of yellow mongoose feeding at carcasses, even during warmer periods when insects were present, may be due to competitive exclusion around carcasses, where slender mongoose dominate. This was indicated by a few incidences of aggression ($n = 4$) directed at yellow mongoose, as well as the departure from the carcass by already feeding yellow mongoose when slender mongoose arrived ($n = 2$). Alternatively, yellow mongoose may not prefer to actively seek out and exploit carcasses for food and rather do so opportunistically when preferred resources are not available.

The feeding behaviour of the slender mongoose at all carcass-baited stations contrasts with those of previous studies in two ways. Firstly, slender mongoose are regarded as primarily solitary foragers and less commonly occurring in pairs (Graw and Manser 2016). Secondly, Vaughan (1976) reported that multiple individuals ($n = 2$) were observed feeding at the giraffe carcass simultaneously, although they kept a minimum of 2 m apart. In our study, at all carcasses stations, two to four slender mongoose were observed feeding at the same time, and despite all the carcasses being considerably smaller than that of the giraffe in Vaughan's (1976) study, the mongoose most often fed alongside one another and on other occasions < 1 m apart, with no negative interactions occurring. It has been suggested that unpredictable resource distribution can alter feeding behaviour from solitary feeding towards non-aggressive food sharing (Overington et al. 2008). Several slender mongoose feeding together may therefore be due to the abundance of food available around and on carcasses.

Despite the skew in seasonal availability of carcasses, it appeared that feeding behaviour differed between colder and warmer months. During the colder periods (winter), the following patterns were observed: there were more mongoose present and feeding simultaneously at carcasses; mongoose appeared later in the mornings and departed earlier in the afternoons; mongoose fed for longer durations; there were more recorded feeding bouts; and mongoose fed predominantly on carcass meat. When temperature increased, fewer mongoose were present, feeding started earlier morning and ended later, feeding durations were fewer and shorter, and most importantly, feeding shifted to insects present in and around carcasses. The cane rat and juvenile reedbuck carcases do however show contradictory results, which may be due to both these carcasses being much smaller than the other carcasses and fewer insects being present.

Vaughan (1976) recorded mongoose digging next to and beneath carcasses, presumably to gain access to developing insect larvae. In our study, when temperatures increased over the study period, the percentage of feeding bouts on carcass meat gradually decreased and the percentage of insects consumed increased. This may largely be due to the relative abundance of insects in the surrounding environment increasing as temperatures increase and rains occur (Mbatyoti 2012; Davies et al. 2015). It is not known whether the species of the carcass, and consequently type of meat, impacted on feeding behaviour.

As far as we are aware, our study provides the first data on the food choice of animals in urban areas through cafeteria styled food choice testing, as well as the first definitive description of the carrion feeding behaviour of the yellow and slender mongoose in an urban environment. Yellow mongoose in the eco-estate favoured bread and also showed a slightly higher preference for dog kibble (compared to the slender mongoose), whereas slender mongoose more frequently occurred at carcasses than yellow mongoose. These differences suggest resource partitioning where yellow mongoose are more likely to make use of anthropogenic items present in the environment, while slender mongoose largely focus on natural items present. Species overlapping in a particular niche dimension differ in another dimension for them to co-exist (Kylafis and Loreau, 2011). Our video footage showed that, in some instances, the yellow and slender mongoose occurred in close proximity, at the same times, yet differed in their feeding behaviour. Despite spatial overlap, this possible resource partitioning may be contributing to the co-existence of the yellow and slender mongoose in this urban area where there is usually an abundance of anthropogenic food items.

In conclusion, the slender mongoose exhibits more of a specialised carnivorous diet, whereas the yellow mongoose is more likely to incorporate anthropogenic items in their diet, suggesting a generalist diet. Furthermore, as predicted, the yellow mongoose appears to be inherently bolder in comparison to the slender mongoose, indicated by shorter latencies to approach novel items (Frost et al. 2007; Kurvers et al. 2012). This makes the yellow mongoose more likely to exploit residential areas, consequently gaining access to anthropogenic food with relatively ease of access, reducing competition with slender mongoose in the natural areas within the estates. Future

studies should assess species distribution and spatial overlap to determine whether the location in which each species mostly occurs determines its food choice and diet.

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Compliance with ethical standards

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. Ethical clearance was obtained from the University of Witwatersrand Animal Ethics Screening Committee (2015/08/37/B). This article does not contain any studies with human participants performed by any of the authors.

Conflict of interest The authors declare that they have no conflict of interest.

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CHAPTER FOUR

Spatio-temporal co-occurrence and overlap of two sympatric mongoose species in an urban environment

Abstract

Small carnivores are becoming increasingly common and are thriving in urban areas. What has received less attention is whether and how resource partitioning among sympatric species in urban areas facilitates their coexistence. We examined the spatial, temporal and combined spatio-temporal occurrence and overlap of co-existing yellow mongoose *Cynictis penicillata* and slender mongoose *Galerella sanguinea* in an urban reserve in South Africa. The reserve comprised of two parts, an Eco-Estate where residential and natural areas are interspersed and contact with residents is greater for wildlife, and a Nature Estate, where contact is reduced by fencing between people and natural areas. Using photographic data from camera traps collected over eleven consecutive months, we found that spatial overlap was greater in the Nature Estate than in the Eco-Estate. Differences between species occurred at a finer habitat scale, particularly in the Eco-Estate: yellow mongoose were more common in open habitats located near human residents, and slender mongoose were more common in covered areas further away from human residents. Although both species demonstrated diurnal bimodal activity, they varied in their peak active periods, with temporal overlap being greater in the Eco-Estate than in the Nature Estate. No complete spatio-temporal overlap (occurrence in the same place at the same time/within a 10 min period) occurred. Resource availability (primarily food) appears to influence the different habitat selection, space use, and activity patterns of yellow and slender mongoose in the two estates. Therefore, we conclude that partitioning along the spatial and/or temporal dimensions aids in the coexistence of these species in an urban environment.

Key words: *camera trap, coexistence, slender mongoose, spatial, temporal, urban areas, yellow mongoose*

Introduction

Rapid expansion of urban areas poses a number of risks to animals (Newsome *et al.,* 2010; Bateman and Flemming, 2012), and can lead to an increase in habitat fragmentation, which decreases the amount of available natural habitats (Duduś *et al.,* 2014; Scott *et al.,* 2014). Nevertheless, the reduced number of natural predators and an increased availability of natural and alternative food resources makes urban areas attractive to some animals which can thrive there (Newsome *et al.,* 2010; Plumer *et al.,* 2014; Wong and Candolin 2015).

Some carnivores are becoming increasingly prevalent in urban areas by exploiting the opportunities available there (Wong and Candolin 2015; Poessel *et al.,* 2017). Those thriving in urban environments tend to be diet generalists, small to medium sized, appear to tolerate and habituate to humans, and are able to exploit anthropogenic resources (Duduś *et al.,* 2014; Scott *et al.,* 2014). For example, the stone marten *Martes foina* and red fox *Vulpes vulpes* are considered as two of the most well adapted small carnivores in urban areas, exhibiting flexibility in their diet (e.g. anthropogenic items) as well as having a considerably high occurrence in, and use of, urban residential areas (Prigioni *et al.,* 2008; Plumer *et al.,* 2014; Scott *et al.,* 2014). Other species well adapted to urban areas are the coyote *Canis latrans* (Murray *et al.,* 2015; Poessel *et al.,* 2017), kit fox *Vulpes macrotis* (Newsome *et al.,* 2010) and Eurasian badger *Meles meles* (Bateman and Flemming 2012). An increase in the occurrence of small and meso-carnivores in urban areas presents the opportunity of morphologically and ecologically similar species overlapping in their resource use. Yet, how these species coexist in urban areas has received little attention.

Niche differentiation theory emphasises that a degree of resource partitioning (spatial, temporal, dietary) between sympatric species must occur in order for them to avoid niche overlap and the consequent interspecific competition (Pianka 1974; Kylafis and Loreau 2011; Lesmeister *et al.,* 2015; Ribeiro 2016). The food, space and time dimensions, either individually or in combination, are considered the foremost resources partitioned to promote coexistence of sympatric species (Prigioni *et al.,* 2008; Ramesh *et al.,* 2012; Frey *et al.,* 2017). Resource partitioning along the spatial niche, such as in habitat selection, is regarded as the principal dimension of differentiation, while temporal partitioning (after diet) is considered rare (Shoener 1974; Cavalini and Nel 1995).

Variation in the temporal niche can include species differing in the timing and level of activity, or in overall diel-activity (e.g. diurnal vs. nocturnal). For example, gray foxes

Urocyon cinereoargenteus occur at lower densities and are less active in areas at times when coyote activity was greater (Lesmeister *et al.,* 2015). Dholes *Cuon alpinus* segregated from leopards *Panthera pardus* and tigers *Panthera tigris* by being primarily diurnal, possibly to avoid competition with the primarily nocturnal felids (Karanth *et al.,* 2017). Similarly, in the spatial niche, species segregate by selecting different habitats, largely influenced by the availability of resources (e.g. food and resting sites; Duduś *et al.,* 2014; Lesmeister *et al.,* 2015). For example, the stone marten and red fox differed in habitat selection in an urban area in Poland, where stone martens were located in, and appeared better adapted to, areas closer to city centres where resting sites were almost exclusively in buildings. In contrast, red foxes selected habitats closer to the urban borders, where resting sites are favourable, but still providing access to anthropogenic items (Duduś *et al.,* 2014). In addition, habitat use niche overlap in a peri-urban area in Portugal was high between the Eurasian badger and red fox, but they exhibited different feeding habits which enabled coexistence (Ribeiro 2016). Despite previous research on resource partitioning, the spatio-temporal co-occurrence of species is poorly understood (Lesmeister *et al.,* 2015).

Here we present the first study on the spatio-temporal co-occurrence and overlap of two herpestid mongoose species, the yellow *Cynictis penicillata* and the slender *Galerella sanguinea,* in a small urban reserve in South Africa. The yellow mongoose is primarily insectivorous and the slender mongoose is an opportunistic carnivore (Nel and Kok 1999; Graw *et al.,* 2016; Cronk and Pillay 2018). Both species are diurnal in non-urban habitats (Mbatyoti 2012; Graw *et al.,* 2016). Yellow mongoose are active during the day between sunrise and sunset (Cavallini and Nel 1995; Mbatyoti 2012), while the slender mongoose reportedly exhibits a slight peak in activity before sunset, and cease activity just after sunset (Maddock and Perrin 1993). Yellow mongoose prefer open grassland and scrub habitats (Skinner and Chimimba 2005), and are not common in dense bush and woodland areas (Mbatyoti 2012). Conversely, slender mongoose are more prominent in dense covered thicket and woodland/forest areas (Ramesh and Downs 2014), and are not common in open grassland (Rapson *et al.,* 2012). Presently, both species inhabit and coexist in an urban areas in South Africa (Cronk and Pillay 2018), and nothing is known about the temporal activity and space use of these species in an urban environment.

We conducted our research in the Meyersdal Nature Area in South Africa, which was divided into 2 parts: an Eco-Estate where wildlife utilise household gardens and corridors between houses, and a Nature Estate, where houses are separated from wildlife by fences,

reducing contact with humans and homes. In both estates, we investigated the spatial and temporal occurrence and overlap of the yellow and slender mongoose through camera trap surveillance. In addition, we specifically investigated whether or not both species were utilising the same spaces at the same time (spatio-temporal overlap). Furthermore, camera traps aided in assessing broad habitat use and the distance from, and utilisation of, the residential areas within both estates for both species.

We had five predictions. 1. Both species would utilize distinct microhabitat types, in accordance with the niche differentiation theory. Yellow mongoose would occur more commonly in open areas and slender mongoose in dense covered areas. 2. In both estates, yellow mongoose would occur more frequently near human residences compared to slender mongoose, since yellow mongoose are more habituated to humans (pers. obs.); slender mongoose would occur more frequently in the natural areas further from human residents. 3. The mongoose species would show overlap in temporal activity profiles in both estates since both species are diurnal. 4. Seasonally, the less favourable conditions during the colder season would lead to both species utilising a wider variety of microhabitats in search for resources and thus show greater overlap in activity and space use in comparison to the warmer season. 5. Spatio-temporal overlap (animals occurring in the same place at the same time) was not expected since the mongoose species were expected to segregate along either the spatial or temporal niche, promoting coexistence (Karanth *et al.,* 2017) in the Meyersdal Nature Area.

Materials and methods

Study site

Field work took place from May 2015 to March 2016 within two adjacent ecological estates, Meyersdal Eco-Estate (26°17'10.4"S 28°05'14.7"E) and Nature Estate (26°17'32.1"S 28°05'23.2"E), in Johannesburg, South Africa (Figure S1). Wildlife occur on both estates but more frequently come into contact with people in the Eco-Estate, which is residentially built-up and interspersed with natural areas and is slightly larger (480ha) than the Nature Estate (300ha). The residential area within the Nature Estate is separated from the natural area by palisade fencing which is permeable to mongoose (Cronk and Pillay, 2018). The dominant vegetation in the area is a grassveld vegetation type, predominantly grasses including thatching grass *Hyparrhenia hirta* and red grass *Themeda triandra*, with dense tree cover on

the borders, housing a wide range of small and large vertebrates. Yellow and slender mongoose are the most abundant carnivores in both estates and from observations, with yellow mongoose being more prevalent than slender mongoose (Cronk and Pillay, 2018). Potential predators of mongoose within these estates included black-backed jackal *Canis mesomelas* and black eagles *Ictinaetus malaiensis*; both sparsely occurring.

Camera trap surveillance

Through an observational pilot study, wildlife trails and areas where both mongoose species were sighted, were identified and recorded as 'sites of occurrence' (hereafter reported as site). We used motion triggered infrared Bushnell Essential® camera traps equipped with high powered batteries and 32GB memory cards, ensuring a minimum of one week uninterrupted data collection. The use of camera traps is beneficial as it incurs very minimal environmental disturbance and is a non-invasive method of data collection (Rovero *et al.,* 2014). Three camera traps were placed at various sites in both the Eco-Estate and Nature Estate (total of 6 cameras). Camera traps were attached to rigid surfaces (rocks/trees) approximately 0.5-1.0 m off the ground, and positioned so the field of view included an active wildlife trail (Jenks *et al.,* 2011; Rovero *et al.,* 2014). Ethical clearance was received (2015/06/22/A) from the Animal Screening and Ethics Committee of the University of the Witwatersrand for camera trap placement. The understory growth at camera sites was cleared to minimize or eliminate the possibility of obstructed images and also of false triggering of the cameras by grass movement.

The cameras were set to capture two consecutive photographs at each trigger, and a delay period of 1 s was set between triggers to ensure multiple captures of any rapid movement of a mongoose. All cameras were active 24 hours a day, and no bait was used. Camera traps were checked once a week to change memory cards, change batteries and to ensure that they were fully functional and had not been tampered with. Camera traps remained at a single site for two weeks, before being moved to a new site approximately 200 m away. In Figure S1, camera traps situated in close proximity were placed in those areas during different seasons (i.e. temporally displaced). In order to minimize autocorrelation within mongoose core home ranges (the areas around dens where activity level is greatest), we ensured that no camera traps were placed near the known mongoose dens. We attempted to balance the number of camera trap sites at each distance category, for each habitat category (Table S1) in order to avoid bias between estates and different categories.

The following information was recorded for each photograph: date; time; and mongoose species present. Since individual mongooses could not be distinguished from camera trap footage, any consecutive captures within a 10 min time frame were considered as a single occurrence (i.e. the same mongoose; Norris *et al.,* 2010). The following was also recorded for each site: GPS location; relative distance to human residents (closest: <200 m; intermediate: 200-400 m; furthest: >400 m); and broad type of habitat/surrounding vegetation (open grassland: large open areas dominated by grasses; or bushy/tree covered: areas dominated by tree cover or dense bushes). This information aided in assessing broad habitat type use as well as relative use of residential areas as a proxy for access to and potential use of anthropogenic items. The relative frequency of occurrence was calculated for each species at each site by dividing the number of photographic captures for each species by the total number of mongoose occurrences (of both species) at each site.

Data analysis

All data were recorded and figures generated using Microsoft Excel® (Microsoft Corporation, 2007) and Statistica (www.statistica.io, version 7.0), and statistical analyses were conducted using R Statistical Software (www.r-project.org, R version 3.4.3). A t-test was used to compare the number of independent captures to establish which species occurred more frequently in both estates. We used recorded data to calculate the frequency of occurrence for each species at each site by dividing the number of captures for each species by the total number of mongoose captures at each site. The data were then square-root transformed to approximate normality and a linear mixed model was used to analyse for significant predictors of frequency of occurrence of each mongoose species. The model comprised of first order effects and interaction effects of the following predictor variables: Estate, Species, Season (cold/warm periods), Habitat type (open/covered vegetation type), and Distance relative to residents (closest, intermediate, furthest) as fixed effects. Site was included as a random variable (random intercept only). Since the study durations for each season were not equal, and in order to balance sample sizes for analysis, sampling periods were categorized as warm (September to February) and cold (March to August) to reflect South Africa's seasons. Tukey post-hoc tests were used to assess significant predictors of occurrence for the significant fixed predictors and their interactions.

To assess activity profiles and temporal overlap, we used the R package '*overlap*' to obtain pair-wise temporal overlap coefficients (Δ; Meredith and Ridout 2014). We compared activity patterns for both species within and between estates, as well as the comparison of overlap of activity within and between colder and warmer periods. Temporal overlap of activity patterns was estimated using the kernel density estimation following the methods proposed by Ridout and Linke (2009). We selected a smoothing parameter of 1.0 since the size of the smallest sample size was greater than 75 (Meredith and Ridout 2014). The overlap coefficient generated (Δ) ranges from 0, indicating no overlap, to 1, indicating complete overlap (Frey *et al.,* 2017).

Photographic rate (number of captures per number of trap days) gives insight into estimating species abundance and distribution (Bowkett *et al.,* 2008; Jenks *et al.,* 2011; Rovero *et al.,* 2014). We calculated the relative abundance index (RAI) for each species (across all sites) in each estate, by taking the sum of all independent captures for each species multiplied by 100, and divided by the total number of camera trap days (occurrence per species per 100 trap days; Jenks *et al.,* 2011). We ran a linear mixed model to test whether Species or Estate were predictors of RAI. In these analyses, χ^2 statistics were used for overall model significance. The Z statistics, including estimate and SE values and confidence intervals (CI), were generated for specific components of the fixed factors. Here, reference categories were selected using sequential entry and/or were based on logically meaningful categories to obtain Z statistics for each component. Furthermore, RAI can also be used as a relative index of space use; hence to account for spatial overlap, we also calculated the RAI for each species at each camera trap site (in both estates), which was then correlated between species at each site using Spearman's rank correlation. We also compared RAI values between warmer and colder periods to assess for seasonal effects. To ascertain spatial overlap at camera trap sites (Ribeiro 2016) between yellow and slender mongoose in each estate, as well as whether spatial overlap varied between cold and warm periods, we used Pianka's Index (Krebs 1989) of overlap, ranging from 0 (no overlap) to 1 (complete overlap):

$$O_{jk} = \frac{\sum_i^n P_{ij} \times P_{ik}}{\sqrt{\sum_i^n P_{ij^2} \times \sum_i^n P_{ik^2}}}$$

Where:

- O = Pianka's measure of resource overlap between species j (yellow) and k (slender)
- Pij = proportion of resource i (occurrence at each site) of the total resources used (total occurrence) by yellow mongoose
- Pik = proportion of resource i (occurrence at each site) of the total resources used (total occurrence) by slender mongoose

Results

We sampled 66 sites with differing surrounding vegetation and relative distance to human residents in both the Eco-Estate and Nature Estate (n=132 in total; Figure S1; Table S1). A total of 1494 photographs of mongoose were obtained in the Eco-Estate and 1374 in the Nature Estate (Table 1). Yellow mongoose occurred significantly more frequently in photographs than slender mongoose in both the Eco-Estate (mean±SE: yellow 77.01±4.54; slender 22.99±4.54; t_{130}=8.42, p <0.001) and Nature Estate (yellow 78.00±4.56; slender 6.88±SE; t_{90}=14.24, p <0.001).

Table 1. Number of independent photographs of yellow mongoose and slender mongoose, per season, in the Eco-Estate and Nature Estate

Season	Eco-Estate		Nature Estate	
	Yellow	**Slender**	**Yellow**	**Slender**
Cold	558	80	544	51
Warm	731	125	722	57
Total	**1289**	**205**	**1266**	**108**

Spatial niche

The yellow and slender mongoose showed different patterns of occurrence at a camera trap site, and the linear mixed effect model showed that there were multiple

significant and non-significant interactions between estate, species, distance relative to residents, and season (Table S2). Significant 4-way interactions occurred between Estate × Species × Season × Habitat (χ^2 (1) = 11.91, p <0.001) and Estate × Species × Distance × Habitat (χ^2 (1), p = 0.04). Tukey post-hoc tests from the model revealed significant differences occurred; the estate and species differences in habitat use and distance from human residents (between seasons) are described below.

Habitat type use

Overall, yellow mongoose occurrence was greater in open than in covered habitats and slender mongoose occurrence was greater in covered than in open habitats (Figure 1). Tukey post-hoc tests from the linear mixed effects model revealed that yellow mongoose occurred in photographs significantly more in open than in covered habitats in the Eco-Estate (p = 0.017) but not in the Nature Estate (p = 0.998). Slender mongoose occurred significantly more in covered than in open areas in the Eco-Estate (p<0.001) and Nature Estate (p = 0.027). Between species, yellow mongoose occurred significantly more often in open habitats than slender mongoose in both the Eco-Estate (p<0.001) and Nature Estate (p<0.001), and slender mongoose occurred significantly more often in covered habitats than yellow mongoose in the Eco-Estate (p<0.001), but not in the Nature Estate (p = 0884).

Between estates, the yellow mongoose and slender mongoose (respectively) did not differ significantly in the use of open (p = 0.442; p = 0.972) or covered (p = 0.574; p = 0.987) habitats (Figure 1). In the Eco-Estate, yellow and slender mongoose did not differ in their occurrence in open and closed habitats between the colder and warmer periods (Figure 2a). Conversely, in the Nature Estate, yellow mongoose occurred more often in covered areas and slender mongoose more often in open areas during the colder periods relative to their occurrence in these habitat types during the warmer periods (Figure 2b).

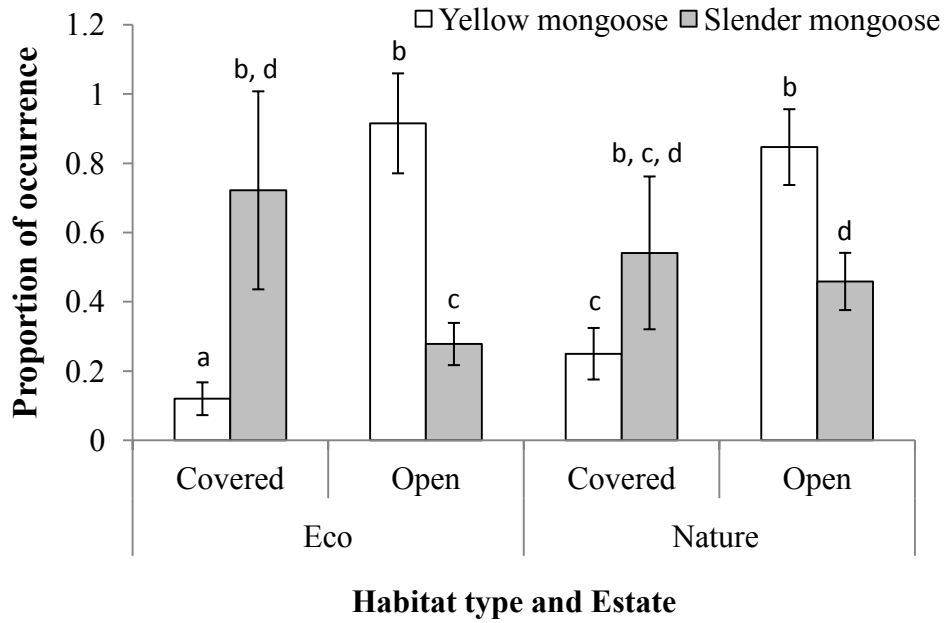

Figure 1. Mean±SE proportion of occurrence (frequency of occurrence over total occurrence per species) of yellow mongoose and slender mongoose in the Open and Covered habitat types in Eco-Estate (Eco) and Nature Estate (Nature). The same alphabet letters above bars denote non significant differences.

Distance from human residents

Post-hoc tests from the linear effects mixed model showed that in both the Eco-Estate and Nature Estate, yellow mongoose occurred significantly more often at sites that were closest (<200m; $p<0.01$ both estates) and at intermediate (200-400 m; $p<0.01$ both estates) distances to human residents than slender mongoose (Figure 3). In contrast, slender mongoose occurred significantly more often at sites furthest (>400m) from human residents than yellow mongoose in the Eco-Estate ($p<0.01$) but not in the Nature Estate. Between estates, yellow mongoose occurred significantly more on camera traps at sites closest to human residents ($p<0.01$) and significantly less at sites furthest from human residents ($p<0.01$) in the Eco-Estate compared to the Nature Estate. Slender mongoose occurred significantly more often at sites furthest from human residents in the Eco-Estate compared to the Nature Estate ($p = 0.02$), and did not differ in occurrence at sites closest to residents between estates ($p = 0.98$); neither species differed in their frequency of occurrence between estates at intermediate distance sites. There was no seasonal variation in occurrence at different distance from human residents.

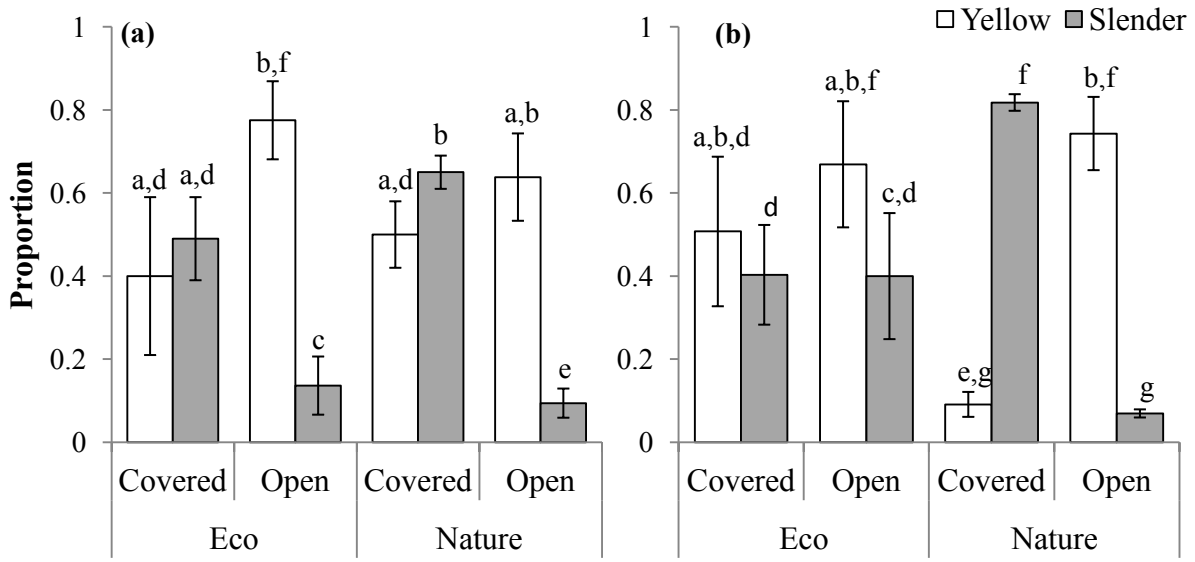

Figure 2. Mean±SE proportion of occurrence (frequency of occurrence over total occurrence) of yellow mongoose and slender mongoose in the Open and Covered habitat types in both the Eco-Estate (Eco) and Nature Estate (Nature) during the colder (a) and warmer (b) periods in the Meyersdal Nature Area. The same alphabet letters above bars denote non significant differences.

