Aspects of the ecology of Cape porcupines on farmlands, peri-urban and suburban areas in KwaZulu-Natal, South Africa

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ABSTRACT

The unprecedented changes in the environmental and ecological processes of the biosphere have led some to believe that we have transitioned into a new geological era from the Holocene. This current era is known as the Anthropocene epoch, termed as such due to the unprecedented human-induced environmental change. Humans have dominated global changes in the environment and climate through the conversion of natural land-use systems into anthropogenic landscapes dominated by agriculture, urban and industrial development. The conversion and destruction of natural habitats into anthropogenic ones have caused shifts in ecosystem functions, and ultimately this has dire consequences for biological diversity globally.

Although many species have gone extinct due to anthropogenic land-use changes, some have persisted and thrive within human-dominated landscapes. These species have adapted well to these landscapes, to the point whereby they have modified their behaviour to exploit anthropogenic resources, and increase in numbers. However, the expansion of human land-use into historically wildlands means that wildlife and humans will increasingly interact with one another. This is cause for concern, particularly with the projection of future anthropogenic land-use expansion and intensification. As a result, there is need to research how wildlife in human-dominated landscapes adapt and how their survival will influence human-wildlife interaction in the future.

Cape porcupines, *Hystrix africaeaustralis*, are one of those species which have benefited from anthropogenic change of the landscape. However, due to their effectiveness in exploiting anthropogenic food and shelter resources, they have been perceived as problematic. This has led to their persecutions in certain areas, particularly within agricultural systems. But they are also becoming increasingly problematic also in suburbia. Therefore, as motivation for this study, we aim to investigate the spatial ecology of Cape porcupines in human-dominated landscapes of farmland and urban areas. This is because there is very little information on their space use and the research on Cape porcupines is outdated. Consequently, due to their potential to become conflict-causing, there is urgency to determine their spatial ecology and contribute knowledge towards their conservation and management in these landscapes.

Therefore, Cape porcupine home range and habitat use along a land-use gradient were investigated. A total of fifteen individual Cape porcupines were captured and fitted with Global Positioning System (GPS) collar transmitters in farmlands of Fort Nottingham, a peri-urban estate near Howick, and in a suburban estate in Ballito, in KwaZulu-Natal, South Africa. Data obtained from the GPS transmitters were used to estimate Cape porcupine home ranges using the Kernel Density Estimator (KDE) (Chapter 2). Overall estimated Cape porcupine home ranges were very small (n = 9, mean ± SE: 39.37 ± 6.33 ha) compared with other *Hystrix* porcupines. Farmland Cape porcupine home ranges (24.57 ha) were the smallest relative to the peri-urban (34.61 ha) and suburban areas (45.18 ha). These results were as expected, since it has been revealed that porcupine home ranges are determined by forage availability. Consequently, these human-dominated habitats have anthropogenic food resources that are constant relative to natural resources. This means that the expansion of human-dominated landscapes will result in the contraction of Cape porcupine home ranges as they benefit from anthropogenic resources.

With the aid of the radio-telemetry data, we also determined Cape porcupine habitat use in the farmland, peri-urban and suburban areas, in KwaZulu-Natal, South Africa (Chapter 3). Habitat use of Cape porcupines were investigated at the landscape-scale (2nd order of selection) and the home range-scale (3rd order of selection). Habitat use of Cape porcupines varied at the two-levels of selection, and individual Cape porcupines utilized different habitats, but generally selected the forest with bushland habitat above other habitats. We thought Cape porcupine habitat use would be determined by habitats dominated by anthropogenic food resources (crops and gardens). However, Cape porcupines utilized natural food resources although they lived in human-dominated landscapes. Their habitat use was determined by the presence of forest with bushland habitat, and to a less extent by croplands or residential gardens. This means that at this point, Cape porcupines opportunistically utilized anthropogenic food resources according to their availability. However, these results should be interpreted with caution since the study duration was limited by battery life of the GPS transmitters (~ 5 months).

This study revealed that Cape porcupine showed individual variation in ranging patterns and habitat use which were likely influenced by forage availability. In addition, Cape porcupines shifted their spatial behaviour depending on the landscape they inhabited. Therefore, the behavioural flexibility of Cape porcupines enabled them to adapt to anthropogenic changing land-use and successfully persist there.