Relative abundance and spatial overlap

For relative abundance, yellow mongoose was detected 138.5 times and 138.0 times, and slender mongoose 22.2 times and 11.9 times per 100 trap days (Jenks *et al.,* 2011), in the Eco-Estate and Nature Estate respectively (Table S3). Relative abundance was significantly affected by species ($\chi^2 = 437.22$, df =1, $p < 0.001$), and was significantly greater in yellow mongoose than slender mongoose in both estates (Estimate = 1.88, SE = 0.21, z = 9.14, $p < 0.001$; CI = 1.49, 2.29). Estate ($\chi^2 = 1.04$, df =1, p = 0.31) and Season ($\chi^2 = 1.14$, df =1, p = 0.28) had no significant effect on RAI. Space use inferred from the RAI (Ramesh *et al.,* 2012) at each site was significantly negatively correlated between yellow and slender mongoose in the Eco-Estate, with a strong positive significant correlation in the Nature Estate (Table 2). Overall, using Pianka's overlap, spatial overlap was greatest between yellow and slender mongoose in the Nature Estate (0.69) compared to the Eco-Estate (0.41), where the overlap was relatively low. In both estates, spatial overlap was greater during colder periods compared to the warmer periods (Table 2).

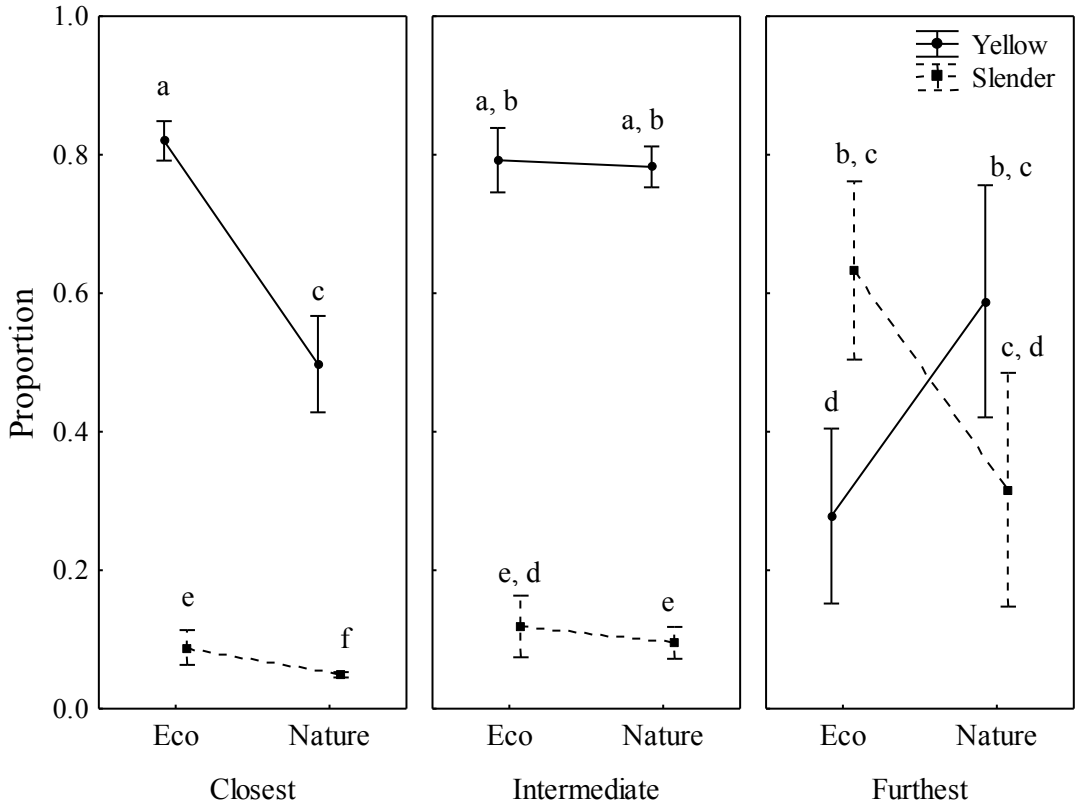

Figure 3. Mean±SE proportion of occurrence (frequency of occurrence over total occurrence per species) of yellow and slender mongoose at three distances classes from residents in the Eco-Estate (Eco) and Nature Estate (Nature). The same alphabet letters above bars denote non significant differences.

Temporal niche

Activity patterns and temporal overlap

The diurnal start and end of time of occurrence on camera trap photographs of yellow mongoose in the Eco-Estate was 06:29 ± 00:28, 18:19 ± 00:37 (mean±SE) and that of slender mongoose was 05:48 ± 00:45, 18:01±01:11. In the Nature Estate, the diurnal start and end times of occurrence for yellow mongoose was 06:14 ± 00:17, 18:36 ± 00:33 and that of slender mongoose was 07:12 ± 01:04, 18:07 ± 00:40. In both estates, yellow mongoose demonstrated a bimodal peak activity, one between 10:00 and 11:00 and another between 16:00 and 17:00 (Figure 4a). Slender mongoose activity was more or less similar throughout the day yet small peaks in activity were observed closer to sunrise (6:00) in the Eco-Estate, and peaks occurred later in the morning and evenings compared to those of yellow mongoose

in the Nature Estate (Figure 4a). Interestingly, while yellow mongoose showed greatly reduced activity during the hottest periods of the day (midday), slender mongoose activity was greater at these times, with no considerable decrease in activity at these times overall. Temporal overlap in activity between yellow and slender mongoose (Table 4) was greater in the Eco-Estate (**Δ**0.78) than in the Nature Estate (**Δ**0.63). Activity patterns of species were also compared between estates (Figure S2). The overlap in temporal activity between the Eco-Estate and Nature Estate was similar for yellow mongoose (**Δ**0.86) and slender mongoose (**Δ**0.83); the high overlap may suggest no difference in the activity patterns between the estates (Table 3).

Table 2. Estimates of spatial overlap between yellow mongoose and slender mongoose, over the entire study period, and per season, within the Eco-Estate and Nature Estate

Interaction	**Eco-Estate**			**Nature Estate**		
Yellow vs. Slender	**Spearman R**	***p***	**Pianka**	**Spearman R**	***p***	**Pianka**
Overall	-0.38	0.002	0.41	0.62	<0.001	0.69
Cold	-0.23	0.255	0.62	0.37	0.058	0.84
Warm	-0.56	<0.001	0.36	0.82	<0.001	0.51

Overall, during the colder months (Figure 4b), activity for both species in both estates appeared to start slightly later and concluded earlier in comparison to the warmer periods (Figure 4c). Bimodal peaks in activity were present in both species in both estates during the colder periods, with the first peak being later in the morning in slender mongoose compared to yellow mongoose (Figure 4b).

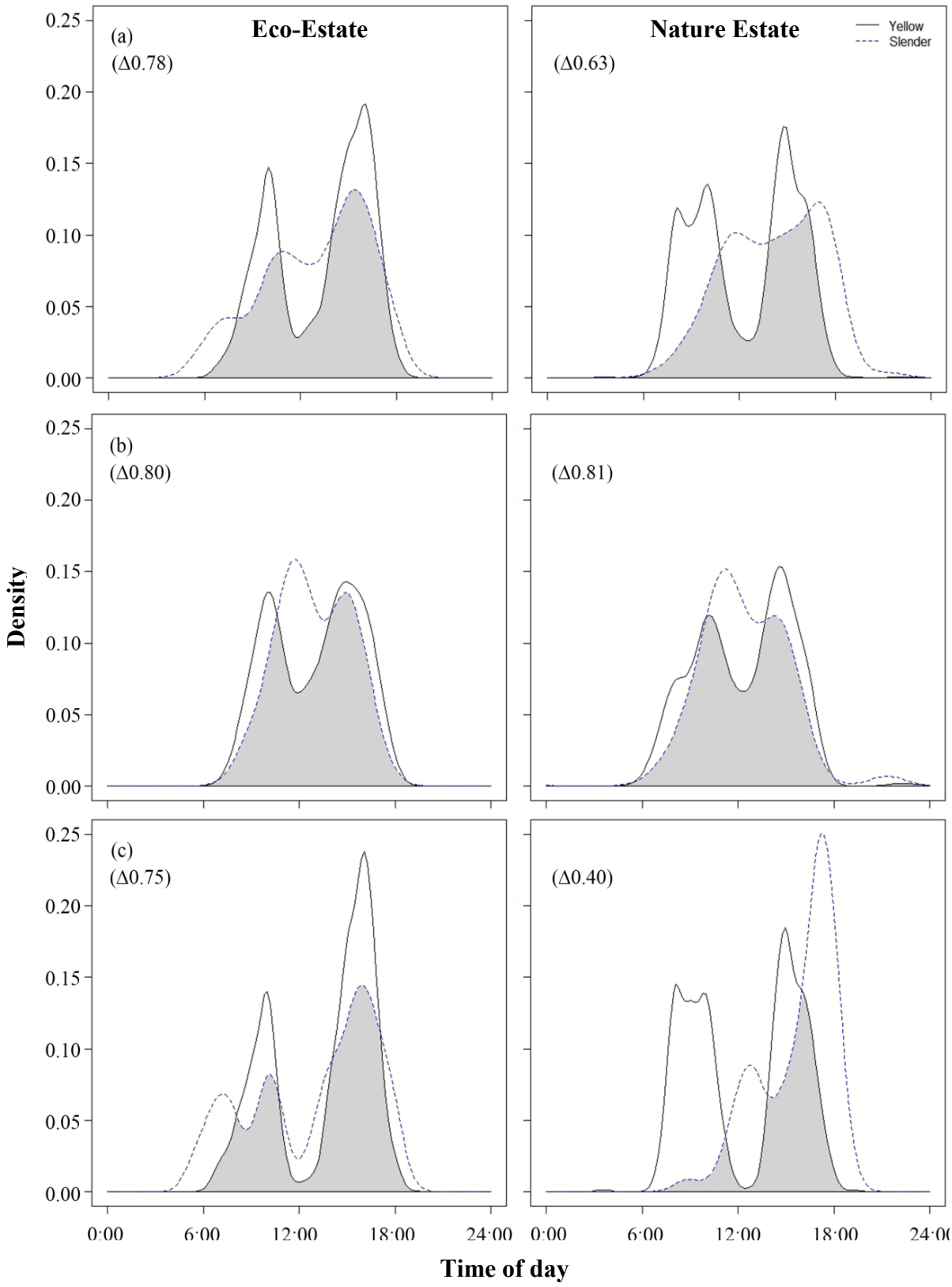

Figure 4. Temporal overlap of yellow (solid line) and slender (dashed line) mongoose activity patterns within the Eco Estate and Nature Estate for the (a) entire study period, (b) colder and (c) and warmer periods. The overlap coefficient (Δ) is the area under the minimum of two density estimates indicated by the grey area below curves.

During the warmer months, slender mongoose activity peaked earlier in the morning in the Eco-Estate, and later in the mornings and evening in the Nature Estate compared to yellow mongoose (Figure 4c). In both estates, yellow mongoose had reduced activity around midday, more so during the warmer months, whereas slender mongoose were comparatively more active at these times during the colder months. Conversely, during the warmer months, slender mongoose had a similar reduction in activity in the Eco-Estate, yet peaked at midday in the Nature Estate (Figure 4a and 4b). Temporal overlap in activity was greater during the colder period (**Δ**0.80; **Δ**0.81) compared to the warmer period (**Δ**0.75; **Δ**0.40) in the Eco-Estate and Nature Estate respectively (Table 3).

Table 3. Estimates of temporal overlap in activity patterns (Δ) between yellow and slender mongoose during the entire study period, and per season, within and between estates. Values in brackets indicate approximate 95% bootstrap confidence intervals

Species interaction	**Eco-Estate**	**Nature Estate**
Yellow vs. Slender	**Overlap Δ**	**Overlap Δ**
Overall	0.78 (0.72-0.83)	0.63 (0.512-0.65)
Cold	0.80 (0.69-0.85)	0.81 (0.69-0.89)
Warm	0.75 (0.69-0.83)	0.40 (0.23-0.40)
	Eco-Estate vs. Nature Estate	
Yellow vs. Yellow	0.86 (0.82-0.88)	
Slender vs. Slender	0.83 (0.75-0.89)	

Spatio-temporal overlap

There were no instances of co-occurrence of yellow and slender mongoose in the same image at the same time in both estates. We then considered evaluating images captured within a 0 - 10 minute time frame (i.e. one species in an image, followed by the other species in a consecutive image captured within 10 minutes), and found 19 (1.27%) such occurrences in the Eco-Estate and 2 (0.15%) in the Nature Estate.

Discussion

We investigated the spatio-temporal occurrence and overlap of yellow and slender mongoose in order to assess mechanisms allowing for their coexistence in an urban setting. The differences in habitat selection, space use, and activity patterns of the two sympatric species suggest that food availability may influence species differences in these mongoose; as discussed below. Yellow mongoose were more common in open habitats located near human residents, and slender mongooses were more common in covered areas further away from residents, and consequently, the species showed greater spatial overlap in a less urbanised than more urbanised area. Temporal overlap was found to be greater in a more urbanised than less urbanised areas, but species varied in peak activity periods. There were no occurrences of complete spatio-temporal overlap.

While several studies have failed to identify strict habitat use differences among co-existing carnivores (Gompper *et al.,* 2016), our study does suggest that, even at a small scale habitat assessment, both mongoose species utilise different habitat types. Habitat use by carnivores is strongly affected by the availability and abundance of food (Pedrini *et al.,* 1995). While the yellow mongoose occurs in a wide range of habitats (Mbatyoti 2012), it prefers open and short grassland vegetation habitats (Skinner and Chimimba 2005), which was also evident in our study. With increasing shrub cover, there is a consequent reduction in the abundance of insects, the main food sources of yellow mongoose (Nel and Kok 1999; Blaum and Rossmanith 2010). The greater occurrence of yellow mongoose in open habitat types may be due to the favourable conditions for obtaining prey, since previous research in this area has shown insects to form the main part of their diet (Cronk and Pillay, 2019). The open habitats dominated by grassland type vegetation might also provide conditions conducive for underground denning (Le Roux *et al.,* 2016); these underground dens were frequently encountered in both estates (per obs.).

As predicted, slender mongoose occurrence was greater in covered areas. While several biotic factors limit the distribution and space use of species, the slender mongoose is reportedly not limited by rainfall and vegetation type and also has a tolerance for a range of habitat types (Smithers 1983; Maddock 1988). Nonetheless, other studies indicate that slender mongoose prefer covered areas with rocky outcrops and associated tree cover, which also supports high densities of their rodent prey (Rood and Wasser 1978; Smithers 1983; Ramesh and Downs 2014); a main component in their diets in the study area (Cronk and Pillay, 2019). The use of cover might also provide protection from aerial predators, as

reported in other small viverrids (Taylor 1975). However, while a pair of resident black eagles occurred at Meyersdal, other large birds of prey were not common here, and incidents of mongoose mortality by raptors were not known in the study area. Another reason for the differences in habitat use could be competitive exclusion. The larger of two competing carnivore species is typically superior (Lesmeister *et al.,* 2015) and subordinate carnivores may shift their habitat use to avoid competition (Mattisson *et al.,* 2011). Maddock (1988) showed that slender mongoose generally avoided open habitats, occurring in covered areas to avoid interactions with the larger Egyptian mongoose *Herpestes ichneumon*, since both species compete for the same food source. Slender mongoose are only slightly smaller than yellow mongoose, so body size alone cannot adequately explain the differences in habitat use.

Within the Eco-Estate, seasonal differences in habitat type use were not apparent as we predicted, even with the availability also of anthropogenic foods. Prey availability and abundance within the Eco-Estate may be more favourable than in the Nature Estate. In contrast, in the Nature Estate, yellow and slender mongoose occurrence during the colder months increased in covered and open habitats respectively. Mongooses did not actively exploit anthropogenic items in the Nature Estate in a previous study (Cronk and Pillay 2018), and therefore utilising different habitat types in colder months may be related to reduced availability of natural food.

Yellow mongoose actively exploit anthropogenic resources and are more habituated to humans (Cronk and Pillay 2018), which may account for their greater presence near human residents in comparison to slender mongoose. The majority of slender mongoose occurrences were located at sites furthest away from residents, particularly in the Eco-Estate, despite relative ease of access to anthropogenic food and other resources. This is possibly due to sites near residents being more open than covered, consequently being more regularly used by yellow mongoose. Furthermore, despite the differences in occurrence at various distances from residents, there was no difference between warm and cold periods in the occurrence of mongoose at different distances from residents.

Studies assessing temporal overlap are largely focussed on species which vary in their diel cycles, being either diurnal or nocturnal (Gerber *et al.,* 2012; Ramesh *et al.,* 2012; Lesmeister *et al.,* 2015; Frey *et al.,* 2017; Karanth *et al.,* 2017), and some report shifts or subtle changes in activity as an adaptation to competition avoidance, habitat disturbances or

resource availability (Norris *et al.,* 2010; Lesmeister *et al.,* 2015; Frey *et al.,* 2017). For example, ring-tailed vontsira (previously mongoose) *Galidia elegans* and broad-striped mongoose *Galidictis fasciata*, which share a similar diet, segregate temporally by being primarily active during dusk/day and night respectively (Gerber *et al.,* 2012). However, in the same study, in the presence of a larger competitor, the small Indian civet *Viverricula indica,* ring-tailed mongoose avoided dusk activity, the preferred activity period of the civet, and the activity of the ring-tailed mongoose was vastly greater at dusk in sites where the civet did not occur (Gerber *et al.,* 2012). In contrast, the activity patterns of yellow and slender mongoose were strictly diurnal in our study. Complete overlap between the two species was potentially reduced by species differences in activity peaks, possibly due to differing foraging times. Maddock (1988) suggested that differences in the activity of prey consumed by similar species should also be considered in the timing of activities, which may also facilitate coexistence. The timing of activity of the main prey of the mongoose in our study area needs to be confirmed to test whether prey activity drives mongoose activity.

Niche partitioning appears evident in the lower spatial overlap between species in the Eco-Estate, although the higher occurrence of yellow mongoose near residents, particularly contributed to the lower spatial overlap, thereby permitting greater temporal overlap. Despite the stronger positive correlation and spatial association (no significant difference in covered habitat use between species and greater spatial overlap), the lower temporal overlap may facilitate coexistence between the two species in the Nature Estate. Moreover, the lower occurrence of mongoose near residents, may account for the greater spatial overlap in Nature Estate in comparison to the Eco-Estate. Taylor (1986) suggested that species overlap is reduced by differences in activity patterns, where foraging at different times may segregate species, which may be evident in our study too; an additional assessment of activity profiles of both species in this study area, noting timing of foraging, may provide further evidence of this.

We specifically investigated spatio-temporal overlap by assessing instances of yellow and slender mongoose occurring in the same place at the same time (or within 10 min of each other). As expected, this was not common. The fact that there were no instances of occurrence in the same place at the same time, and only few instances of occurrences within a 10 min period (0.77% of all occurrences), suggests that resource partitioning, either along the spatial and/or temporal niche, is evident. In contrast, in a previous study in the same population, individuals of both species fed on a reedbuck *Redunca arundinum* carcass at the

same time in winter (Cronk and Pillay 2018). Even so, the majority of these joint feeding occurrences resulted in the slender mongoose aggressively vocalising and lunging towards the yellow mongoose, chasing it away after a short period (Cronk and Pillay 2018). This suggests that under certain conditions, e.g. an abundance of food resources at a large carcass during winter, spatio-temporal overlap is possible for short periods.

In conclusion, we showed that in an urban area, the spatio-temporal ecology of small co-existing carnivores is still strongly influenced by food resources. The combined spatio-temporal overlap has not been widely assessed in coexistence studies, more particularly in urban ares. However, it has been reported that segregation or overlap along the combined spatio-temporal niche does not necessarily emulate the findings of spatial and temporal overlap separately (Karanth *et al.,* 2017), which was also the case in our study. The likelihood of access and the potential to exploit anthropogenic items appears to influence whether resource partitioning along the spatial (including differing habitat and site use) or temporal niche is more apparent in this urban setting, but with low combined spatio-temporal overlap. Future studies would benefit from assessing prey availability and abundance to reiterate the outcomes on prey resources affecting spatio-temporal occurrence.

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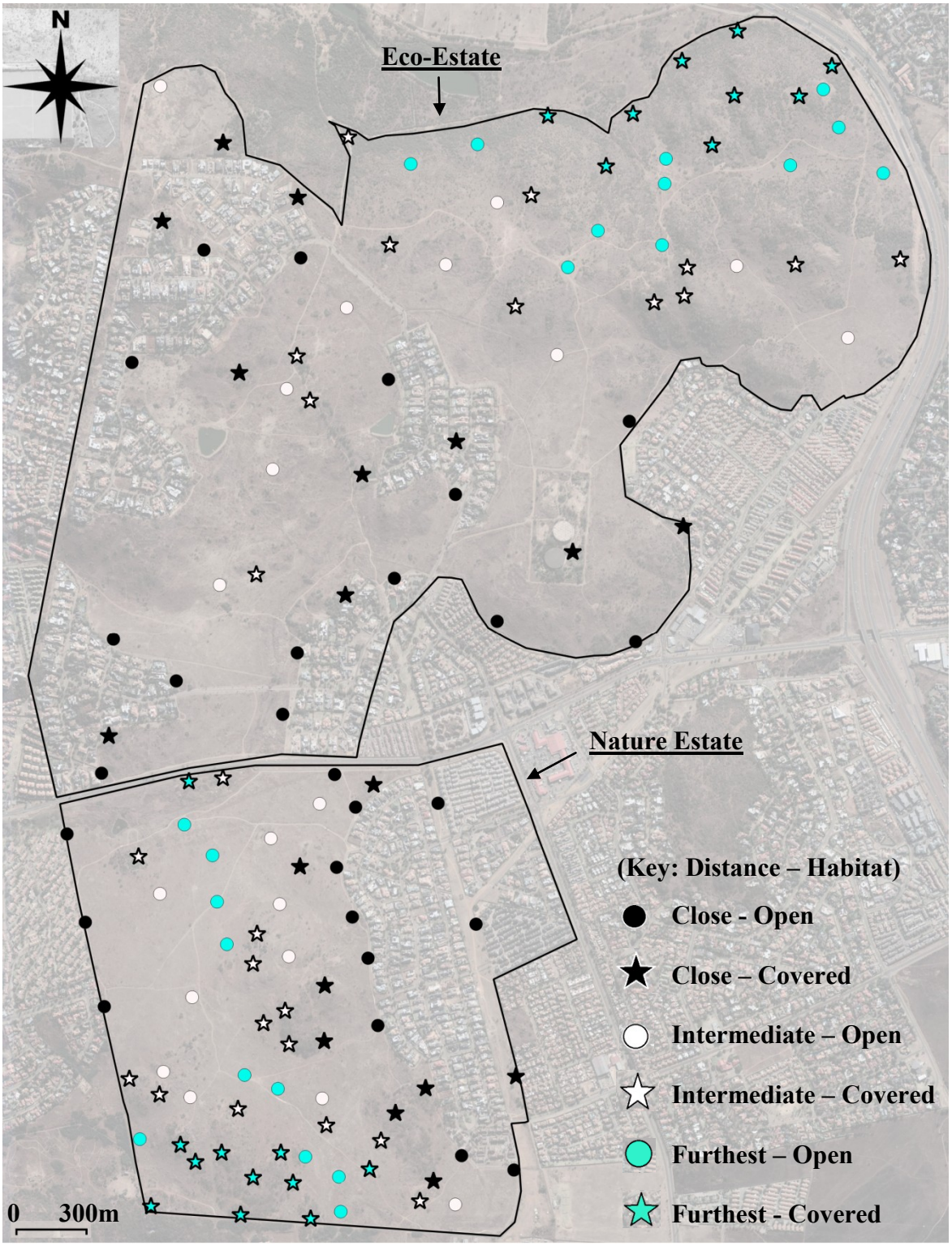

Figure S1. Locations of camera traps in the open and closed habitat categories at varying distances from human residents, in the Eco-Estate (top) and Nature Estate (bottom).

Table S1. Number of sites sampled in the different vegetation types, and various distance from human resident categories

Distance	Eco-Estate		Nature Estate	
	Open	Covered	Open	Covered
Closest	14	10	13	8
Intermediate	10	12	10	13
Furthest	11	9	10	12

Table S2. Outcomes of a linear mixed effects model analysing the predictors of occurrence of mongoose. Test statistics in bold indicate significant predictors of occurrence

Effects and interactions	Occurrence		
	χ^2	*d.f.*	*P*
Estate	**7.43**	**1**	**0.01**
Species	**387.99**	**1**	**<0.001**
Season	0.74	1	0.39
Distance to residents	**24.55**	**2**	**<0.001**
Habitat	0.41	1	0.52
Estate*Species	0.04	1	0.84
Estate*Season	0.001	1	0.98
Estate*Distance	**20.26**	**2**	**<0.001**
Estate*Habitat	0.93	1	0.33
Species*Season	2.90	1	0.09
Species*Distance	**66.84**	**2**	**<0.001**
Species*Habitat	**47.44**	**1**	**<0.001**
Season *Distance	5.16	2	0.08
Season *Habitat	0.001	1	0.97
Distance*Habitat	2.76	2	0.25
Estate*Species*Season	**5.89**	**1**	**0.02**

Estate*Species*Distance	**38.99**	**2**	**<0.001**
Estate*Season*Distance	0.30	2	0.86
Estate*Season*Habitat	0.05	1	0.83
Estate*Species*Habitat	0.85	1	0.36
Estate*Distance*Habitat	0.03	1	0.87
Species*Season*Habitat	**5.94**	**1**	**<0.001**
Species*Season*Distance	0.93	2	0.63
Season*Distance*Habitat	0.79	1	0.38
Species* Distance*Habitat	**13.97**	**2**	**<0.001**
Estate*Species* Season*Distance	3.21	2	0.20
Estate*Species*Season*Habitat	**11.91**	**1**	**<0.001**
Estate*Species*Distance*Habitat	**3.93**	**1**	**0.05**
Estate*Season*Distance*Habitat	0.01	1	0.98
Species*Season*Distance*Habitat	0.83	1	0.36

d.f. – degrees of freedom

Table S3. Relative abundance of the yellow mongoose and slender mongoose over the entire study period, and per season, within the Eco-Estate and Nature Estate

Season	**Eco-Estate**		**Nature Estate**	
	Yellow	Slender	Yellow	Slender
Overall	139.50	22.19	138.09	11.69
Cold	147.62	21.16	143.92	13.49
Warm	133.88	22.89	132.23	10.44

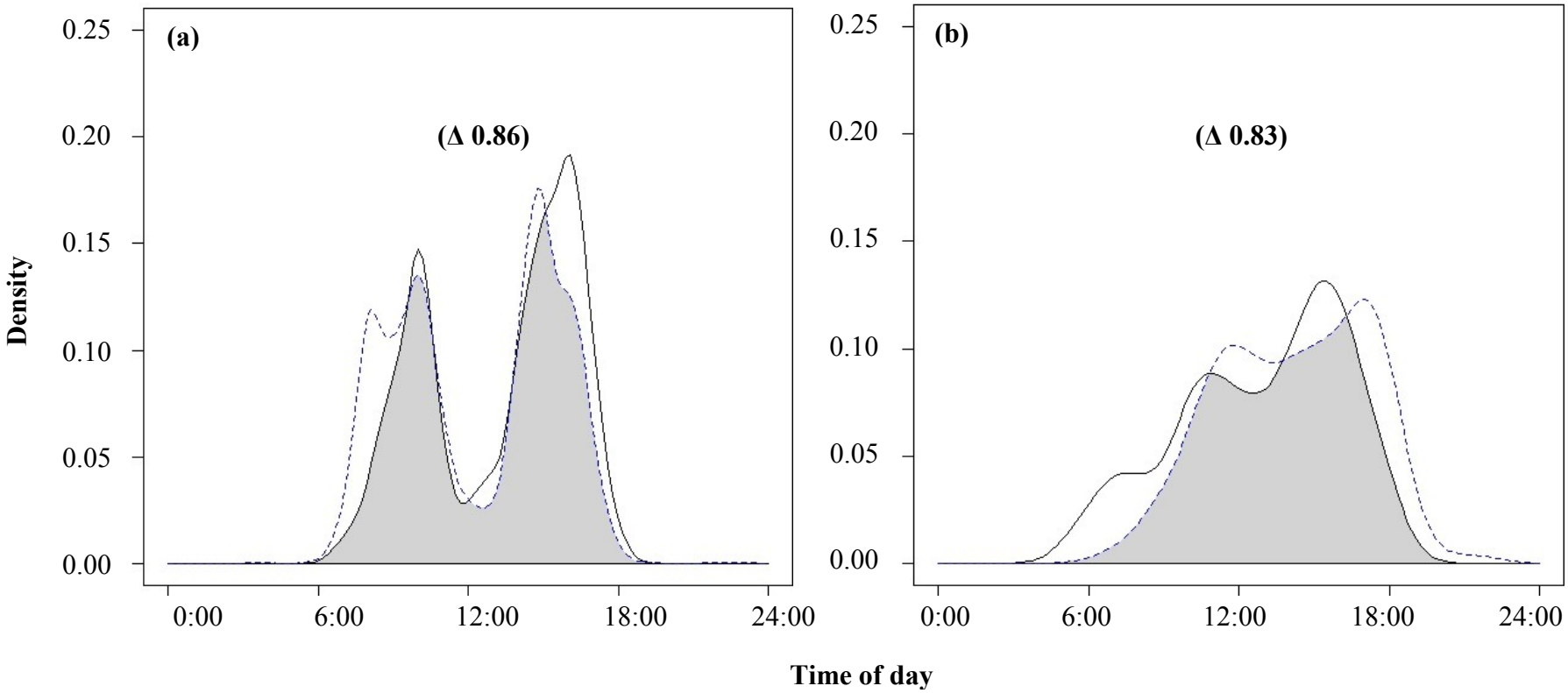

Figure S2. Temporal overlap of (a) yellow mongoose and (b) slender mongoose activity patterns in the Eco-Estate (solid line) and Nature Estate (dashed line). The overlap coefficient (Δ) is the area under the minimum of two density estimates (indicated by the grey area below curves).

CHAPTER FIVE

Home range and space use of yellow mongoose C*ynictis penicillata* in an urban environment

ABSTRACT

Urban areas provide small carnivores with an abundance of resources and reduced predation risk, resulting in higher population densities and greater survival rates, in comparison to more natural areas. Animals thriving in urban areas tend to have greatly reduced home range sizes in response to increased resource availability. I investigated the home rage size of yellow mongoose *Cynictis penicillata* in an urban area and the extent to which their home ranges overlapped with human residential gardens. I assessed the home range sizes of 8 collared and GPS tracked individuals in two residential wildlife estates in Meyersdal, South Africa: an Eco-Estate which was a built up residential area interspersed with natural areas; and a Nature Estate with reduced contact between animals and human residents. I used three methods to calculate home range size at the 50%, 95% and 100% isopleth levels, namely Minimum Convex Polygon (MCP), Kernel Density Estimates (KDE) and Local Convex Hull (LoCoH). There were no significant differences in the results produced by all methods, with the exception that the core area measured by LoCoH was significantly smaller than the MCP and KDE methods. I found no statistically significant difference in home range size between estates or sexes, but home range sizes were slightly larger in the Nature Estate, and male home ranges were larger than those of females. Compared to previous studies in the species, home range sizes according to all methods were considerably smaller. Seasonal variation in home range could not be statistically compared, but similar to non-urban populations, I observed smaller home range sizes during the breeding season (winter and spring) and larger sizes during the non-breeding season (autumn and summer). Overlap with human residents was evident in both estates but to a greater extent in the Eco-Estate, and seasonal overlap with residents was greatest during autumn and winter. Our study shows that yellow mongoose modify their home ranges in response to urbanisation, which might be a consequence of abundant and easily accessible available resources, particularly during colder periods.

Key words: *home range size, resource availability, urbanisation, yellow mongoose*

Introduction

Expanding urbanisation is a continuing threat to biodiversity, fragmenting and diminishing natural habitats available for wildlife (Gould and Andelt , 2013; Šálek *et al*., 2015). While wildlife faces new challenges in these changing environments, some species succeed in urban areas, resulting in increased population densities, primarily as a result of readily available resources and reduced predation pressure (Gehrt *et al*., 2009; Mc Kinney 2008; Bateman and Flemming, 2012). Urban adapters and exploiters are typically species' that modify aspects of their behaviour, diet, and habitat use in order to flourish in urban areas (Bateman and Flemming, 2012; Fuller *et al*., 2010). This is particularly true for several small-medium sized carnivores, all predominantly omnivorous, that are able to exploit anthropogenic food sources (Riley 2003), such as red fox *Vulpes vulpes* and Eurasian badger *Meles meles* (Young *et al*., 2015), stone marten *Martes foina* (Herr 2008), and coyote *Canis latrans* (Gehrt 2007; Poessel *et al*., 2013).

The ecology of urban wildlife is a growing area of study, and understanding how anthropogenic forces drive changes in species' biology is crucial for management and conservation of these species (Gehrt *et al*., 2009; Šálek *et al*., 2015). An essential aspect of previous urban ecology research includes the effects of urbanisation and concomitant changes on the home ranges of urban wildlife in comparison to their non-urban counterparts (Šálek *et al*., 2015). An animals' home range can vary greatly within and between species, and is determined by a range of factors, such as population density, sex, and body size, food availability, and suitable habitat availability (Gehrt and Fritzell, 1997; Dahle *et al*., 2006; Gould and Andelt 2013; Sanchez and Hudgens, 2015; Walton *et al*., 2017).

Several studies have shown that carnivores occupying human-altered landscapes typically have smaller home range sizes than those occurring in more natural areas (Randa and Yunger, 2006; Herr 2008; Riley *et al*., 2010; Bateman and Flemming, 2012; Walton *et al*., 2017). For example, bobcats *Lynx rufus* in more urbanised zones had home range sizes 2-4 times smaller than those in more rural zones (Riley 2003). Similarly, rural forest dwelling stone martens had an average home range size of 361 ha (Genovesi *et al*., 1997) compared to 74.8 ha of their urban dwelling counterparts (Herr 2008). Home range sizes of red foxes was 3-4 times smaller in areas with a greater percentage of human impact compared to those with little to no human presence (Walton *et al*., 2017). This decrease in home range size in the species listed above has been largely attributed to the relative ease of finding food and shelter, thus eliminating the need to cover a large area to meet energetic requirements (Gehrt

and Fritzell, 1997; Gould and Andelt, 2013). Furthermore, with increasing population densities of wildlife in urban areas (Šálek *et al*., 2015), the likelihood of encountering a mate is greater, thereby negating the need of a large home range to find a mate, particularly for males (Gehrt and Fritzell, 1997).

The yellow mongoose *Cynictis penicillata* is endemic and widespread throughout Southern Africa, including urban areas (Cronk and Pillay, 2018), inhabiting scrub and open grassland habitats (Blaum *et al*., 2007), is diurnal (Skinner and Chimimba, 2005; Mbatyoti 2012), and primarily insectivorous (Nel and Kok, 1999; Cronk and Pillay, 2018). It is relatively small and males are slightly heavier (± 790 g and a body length of ±563 mm) than females (± 734 g and a body length of ±554 mm; Skinner and Chimimba, 2005; Mbatyoti 2012). The mating period begins in early July and, following an average of 42-62 day gestation period, offspring are born from August (commonly mid-October), but this can extend until March as females can produce two litters in the same breeding season (Zumpt 1976; Rasa *et al.*, 1992; Balmforth 2004; Mbatyoti 2012). Litters vary between 2 and 5 pups (Rasa *et al*., 1992). The species has a cooperative breeding system, whereby non-breeding members of a group feed and care for young (Rasa *et al.,* 1992; Balmforth 2004). The yellow mongoose has also been observed to bring large prey back to young at dens, typical of social felids and canids but not of other herpestids (Rasa *et al*, 1992; pers obs).

Home range sizes of the yellow mongoose have been recorded as a minimum of 26 ha (Balmforth 2004) and a maximum of 250 ha (mean of 70 ha; Taylor and Meester, 1993; Le Roux 2008; Mbatyoti 2012), with male home ranges being more than twice that of the females home ranges (Zumpt 1976; Mbatyoti 2012). Home range sizes vary seasonally, with both sexes reducing home range sizes during colder periods (Mbatyoti, 2012). Male home ranges overlap with those of other males but not in their core use area (Cavallini 1993). In addition, the home ranges of males typically include those of their offspring (Le Roux 2008) and of several females; however, females from different dens have non-overlapping home ranges (Cavallini 1993). No previous studies have investigated the effects of urbanisation on the home range size, nor have any determined the spatial distribution, of the yellow mongoose in an urban area, particularly overlap with human residential areas.

I investigated the home range size, as well as the overlap of home ranges with human residential areas, of yellow mongoose inhabiting two ecological estates in an urban area (Meyersdal Nature Area) in Johannesburg, South Africa. Field work was conducted in a

Nature Estate, where houses were separated from wildlife by palisade fences, reducing contact with humans and homes (but still permeable to mongoose) and an Eco-Estate where wildlife openly utilise corridors between houses and enter household gardens (Cronk and Pillay, 2018).

Using data obtained from radio-collared individuals, I made 4 predictions, 1. (a) Home range sizes of mongoose in the Eco-Estate (more urbanised) would be smaller than those in the Nature Estate (less urbanised). (b) Home range sizes of these mongoose would be smaller than those recorded in non-urban populations. 2. In both estates, home ranges of males would be larger than those of females, consistent with what has been observed in naturally occurring yellow mongoose. 3. In the Nature Estate, home range size would vary monthly/seasonally, being smaller during colder periods in order for mongoose to conserve energy due to less abundant prey (Cronk and Pillay, 2018). In the Eco-Estate, I did not predict home range sizes to vary since home ranges were expected to include anthropogenic food resources year round, which yellow mongoose prefer over naturally occurring insects (Cronk and Pillay, 2018). 4. (a) Overall, overlap with human residential areas would be greater in the Eco-Estate than in the Nature Estate. (b) I predicted overlap with human residential areas to be greatest during colder periods/months since the yellow mongoose were expected to make greater use of these resources during colder periods.

Materials and methods

Study site

The study was conducted between March 2016 and April 2018 in two ecological estates in the South of Johannesburg, South Africa. Field work took place within the Meyersdal Eco-Estate (26°17'10.4"S 28°05'14.7"E) and Nature Estate (26°17'32.1"S 28°05'23.2"E), which are separated by a double lane tarred main road. Both estates enclose a grassveld habitat with numerous mammal game species as well as less abundant small carnivores, including serval *Leptailurus serval*, black-backed jackal *Canis mesomelas* and Cape fox *Vulpes chama*. The yellow mongoose is the most abundant carnivore in the Meyersdal Nature Area (pers. obs.). The human residential area in the Meyersdal Eco-Estate (26°17'10.4"S 28°05'14.7"E; 480ha) is scattered within the nature area where animals frequently come into contact with humans. The Nature Estate (26°17'32.1"S 28°05'23.2"E; 300ha) is smaller where the nature area is separated from the residents by palisade fencing.

Trapping and collaring

Between 2016 and 2017, I captured and equipped 8 yellow mongoose with GPS tracking collars. Collars were manufactured by Africa Wildlife Tracking (HAWK-UHF device, AWT CC, Pretoria, South Africa), weighed between 65g and 85 g, and were designed with an easy release point that would break when snagged. All animal capture and handling procedures were approved by the Animal Ethics and Screening of the University of the Witwatersrand (2015/08/37/B).

I used single-door humane animal traps (80x29x33 cm - constructed from high tensile galvanised wire mesh) placed at independent sites (different regions of the estate approximately 1 km apart) in an attempt to avoid capturing individuals that are likely to congregate in social groups, which would result in spatial correlation between individual mongooses. Traps were camouflaged as best as possible with the surrounding vegetation, and set out in the early morning before mongoose activity was expected to start (Chapter 4). Using information obtained in a pilot study, traps were baited with off-cut deli meats and provided with water. Traps were checked every hour to ensure that a trapped mongoose did not become stressed by spending too much time in the trap. During trap checks, traps were re-baited if the bait had dried out or if it was removed by animals without triggering the trap door. Non-targeted animals that were captured, such as the rock hyrax *Procavia capensis*, were released and traps reset.

When a yellow mongoose was trapped, traps were covered with a dark towel to reduce any further distress to the mongoose, and the cage and mongoose were transported to an isolated and shaded site in each estate where the collaring process took place. The mongoose was immobilized using a dosage of 0.06 ml/kg Medetomidine and 6mg/kg Ketamine, which was administered intramuscularly by Dr Jill Drake, a registered veterinarian. Following a period of approximately 20 min, to ensure the animal was fully anaesthetized, various data and measurements were recorded before fitting the collar. These measurements included sex, weight (in g), and body (nose to tip of tail) and tail lengths (in mm). Mongoose were assigned an age class (adult/sub-adult) based on tooth wear and colouration (Herr 2008; Mbatyoti 2012; Walton *et al*., 2017). Mongoose were collared if the collar weighed less than 15% of body weight, otherwise they were released at the point of capture. Once the collar was fitted, the mongoose was returned into the trap, and an anaesthetic reversal of 0.3 mg/kg Atipamezole was administered. The veterinarian monitored

when the mongoose was mobile again in order to assess whether there was any discomfort or distress from the collar. They were subsequently released at the site of capture. The study was conducted over a two-year period.

Tracking

Yellow mongoose are diurnal, and I did not expect them to be active outside their dens in the evening (Chapter 4). Thus, to extend battery life of the collars. I selected a 3-hour interval for recording of GPS locations between 5am and 7pm. To collect data from the collars, I located collared individuals by means of the triangulation method, using a hand-held H antenna (AWT CC, 433 MHz), and a portable VHF receiver (HAWK 433 MHz transceiver, AWT CC). Each collar had a reception range of ±1km, and data could be downloaded from within a ±50m range of a collared mongoose. Tracking took place on foot. All GPS fixes were automatically stored on the collar, which required a single download from the receiver every 2 weeks. The receiver was connected to a computer and GPS coordinates were then downloaded for later analysis.

Estimation of home range size

Home range size was classified by the area navigated by each collared mongoose while engaging in daily activities. Home range size was established using three methods: Minimum Convex Polygon (MCP), Kernel Density Estimates (KDE), and Local Convex Hull (LoCoH) using the 'adehabitatHR' package in R. The MCP method constructs polygons by connecting the outermost locations with straight lines (Herr 2008). This often includes areas rarely visited, particularly at the 100% isopleth, incorporating outliers that may overinflate home range size in comparison to the other methods (Rautio *et al*., 2013). These outliers at the 100% MCP may include use of residential areas, which is particularly important for urban animal studies (Riley 2006), and was thus included in our analyses. The MCP was also useful in calculating the home range size of urban coyotes by including important areas excluded from other analyses (Poessel 2015). While this estimator has been criticized for many reasons (such as that high use areas cannot be distinguished, and it may overinflate home range size by including locations used infrequently), it is the most widely used method and is thus useful in comparisons with previous home range studies, including those of yellow mongoose (Herr 2008; Mbatyoti 2012; Rautio *et al*., 2013; Poessel 2013)

The kernel density estimates (KDE) method calculates a home range based on the 'utilisation distribution' and produces isopleths defining the area that contains a specific percentage of the overall density distribution of location points (Balmforth 2004). While widely recommended, the KDE has also been criticized for its requirements of parameters that need to be set by the user, such as the bandwidth selection/smoothing parameter (*h;* Harless *et* al., 2010; Lichti and Swihart, 2011; Gould and Andelt 2013). While 'least-squares cross validation' is most commonly chosen bandwidth selection (h_{lscv}; Germain *et al*., 2008), it is predominantly used in studies using VHF collar data (Walter *et* al., 2011), and problems have been encountered with GPS data (Hemson *et al*., 2005). Authors caution against this method as the risk of failure of h_{lscv} in determining home range size also increases when the distribution of GPS locations contain a tight cluster of points, and for more than 150 GPS data points (Walter *et al*., 2011; Hemson *et al*., 2005), which was common in our study. I therefore selected the default *ad hoc* method for the smoothing parameter (Calenge 2006), which has been shown to outperform other parameter selections (Kie 2013). Because this method produces contours based on location density, the 100% isopleths cannot be calculated, since the 100% contours generated would be infinite (Balmforth 2004); this might be why the majority of studies generally report only 95% KDE (Gilchrist and Otali, 2002). The kernel method is useful for identifying areas that are of importance to individuals, and reveals finer details of utilization distribution patterns (Hemson *et* al., 2005; Harless *et* al., 2010; Chirima and Owen-Smith, 2017), and many researchers consider its accuracy and prefer this method (Powell 2000). It may also be useful in assessing home range in fragmented urban areas, since it allows for the detection of detached areas of activity (Grinder and Krausman, 1998).

The LoCoH method takes a different approach by establishing vectors between each of the GPS points in a dataset as well as with *x*-number of nearest neighbours in such a way that the length of the vectors equals a specific value (Getz *et al*., 2007). Once all of the vectors have been established, the resultant area delimited by the points involved is merged to construct a single polygon (Getz *et al*., 2007). The LoCoH method demands large sample sizes to adequately estimate home range size, and has also been shown to underestimate home range size (Adam *et al*., 2015; Gregory 2017). This method takes into account hard boundaries, such as roads or rocky outcrops (Getz *et* al., 2007; Lichti and Swihart 2011; Walton *et al*., 2017), which may include areas not/infrequently used by animals (which other estimates may account for).

The kernel method has been shown to have the best fit for home range data than estimators derived by polygon methods (Walter *et al*., 2011), while more recently, other studies found the LoCoH preferable (Chirima and Owen-Smith, 2017; Stark *et al.,* 2017; Walton *et al*., 2017). Both KDE and LoCoH reportedly better define home range boundaries than the conventional MCP (Lichti and Swihart, 2011). However, MCP has been found to be more accurate than KDE when sample sizes were small (Boyle *et al*., 2009) and MCP is useful in assessing monthly and seasonal home range sizes (Grueter *et al*., 2009). Because each of the three methods has its own advantages and disadvantages, it is recommended to use multiple methods of analysis and to compare the consequent results (Chirima and Owen-Smith, 2017; Gregory 2017). All three methods were employed here, measuring the 50% and 95% isopleths to delineate core use area and home range size respectively. Core use areas are described as the areas encompassed by the home range that are used most intensively (Balmforth 2004). The 100% isopleths (total space use) were also considered for comparison between methods and with previous studies.

Home range overlap with residents

Home range overlap with human residential areas of each mongoose was determined by calculating the percentage of GPS fixes located within residential gardens, as well as assessing the percentage of the mapped home range polygons (from MCP) that overlapped with residential areas (houses; Herr 2008).

Data analysis

All GPS data were downloaded from the receiver and recorded in Microsoft Excel® (Microsoft Corporation, 2007). Statistical analyses were conducted using R Statistical Software (www.r-project.org, R version 3.4.3).I established the home range size for each mongoose by calculating 50%, 95% and 100% isopleths, according to all three methods (MCP, KDE, LoCoH) using the R package adehabitatHR (Calenge 2006). When I calculated 100% KDE, the model did not converge and subsequently unrealistically large home range sizes were generated, and were hence not included in analyses (see Balmforth 2004).

I ran several general linear models (lmer) in R for statistical analysis of the predictors of home range size for each method. The models comprised of Estate and Sex as first order effects and an Estate*Sex interaction effect; models were run individually for each method

and at each isopleth level (8 models in total). Fisher's post-hoc tests were used to identify differences in the fixed predictors. Since sampling took place at different periods in two years, sampling intervals were unbalanced among individuals (i.e. individuals were not all sampled in all seasons); thus, season was not included in these models. I then compared home range sizes among the different methods using paired t-tests to determine significant differences in home range estimation methods. I compared male and female home range size (without factoring in estate in order to assess the yellow mongoose population as a whole), using two-sample t-tests in order to compare female and male home range sizes to other studies on non-urban yellow mongoose. Because season was not included in the statistical models, I plotted monthly home range sizes for each mongoose instead. I then calculated the rate of change of home range size from month to month using the monthly results of all three methods in order to establish temporal variation in home range size:

$$\sum_{n-1}^{n} \frac{t_2 - t_1}{(t_1 + t_2)}$$

- n = total number of months sampled per mongoose
- t = each month sampled

The resultant rate of change was then divided by the number of months sampled to determine an average monthly rate of change per individual. Furthermore, for comparison with previous studies, I compared home range sizes by season sampled for each mongoose separately by grouping the months sampled for each individual into seasons. Seasons were identified as Spring - September to November, Summer – December to February, Autumn – March to May, and Winter – June to August.

Overlap with human residents was assessed as the percentage of GPS locations found within residential areas, as well as the percentage of the home range polygons (MCP 50%, 95% and 100%) overlapping with residents (Herr 2008). I used general linear models to assess whether Estate and Sex were significant predictors of the percentage of overlap with residents. This was further assessed between seasons to establish variation in use of residential areas per individual mongoose. Since images generated for the KDE method display utilization distribution, these were used to visually identify any shifts in the density of locations with use of residential areas between seasons. MCP polygons (50%, 95% and 100%) and kernel density estimate images (showing utilization distribution of the 50% and 90%) were generated using R, and graphically represented using Quantum GIS (QGIS 3.2 Bonn; http://www.qgis.org).

Results

Home range size

I collared two male (1 adult, 1 sub-adult) and two female (both adult) yellow mongoose in the Eco-Estate, and three male (1 sub-adult, 2 adult) and one female (adult) yellow mongoose in the Nature Estate (Table S1). Mean body mass and sizes (±SE) were 842 (43.94) g and 34.72 (0.79) cm, and 814 (64.51) g and 35.85 (0.35) cm for males and females respectively (Table S1). While I had aimed to capture 2 individuals of each sex in each estate, it proved difficult to capture a second female in the Nature Estate. Unexpectedly, in the Nature Estate, two males inhabiting the same den were captured and collared (Nm1 and Nm3; Figure 1). From March 2016 to April 2018, the 8 yellow mongoose were tracked for periods varying from 3 to over 5 months. The fate of the collared animals was not known, with the exception of two individuals which were seen at dens without their collars. Re-capturing of mongoose was attempted, but mongoose were reluctant to enter cages for removal of collars. Due to the easy release point on collars fitted by the manufacturers, it was expected that the wear on this point of all collars caused release of collars in all instances.

On average, 373 ± 23 GPS locations (location error estimate of 2-3 m) were recorded per mongoose (Table S1), which exceeded the required minimum of 50 location points for home range estimation for yellow mongoose considered by Le Roux (2007), and also a sufficient number of fixes to assess yellow mongoose home ranges, which stabilize at 100 – 250 location points (Balmforth 2004). These GPS locations were used to plot the MCP home range polygons for each collared mongoose (Figure 1) as well as represent the utilization distribution of locations by the KDE method (Figure S1).

Home range size varied considerably between different home range estimators (Table 1). The MCP core use (50%) and home range size (95%) estimates were significantly larger than the corresponding KDE estimates (paired t-test, 50% : $t_7 = 4.15$, $p = 0.004$; 95% : $t_7 = 4.35$, $p = 0.003$), and LoCoH estimates (paired t-test, 50% : $t_7 = 5.81$, $p < 0.001$; 95% : $t_7 = 3.71$, $p = 0.008$); while MCP and LoCoH were similar in estimating total space used (paired t-test, 100% : $t_7 = 1.36$, $p = 0.215$). KDE estimates were significantly greater than LoCoH at the 50% level ($t_7 = 5.39$, $p = 0.001$) and 95% level ($t_7 = 3.23$, $p = 0.015$).

The total home range size (MCP and LoCoH 100%) ranged from 8.56 to 26.09 ha, with an average of 14.94 ± 4.11 ha in the Eco-Estate, and 2.15 to 30.29 ha with an average of

20.59 ± 3.62 (MCP) and 19.70 ± 3.98 ha (LoCoH) in the Nature Estate (Table 1). The 100% home range of the mongooses did not overlap (Figure 1), except for a slight overlap in the 100% MCP of two males from the different estates (Em1 and Nm2; Figure 1), evidence that mongoose sometimes move between the two estates. The 95% home range size ranged from 4.06 to 19.09 ha with an average of 10.88 ± 2.83 ha (MCP), 9.93 ± 2.74 ha (KDE) and 8.61 ±3.02 ha (LoCoH) in the Eco-Estate, and 17.59 ± 2.90 ha (MCP), 15.16 ± 2.48 ha (KDE) and 10.36 ± 1.77 ha, in the Nature Estate (Table 1). The core use areas were located around the known den sites (Figure 1). Core home ranges (50%) were smallest according to the LoCoH method, and ranged from 0.04 to 5.99 ha, with an average of 3.05 ± 1.01 ha (MCP), 2.55 ± 0.76 (KDE), and 0.15 ± 0.07 ha (LoCoH) in the Eco-Estate, and 0.04 to 5.53 ha, with an average of 3.92 ± 0.73 ha (MCP), 2.65 ± 0.73 ha, and 0.15 ± 0.07 ha (LoCoH) in the Nature Estate (Table 1).