Keywords: *Hystrix africaeaustralis*, land-use change, GPS telemetry, Kernel Density Estimator, behavioural plasticity, food availability and distribution

PREFACE

The data described in this thesis were collected in KwaZulu-Natal, Republic of South Africa, from June 2016 to July 2017. Experimental work was carried out while registered at the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, under the supervision of Professor Colleen T. Downs, and co-supervision of Dr Amy-Leigh Wilson.

This thesis, submitted for the degree of Master of Science in the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, School of Life Sciences, Pietermaritzburg campus, represents original work by the author and has not otherwise been submitted in any form for any degree or diploma to any University. Where use has been made of the work of others, it is duly acknowledged in the text.

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Samukelisiwe Princess Ngcobo

January 2018

I certify that the above statement is correct and as the candidate's supervisor I have approved this thesis for submission.

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Professor Colleen T. Downs
Supervisor
January 2018

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DECLARATION 1 - PLAGIARISM

I, Samukelisiwe Princess Ngcobo, declare that

1. The research reported in this thesis, except where otherwise indicated, is my original research.
2. This thesis has not been submitted for any degree or examination at any other university.
3. This thesis does not contain other persons’ data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.
4. This thesis does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:
    a. Their words have been re-written but the general information attributed to them has been referenced
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DECLARATION 2 - PUBLICATIONS

DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis.

Publication 1

SP Ngcobo, A-L Wilson & CT Downs

Home ranges of Cape porcupines on farmland, peri-urban and suburban areas in KwaZulu-Natal, South Africa

Author contributions:

SPN conceived paper with CTD. SPN and ALW collected the data. SPN analysed data, and wrote the paper. CTD and ALW contributed valuable comments to the manuscript.

Publication 2

SP Ngcobo, A-L Wilson & CT Downs

Habitat selection of Cape porcupines along a suburban-farmland gradient in KwaZulu-Natal, South Africa

Author contributions:

SPN conceived paper with CTD. SPN and ALW collected the data. SPN analysed data, and wrote the paper. CTD and ALW contributed valuable comments to the manuscript.

Signed: ……………………………………………………

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January 2018

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CHAPTER 1

INTRODUCTION

We are currently living in a new geological epoch, the Anthropocene, where humans have become an important driver of environmental change (Crutzen and Stoermer 2000; Crutzen 2002; 2006). This geological transition from the Holocene era, although accepted by many, is still quite a recent term that is not as yet formally considered (Zalasiewicz et al. 2008; Steffen et al. 2011). Likewise, the beginning of the Anthropocene epoch is still an on-going debate (Corlett 2015), but all seem to concede that global environmental processes have indeed exceeded the boundaries of the Holocene into a new geological time zone (Steffen et al. 2007; 2011; Braje and Erlandson 2013; Ribot 2014; Lewis et al. 2015; Waters et al. 2016).

Regardless, it has reached a point whereby anthropogenic environmental change far exceeds the rate of natural environmental change (Gaffney and Steffen 2017). Gradually, the terrestrial biosphere has shifted from being predominantly wildland, into one which is now dominated by human settlements and agricultural lands (Ellis et al. 2010). Underlying drivers for this unprecedented land transformation is the ever-increasing human population, associated with an increase in the rate of resource consumption (Foley et al. 2005; Falcucci et al. 2007; Ceballos et al. 2017). Consequently, this places huge demands on agricultural production, as well as on natural resources (Foley et al. 2011).