Table 1. Home range sizes from three estimates (MCP, KDE, LoCoH) of individual male (m) and female (f) yellow mongoose in the Eco-Estate (E) and Nature Estate (N).

Mongoose identity	Tracking duration in days (no. of fixes)	Home range size (ha)							
		MCP			KDE		LoCoH		
		50%	95%	100%	50%	95%	50%	95%	100%
Em1	110 (299)	2.77	10.13	16.17	2.32	8.76	0.27	8.59	16.16
Ef1	113 (309)	1.63	7.42	8.93	1.43	6.76	0.04	4.06	8.93
Em2	152 (445)	5.99	19.09	26.09	4.76	17.98	0.23	17.17	26.08
Ef2	162 (486)	1.81	6.9	8.57	1.69	6.23	0.04	4.62	8.54
Nm1	139 (354)	5.53	20.31	21.04	4.15	17.46	0.13	13.9	21.02
Nm2	125 (335)	4.77	24.48	30.29	3.60	20.97	0.33	12.19	30.27
Nm3	137 (391)	2.8	12.62	13.16	1.15	10.15	0.08	5.80	12.15
Nf1	129 (368)	2.58	12.95	17.87	1.68	12.06	0.04	9.52	15.33

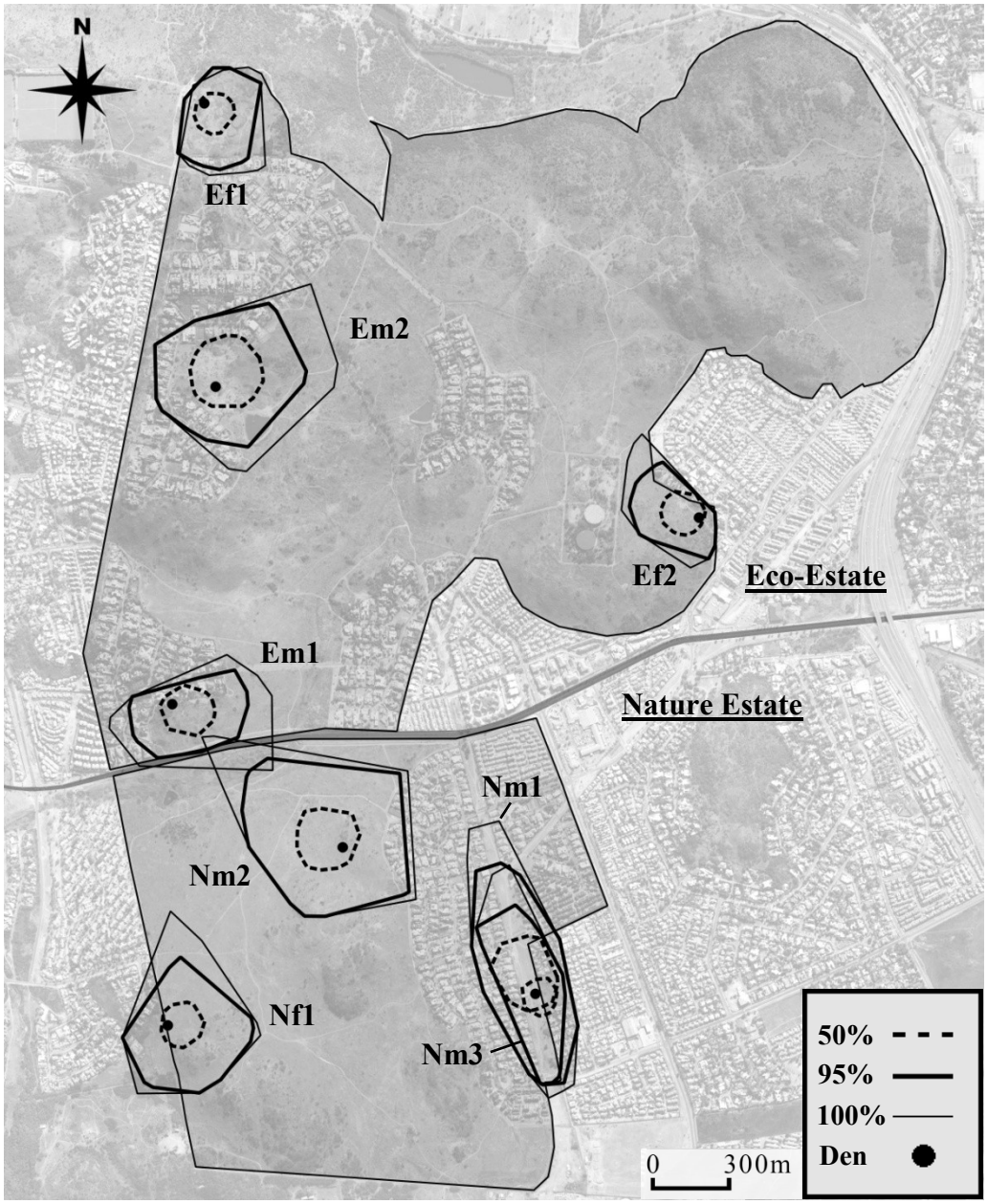

Figure 1. MCP home range (50%, 95% and 100%) plots of 8 yellow mongoose overlaid on aerial maps of the Eco-Estate and Nature Estate, separated by a double lane tarred road.

The results of general linear models (Table 2) revealed that Estate, Sex and Estate*Sex were not significant predictors of home range size according to the MCP method (50%, 95% and 100%; Figure 1), KDE method (50% and 95%) and LoCoH method (50%, 95% and 100%). While male and female mongoose home range sizes in the Nature Estate appeared to be larger than the corresponding sex in the Eco-Estate, all models indicated that estate and sex had no apparent effect on home range size. Overall, while not significant, all

home range size estimates of male mongoose in the Eco-Estate were larger than those of female mongoose in the Eco-Estate, and this was also evident for the most part in the Nature Estate; however, the females had slightly larger home range sizes than that of the sub-adult in the Nature Estate (Nm3; Table 1).

Table 2. Outcomes of General Linear Models analysing the predictors of home range size of yellow mongoose for three estimates (MCP, Kernel, LoCoH). No analysis was done for the 100% KDE because this could not be computed.

Effects and interactions	Home range size estimate								
	50%			95%			100%		
	F	*df*	*P*	*F*	*df*	*P*	*F*	*df*	*P*
				MCP					
Estate	0.13	1	0.73	1.62	1	0.27	0.79	1	0.43
Sex	3.69	1	0.13	2.83	1	0.17	2.24	1	0.21
Estate*Sex	0.14	1	0.73	0.02	1	0.88	0.67	1	0.46
				KDE					
Estate	0.04	1	0.85	1.16	1	0.34			
Sex	2.27	1	0.21	2.01	1	0.23			
Estate*Sex	0.10	1	0.76	0.12	1	0.74			
				LoCoH					
Estate	0.25	1	0.64	0.20	1	0.68	0.35	1	0.59
Sex	5.93	1	0.07	2.17	1	0.21	2.66	1	0.18
Estate*Sex	0.22	1	0.66	1.29	1	0.32	0.35	1	0.59

Male vs. female home range size

Removing the Estate from the analyses, male yellow mongoose home range sizes were generally almost twice as large as those of female yellow mongoose for all methods (Table 2), but this difference was not significant for the majority of methods used (Table 3). Statistical significance was apparent in the core home range sizes (50%) according to the

MCP and LoCoH method, with males having significantly greater home range size than female, but this difference was not evident according to the KDE method.

Table 3. Mean (±SE) home range sizes (in hectares) based on three estimates (MCP, Kernel, LoCoH) for three isopleths, of yellow mongoose in the Meyersdal Nature Area. Test statistics in bold indicate significant differences in home range size between female and male mongoose.

Method	Mean (±SE) home range size		*t-value*	*df*	*P*
	Female	Male			
MCP 50%	**2.01 (0.29)**	**4.37 (0.68)**	**-2.55**	**6**	**0.04**
MCP 95%	9.09 (1.94)	17.33 (2.62)	-2.19	6	0.07
MCP 100%	11.79 (3.04)	21.35 (3.13)	-2.02	6	0.09
KDE 50%	1.64 (0.11)	3.19 (0.65)	-1.79	6	0.12
KDE 95%	8.35 (1.86)	15.07 (2.38)	-1.95	6	0.09
LoCoH 50%	**0.04 (0.00)**	**0.21 (0.05)**	**-2.75**	**6**	**0.03**
LoCoH 95%	6.07 (1.73)	11.53 (1.99)	-1.86	6	0.11
LoCoH 100%	10.94 (2.19)	21.15 (3.27)	-2.19	6	0.07

Monthly variation in home range size

The general patterns for the increase or decrease in home range size by individual mongoose on a monthly basis was similar for all estimate methods (Figure 2, Figure 3). The rate of change in home range size for each mongoose showed that, with the exception of Em2, all isopleths were also consistent with either an increase or decreasing rate of change (Table 4); the highest variability in home range sizes was observed according to the KDE method. Overall, there was greater variability in monthly home range size within the Nature Estate compared to the Eco-Estate. Within the Eco-Estate, female mongoose showed greater variability in home range size than males; this could not be established for the Nature Estate due to only one female being collared in the Nature Estate. Mongoose that were tracked

during months that included March/April to July/August (Em1, Ef1, Nm1, and Nm2) showed a decrease in monthly home range size, and an overall decreasing rate of change, while the remaining individuals sampled showed a general increase in home range size (Figure 2 , Figure 3) and rate of change (Table 4). The seasonal home range sizes generated using all three estimates is presented in Table S3, showing similar patterns evident across the three estimates. For example, according to the 95% MCP method, seasonal home range sizes revealed that for females, home ranges sizes in spring were the smallest (mean = 1.76 ha), followed by winter (3.11 ha), summer (4.27 ha) and then autumn (7.51 ha), while for males, winter was the smallest (9.02 ha), followed by, summer (11.86), spring (12.14 ha) and then autumn (13.69 ha; Table S3).

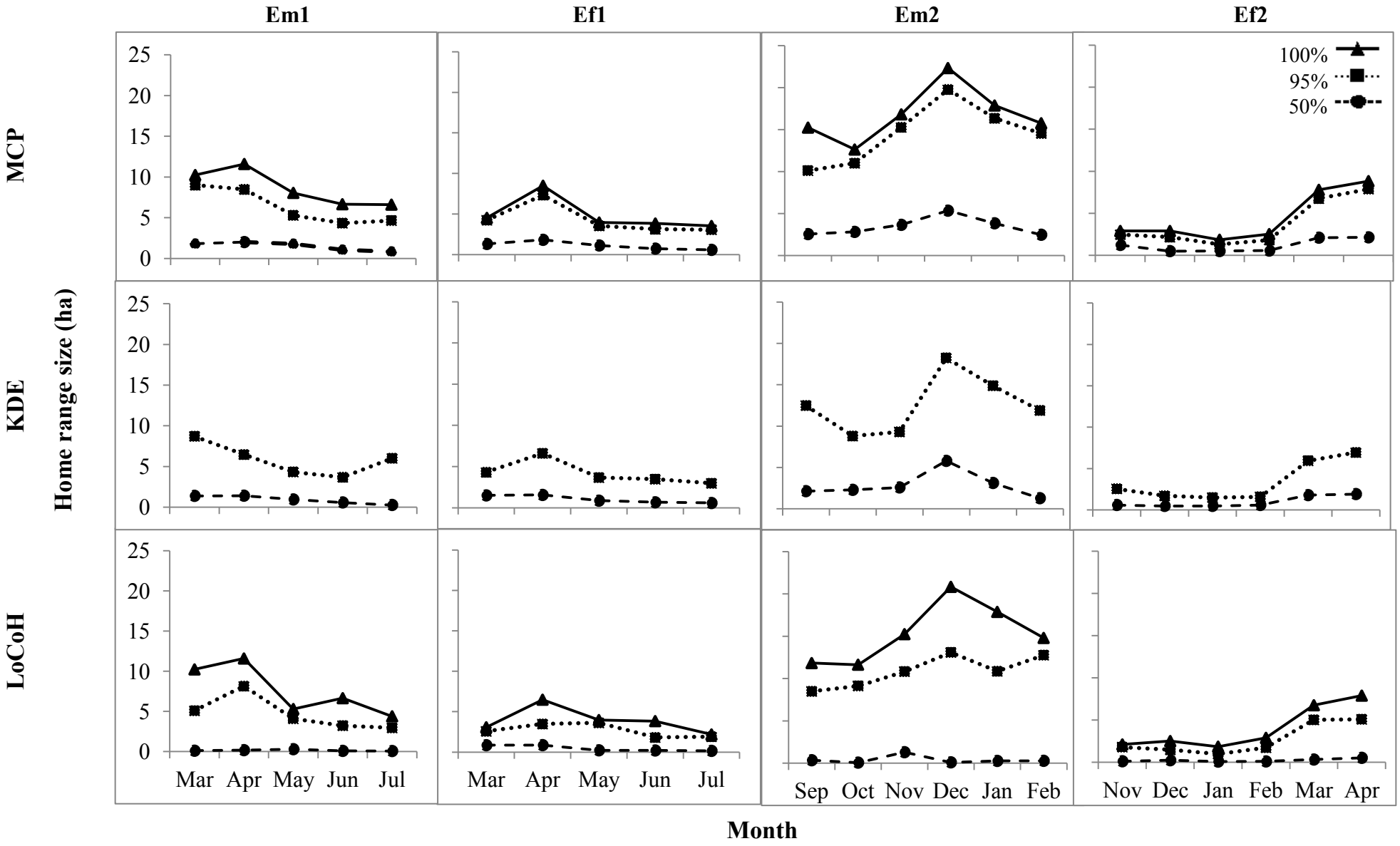

Figure 2. Monthly home range sizes, derived from three estimates (MCP, KDE, LoCoH), of each mongoose within the Eco-Estate.

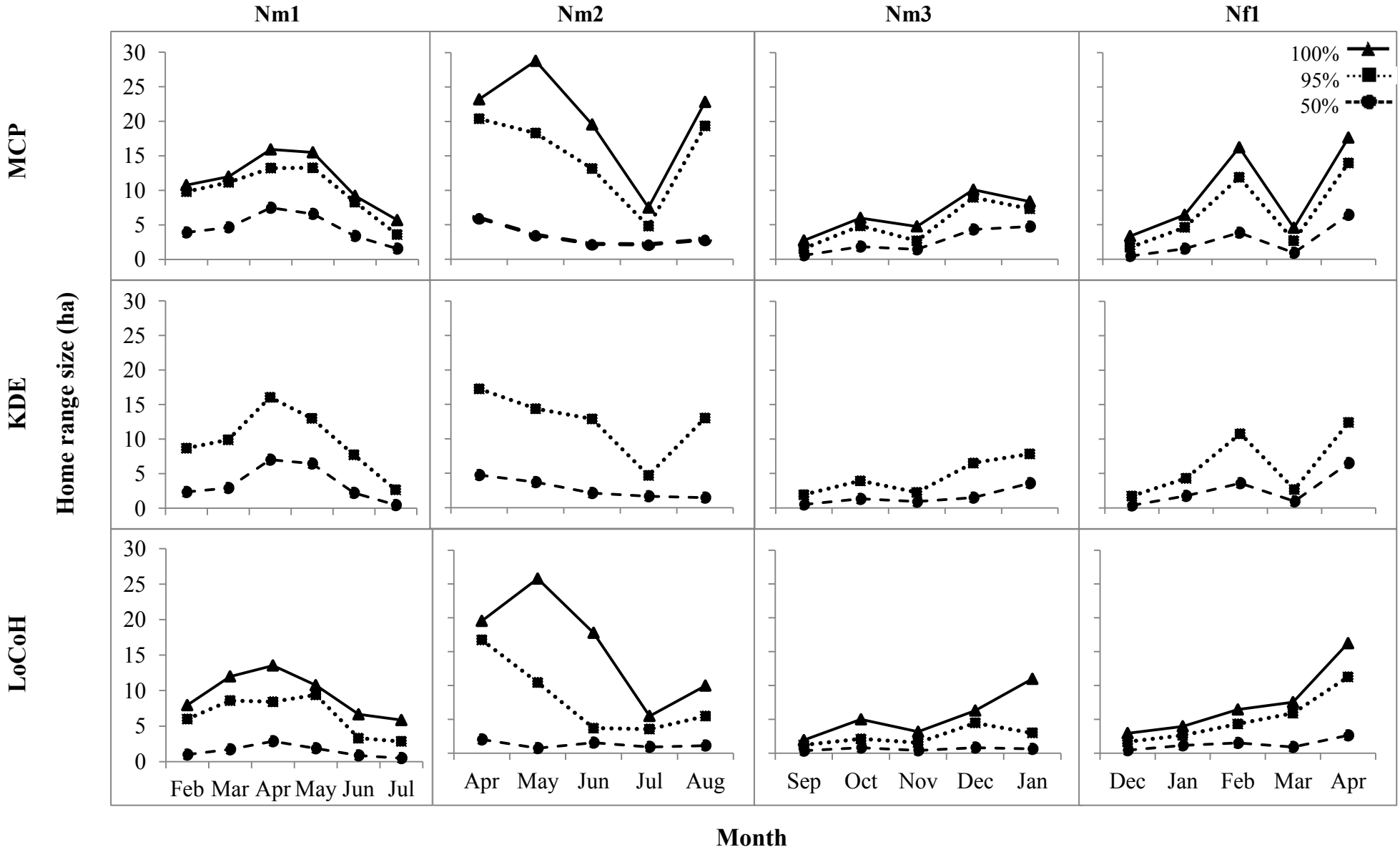

Figure 3. Monthly home range sizes, derived from all three estimates(MCP, KDE, LoCoH), of each mongoose within the Nature Estate.

Table 4. Overall rate of change in home range size (and rate of change per month in brackets) for male (m) and female (f) yellow mongoose in the Eco-Estate (E) and Nature Estate (N) based on three estimates (MCP, Kernal, LoCoH). Shaded areas show negative rate of change.

Name	Tracking period	Rate of change in home range size (rate of change per month)							
		MCP			KDE		LoCoH		
		50%	95%	100%	50%	95%	50%	95%	100%
Em1	March '16 to July '16	-0.26 (-0.05)	-0.33 (-0.07)	-0.22 (-0.04)	-0.43 (-0.09)	-0.19 (-0.04)	-0.17 (-0.03)	-0.08 (-0.02)	-0.32 (-0.06)
Ef1	March '16 to July '16	-0.39 (-0.08)	-0.15 (-0.03)	-0.12 (-0.02)	-0.46 (-0.09)	-0.18 (-0.04)	-0.31 (-0.06)	-0.14 (-0.03)	-0.10 (-0.02)
Em2	September '16 to February '17	-0.01 (0.00)	0.18 (0.03)	0.02 (0.00)	-0.24 (-0.04)	-0.03 (-0.01)	-0.15 (-0.03)	0.12 (0.02)	0.20 (0.03)
Ef2	November '16 to April '17	0.22 (0.04)	0.43 (0.07)	0.44 (0.07)	0.54 (0.09)	0.42 (0.07)	0.14 (0.02)	0.44 (0.07)	0.47 (0.08)
Nm1	February '17 to July '17	-0.06 (-0.01)	-0.08 (-0.01)	-0.07 (-0.01)	-0.01 (0.00)	-0.06 (-0.01)	-0.05 (-0.01)	-0.33 (-0.06)	-0.15 (-0.03)
Nm2	April '17 to August '17	-0.50 (-0.1)	-0.08 (-0.02)	-0.02 (0.00)	-0.46 (-0.09)	-0.33 (-0.07)	-0.27 (-0.05)	-0.37 (-0.07)	-0.28 (-0.06)
Nm3	September '17 to January '18	0.43 (0.09)	0.15 (0.03)	0.15 (0.03)	0.48 (0.10)	0.31 (0.06)	0.26 (0.05)	0.03 (0.01)	0.38 (0.08)
Nf1	December '17 to April '18	0.35 (0.07)	0.27 (0.05)	0.19 (0.04)	0.51 (0.10)	0.47 (0.09)	0.37 (0.07)	0.38 (0.08)	0.29 (0.06)

Home range overlap with human residents

As expected, the 100% MCP encompassed the majority of GPS locations and had the greatest percentage of polygons overlapping with human residents for all mongoose individuals (Table S3; Figure 4). Linear models indicated that both % GPS location and % polygon overlap with residents was not significantly affected by Estate, Sex and their interactions (Table S4). There was a trend of estate and sex which approached significance for the percentage of GPS locations overlapping with human residents at the 95% MCP isopleth level (Estate: $F = 4.94$, $d.f. = 2$ $p = 0.09$; Sex: $F = 7.34$, $d.f. = 2$, $p = 0.05$). There were more occurrences (n) of recorded GPS locations overlapping with human residents within the Eco-Estate (50% = 45; 95% = 225; 100% = 270) than in the Nature Estate (50% = 37; 95% = 90; 100% = 110), but the difference between estates was not significant for each isopleth level (p = 0.85; p = 0.14 and p = 0.22; 50%, 95% and 100% respectively).

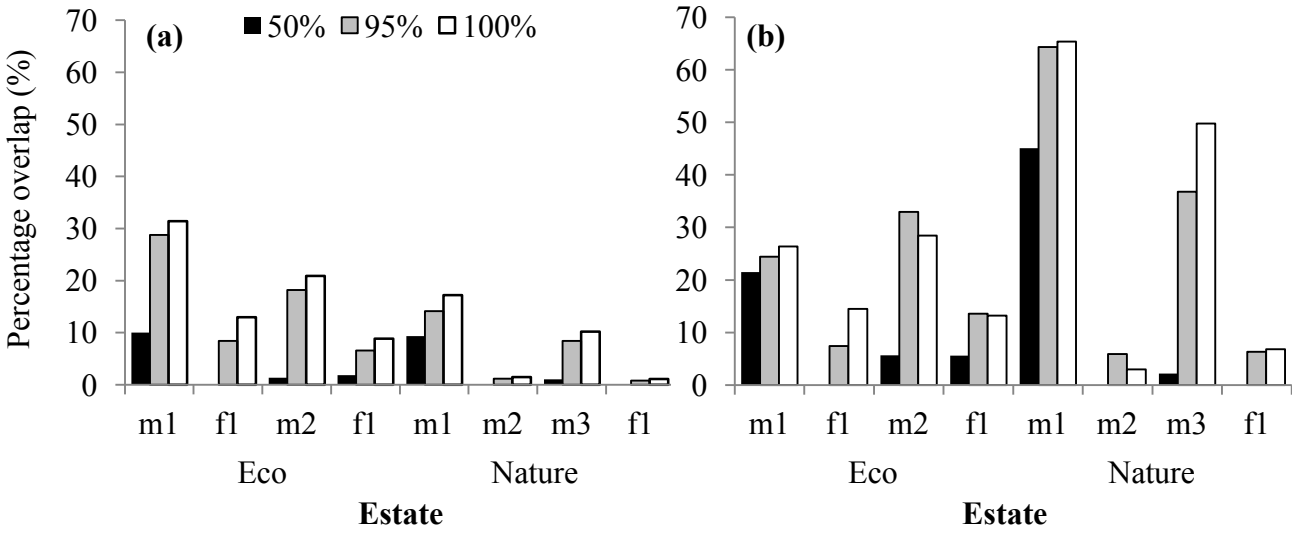

Figure 4 Percentage GPS location (a) and polygon overlap (b) with human residents for each individual yellow mongoose (m = male; f=female) in the Eco-Estate and Nature Estate according to the MCP method (50%, 95% and 100%).

As a percentage of the GPS locations recorded for each individual, the average percentage overlap was also higher in the Eco-Estate (50% = 3.31%; 95% = 15.49%; 100% = 18.53%) than in the Nature Estate (50% = 2.59; 95% = 6.14%; 100% = 7.51%; Table S3), but this difference between estates was also not significant for each isopleth level (p = 0.829; p = 0.171 and p = 0.131).

In the Eco-Estate, percentage GPS and percentage polygon overlap were proportionately similar for all mongooses, whereas in the Nature Estate, this was evident only for Nm2 and Nf1 (Table S3; Figure 4); in contrast, the percentage polygon overlap for Nm1 and Nm3 was disproportionately greater that the percentage of GPS locations (Table S3; Figure 4). It is important to note that the home range polygons generated by the MCP method for Nm1 and Nm3, particularly the 95% and 100% isopleths, substantially overlapped with the residential gardens despite the lower percentage of GPS locations occurring within these borders. This is likely due to the fact that these mongoose were located in a corridor between houses (Figure 1). I assume that this may have influenced the comparison of overlap with residents between estates, resulting in no significant predictors in the models (Table S4).

Percentage overlap with human residents was greater during the colder seasons (autumn and winter) than the warmer seasons (spring and summer) for both % GPS location overlap and % polygon. In the Eco-Estate, despite the larger home range sizes and number of recorded GPS locations during autumn for Em1, % GPS overlap with residents was greater during winter than autumn, and for Ef1, greater in autumn than winter (Table 5); while % polygon overlap was greater in winter for Em1 and greater in autumn for Ef1; likely due to the winter home range size of Em1 being proportionately larger than for Ef1. Kernel density images generated for these two individuals showed a change in the intensity of use of residential areas for these two mongoose only (Figure 5), consistent with the results of the MCP method; utilization distribution for the remaining yellow mongoose did not appear to shift (Figure 5). There were similar overlap percentages with human residents in spring and summer for both measures (percentage overlap and polygon overlap) for Em2; the percentage overlap for both months being lower than for the male (Em1) sampled during autumn and winter. Mongoose Ef2 was sampled over 3 seasons, and the overlap percentage with residents for both estimates was greatest during autumn, similar to the other female (Ef1). GPS coordinate overlap with human residents was higher during spring than summer, but polygon overlap (while very similar) was slightly greater during summer than spring (Table 5).

In the Nature Estate, the greatest overlap with human residents was observed in autumn and winter for Nm1. While polygon overlap for summer was similar to autumn and winter, the number of GPS locations overlapping with human residents during this season was far less during summer in comparison to autumn and winter. Similarly, Nm2 had greater % GPS location overlap with residents during winter than in autumn (Figure 6), but the opposite was true for % polygon overlap.

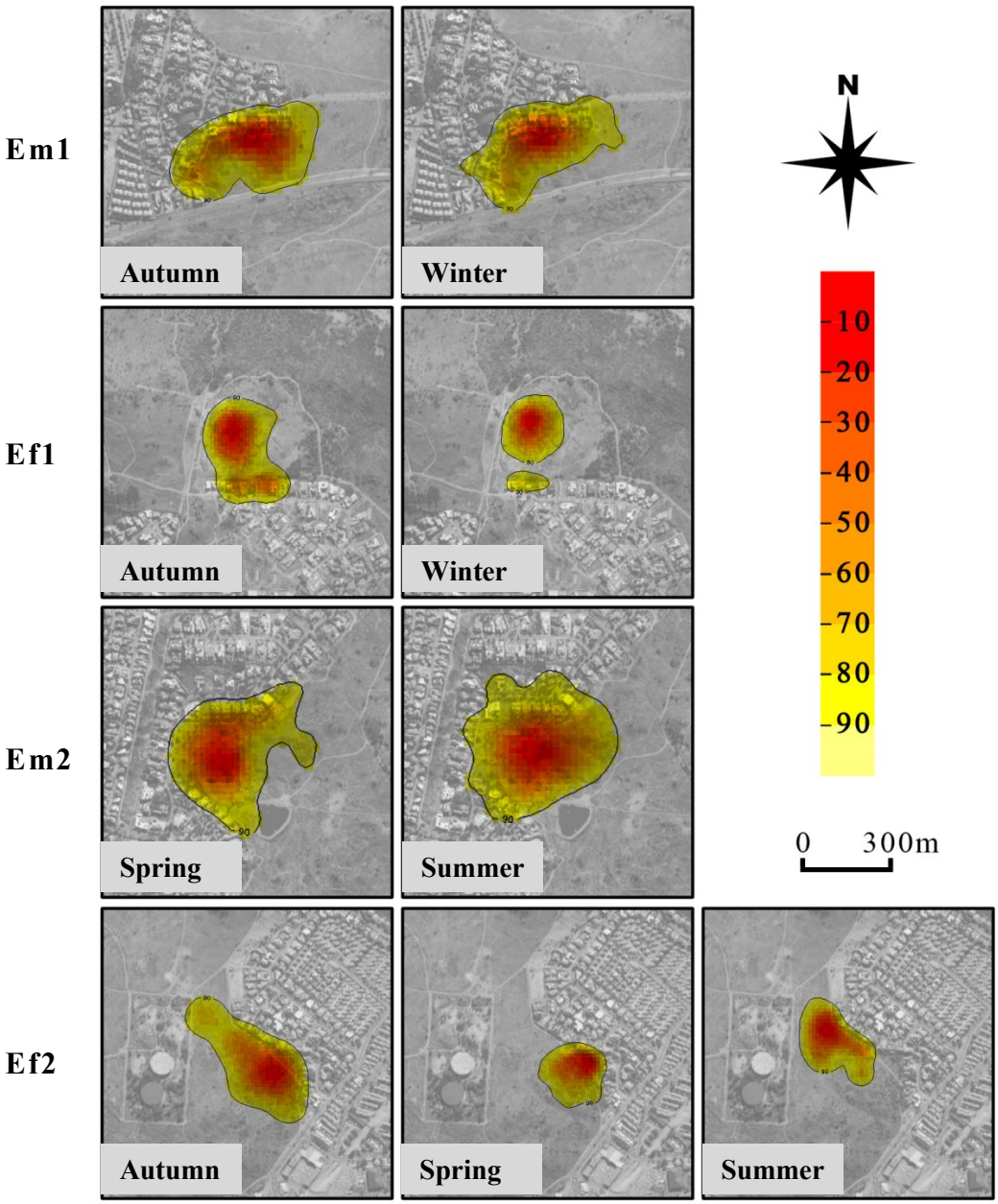

Figure 5. Location utilization density per season (by the kernel method) of individual yellow mongoose overlaid on aerial photographs of the Eco-Estate. More red stipulates core use areas, while the more yellow represents wider area of use and extends to the 95% home range use.

Percentage GPS location overlap with residents for Nm3 was the second highest on the estate, and was similar between seasons. The percentage polygon overlap however was substantially greater during summer than during spring at the 100% isopleth. Similar to the overall seasonal home range overlap, this was likely due to the location of the home ranges within the estate, in the corridor. The female mongoose was located furthest away from

residents and had the little to no overlap with residents except at the complete home range level (100% MCP; Figure 6; Table 5) mainly during autumn.

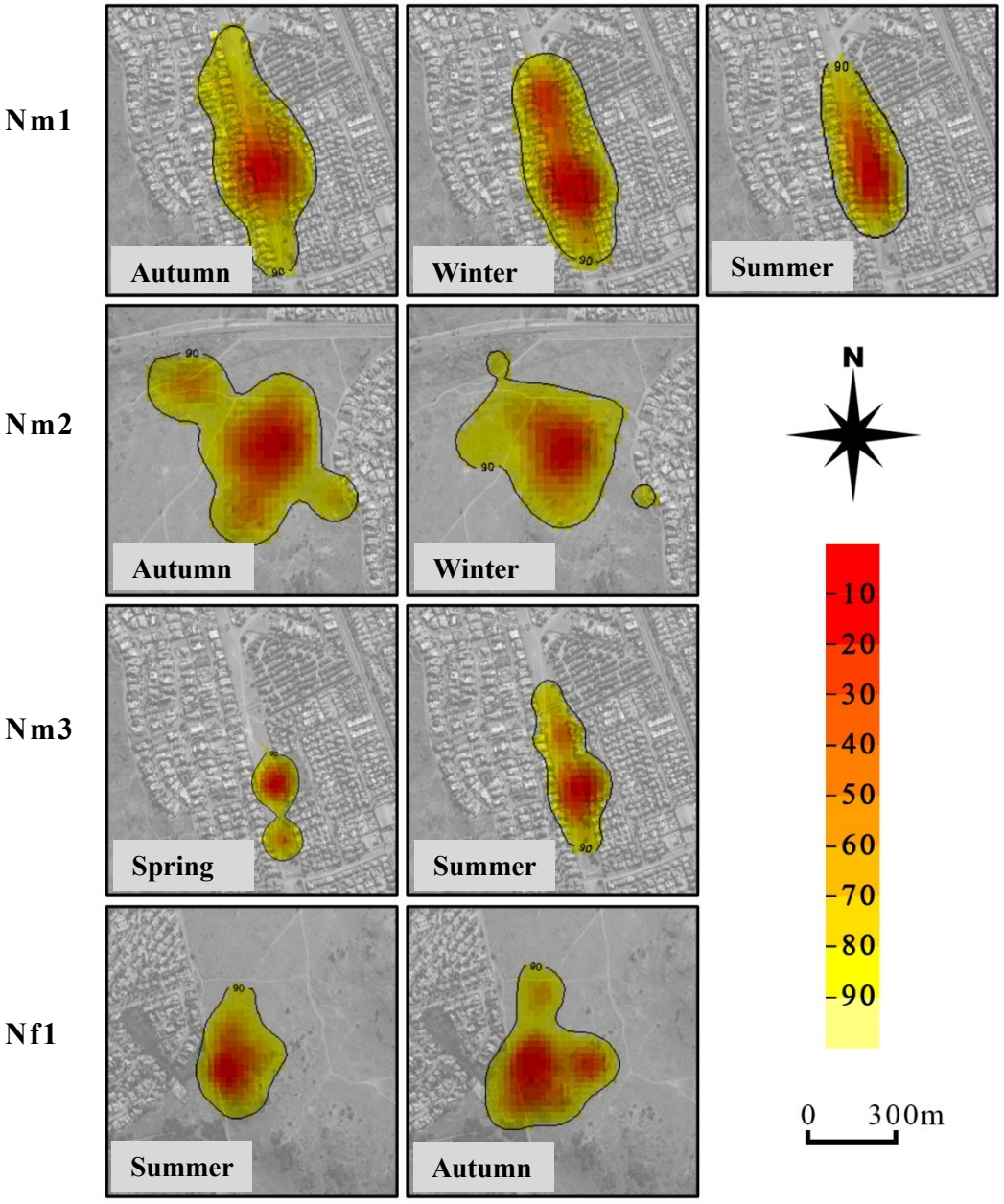

Figure 6. Location utilization density per season (by the kernel method) of individual yellow mongoose overlaid on aerial photographs of the Nature Estate. More red stipulates core use areas, while the more yellow represents wider area of use and extends to the 95% home range use.

Table 5. Percentage of total GPS locations (where n = number of GPS locations) and percentage of polygon size (MCP method) overlapping with residents, per season, at each isopleths level for each individual.

Name	Season	Percentage overlap with residents (%)					
		% GPS locations (n)			% Polygon (MCP)		
		50%	95%	100%	50%	95%	100%
Em1	Autumn	5.24 (11)	26.19 (55)	29.05 (61)	28.79	27.08	28.25
	Winter	21.35 (19)	34.83 (31)	37.08 (33)	27.10	28.98	44.80
Ef1	Autumn	0.00 (0)	8.06 (17)	11.37 (24)	0.00	17.44	15.32
	Winter	0.00 (0)	9.18 (9)	16.33 (16)	0.00	1.93	5.65
Em2	Spring	0.00 (0)	21.37 (56)	23.28 (61)	0.00	17.70	26.26
	Summer	6.12 (6)	26.53 (36)	32.65 (32)	8.29	25.74	31.28
Ef2	Autumn	3.83 (7)	14.75 (27)	18.03 (33)	0.00	12.80	13.73
	Spring	0.00 (0)	5.41 (2)	10.81 (4)	0.00	5.21	9.51
	Summer	0.75 (0)	1.13 (3)	2.26 (6)	0.00	5.62	10.34
Nm1	Autumn	7.72 (19)	12.60 (31)	15.04 (37)	47.76	41.99	43.97
	Winter	15.85 (13)	20.73 (17)	26.83 (22)	0.00	7.75	63.25
	Summer	3.85 (1)	7.69 (2)	7.69 (2)	29.07	52.93	52.37
Nm2	Autumn	0.00 (0)	1.02 (1)	1.02 (1)	0.00	7.00	8.92
	Winter	0.00 (0)	1.23 (3)	1.64 (4)	0.00	1.00	3.17
Nm3	Spring	1.17 (3)	8.56 (22)	10.51 (27)	13.11	8.71	10.64
	Summer	0.75 (1)	8.21 (11)	9.70 (13)	13.61	43.08	51.30
Nf1	Summer	0.00 (0)	0.00 (0)	0.43 (1)	0.00	0.00	0.13
	Autumn	0.00 (0)	1.0 (2)	2.21 (3)	0.00	5.64	6.12

Discussion

I investigated the home range size and overlap with human residents of yellow mongoose in an urban area. I used three home range estimates (MCP, KDE, and LoCoH) to investigate various aspects of home range parameters. The estimates produced largely similar outputs for the overall and monthly/seasonal home ranges at three isopleths (50%, 95% and 100%), with the exception of the smaller 50% LoCoH estimates. The LoCoH does reportedly underestimate home range size (Gregory 2017), and it may be that the significantly smaller core home range sizes generated by the LoCoH method were the result of the duration of data collection per individual and the small sample size. The method requires large sample sizes to adequately assess home range sizes (Adam *et al*., 2015). Therefore, our analysis using three estimates provided an exhaustive assessment of home range characteristics of the yellow mongoose in our study. In addition, the use of different methods allowed for comparison with several other published studies that used different methods.

Several studies support the conclusion that animals occurring in urban areas have home range sizes comparatively smaller than their non-urban dwelling counterparts (Riley 2003; Randa and Yunger, 2006; Gehrt 2007; Herr 2008). Due to the decrease in home range size attributed to the increase in level of urbanisation (Walton *et al*., 2017), I expected home range sizes of yellow mongoose to be smaller in the more urbanised Eco-Estate than in the less urbanised Nature Estate (prediction 1a). Indeed, according to all methods of analysis, the home range sizes of yellow mongoose in the Nature Estate were larger, on average, than those in the Eco-Estate, although the difference was not significant. Despite our attempts to avoid collaring individuals from the same den, two individuals collared in the Nature Estate shared the same den, which was located in a corridor situated between two blocks of residents. This may have largely impacted on the results of the home range size comparison between estates.

The Nature Estate was expected to be less urbanised since animals here had reduced contact with human residents due to houses being separated from the natural areas of the estate by a fence. Consequently, since only two of the four mongoose sampled in the Nature Estate were sampled in the 'natural area' of the estate and two in a narrow corridor between residents, I could not adequately assess space use in the less urbanised estate. Nonetheless, the two individuals occurring in the natural part of the Nature Estate (Nm2 and Nf1) had home range sizes larger than mongoose in the Eco-Estate (Table 1). The female mongoose in

the Nature Estate (Nf1) had a home range size twice as large as that of both females in the Eco-Estate (Ef1 and Ef2), and the male (Nm2) had a home range size larger than that of both males in the Eco-Estate (Em1 and Em2).

As predicted, home range sizes of yellow mongoose in this study were smaller than those of yellow mongoose from previous studies conducted on non-urban populations (prediction 1b; Table 6). The majority of these were conducted in nature reserves, which consist of natural, protected green areas with none to minimal human impact, and a farmland with both anthropogenic impacts (housing and farming), as well as large natural green spaces. The mean 95% and 100% MCP home range sizes of yellow mongoose in the Meyersdal Nature Area were smaller than those reported by Mbatyoti (2012) in the Great Fish River Reserve. Similarly at the 100% MCP, home range sizes were smaller than those obtained in the West Coast National Park (Cavallini 1993) and farmlands in the Western Cape (Balmforth 2004). Balmforth (2004) attributed the smaller male home range sizes to the limited number of locations collected for males. At the 95% KDE, home range sizes in this study were also smaller than those of yellow mongoose in the Kuruman River Reserve (Le Roux *et al*., 2008) and farmlands (Balmforth 2004).

Larger home range sizes are generally correlated with smaller population densities in both urban (Gerht 2007; Gould and Andelt, 2013) and non-urban areas (Dahle *et al*., 2006; Sanchez and Hudgens, 2015). A comparison between the results of previous studies on yellow mongoose home range sizes conform to this statement (Table 6). The much larger home range sizes of yellow mongoose occurred under comparatively low population densities (Cavallini 1993; Le Roux *et al.,* 2008; Mbatyoti 2012), while 2 – 3 times smaller home ranges were found in a medium density population (Balmforth 2004). Earlé (1981) reported substantially smaller home range sizes in an extremely high density population (Table 6), but these were largely anecdotal measurements by observation rather than radio/GPS tracking, and have been regarded as an underestimate of home range size. In my study area, from known number of individuals at some dens and the known estate sizes, I estimated the population density to be between 30 and 40 individuals per 100 hectares. I calculated the density by calculating the area encompassing all known dens, and multiplied that by the sum of the individuals at these dens to obtain an average population density for each estate. This value was divided by total estate size (in ha).

Table 6. A comparison of the home range sizes of yellow mongoose in our study, and in previous studies using different methods of estimations.

Area type	Population density (n/ 100 ha)	Method used	Home range size (ha)		Study
			Female	Male	
urban	30 - 40	95% MCP	9.09	17.33	This study
		100% MCP	11.79	21.23	
		95% KDE	8.35	15.06	
reserve	133 - 200	Visual observation	5 - 6		Earlé 1981
reserve	6 – 7	100% MCP	27	102	Cavallini 1993
farmland	23 - 26	100% MCP	26	25	Balmforth 2004
		95% KDE	17.54	20.65	
reserve	4 - 14	95% KDE	20	76	Le Roux *et al*., 2008
reserve	4 - 10	95% MCP	22	48	Mbatyoti 2012
		100% MCP	30	70	

Species flourishing in urban areas generally attain much higher population densities than in non-urban areas due to greater food availability and reduced predation pressure (Herr 2008; Gehrt *et al*., 2009; Bateman and Flemming, 2012). For example, a decrease in home range size, along with an increase in population density as the level of urbanisation increased, has been reported in the red fox, coyote, and racoon (Šálek *et al*., 2015). This estimate of population density could be expected since the home range sizes in my study were considerably smaller than in the other studies where population densities were lower, thereby concurring that population densities and home range sizes may be interlinked. Therefore, it is possible that the smaller home range sizes in our study may be the result of a higher population density in Meyersdal, and not just the greater resource availability. The two males (Nm1 and Nm3) with overlapping home ranges (particularly range cores) in the Nature Estate indicates similar home range use and possibly a single group home range, reminiscent of the medium-high density yellow mongoose populations previously studied (Earlé 1981;

Balmforth 2004). Hence, I could infer that this too is perhaps a high density population, but this needs to be confirmed through population censuses.

Similar to previous yellow mongoose studies (Cavallini 1993; Balmforth 2004; Le Roux *et al*., 2008; Mbatyoti 2012), male home range sizes, while not statistically significant (for this and these other studies), were larger than those of females (prediction 2). Differences in home range sizes between males and females in mammals have been ascribed to body mass/size (Dahle *et al*., 2006; Gould and Andelt, 2013). Larger individuals are expected to have larger home range sizes, encompassing more resources in order to meet the necessary daily energetic requirements (Ghert and Fritzell, 1997; Riley 2003). However, as urban environments have an abundance of available food resources (Riley *et* al., 2010; Bateman and Flemming, 2012; Šálek *et al*., 2015), energetic requirements are met quicker in confined spaces, reducing home range sizes (Gilchrist and Otali, 2002; Gould and Andelt, 2013). Body mass did not appear to influence in this study since collared females were heavier than some males, yet their home range sizes were still smaller.

Home range size of female mammals is largely affected by the distribution and abundance of food. For males on the other hand, in addition to food, mate seeking and territorial/mate defence strongly influence home range sizes (Balmforth 2004; Nilsen *et al*., 2005; Mbatyoti 2012). The higher population densities in urban areas (Šálek *et al*., 2015) increase the chances of encountering a mate (Gehrt and Fritzell, 1997). I did not study the interactions of all individuals in a group, or with neighbouring groups in the estate. I could not demonstrate home range overlap between the sexes, and therefore could not determine whether the polygamous nature of male yellow mongoose searching for females outside of the denning groups is evident in our study. Other studies showed that male yellow mongoose extend their home ranges to overlap with females of other groups for mating opportunities (Cavallini 1993; Balmforth 2004; Mbatyoti 2012). While abundant resources in urban areas decrease territorial defence behaviours (Šálek *et al*., 2015), higher population densities on the other hand naturally increases intruder pressure, potentially making territorial defence important (Stenseth *et al.,* 1992; Cavallini 1993; López-Sepulcre and Kokko, 2005). Territories and territorial defence in urban areas would need to be assessed to establish whether these are affecting the larger male yellow mongoose home range sizes in our study. Additionally, since female yellow mongoose are cooperative breeders (Vidya *et al.,* 2009; Rasa *et al.,* 1992), home ranges of mothers and helpers may also be limited in size in

comparison to males simply due to the need to stay close to dens to rear young (Balmforth 2004). However, this was not assessed and should be addressed in future studies.

Our data set was not large enough to fully evaluate seasonal variation in home range size of each individual. Instead, I assessed the change in home range size between months for individuals, and found that home range size decreased in coldest months and increased in warmer months, for individuals for which data were available. Thus, as I predicted, home range sizes of yellow mongoose in the Nature Estate did appear to vary seasonally. However, contrary to our expectations, home range sizes also varied seasonally in the Eco-Estate, decreasing in the coldest months in both estates. While I expected home range sizes in the Eco-Estate not to vary seasonally as a result of greater exposure of the mongoose to and overlap with human residents and anthropogenic resources, it has been established that mongoose in the Nature Estate also made use of residential areas (Nm1 and Nm3, likely due to where they were located in the estate). Therefore, anthropogenic resources aside, the less abundant main prey availability (e.g. insects; Cronk and Pillay, 2019) during the colder periods may have restricted home range sizes of both sexes, in both estates, as a means of minimising energy expenditure when natural resources were limited (Mbatyoti 2012). Additionally, our previous research (Cronk and Pillay, 2019) as well as other studies on the diet composition (Nel and Kok, 1999; Skinner and Chimimba, 2005) showed that yellow mongoose increase their consumption of small mammals and birds during the coldest months. Therefore, energetic requirements may also be met quicker when consuming these more profitable foods (vertebrate prey) during this colder period. This may have influenced the reduced home range sizes in yellow mongoose in both estates during colder months, since the occurrence of small vertebrates in the scat of yellow mongoose in both estates increased during this period, in addition to the concurrent increase in occurrence of anthropogenic resources in yellow mongoose scat the Eco-Estate (Cronk and Pillay, 2019).

Contrary to the suggestion that home range sizes of yellow mongoose are smaller during colder periods, home range were relatively larger in autumn than summer/spring for the same individual (Ef2, Nm1, Nf1). Since autumn falls outside of the breeding period of yellow mongoose (Zumpt 1976; Rasa *et al.*, 1992; Mbatyoti 2012), the smaller home range sizes in summer/spring may be attributed to mate guarding for males and nursing activities of females. However, the breeding period of yellow mongoose has been reported to extend up to March (Rasa *et al.*, 1992; Mbatyoti 2012), which may account for smaller summer than autumn home ranges for the above mentioned individuals despite warmer temperatures.

Based on personal field observations during the study period, young were seen at dens between August and October, so there was no reason to suspect that breeding periods differ in this urban setting from a non-urban setting. While the seasonal variation of home range size in yellow mongoose has not been extensively researched, the results of our study are similar to previous studies that showed that home range sizes in non-breeding period (summer and autumn) are larger than home range sizes during the breeding period (winter and spring; Balmforth 2004; Mbatyoti 2012).

The overlap of small carnivores with human residents and residential gardens in urban areas has not been widely assessed previously, despite gardens representing a large portion of urban spaces (Gaston *et al*., 2005). By using the methods described by Herr (2008) as 'determination of urban overlap', I was able to assess whether, and to what extent, home ranges of yellow mongoose overlapped with residential gardens. Animals making use of urban gardens have ease of access to anthropogenic foods, such as rubbish bins, pet food, garden fruits/plants and bird feeders (Gaston *et* al., 2005; Bateman and Flemming, 2012). While I could not assess whether animals simply pass through gardens instead of making use of any resources within their boundaries from our MCP polygons, KDE images showed the density of locations, which aided in interpreting overlap with residents (discussed below).

There was no significant difference in overlap of mongoose with human residents between estates. Yet, collared mongoose in the Eco-Estate did have greater overall overlap with human residents as predicted (prediction 4a). Our results of similar high overlap of mongoose with residents in the Nature Estate were unexpected and likely due to range limitation (for Nm1 and m3) based on their den being located in a narrow corridor between houses boundary walls. This potentially would have impacted on the differences in overlap between estates, since mongoose in the Nature Estate located furthest away from human residents (Nm2 and Nf1) had little to no overlap with human residents in either percentage GPS locations or polygon overlap metrics. Overall KDE images showed that those mongoose denning closest to residents (i.e. Em1, Em2, Nm1 and Nm3) overlapped with residents with a greater percentage of their home range polygons; if dens were located further away from residents, a small, separate area of concentration within their home ranges, overlapped with residents (Figure S1 i.e. Ef1 and Nm2). Where portions of home ranges overlapped with human residents on these estates, I assumed they made use of the resources available in residential gardens (Gaston *et al*., 2005; Bateman and Flemming, 2012). I conclude from

these results that yellow mongoose do overlap with residents and make use of gardens, and they do so to a greater extent when they are located closer to the residents.

Both percentage GPS location and polygon size overlap with human residents was greater during the colder seasons (autumn/winter) than during the warmer seasons (spring/summer), specifically at the 95% and 100% MCP isopleths. Similarly, stone martens spent most of their time during autumn and winter within residential gardens (Herr 2008). Yellow mongoose sampled in both autumn and winter, had the greatest overlap with human residents (prediction 4b). While I did not find significant differences in home range size between seasons, the location density images generated by the kernel method (Figure 5, Figure 6) aided in assessing how yellow mongoose made use of residential areas during the different seasons. In particular, in mongoose sampled during colder seasons (Em1, Ef1, and Nm2), areas of concentration (more red in images) overlapped more with residents, than the remainder of mongoose sampled during warmer seasons. As opposed to colder seasons, the overlap with human residents in mongoose sampled in warmer seasons fell largely in the 95% home range, (more yellow) indicating opportunistic use. These results demonstrate that the mongoose could have exploited anthropogenic food resources from gardens more readily during colder seasons, like in the stone marten (Herr 2008). Similarly, anthropogenic items were found in the scat of yellow mongoose year round in the Eco-Estate, with a greater occurrence in scat during colder periods (Cronk & Pillay, 2019). Core areas of concentration of home ranges located near anthropogenic resources (e.g. garbage dumps) has also been recorded in banded mongoose *Mungos mungo* (Gilchrist and Otali 2002), and similarly, the occurrences of raccoons were significantly positively correlated with relatively high residential land use areas (Randa and Yunger, 2006).

In conclusion, I showed that yellow mongoose in an urban area utilise residential gardens during the coldest periods when the availability of their main prey, particularly insects, is at its lowest. The short duration that each individual was tracked generated inconclusive results regarding seasonal variation in home range size, but I showed that similar to non-urban yellow mongoose, home ranges sizes were smallest during the breeding seasons. The small sample size made it difficult to assess home range size of mongooses between the estates, and therefore describing the study area on a more/less urban gradient proved challenging. Our study does show smaller home range sizes of urban than non-urban yellow mongoose. Yet, whether this was a function of either or both of the ease of access

to/greater resource availability in urban areas and a consequence of greater population densities, needs to be further studied.

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Supplementary Material

Table S1. Characteristics of male (m) and female (f) mongoose collared and tracked in the Eco-Estate (E) and Nature Estate (N).