Anthropogenic effects on biodiversity

Human activities affect biodiversity in numerous ways that are multidimensional and complex in their nature and magnitude (McGill et al. 2015). These factors negatively affect biodiversity to such extents that ecosystem function becomes degraded, and shall continue in that trajectory as human activity become increasingly dominant on the planet (Hooper et al. 2005). Habitat loss and fragmentation (land-use change), overexploitation, invasive species, and anthropogenic climate change are some of the factors which, according to the Living Planet Report of 2016, threaten vertebrate populations worldwide (Newbold et al. 2015; Ceballos et al. 2015; McGill et al. 2015; Ripple et al. 2016; Tilman et al. 2017). Anthropogenic land-cover change is a more direct effect of human transformation of the landscape, and is one of the primary factors upon-which other factors hinge upon (Ellis 2011). Land-cover changes as a result of human activities lead to habitat destruction (loss, fragmentation, degradation), which directly affects species biodiversity by removing habitats and resources upon which species depend upon (National Research Council 1999). Consequently, as land-use change intensifies, there is growing concern that biodiversity will face increased risk of species extinctions and the decline of population numbers (Tittensor et al. 2014). Terrestrial biomes are particularly more susceptible since the majority of land-use changes occur in the terrestrial surface (Ojima et al. 1994; Sala et al. 2000).

Land-use change

Human-induced changes in land-use have been responsible for habitat destruction and is the main driver of global biodiversity declines (Pimm and Raven 2000; Sala et al. 2000; Newbold et al. 2015). This habitat destruction refers to habitat loss and fragmentation whereby complete areas are removed or modified into small, isolated patches (Cheptou et al. 2017). Common causes include agriculture (expansion and intensification), infrastructure development (urbanisation) and extraction practices (harvesting of natural resources) (Dirzo and Raven 2003). According to Newbold et al. (2016), at least 62% and 65% of terrestrial biomes and biodiversity hotspots respectively, have exceeded the planetary threshold for global biodiversity loss. Therefore, the few species that are able to adapt and thrive within human-modified landscapes are replacing the majority that are unable- which will eventually cause homogenisation of biodiversity (McKinney and Lockwood 1991; McKinney 2006). To date, about 20% of terrestrial vertebrates (of which 13% are bird species) (Tilman et al. 2017), 45% are invertebrates (Dirzo et al. 2014), 41% are amphibians (IUCN 2014) and at least 21% of vascular plants (Pimm and Raven 2017), are facing threats of extinction. According to Tilman et al. (2017), 80% of terrestrial mammal and bird species are directly threatened by habitat loss associated with expansion and intensification of agriculture and urbanisation.

Biodiversity in farmland and urban areas

Biodiversity within farmland areas

Agriculture and urbanisation are by far the greatest threats to biodiversity globally (Ricketts and Imhoff 2003; Grimm et al. 2008). Both land-use types directly and indirectly affect biodiversity. That is, directly through habitat loss and fragmentation, and indirectly through the increased human population and dominance of human activities (urbanisation) and through chemical pollution and degradation of water resources due to the addition of agrochemicals (intensive agriculture) (Tilman et al. 2001; de Oliveira et al. 2011; Oliver and Morecroft 2014).

Farmland areas consist of a mix of production cover types and natural vegetation habitat types, proportions of which generally vary with farming practice, as well as management level (i.e. farming intensity) (Kleijn et al. 2011). For instance, low intensity farming usually involves low disturbance levels (in terms of livestock impacts, soil disturbance and agrochemical inputs) and high spatial heterogeneity (Duru et al. 2015). Whereas, characteristic landscape composition of intensive farming systems is generally vice-versa (Tscharntke et al. 2005; Berg et al. 2015). Low intensity farmlands usually favour species with broad ecological requirements because of the heterogeneous habitat composition within these landscapes (Doxa et al. 2010; Kleijn et al. 2011). However, intensive farming practices generally promote specialising species due to them having fewer habitat cover types and niches (Padmavathy and Poyyamoli 2013).

Biodiversity in farmlands is influenced to a great extent, by landscape composition, with heterogeneous landscapes consisting of higher diversity of biota compared with the more homogenous farmland landscape (Benton et al. 2003; Fahrig et al. 2011; Monck-Whipp et al. 2018). Heterogeneous landscapes provide different cover types and higher structural complexity (i.e provide more habitat types), thus increasing local biodiversity because of the different species which these landscapes can support (Fahrig et al. 2011). However, landscape heterogeneity is good in high intensity farming systems, but not so much in low intensity farming systems, and also varies depending on the target species or groups under investigation (Batáry et al. 2011; Medan et al. 2011).