Name	Capture date	Body mass (g)	Body length (cm)	Tail length (cm)	Age class	Tracking duration in days (no. locations)
Em1	20-Mar-16	750	32.7	27.2	sub-adult	110 (299)
Ef1	20-Mar-16	892	33.4	24.1	adult	113 (309)
Em2	4-Sep-16	768	36.6	25.5	adult	152 (445)
Ef2	20-Nov-16	686	36.2	26.7	adult	162 (486)
Nm1	18-Feb-17	818	33.5	25.2	adult	139 (354)
Nm2	26-Apr-17	882	34.3	24.6	adult	125 (335)
Nm3	2-Sep-17	992	36.5	25	sub-adult	137 (391)
Nf1	10-Dec-17	864	35.5	24.5	adult	129 (368)

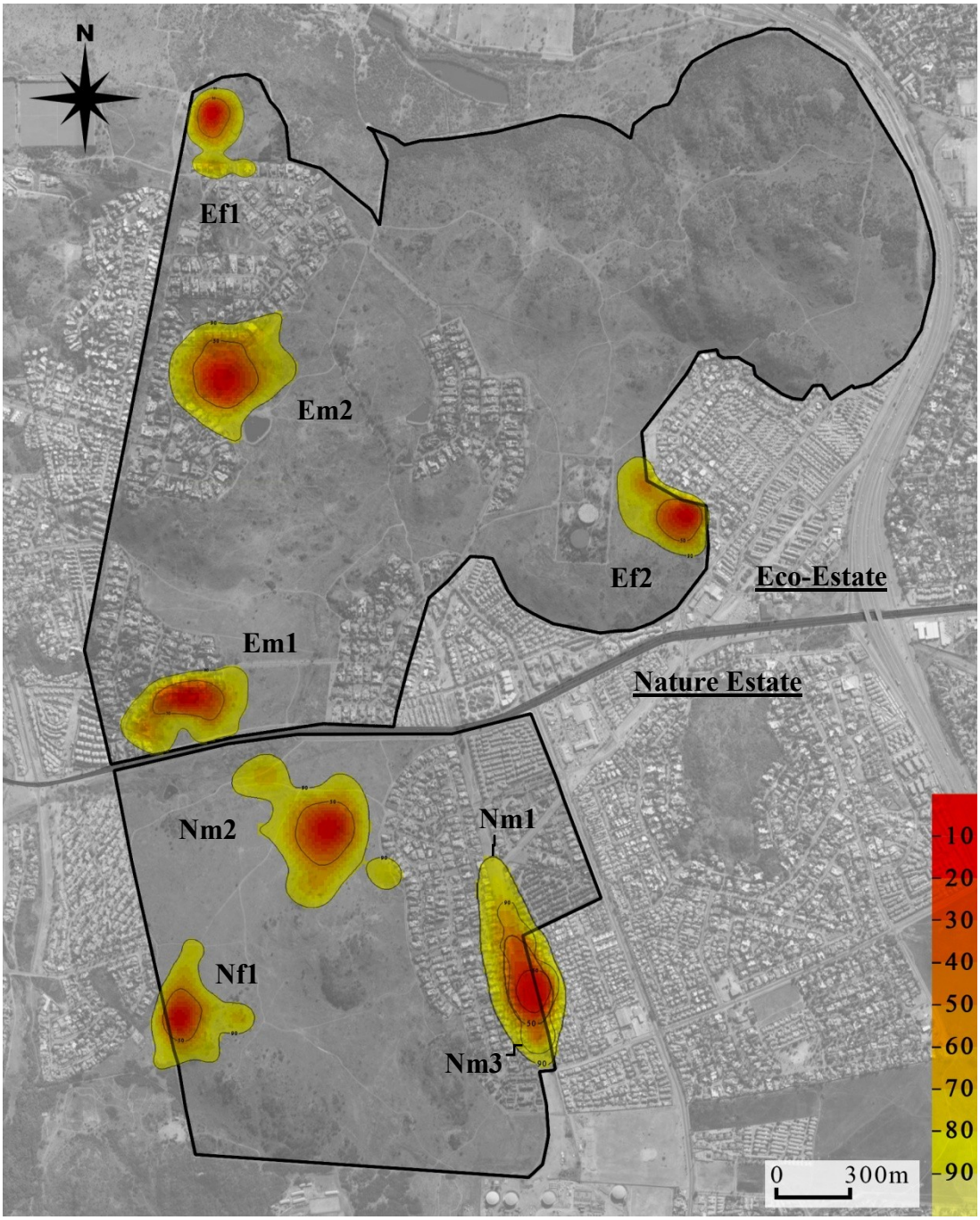

Figure S1. Location utilization density (by the kernel method) of individual yellow mongoose in the Eco-Estate and Nature Estate, separated by a double tarred road. More red stipulates core use areas, while the more yellow represents wider area of use and extends to the 95% home range use.

Table S2. Seasonal home range sizes, based on three estimates (MCP, KDE, LoCoH), of female (f) and male (m) yellow mongoose in the Eco-Estate (E) and Nature Estate (N).

Name	Season	MCP			KDE		LoCoH		
		50%	95%	100%	50%	95%	50%	95%	100%
Em1	Autumn	1.86	8.50	9.04	1.24	6.49	0.19	5.78	9.04
	Winter	0.94	4.49	6.63	0.42	4.84	0.08	3.09	5.52
Ef1	Autumn	1.43	5.06	5.67	1.31	4.87	0.65	3.33	5.18
	Winter	0.67	3.11	3.69	0.63	3.22	0.19	1.87	3.02
Em2	Spring	3.02	12.15	14.57	2.33	10.19	0.57	9.48	12.91
	Summer	3.57	13.90	14.33	3.39	11.67	0.22	8.91	14.17
Ef2	Autumn	2.11	7.32	8.30	1.85	6.44	0.21	5.06	7.32
	Spring	0.52	1.76	2.29	0.52	1.59	0.05	1.39	2.28
	Summer	1.23	2.47	2.89	0.59	2.55	0.06	1.90	1.91
Nm1	Autumn	6.23	13.21	15.14	5.48	12.98	2.15	8.79	12.76
	Winter	2.48	5.95	7.29	1.34	5.19	0.68	5.99	7.94
	Summer	3.90	9.81	10.75	2.35	8.69	0.98	8.07	9.75
Nm2	Autumn	4.77	19.34	25.49	4.22	15.81	1.37	13.58	24.17
	Winter	2.42	12.09	15.95	1.74	10.19	1.19	4.24	11.08
Nm3	Spring	1.27	2.51	3.48	0.90	2.03	0.52	1.12	2.34
	Summer	4.51	9.39	9.72	2.54	7.68	0.71	3.71	8.63
Nf1	Summer	1.94	6.07	8.33	1.89	5.59	1.02	2.87	4.11
	Autumn	3.67	10.16	8.76	3.73	7.54	1.76	8.59	11.38

Table S3. Percentage of total GPS locations and percentage of polygon overlapping with residents for three isopleths (MCP method) for each individual mongoose.

Mongoose identity	Percentage overlap with residents (%)					
	% GPS locations (n)			% Polygon		
	50%	95%	100%	50%	95%	100%
Em1	10.03 (30)	28.76 (86)	31.44 (94)	21.53	24.40	26.39
Ef1	0.00 (0)	8.41 (26)	12.94 (40)	0.00	7.44	14.49
Em2	1.35 (6)	18.20 (81)	20.90 (93)	5.65	32.96	28.43
Ef2	1.85 (9)	6.58 (32)	8.85 (43)	5.60	13.56	13.21
Nm1	9.32 (33)	14.12 (50)	17.23 (61)	45.08	64.30	65.35
Nm2	0.00 (0)	1.19 (4)	1.49 (5)	0.00	5.90	3.00
Nm3	1.02 (4)	8.44 (33)	10.23 (40)	2.22	36.82	49.73
Nf1	0.00 (0)	0.00 (0)	0.02 (4)	0.00	6.33	6.83

Table S4. Outcomes of General Linear Models analysing the predictors of the percentage of GPS locations and the percentage of home range polygons overlapping with human residents.

Effects and interactions	Overlap with human residents								
	50%			95%			100%		
	F	***df***	***P***	***F***	***df***	***P***	***F***	***d.f.***	***P***
	% GPS locations								
Estate	0.05	2	0.84	4.94	2	0.09	5.16	2	0.09
Sex	1.35	2	0.31	7.34	2	0.05	5.71	2	0.08
Estate*Sex	0.03	2	0.87	0.95	2	0.38	0.41	2	0.56
	% Home range polygon								
Estate	0.07	2	0.79	0.35	2	0.59	0.43	2	0.55
Sex	0.82	2	0.42	2.09	2	0.22	1.56	2	0.28
Estate*Sex	0.03	2	0.87	0.12	2	0.75	0.29	2	0.62

CHAPTER SIX

Distribution of yellow and slender mongoose species in the greater Johannesburg area: a citizen science approach

Abstract

The yellow mongoose *Cynictis penicillata* and slender mongoose *Galerella sanguinea* are two small carnivores with similar ecologies. Both are widely distributed in southern Africa, and coexist in the central portions of South Africa. What is not known is the extent of their occurrence and coexistence in urban areas. My aim was therefore to assess their occurrence, some aspects of their habitat use and extent of overlap in the greater Johannesburg area, a highly populated urban area. I used a citizen science approach to encourage the general public to report sightings of yellow and slender mongoose in the greater Johannesburg area. Citizens were approached using online public platforms where people could report the sighting and location of the species. I created a survey consisting of questions pertaining to their location, some aspects of mongoose behaviour (such as their active periods and their response to human presence), and also the opinions of the citizens regarding their presence in Johannesburg. The project ran for three and a half years, resulting in a total of 187 yellow mongoose and 98 slender mongoose sightings. From the additional survey questions it was apparent that both species were diurnal, most commonly sighted individually, were often seen travelling and foraging, and occurred in urban green spaces such as parks, river sides and in residential gardens. Using MCP polygons to map the occurrence of each species, I found a wider area of occurrence in the slender than in the yellow mongoose (at the 95% and 100% isopleth level). In contrast, at the 50% core area of occurrence, the yellow mongoose occurred over a larger area than the slender mongoose. Overlap between the species was extensive at all isopleth levels. Thus, yellow and slender mongoose are widely distributed in the greater Johannesburg area, coexisting over a large portion, but areas of individual species occurrence separately was still evident.

Key words: *coexistence, distribution, slender mongoose, urban Johannesburg, yellow mongoose*

Introduction

The yellow *Cynictis penicillata* and slender *Galerella sanguineus* mongoose are small carnivores of the family *Herpestidae*. Both species are widely distributed throughout southern Africa (Skinner and Chimimba, 2005), with yellow mongoose occurring further south and slender mongoose extending further north, with overlap in central southern Africa. Current distribution maps for yellow (Do Linh San *et al.,* 2015) and slender (Do Linh San and Maddock, 2016) show that these species overlap within a portion of their geographic range; however, their co-occurrence in the same locality has not previously been documented (Figure 1).

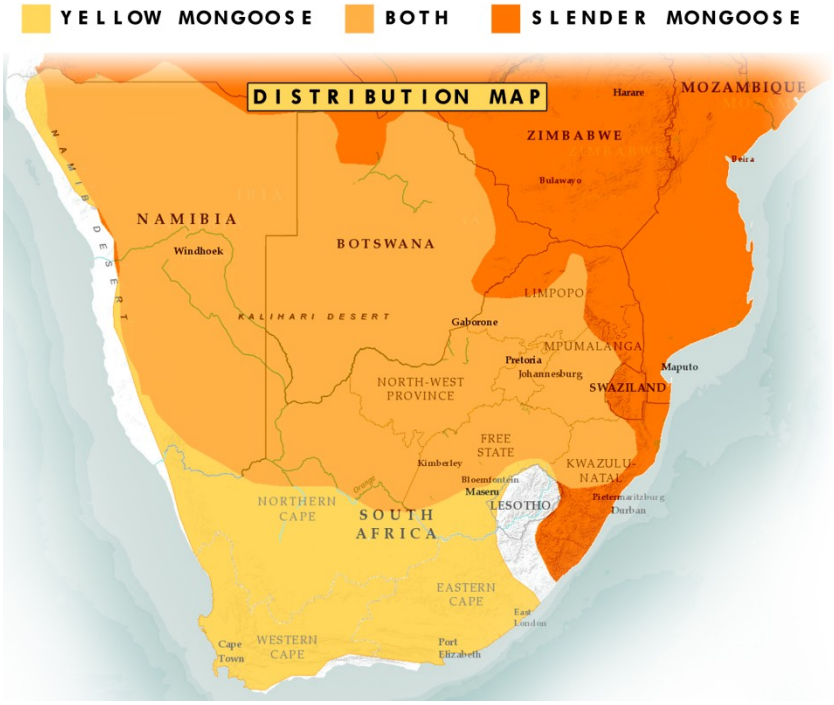

Figure 1. A composite map showing the current published distribution and overlap of the yellow and slender mongoose in Southern Africa (generated using maps produced by Do Linh San *et al.,* 2015; Do Linh San and Maddock, 2016).

A more detailed map using quarter degree squares for each species was available in the Mammal Red List of Mammals of South Africa, Lesotho and Swaziland produced in 2016, showing historical and more recent distributions of the species (Figure 2; Do Linh San *et al*., 2016; Le Roux *et al.,* 2016). These maps showed that the yellow mongoose has a wider distribution in South Africa, and a general shift northwards in the last 20 years.

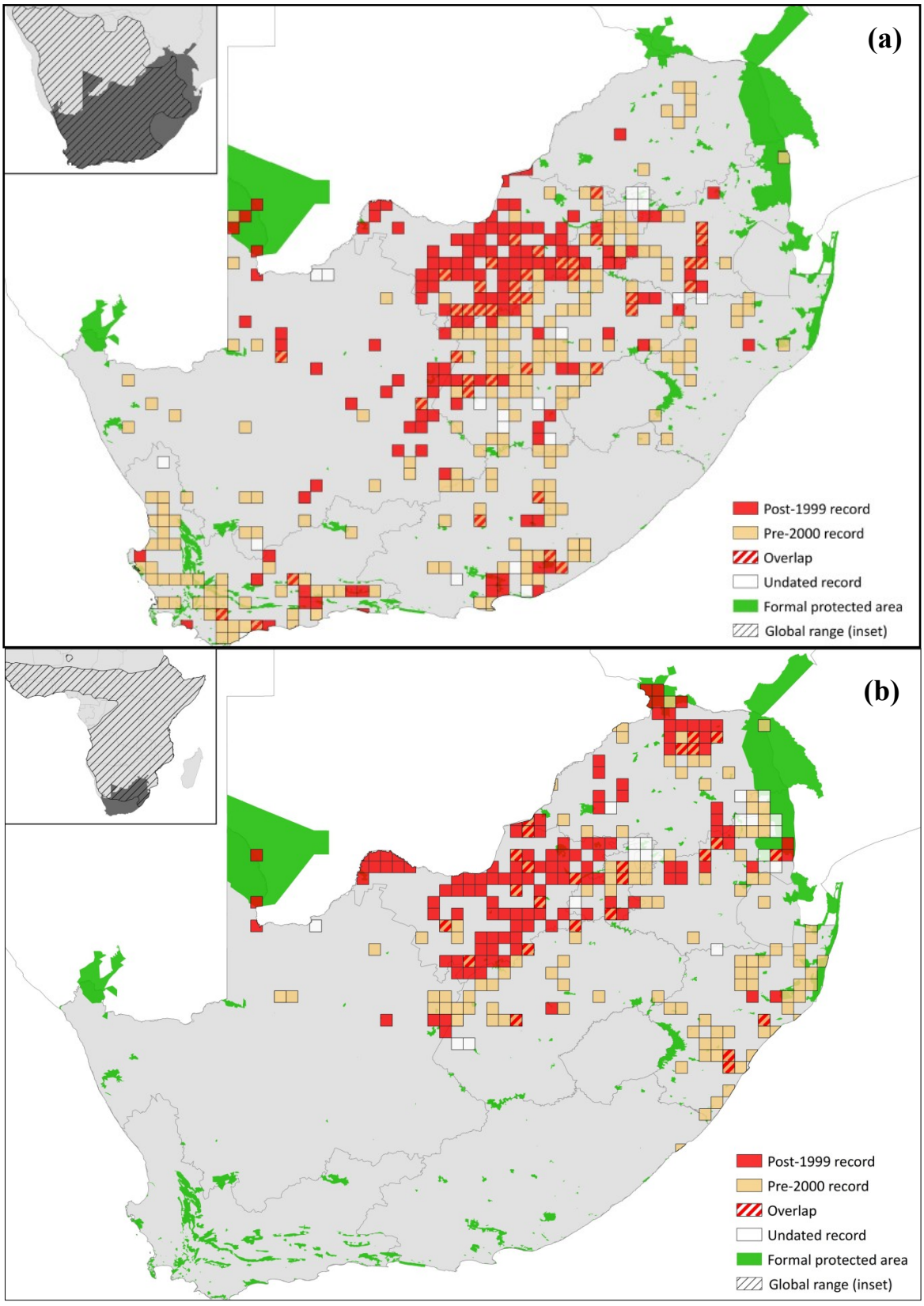

Figure 2. Quarter degree square distribution records of yellow (a) and slender (b) mongoose in South Africa; conservation assessment in The Red List of Mammals of South Africa, Lesotho and Swaziland (Do Linh San *et al*. 2016 and Le Roux *et al.* 2016).

The slender mongoose maintained a northerly distribution, decreasing in the eastern regions of South Africa in the last 20 years. These maps do not specifically report the occurrence of the species in urban areas. From these maps overlap in the distribution is evident in the Gauteng Province, South Africa, but the extent of occurrence and overlap is not clear in the greater Johannesburg area (Figure 2). A closer look at the maps in Figure 2 shows that regions of the greater Johannesburg area have no occurrence of either species, but it is difficult to determine which areas in Johannesburg these regions represent (Figure 3). In both sets of maps (Figures 1 and 2), it is not clear whether yellow and slender mongoose co-occur sympatrically or allopatrically in their broad geographic areas of overlap. If they coexist sympatrically, my previous studies have shown that yellow and slender mongoose partition use of food resources (yellow mongoose scats showed greater occurrence of anthropogenic foods, while those of slender mongoose had greater occurrence of vertebrate remains; Cronk and Pillay, 2018; 2019), and differ spatio-temporally (yellow mongoose were more common in open areas near residents and slender mongoose in covered areas further form residents; Chapter 4).

In previous chapters, I showed that the two mongoose species coexist in an urban area in the south of Johannesburg South Africa (Meyersdal Nature Area; Cronk and Pillay, 2018), but this has not been established elsewhere in Johannesburg. Since I assumed that these species' distributions are shifting (Figure 2), I investigated whether the coexistence and overlap of these two species is unique to the Meyersdal Nature Area or more widespread in the urban Johannesburg area. I used a citizen sciences approach, asking the public (through various online platforms) to 1) report sightings of yellow or slender mongoose; and 2) answer questions pertaining to the behaviour of the mongoose sighted, and their personal opinions about mongoose occurrence in the greater Johannesburg area.

Materials and methods

I surveyed the public in the greater Johannesburg area (26.170315 S, 27.971777 E), and also included neighbouring areas of the West Rand (including Krugersdorp and Muldersdrift) and East Rand (including Alberton, Germiston, Edenvale and Kempton Park; Figure 4). Johannesburg is one of the 50 largest urban assemblages in the world, and the largest city in the world that is not located alongside large bodies of water (coastlines, river). Since 1990, the human population in the urban areas of Johannesburg has increased from ±1.9 million to ±5.5 million currently (Johannesburg Population, 2018).

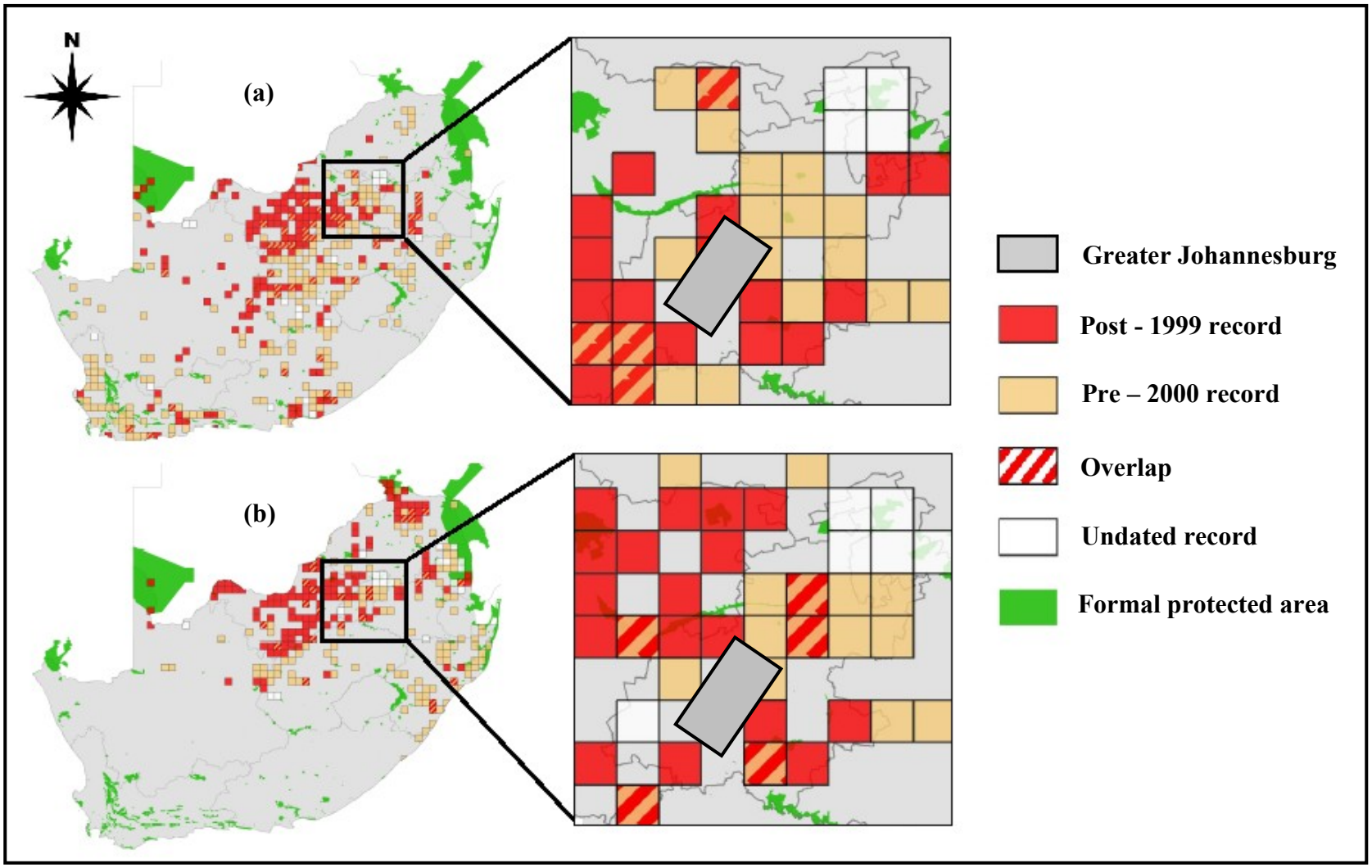

Figure 3. A zoomed in map of the approximate location of the greater Johannesburg area to show the occurrence of yellow mongoose (a) and slender mongoose (b). Generated from Do Linh San *et al*. 2016 and Le Roux *et al.* 2016.

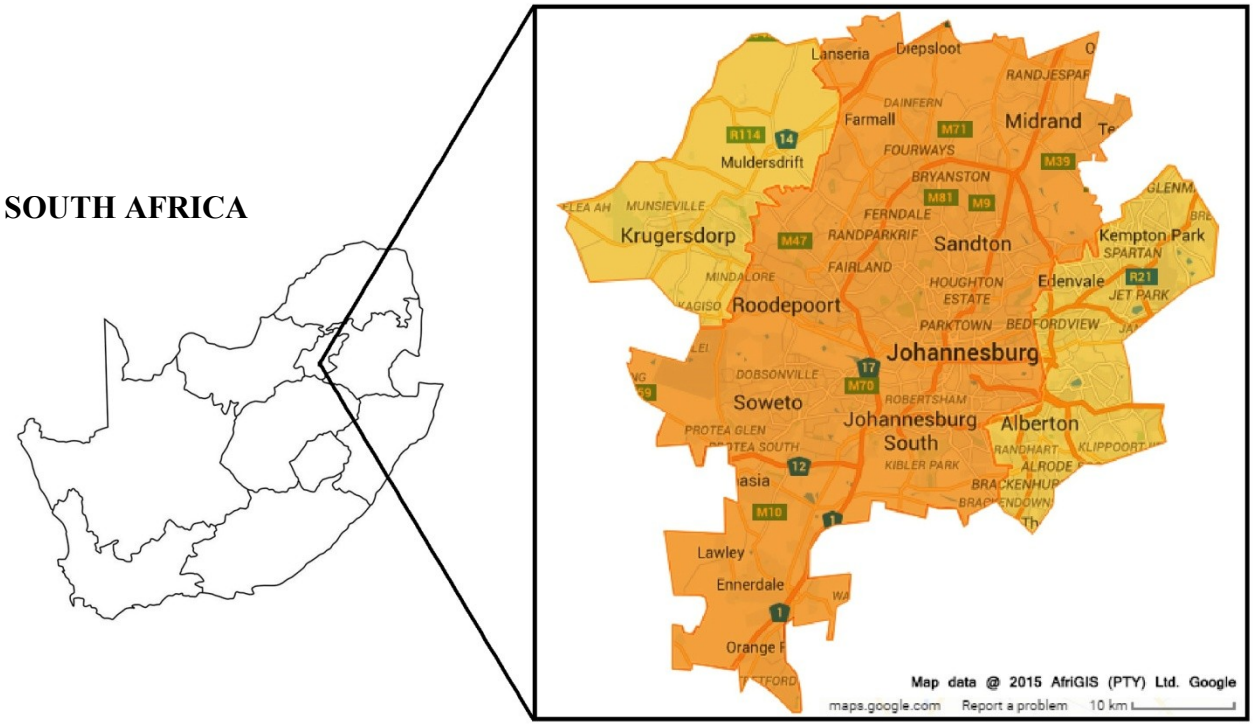

Figure 4. Map outline of the greater Johannesburg area (centre in orange), including outskirts of the West Rand (left in yellow) and East Rand (right in yellow) areas, in Gauteng, South Africa (inset). Image provided by Google Maps (Google: maps.google.com).

Data collection

I used citizen science as my main method of data collection. Citizen science research is a useful sampling tool that potentially produces large data sets, is comparatively cheaper than traditional data collection methods, and allows for large areas to be covered including areas that are inaccessible to researchers (such as private property; Dickinson *et al*., 2010). In 2015, I created the "The Urban Mongoose Project" in order to inform the public of my research, and to encourage responses from citizens about where these mongoose occurred in the greater Johannesburg area. The project was presented to the public in a Facebook page (https://www.facebook.com/THEURBANMONGOOSEPROJECT/) and a poster. Additionally, I created an email account for correspondence with the public (MongooseCity@gmail.com), which was used to receive mongoose sightings. The Facebook page was the main platform for reporting of sightings, and the page was updated frequently, answering questions from the general public and providing additional information about the

species. Posters were put up at shopping centres and other public spaces, where permitted, around Johannesburg (e.g. university campuses, veterinary centres, garages). The poster contained the aim of this project, some general information on each species, a picture and information to help identify each species, and also information on where sightings could be reported (Supplementary Material 1).

When reporting sightings, the public were requested to provide a location (a physical address or GPS co-ordinates for accuracy) as well as the approximate date when the sighting was made; this allowed me to determine whether this reflects the current distribution vs. sightings of mongoose from, for example, a few years previously. Since time frames were given, seasonal data could not be assessed. I created a survey that contained 16 questions pertaining to the yellow or slender mongoose occurrence (Supplementary Material 2). These questions included additional information on the sighting (e.g. time of day, number of individuals seen), as well as questions about the personal opinions of having these mongoose in urban areas. Those completing the survey were given the option to complete whichever questions they wanted and did not need to complete the entire survey. I followed this protocol in order to minimize the risk of their losing interest in completing a long survey. The public could choose to report sightings via Facebook, by email, or through the survey, and all data were stored anonymously.

Data analysis

Reponses from the survey were automatically recorded in an Excel spreadsheet for later analysis. Locations of sightings from these surveys were all converted to GPS co-ordinates to create a list of location points; additional sightings reported on the Facebook page or via the email address were converted to GPS co-ordinates and added to this list. All reported locations were plotted using Google Maps. Each plot was colour coded for species, and the resultant plotted maps were exported into QGIS (QGIS Development Team, Version 3.2.3, 2018) for further analysis.

I used the MCP polygon method to illustrate the extent of occurrences around Johannesburg. MCP polygons provides a simple illustration of the areas that encompass a set percentage of recorded GPS locations, and since I only had one GPS point for each sighting, it is beneficial as I could include all points in generating polygons. I used the R package adehabitatHR (Calenge 2006) to construct MCP polygons that encompass 50% (referred to as

the core area where majority of sightings occurred; Balmforth 2004), 95% and 100% of locations recorded for each species to determine where the majority of sightings occurred, and where overlap might occur between the species. These polygons were exported into QGIS, and overlaid with the plotted locations for comparison between species. The results of this study were all qualitatively assessed and no statistical analysis was performed. Those that reported sightings using the survey rarely completed the entire survey (only about 35% answered all questions) and the number of responses to each question overall was therefore inconsistent. Thus, some of these questions are discussed based on only a percentage of responses.

Results

The Urban Mongoose Project Facebook page and survey remained active from its inception in May 2015 until December 2018. During this period, a total of 285 sightings were reported through the various platforms, all of which were plotted using Google Maps (Figure 5). From the survey, 128 sightings were reported for yellow, and 64 for slender mongoose. In addition, from the Facebook Page and email account, 59 were reported for yellow, and 34 for slender mongoose. Reported sightings where respondents were unsure of the species (n = 6) were excluded from assessment. The peak in responses was in late 2015/early 2016, although citizens were still reporting sightings up until November 2018 (Figure 6). For the majority of reports, the mongoose was seen within the past week or past month, and less than 5% of reported sightings fell into 'seen more than one year ago' category (Figure 7). I therefore assumed that the reports reflected the prevailing distribution of mongoose in the greater Johannesburg area.

The majority of sightings were clustered in the Johannesburg north and Johannesburg south areas (Figure 5). A large central portion of the Johannesburg area and furthest reaches into the Johannesburg south area had no reported sightings. Sporadic reports were received from the East Rand and West Rand which border greater Johannesburg (Figure 4). The Meyersdal Nature Area is located on the border of Greater Johannesburg and the East Rand (Supplementary material 3). Since my previous research (Chapters 2 – 5) was conducted in the Meyersdal Nature Area, people there were more familiar with my project. Hence, I expected sightings to be reported in this area. Nonetheless, I included all of these reported sightings since it represents the prevailing distribution of mongoose in urban regions.

The responses showed areas of occurrence where the yellow mongoose were more common than the slender mongoose, and vice versa. I measured a 10 km radius around isolated mongoose sightings plotted on the map and found that there were instances where reported sightings of one species did not include the sighting of the other species within a 10 km radius (Figure 5). This was solely based on what respondents reported, and hence may not be an exhaustive appraisal mongoose occurrence.

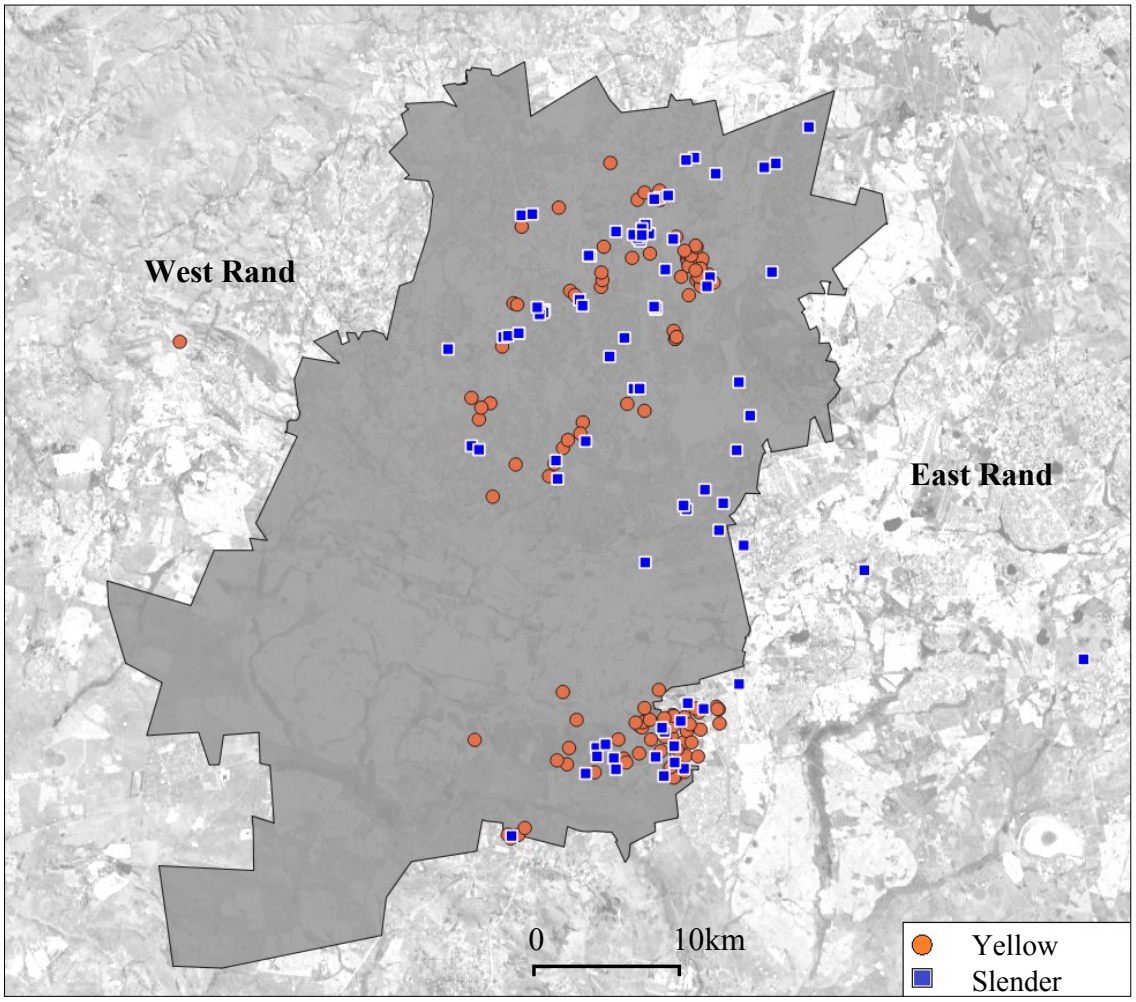

Figure 5. Locations of reported sightings of yellow and slender mongoose from 2015 to 2018 in the greater Johannesburg area (dark grey outlined area) reported via Facebook, email and a survey.

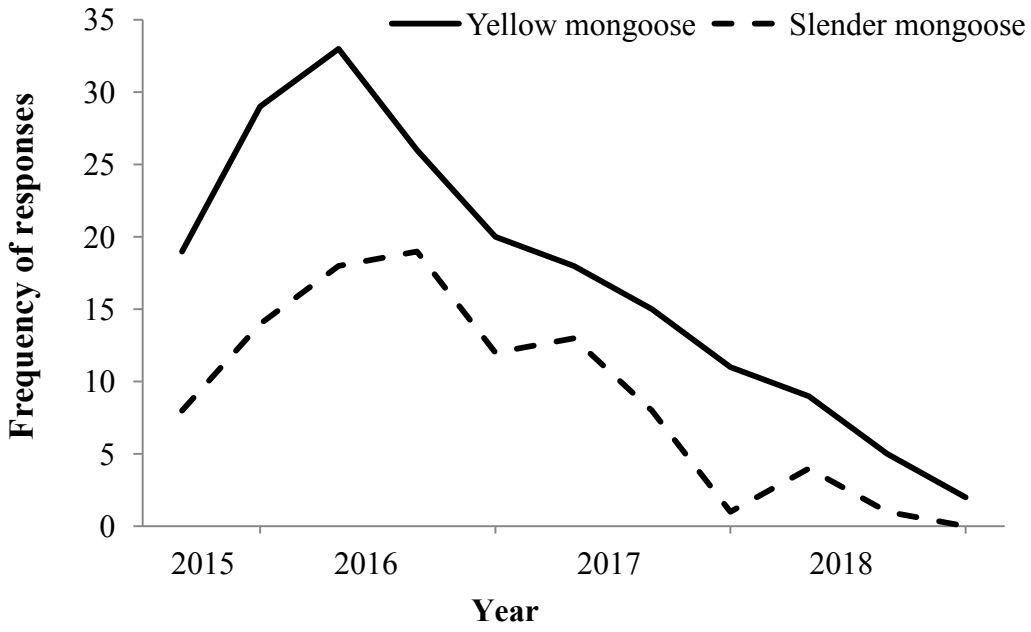

Figure 6. Frequency graph showing the number of responses over the entire study period (mid 2015 - end 2018).

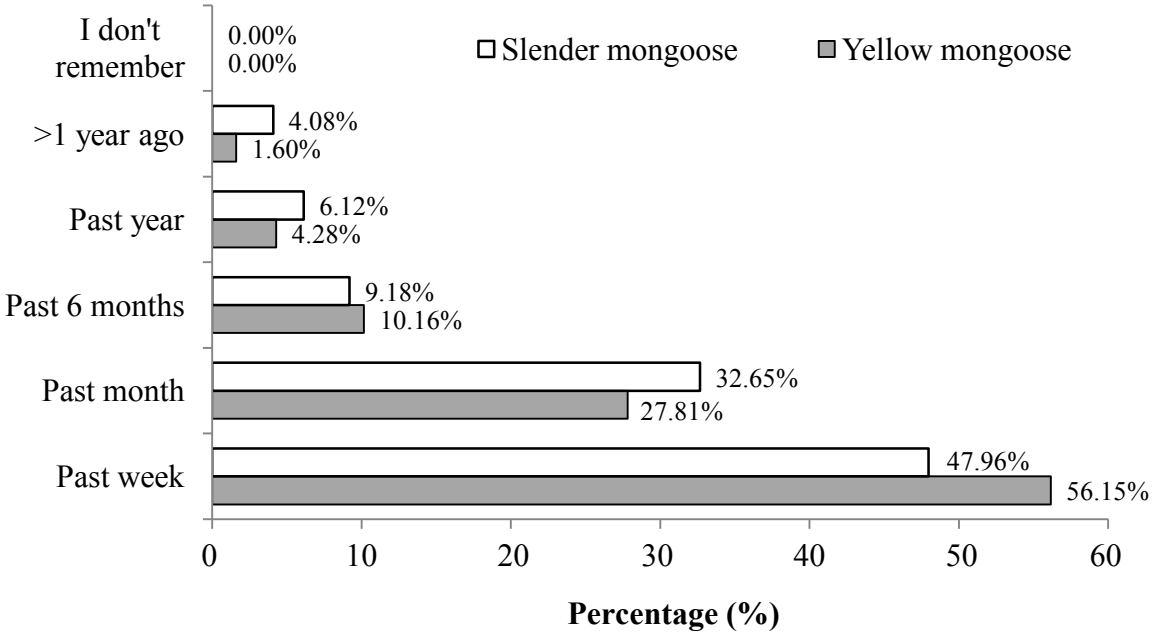

Figure 7. Responses from the public regarding when last yellow or slender mongoose were sighted in the greater Johannesburg area.

A high degree of overlap was evident in the MCP polygons generated (Figure 8). At the 100% isopleth level, which included all sightings for each species, the polygons covered an area of 122.34 km^2 for yellow mongoose, and 136.28 km^2 for slender mongoose (Table 1). Since a single sighting of yellow mongoose was reported in the West Rand, and isolated sightings of only slender mongoose in regions of the East Rand (Figure 7), this greatly extended the polygons for each species at the 100% isopleth level. The area of overlap was greatest at this level (100.92 km^2), centralised around the westerly occurrence for slender mongoose and easterly occurrence of yellow mongoose. For the 95% isopleth level, the area of occurrence for slender mongoose (107.52 km^2) remained greater than yellow mongoose (94.44 km^2). The area of overlap between species at the 95% isopleth level (87.73 km^2) encompassed the majority of yellow mongoose sightings included in the 95% polygon (excluding n = 6), while several more locations of the slender mongoose's 95% polygon fell outside of the area of overlap (n = 19).

Similarly to the 100% isopleth, the occurrence of both species at the 95% isopleth level included the Meyersdal Nature Area south of Johannesburg. Interestingly, at the 50% isopleth level, the area of occurrence was smaller for slender mongoose (60.54 km^2) than yellow mongoose (84.29 km^2). The area of overlap between the species (57.02 km^2) encompassed almost the entire 50% polygon of slender mongoose in the north of Johannesburg, while the yellow mongoose's 50% polygon showed its range still extended into the Meyersdal Nature Area (Figure 7).

Table 1. The size of the area (in km^2) of occurrence, and the size of the overlap area of the yellow and slender mongoose in greater Johannesburg, South Africa.

Isopleth level	Occurrence area (km^2)		Overlap area (km^2)
	Yellow mongoose	Slender mongoose	
100%	122.34	136.28	100.92
95%	94.44	107.52	87.73
50%	84.29	60.54	57.02

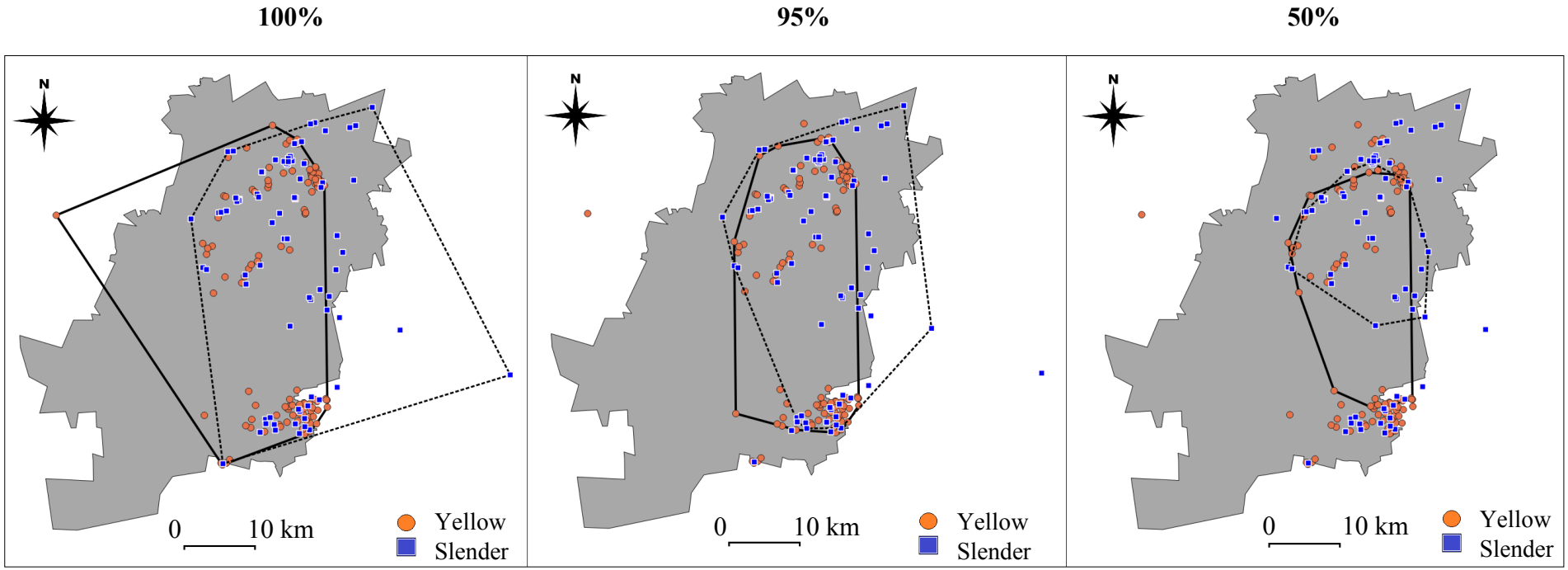

Figure 8. The polygons generated at the 100%, 95% and 50% MCP isopleths showing overlap between reported sightings of yellow mongoose (solid line) and slender mongoose (dotted line) in the greater Johannesburg area.

Summary of responses to survey questions

The surveys revealed that mongoose were seen all year around (60% of respondents), and were mostly active during the daylight hours (8 am to 5 pm; 71%), followed by early evenings (20%). The remainder were reportedly seen at times either in the early morning (before 8 am; 6%), or later evenings (after 5 pm; 3%). Mongoose were most commonly observed travelling (73% yellow; 78% slender) followed by foraging/feeding for yellow mongoose (26%; only 2.4% reported for slender mongoose) and sunbathing for slender mongoose (9.8%). Mongoose were sighted mostly individually (53% yellow; 91% slender), followed by pairs (25 % yellow, 6% slender), and groups of 3 up to 5 individuals (22% yellow; 3% slender). Interestingly, none reported larger groups in a single sighting. The most common reactions of the mongoose to human presence was, for yellow and slender respectively: i) ran away (53%; 49%); ii) walked away (21%; 10%); and iii) didn't appear to notice/care about a person's presence (26%; 37%). Mongoose were generally observed in urban green areas including parks, golf courses, school fields, and along rivers of residential estates, likely because they are more visible in these open spaces. Both species were also commonly seen in residential gardens, with yellow mongoose being more common. Several respondents (n = 41) reported that mongoose fed in their gardens, investigated garbage bins and ate from dog food bowls left outside. Additionally, one respondent reported that a slender mongoose caught and killed his garden rabbits, and another reported a yellow mongoose catching and killing a bird in their garden. Nevertheless both respondents had a positive response about their presence despite the above mentioned encounters.

When asked about their personal opinions on the mongoose being present in our urban areas, the most common responses were 'they are part of our biodiversity' and 'they are cute and don't bother me'. Almost 100% of respondents to the question scored their occurrence as positive, and that they should be conserved, while one respondent highlighted the concern of mongoose being rabies carriers and should be chased away when seen in gardens.

Discussion

Previous published accounts of the distribution of yellow and slender mongoose have not addressed their occurrence in urban areas in South Africa, except for my recent studies (Cronk and Pillay, 2018; Cronk and Pillay, 2019). The aim of this study was therefore to

investigate the occurrence and areas of overlap within a large urban region, the Greater Johannesburg area. Citizens reported that mongoose were mostly sighted within the past year, indicating that the data are representative of the prevailing occurrence patterns in the Johannesburg area. The lack of reported sightings in some regions of Johannesburg (particularly the west and south of Johannesburg) may have been as a result of the extremely built up residential, mining and industrial areas located in these regions. Furthermore, the lack of green space and extremely high human density in central Johannesburg is not conducive to mongoose occurrence and might explain the lack sightings here. In addition, the citizens living in these areas generally fall into the low income bracket, with limited/no access to the online platforms, unfamiliarity with my project, or simply a lack of interest in the research, which may all have contributed to no reported sightings for these regions. Consequently, a lack of sightings may not be a true reflection of mongoose occurrence in these areas.

Previous assessments of the distribution of both species (Do Linh San *et al.,* 2015; Do Linh San *et al*., 2016; Do Linh San and Maddock, 2016; Le Roux *et al.,* 2016) made no mention of their occurrence in urban areas, including the greater Johannesburg area. I had hoped that responses from the survey would aid in my assessing whether the mongoose occurrence in urban areas is a recent phenomenon, but my data set did not provide such confirmation. I did however receive one response stating that it was the first time in 15 years of living on a property that the owner had seen yellow mongoose in the garden, citing a new business development nearby her house as the reason for them leaving that open site and entering her garden – this however could not be confirmed. Furthermore, another respondent reported they had not previously seen slender mongoose on their plots located in northern Johannesburg, where both species occur in recent years.

It is not clear from the historical distribution maps which regions of greater Johannesburg have had previous records of mongoose occurrence (Figure 3). However, from the distribution generated in my study (Figure 5), it would appear that occurrence is largely similar to historical maps in that they do occur in Johannesburg, but also spreading further through greater Johannesburg. This could indicate fewer occurrences in the area previously, and an increase in their occurrence more recently coinciding with development and expansion (commercial and residential buildings) diminishing natural green spaces for wildlife, which then enter gardens etc. Alternatively, the shift in the distribution northwards in both species in South Africa (post 1999; Do Linh San *et al*., 2016; Le Roux *et al*., 2016), particularly so in

the slender mongoose would indicate a more recent occurrence in Johannesburg within the past 20 years. The historical distribution of the slender mongoose (Figure 3b) appears to show much less of an occurrence in greater Johannesburg than the same maps for yellow mongoose (Figure 3a). Yet, in my study (Figure 5), it would appear that the distribution of both species covers a wider area than previously recorded, and now appears to include urban areas.

It is evident that the occurrence of yellow and slender mongoose is not unique to the Meyersdal Nature Area, since there were a few concentrated areas of occurrence ±40 km to the north of Meyersdal. My findings suggest that there are some areas where yellow mongoose were sighted and not slender, and vice versa. Therefore, in line with their nationwide distribution, it may just be that there are locations more suited to each species, or more likely that the other species was just not sighted/reported. Alternatively, as previously mentioned, resource partitioning has been observed in the Meyersdal mongoose populations, (Cronk and Pillay, 2018, 2019). This may account for the general population of yellow and slender mongoose having variable occurrence in greater Johannesburg based on available resources in these areas. This, however, will need to be addressed by systematic assessments of the resource composition (e.g. food abundance and availability, habitat type) of the different areas where each species occurred in Johannesburg.

Based on the responses to survey questions, I was able to assess some of the habits of the sighted urban yellow and slender mongoose. Similar to previous chapters, mongoose were diurnal (Chapter 4), reportedly fed on anthropogenic foods available (Cronk and Pillay, 2019), and yellow mongoose occurred more frequently in residential gardens and were less perturbed by human presences (Chapter 4). Given that human-wildlife conflict in urban areas is a potential concern, based on the responses to the survey, yellow and slender mongoose integrate well within human settlements in the greater Johannesburg area, and there does not appear to be a threat of human persecution. Since the general consensus was a positive opinion regarding their occurrence in urban Johannesburg, there is an expectation that these species will continue to thrive in urban areas provided their access to suitable habitat, and preferential resources (including access to, and use of, residential properties and anthropogenic resources).

The GPS locations and polygons generated show potentially high overlap between yellow and slender mongoose throughout the greater Johannesburg area, including residential

gardens. It is interesting that the slender mongoose had a greater area of occurrence overall (both 95% and 100% isopleths), yet the core area (50%) of yellow mongoose occurrence covered a larger area. I initially thought that including sightings in Meyersdal would bias the results by over representing occurrence due to the knowledge of residents about my project. However, despite the known occurrence of slender mongoose in Meyersdal, their core area of occurrence (from reported sightings) excluded the Meyersdal area. Since the core area for yellow mongoose still included Meyersdal (as well as the northerly regions included in the slender mongoose core area), it may suggest that the yellow mongoose are more generalist, and the slender mongoose is rather more focused in the northerly regions due to preferential resources. Alternatively, Meyersdal may be anomalous in that it provides suitable habitats supporting both species, whereas these other northerly regions may not. Nonetheless, similar to the historical maps, these polygons show that both co-occurrence and separation between the species is evident in the greater Johannesburg area.

I showed that both yellow and slender mongoose occur in the greater Johannesburg area, separately and in overlapping areas. Since the greatest response to the project occurred in the early stages of its inception, the occurrence of yellow and slender mongoose may still be under assessed at this time, since almost four years had lapsed since the start of the project. With dwindling interest in the project over time, the sightings of both species in urban areas were not always reported, such that their distribution may be even greater than reported here. Nonetheless, the results of this study give a good indication of the current presence of these species in urban Johannesburg which has not previously been recorded. The reported use of anthropogenic resources appears to aid largely towards their apparent thriving in urban Johannesburg. I therefore suggest that these species are also coexisting in urban settings in other parts greater Johannesburg and by extension perhaps nationally, occurring in and exploiting urban gardens just as they do in the Meyersdal estates. Since the degree of resource partitioning was not assessed over the entire greater Johannesburg area, I believe Meyersdal can be used as a proxy to infer how yellow and slender mongoose coexist in urban areas in Johannesburg.

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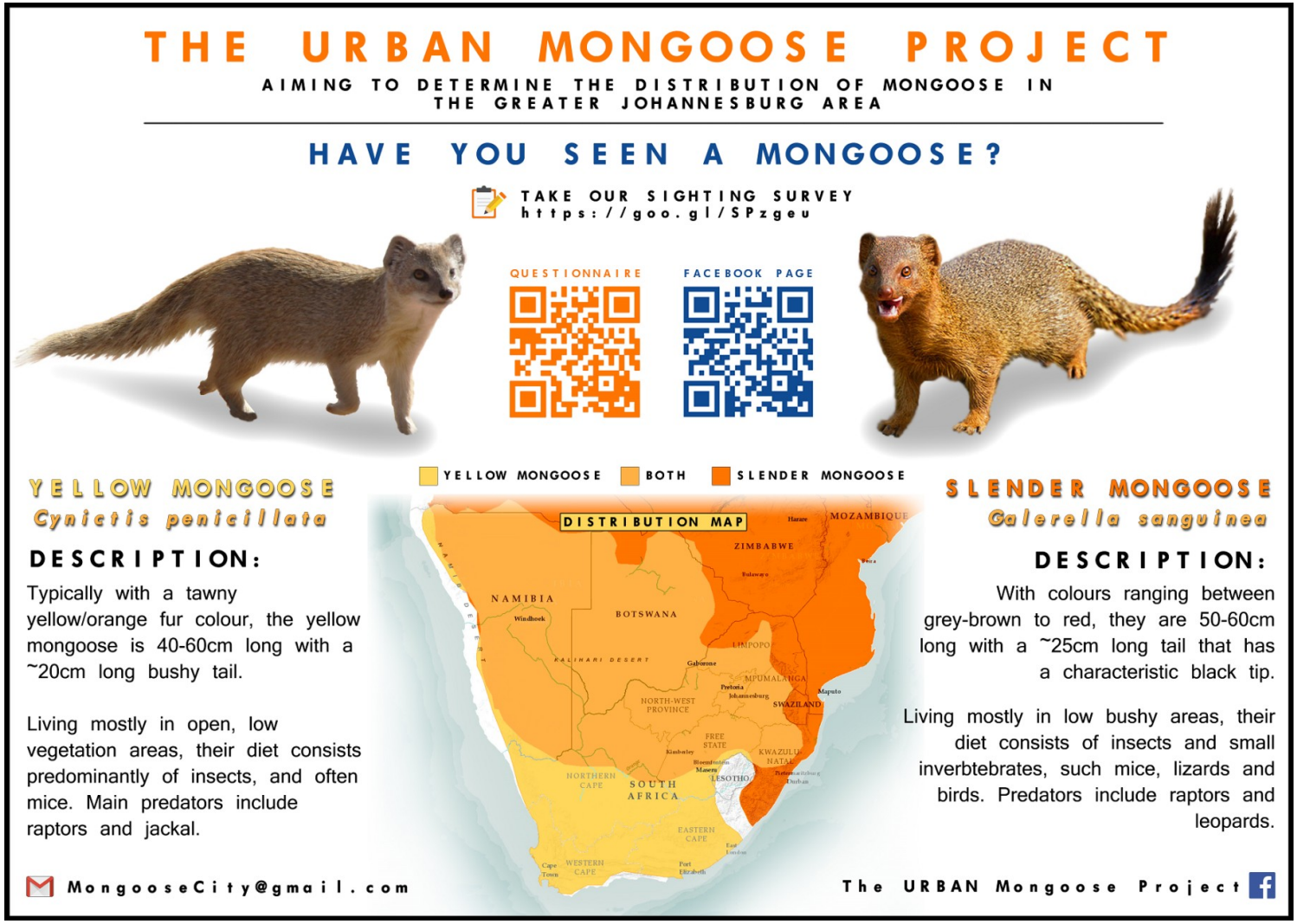
Supplementary material 1



The Urban Mongoose Project poster that was distributed to members of the public in the greater Johannesburg area

Supplementary material 2

Mongoose sightings in the Greater Johannesburg Area

My name is Nadine Cronk. The aim of my survey is to try and establish where the yellow mongoose (*Cynictis penicillata* - Witkwasmuishond) and the slender mongoose (*Galerella sanguinea* - Swartkwasmuishond) occur within the greater Johannesburg area and whether they are successfully living in urban centres. Should any further information be required, participants can either look at our Facebook page - www.facebook.com/THEURBANMONGOOSEPROJECT/; or send any enquiries to the MongooseCity@gmail.com. Participants are urged to read through the following before agreeing to participate.