Due to varying levels of pressures from agricultural intensification and expansion, wildlife populations in agricultural landscapes experience loss of their habitats, fragmentation of the remaining habitat, as well as modification of the surrounding landscape matrix (Tilman et al. 2001; Kleijn et al. 2011). As a result, species diversity generally declines with increasing levels of agricultural intensity, mainly because of the reduced ability of some species to compete for resources and establish viable populations within the intensively managed farmlands which are associated with the loss of habitat, reduction in habitat quality and have a simplified landscape (Feber et al. 2007; Holzschuh et al. 2007; MacDonald et al. 2007; Boutin et al. 2011).

Biodiversity within urban areas

Urbanising systems are those with novel modifications of the landscape, which consist of varying levels of natural vegetation juxtaposed within human-dominated landscapes, mainly characterised by an increase in consumption rates and industrial development (Pickett et al. 2011). Regardless of their relative small terrestrial surface cover (about 2.4% of the global surface- Potere and Schneider 2007; Seto et al. 2012), the urban ecological footprint extends beyond city limits, even affecting surrounding areas and affecting local, regional and/or global changes in biodiversity. Urban biodiversity is influenced by natural habitat area, connectivity, as well as vegetation structural composition (Goddard et al. 2009; Shanahan et al. 2011; Aronson et al. 2014; Beninde et al. 2015; Lepczyk et al. 2017).

Wildlife in cities: how are they influenced by urbanisation?

Firstly, as a consequence of urban development, native species diversity and abundance become reduced, particularly along city centers- as there is a high proportion of built-up areas (McKinney 2008). In addition, native species become replaced by non-native species, which leads to biotic homogenization (McKinney 2002; 2006; Goddard et al. 2009). Secondly, due to urban production and consumerism (connected to urban affluence and a proportional rise in consumption levels- especially dietary shifts to animal-based products), there has been a considerable increase in pasture land, which is one of the most extensive agricultural land-use type globally and a major cause of habitat loss (pastures/rangelands cover about 20-26% of the terrestrial surface globally) (Ellis et al. 2010). Thirdly, trade and logistics within urban areas directly affects biodiversity through its contribution towards air pollution, invasive species introductions and climate change (Goddard et al. 2009). Fourthly, urban heat islands (i.e. higher urban temperature relative to surrounding areas- due to temperature differences compared with adjacent areas) consequently results in habitat modification, leading to changes in indigenous species composition (de Oliveira et al. 2011).

How wildlife responds to anthropogenic environmental change

Wildlife are subjected to environmental conditions that have been altered by human activities for centuries (Western 2001). Wild populations can respond to novel habitats in several ways: they could either 1) disperse, 2) adjust (phenotypic), 3) adapt (genetic) or 4) perish (McDonnell and Hahs 2015). However, options of dispersal and adapting are usually limited when dealing with anthropogenic changes (Wong and Candolin 2015). For instance, there are likely barriers to movement caused by habitat fragmentation or physical barriers that would limit dispersal. In addition, human-induced environmental changes are generally abrupt, and there is a short time period given for species to respond to these changes, so adaptation through genetic changes is limited (Sih et al. 2011). As a result, species have a greater chance to persist if they adjust their behaviour according to their environment. This behavioural adjustment occurs when the genotype produces multiple phenotypes that will suit the environment (plasticity) in which the animal finds itself in and will contribute to its fitness (Reed et al. 2010). However, species that fail to adjust may be excluded from these human-altered environments (Chevin et al. 2010). The most novel environments altered by humans include urbanised areas, whereby wildlife are challenged by the destruction and loss of natural resources (from habitat loss and fragmentation), as well as increased human disturbance levels such as infrastructure development, road construction, traffic caused by vehicles, and pollution, etc. (Lowry et al. 2013). In addition, urban areas introduce wildlife to altered light, noise, and temperature (heat-island effect) impacts (McDonnell and Hahs 2015). As a result, urban areas are novel environments that resemble little to nothing of the historical, and organisms inhabiting these landscapes are required to adapt specifically (Hunter 2007). A number of species have gone extinct from local urban areas, including plants (Hahs et al. 2009; Duncan et al. 2011), herpetofauna (Hamer and McDonnell 2010), mammals (Van der Ree and McCarthy 2005) and birds (Husté and Boulinier 2007; Aronson et al. 2014).