Consent to participate:
• I have had the opportunity to ask questions and have had them answered
• I understand that all personal information will remain confidential and that data gathered in this study may be stored anonymously and securely, and may be used for future research.
• I understand 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 understand the details of the research and give my consent for my participation in the survey

Question 1

Are you aware that there are different species of mongoose occurring in Johannesburg?
☐ Yes

☐ No

Question 2

If you answered yes to Question 1, how did you know there are mongooses in Johannesburg?
☐ I have seen them

☐ Family or friends have seen them

☐ Other:

Question 3

Have you personally seen either yellow or slender mongoose in Johannesburg? **(Complete page 2 to 9 if you have seen both mongoose species).**

☐ Yes; seen a yellow mongoose (go to page 2)

☐ Yes; seen a slender mongoose (go to page 6)

☐ No

Personal sightings of yellow mongoose

Question 1.1

If you answered yes to Question 3, could you specify when you saw a yellow mongoose?

- ☐ The past week
- ☐ The past month
- ☐ The past 6 months
- ☐ The past year
- ☐ > 1 year ago
- ☐ I don't remember

Question 1.2

If you have seen the yellow mongoose in the greater Johannesburg area, please provide the GPS co-ordinates or a physical address for the location/s. (NB. This will be kept anonymous).

_____

Question 1.3

What best describes how often you see yellow mongooses?

- ☐ Daily
- ☐ Weekly
- ☐ Monthly
- ☐ Once a year
- ☐ I've seen a yellow mongoose once

Question 1.4

What time of the year do you mostly see yellow mongoose?

- ☐ Summer (December-February)
- ☐ Autumn (March-May)
- ☐ Winter (June-August)
- ☐ Spring (September-November)

Question 1.5

What time of the day do you mostly see yellow mongooses?

- ☐ Early morning/dawn (5-8 am)
- ☐ During the daylight hours (8 am-5 pm)
- ☐ Early evening (5-7 pm)
- ☐ Night (7 pm onwards)

Question 1.6

What was the yellow mongoose doing when you saw it?

- ☐ Eating
- ☐ Sleeping
- ☐ Laying in the sun
- ☐ Running
- ☐ Other: _____

Question 1.7

What best describes the yellow mongoose's reaction to your presence? (Check all boxes that apply).

- ☐ Ran away
- ☐ Walked away
- ☐ Snarled at you
- ☐ Followed you
- ☐ Didn't appear to notice you
- ☐ It chased or attacked you
- ☐ It chased or attacked your pet
- ☐ Other: _____

Question 1.8

What were you doing at the time when you saw a yellow mongoose? (e.g. jogging or driving).

Question 1.9

Can you recall how many you saw together in one sighting?

- ☐ 1
- ☐ 2 individuals
- ☐ 3-5 individuals
- ☐ 5+ individuals (specify number: _____)

Question 1.10

What is your general opinion of the yellow mongooses?

- ☐ Positive
- ☐ Negative

Question 1.11

Based on the previous question, on a scale of 1 - 10, please elaborate on your answer.

Question 1.12

Have they caused any damage to you (or someone else you may know) property or person?

- ☐ Yes
- ☐ No

Question 1.13

If you answered yes to Question 1.12, please elaborate on your answer as well as providing information on how you dealt with the situation.

Question 1.14

Would you like to continue seeing yellow mongoose in Johannesburg?

- ☐ Yes
- ☐ No

Question 1.15

If you answered yes to Question 1.14, please specify why.

- ☐ They are part of our biodiversity
- ☐ They manage pests (e.g. insects)
- ☐ Urban areas make it safer for them
- ☐ They are cute and don't bother me

Question 1.16

If you answered no to question 1.14, please specify why.

- ☐ They are pests
- ☐ They carry diseases
- ☐ They bother my pets
- ☐ They damage my property

Personal sightings of slender mongoose

Question 2.1

If you answered yes to Question 3, could you specify when you saw a slender mongoose?

- ☐ The past week
- ☐ The past month
- ☐ The past 6 months
- ☐ The past year
- ☐ > 1 year ago
- ☐ I don't remember

Question 2.2

If you have seen the slender mongoose in the greater Johannesburg area, please provide the GPS co-ordinates or a physical address for the location/s. (NB. This information will be used to plot occurrences on a map and will be kept anonymous).

_____

Question 2.3

What best describes how often you see slender mongooses?

- ☐ Daily
- ☐ Weekly
- ☐ Monthly
- ☐ Once a year
- ☐ I've only seen a slender mongoose once

Question 2.4

What time of the year do you mostly see slender mongoose?

- ☐ Summer (December-February)
- ☐ Autumn (March-May)
- ☐ Winter (June-August)
- ☐ Spring (September-November)

Question 2.5

What time of the day do you mostly see slender mongooses?

- ☐ Early morning/dawn (5-8 am)
- ☐ During the daylight hours (8am-5 pm)
- ☐ Early evening (5-7 pm)
- ☐ Night (7 pm onwards)

Question 2.6

What was the slender mongoose doing when you saw it?

- ☐ Eating
- ☐ Sleeping
- ☐ Laying in the sun
- ☐ Running
- ☐ Other: _____

Question 2.7

What best describes the slender mongoose's reaction to your presence? (Check all boxes that apply).

- ☐ Ran away
- ☐ Walked away
- ☐ Snarled at you
- ☐ Followed you
- ☐ Didn't notice you
- ☐ It chased or attacked you
- ☐ It chased or attacked your pet
- ☐ Other: _____

Question 2.8

What were you doing at the time when you saw a slender mongoose? (e.g. jogging or driving).

Question 2.9

Can you recall how many you saw together in one sighting?

- ☐ 1
- ☐ 2 individuals
- ☐ 3-5 individuals
- ☐ 5+ individuals (specify number: _____)

Question 2.10

What is your general opinion of the slender mongooses?

- ☐ Positive
- ☐ Negative

Question 2.11

Based on the previous question, on a scale of 1 - 10, please elaborate on your answer.

Question 2.12

Have they caused any damage to you (or someone else you may know) property or person?

- ☐ Yes
- ☐ No

Question 2.13

If you answered yes to Question 1.12, please elaborate on your answer as well as providing information on how you dealt with the situation.

Question 2.14

Would you like to continue seeing slender mongoose in Johannesburg?

- ☐ Yes
- ☐ No

Question 2.15

If you answered yes to Question 1.14, please specify why.

- ☐ They are part of our biodiversity
- ☐ They manage pests (e.g. insects)
- ☐ Urban areas make it safer for them
- ☐ They are cute and don't bother me

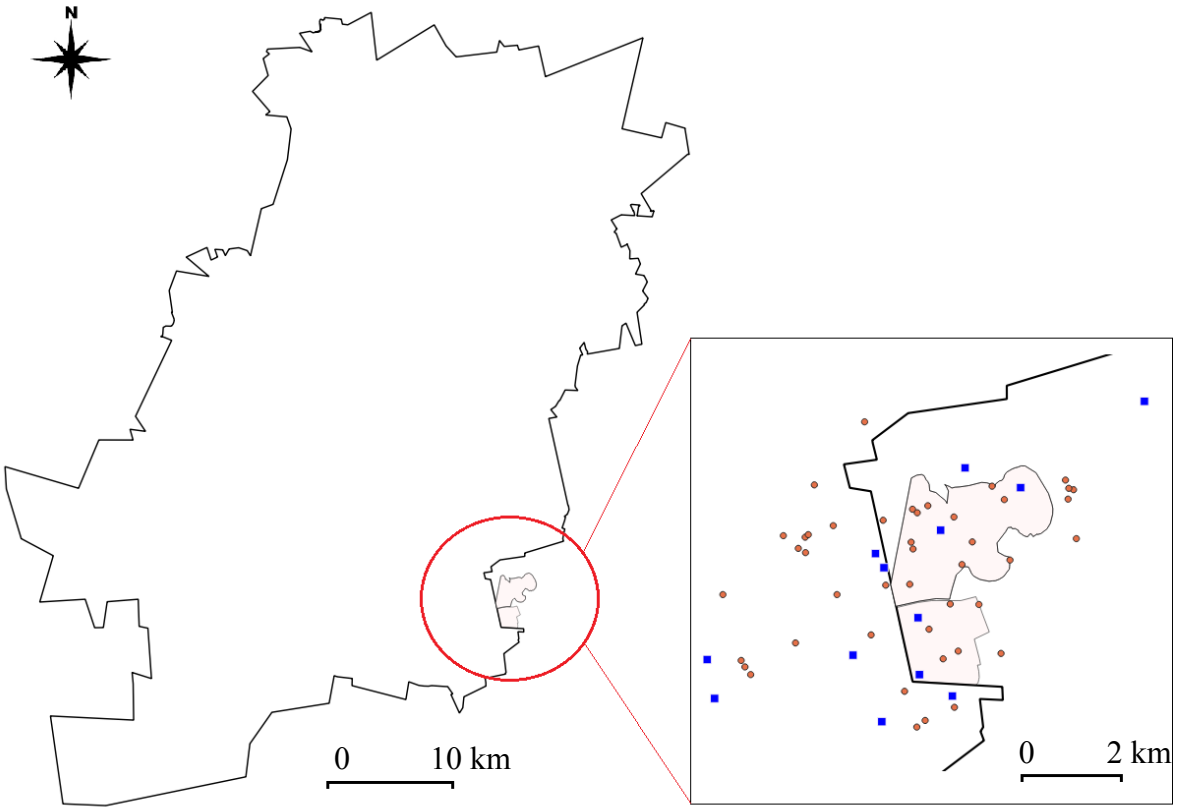
Question 2.16

If you answered no to question 1.14, please specify why.

- ☐ They are pests
- ☐ They carry diseases
- ☐ They bother my pets
- ☐ They damage my property

THANK YOU!!

Supplementary material 3



Mapped outline of the greater Johannesburg area showing the location of the Meyersdal Nature Area (encircled) and inset showing reported sightings of yellow mongoose (orange circles) and slender mongoose (blue squares) by the public in and around the Meyersdal estates.

CHAPTER SEVEN

General Discussion

As the human population continues to grow, urbanisation brings about anthropogenically driven change of natural landscapes (McKinney 2002). Urban areas provide a plethora of resources, and animals that are able to effectively exploit these resources tend to thrive there (Bateman and Flemming, 2012; Duduś *et al.,* 2014; Šálek *et al*., 2015). Since urban expansion could inevitably result in more wildlife occurring in urban areas, biologically similar species are bound to co-occur there. In order to contribute to the conservation of urban wildlife that are affected by human-induced environmental change, it is imperative to understand the ecology of these species, including how they could coexist in urban areas, in order to introduce effective management plans where necessary.

Yellow and slender mongoose are common small carnivores in southern Africa, but the ecology of these species in an urban environment was not addressed until the current study. While studies on the coexistence of each of these species with other carnivores has been widely studied, none has included studying the ecology and coexistence of these two species, nor am I aware of any studies based on the coexistence of two such biologically similar species (in all aspects of diet, space, activity, and distribution) in an urban environment.

In this thesis, I investigated the possible mechanisms of coexistence through resource partitioning between these sympatric mongoose species in an urban area. Considering three main niche dimensions for each species, namely diet, habitat, and spatio-temporal occurrence, I also evaluated the overlap between these two species in each dimension, and where possible, assessed seasonal variation in the overlap. In addition, I assessed the home range and overlap with human residents in the yellow mongoose, and evaluated the occurrence of these two species over a larger urban region, the greater Johannesburg area. This study was conducted from March 2015 to December 2018 and the primary study site was the Meyersdal Nature Area, on the border of the south of Johannesburg. Data collection took place within two estates, the Meyersdal Eco-Estate and Nature Estate, described as more and less urbanized estates respectively (Cronk and Pillay, 2018).

Summary of objectives and findings

This study had five main objectives. Firstly, I assessed the diet of yellow and slender mongoose through scat analysis, and determined dietary overlap (Chapter 2). I showed that the diets for both species were similar to non-urban counterparts in the occurrence of insect and vertebrate food items, with insects being more prevalent in yellow mongoose and vertebrate prey being more frequent in slender mongoose scat. While diet has been shown to vary geographically in both species (Skinner and Chimimba, 2005), the general consensus from my study is that the yellow mongoose is primarily insectivorous and the slender mongoose is a generalist carnivore. I also showed that the yellow mongoose more frequently consumed anthropogenic resources. Seasonal variation was evident in the occurrence of food items in scats: insects occurred more frequently in scat in warmer months in both species, while the transition to colder periods showed reduced occurrence of insects and an increase in anthropogenic items in yellow mongoose and vertebrate prey in slender mongoose scat. Seasonal variation in prey availability is largely responsible for these shifts in diet (Nel and Kok, 1999; Poessel *et al*., 2017). In a comparison between estates, anthropogenic items did not occur in scat collected in the Nature Estate while it formed part of the diet of mongoose in the Eco-Estate, particularly for the yellow mongoose during colder periods. Previous studies have shown that higher density housing and closer contact with human residents in urban areas results in greater consumption of anthropogenic food items by wildlife (Poessel *et al*., 2017). Animals supplement their diets in winter with athropogenically provided food items, especially since urban areas provide nutritional seasonal food security (Bateman and Flemming, 2012). Dietary overlap was lower in the Eco-Estate, likely due to the more varied food items (including anthropogenic items) in the scat of both species of mongoose in this estate. Seasonally, overlap was greatest in summer and lowest in winter in both estates. Changes in dietary composition may be due to interspecific competition, and during periods of low resources abundance (e.g. in this case, insects in winter), species increase the diet breadth and consumption of other available resources (Pavey *et* al., 2008) consequently reducing dietary overlap (Heng *et al*., 2018).

In Chapter 3, I had predicted that yellow mongoose would choose insects over meat (simulating vertebrate prey) on the basis of previous studies showing a more insectivorous diet in yellow mongoose (supported by Chapter 2). However, since both species chose meat first, I am inclined to conclude that both species have a preference for meat (vertebrates) over insects. Since food choices are predicated on choosing the most profitable prey while

expending the least amount of energy (Verdolin 2006), for yellow mongoose this may be hunting for insects versus small vertebrates (i.e. meat). However, the relative ease of access of the food items presented in the food choice tests eliminated the need for the finding/hunting and capturing of any food/prey. Hence, this largely could have impacted on the choices of the yellow mongoose.

Secondly, I investigated food choice and feeding behaviour. I predicted that meat and insects would be favoured in food choice tests for both species (since they are carnivores), and that yellow mongoose would display a more bold approach to novel items than the slender mongoose. I also expected that carrion baited feeding stations would be more frequented by slender mongoose (since they were previously shown to do so; Vaughan 1976). I showed that both species preferred meat above all, followed by insects. Between estates, however, yellow mongoose in the Eco-Estate preferred bread over insects. The latency to approach and consume provided food was lower in yellow than in slender mongoose, suggesting a more bold temperament (Chapman *et al.,* 2012; Lowry *et al.,* 2013). Additionally, slender mongoose occurred significantly more often at carcass baited stations, consuming meat off the carcasses (more so in winter), and appeared to aggressively exclude yellow mongoose.

Thirdly, I predicted that yellow mongoose would occur in open areas near residents, while slender mongoose would occur in dense/covered areas further away from residents. Bold, more habituated individuals (i.e. those with a tolerance for humans; Gehrt *et al*., 2010) characterise species adapted to urban areas (Luniak 2004; Bateman and Flemming, 2012), so I expected the more habituated species (yellow mongoose; Cronk and Pillay, 2018) to occur more frequently near residents. As a result, I expected no spatial overlap, but some temporal overlap (with overlap increasing during less challenging colder periods), and no combined spatio-temporal overlap. Here, I showed that: yellow mongoose were more common in open habitats near human residents and slender mongoose in covered habitats further away from human residents, with no seasonal variation, indicating low spatial overlap; both species exhibited bimodal peaks in activity that differed between species (slender mongoose peaking in activity earlier and also later in the day than yellow mongoose); temporal overlap was evident, and was greater in the Eco-Estate; and no complete spatio-temporal overlap was evident.

Fourthly, I assessed home range and overlap with residents in the yellow mongoose. I hypothesized smaller home range sizes overall in these urban mongoose in comparison to

other studies in the literature, larger home range sizes in the Nature Estate, larger home ranges in males, greater overlap with human residents in the Eco-Estate, and seasonal variation in home range size and in overlap with human residents. I showed that home range sizes were, on average, smaller than those in other studies conducted on non-urban populations (e.g. Balmforth 2004; Le Roux *et al.,* 2008). Several studies have shown that home range sizes of carnivores decrease in urban areas due to an increase in resource availability and population densities (Herr 2008; Gould and Andelt, 2013; Šálek *et al*., 2015; Walton *et al*., 2017). While not statistically significant (as in previous studies; e.g. Zumpt 1976), home range sizes were slightly larger in males than in females, larger in the Nature Estate compared to the Eco-Estate, and varied seasonally with home range sizes being larger in the autumn and summer seasons (non-breeding period). It was also evident that overlap with human residents was greater in the Eco-Estate, particularly during colder periods. Generally, the spatio-temporal availability of food largely impacts the home range size and spacing in carnivores, (Elfström *et al.,* 2014). Thus, the greater use of anthropogenic resources in the Eco-Estate (Chapter 2) could have resulted in their smaller home range sizes in winter. Since two of the mongoose made excursions between the estates, there is potential for pseudo-replication between estates; however, findings in the data chapters were considered to be sufficient to distinguish estates.

Lastly, I used a citizen sciences approach to determine the occurrence and areas of overlap of yellow and slender mongoose in greater Johannesburg. Results showed that slender mongoose occurred over a larger area than yellow mongoose, and that both species overlapped extensively throughout greater Johannesburg, particularly concentrated in the north of Johannesburg. However, areas of individual species occurrence were also evident. Citizens that reported sightings mostly had a positive attitude to the presence of the mongoose in urban areas.

Evidence of resource partitioning facilitating coexistence

The results of my study show that resource partitioning does not appear evident in one niche dimension exclusively, but rather that the differences in the use of a combination of diet, space and spatio-temporal habitat use, facilitates coexistence between the yellow and slender mongoose.

While the dietary overlap index was relatively high (Chapter 2), at a finer scale, these mongoose species differ in the relative frequency and timing of individual components in scats, thereby presenting evidence for trophic resource (i.e. available food/prey) partitioning. Similarly, dingoes *Canis lupus dingo* and foxes *Vulpes vulpes* have been shown to have extensive dietary overlap (Pianka's index >0.8), yet these species differed in the relative size of the prey consumed, indicating significant differences in diet (Cupples *et al.,* 2011). Moreover, the preference for anthropogenic items (Chapter 3), along with the greater occurrence of anthropogenic items in yellow mongoose scat (specifically in the Eco-Estate with greater human resident contact), and the affinity for mammals (Chapter 2) and carrion in slender mongoose (Chapter 3), suggest that within this estate, particularly, differences in diet and food preference aids in species coexistence. In the Nature Estate, while dietary overlap was even greater than in the Eco-Estate, the mongoose species still differed in the main food items consumed. Additionally, since I could not measure indigestible anthropogenic items (Allen *et al.,* 2016), the use of anthropogenic resources by both mongoose species may be even greater than reported, but I expect this occurrence will remain higher in yellow mongoose.

In the Eco-Estate, the yellow mongoose occurred more frequently closer to human residents (Chapter 4), in particular residential gardens in winter (Chapter 5), which would explain the higher occurrence of anthropogenic items in the diet during this time (Chapter 2). The citizens survey results also showed yellow mongoose were sighted regularly feeding in residential gardens (Chapter 6), which supports the findings that yellow mongoose are more inclined to occur near residents and use anthropogenic resources, but also shows that slender mongoose, to a lesser extent, also occur in gardens. An important caveat here may be that the yellow mongoose population size and density is larger than that of slender mongoose in urban areas, which may explain their more frequent sightings. While slender mongoose were often visible (by direct observation and camera traps), the number and locations of dens were not easily located, and therefore population density could not be determined. The population density of non-urban slender mongoose, however, is estimated between 1 and 10 individuals per 100 ha (Rood and Waser, 1978; Graw *et al*., 2016), which is lower than that of yellow mongoose (Chapter 5). If the population density of slender mongoose is lower at my study sites, as assumed here, it is not known whether this is a cause or a consequence of its coexistence with yellow mongoose.

The greater occurrence of yellow mongoose in open habitats (Chapter 4) supports reports in previous studies that suggest that this is a result of higher insect availability (their

main prey) in these types of habitats (Nel and Kok 1999; Blaum and Rossmanith, 2010; Cronk and Pillay, 2019). Slender mongoose on the other hand were more common in more dense and covered areas (Chapter 4), and this habitat supports their main prey, small mammals (Ramesh and Downs 2014; Cronk and Pillay, 2019). Additionally, the occurrence of slender mongoose more commonly further away from residents (Chapter 4) might explain the greatly reduced occurrence of anthropogenic items in their scat compared to yellow mongoose (Chapter 2). The use of different micro-habitat types by carnivores is strongly affected by food availability and abundance (Pedrini *et al.,* 1995). Hence, I conclude that spatial partitioning is indeed evident, and since habitat preferences appear to be related to specific diet differences of the two mongoose species, a combination of diet and space largely contribute to their niche partitioning.

Complete temporal partitioning in overall diel activity was not evident as both species remained diurnal in urban areas as they do in non-urban areas (Skinner and Chimimba, 2015). The main active periods of both mongoose species occurred from early morning (sunrise) to just after sunset, but both had varying peak active periods, with the slender mongoose peaking earlier in the mornings and later in the evenings. Since the differences in the activity of the main prey types affect the foraging times of viverrids (Maddock, 1988), this may explain the differing peaks in active periods between species, which may suggest some temporal partitioning. This however further supports the notion that diet and prey availability play a large role in species coexistence in my study. Nonetheless, in the Eco-Estate, different spatial occurrence and lower spatial overlap naturally permits greater temporal overlap (i.e. both species being active in different areas at the similar times). Yet, in the Nature Estate, the greater spatial overlap had a concurrent reduction in temporal overlap (i.e. the mongoose occurred in the same space but at different times), providing evidence that mongoose may also incorporate temporal partitioning when necessary.

Based on the short survey of mongoose occurrence in Johannesburg, there are areas of individual occurrence and overlap between the species. Areas where these species overlap may offer similar cases of coexistence as in the Meyersdal estates. Thus, this study provides a better understanding of mongoose coexistence in the urban context as a whole. Moreover, while this coexistence does not appear unique to the Meyersdal area compared to a larger urban region (greater Johannesburg), it does appear that there are mechanisms of coexistence of mongoose in Meyersdal, that may be unique compared to those of mongoose in non-urban areas. It would be interesting to assess their coexistence in non-urban areas (removing the anthropogenic influence), to ascertain how they partition resources in areas of overlap.

Conclusion

I studied aspects of yellow and slender mongoose ecology pertaining to diet, activity and space use, and assessed how these species differ in their use of these resources as a mechanism facilitating coexistence. I used a combination of different techniques in these experiments to establish where species overlapped, and where and how they differed in these niche dimensions. My thesis contributes to the growing body of knowledge on urban ecology and particularly on the nature of yellow and slender mongoose occurring in urban areas. To my knowledge, my study provides the first empirical assessment of the diet, spatial and temporal occurrence and overlap of closely related carnivore species in an urban environment in order to evaluate their coexistence.

My results showed that, similar to other studies, urban wildlife will incorporate accessible anthropogenic resources in their diets and therefore will occur in close contact with human residents to do so. In line with the niche differentiation theory, different species partition resources to avoid interspecific competition, which aids in coexistence. Here, the yellow mongoose was more habituated to humans, more commonly using anthropogenic resources, while, in contrast, the slender mongoose has a specialized carnivorous diet more inclined to vertebrate prey in naturally covered habitats. In addition, slender mongoose aggressively excluding yellow mongoose from carcasses provides evidence of direct interference competition (Adams 2005). Furthermore, the smaller home range sizes in yellow mongoose may be a consequence of their behavioural responses to the changing environmental resources in urban areas. As defined by Blair (2001), the yellow and slender mongoose are both typical ‘urban adapters’ (more so for the yellow mongoose), likely to continue to thrive in urban areas and expand in their distribution within the urban landscape in South Africa. I found evidence that supports the findings that urban areas may be providing an abundance of resources that are able to support large coexisting populations. However, these species appear to also be displaying similar phenotypic characteristics as their non-urban counterparts, which may allow coexistence in the wild, particularly in the Nature Estate. In the Eco-Estate, on the other hand, both species appear to be responding flexibly to the urban environment over short geographic distances by incorporating anthropogenic items into their diets. This was more evident in the yellow mongoose which appears to exploit anthropogenic resources to a greater extent, giving them an advantage over slender mongoose in this urban setting.

Future studies

Since I concluded that urban areas provide increased food resources availability, an important consideration for future studies would be to include a prey availability and distribution analysis to test the conclusions based on diet and food choice raised here (Chapter 2 and Chapter 3). Furthermore, conducting a thorough analysis of the population density of each species would further help describe some of the outcomes in this study (e.g. home range size being related to population density in Chapter 5). Future studies would also benefit from investigating home range sizes of the slender mongoose concurrently with that of yellow mongoose to better interpret coexistence in the context of home range use and overlap between species. These studies should consist of a considerably larger sample size of simultaneously collared and tracked individuals. Lastly, studies would benefit from multiple study areas (both urban and non-urban) where these mongoose species coexist to assess whether these findings are unique to the Meyersdal area, or whether these mechanisms of coexistence are generally employed in all areas where they co-occur.

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