Regardless, many species appear to thrive in these landscapes and have actually increased their population numbers (Luniak 2004). These individuals have been termed by McKinney (2002) as urban adapters or exploiters, terming species which can use urbanised landscapes and species that thrive within them. Indeed, this reveals that urban species seem to be more resilient than was previously believed (Alberti and Marzluff 2004). With species adaptations being driven by the magnitude of anthropogenic environmental changes (Kueffer 2015). These act as selective pressures which, as they increase, will likely force organisms to either adapt or face local extinctions (Hendry et al. 2011). Research has revealed a number of ways species respond and adapt to urban environments including, behavioral responses (Lowry et al. 2013; Snell-Rood 2013; Sol et al. 2013; Wong and Candolin 2015; Miranda 2017), genetic responses (Delaney et al. 2010; Konorov and Nikitin 2015; Brans et al. 2017; Harris and Munshi-South 2017), and hormonal response (Fokidis et al. 2009; Bonier 2012). As a result, studies have revealed that urban wildlife seem to behave differently from their rural conspecifics in terms of behaviour, diet, movements and territoriality, exposure to disease, and physiology (Evans et al. 2010; McLeery 2010; Seress et al. 2011; Miranda et al. 2013; Uchida et al. 2016; Carrete and Tella 2017).

Therefore, species inhabiting urban landscapes bear adaptations that enable them to overcome anthropogenic disturbances and risks and allow them to benefit from anthropogenic resources (Sato 2017). For example, due to natural resources being reduced in urban landscapes, urban wildlife make use of anthropogenic resources for food and shelter (Widdows and Downs 2015, 2016, 2018; Widdows et al. 2015). As they exploit these resources, some species tend to achieve higher numbers compared with the wild (Beckmann and Lackey 2008; Bateman and Fleming 2012). Also, since urban areas experience high levels of anthropogenic disturbance, animals have to be cautious when utilising urban resources because of the risks involved.

On the one hand, some animals respond by changing their spatial behaviour and diel activity patterns in order to avoid human activities (Tuomainen and Candolin 2011). For instance, Dowding et al. (2010) revealed that urban European hedgehogs *Erinaceus europaeus* shifted their spatial and temporal patterns to avoid peak human activities. While, on the other hand, some species benefit from associating with human habitation. According to Møller (2010) birds nesting in close proximity to human habitations experienced high fitness rates compared with those that nested outside (i.e. protection from predation). In response to anthropogenic noise, birds either adjust their vocal frequency according the noise level (Francis et al. 2011) or they avoid or become displaced from noisy places (Duarte et al. 2011; Proppe et al. 2013).

Regardless of the species adaptation to urban landscapes, some wildlife species have benefitted from anthropogenic resources to the point whereby there are large increases in their populations, ultimately becoming increasingly problematic. Because of this, there is increased encounter rates between humans and wildlife, causing opportunities for conflict to become enhanced (Destefano et al. 2005). These over-abundant species end up becoming a nuisance, damaging property, and or threatening the wellbeing of humans (Soulsbury and White 2016). Therefore, with urban areas projected to expand globally (Seto et al. 2012), there is an increased likelihood of negative interactions between humans and wildlife as they coexist within urban environments. As a result, there is an increased urgency to investigate the future implications of anthropogenic environmental change and how wildlife will respond as they experience these novel environmental conditions.

***Hystrix* sub-genus distribution**

Cape porcupines (*Hystrix africaeaustralis*) are Africa's largest rodents and they have a wide distribution throughout southern Africa (Skinner and Chimimba 2005). Along the north-eastern edge of their distribution in Tanzania, they are sympatric with the very similar crested porcupine (*H. cristata*) (Barthelmess 2006), which is distributed along North Africa (IUCN 2016). Another very similar species of the sub-genus *Hystrix* is the Indian crested porcupine (*H. indica*), which is found along western Asia (IUCN 2016). All these species are similar in appearance, habitat and ecology, as well as general biology (Corbet 1991).

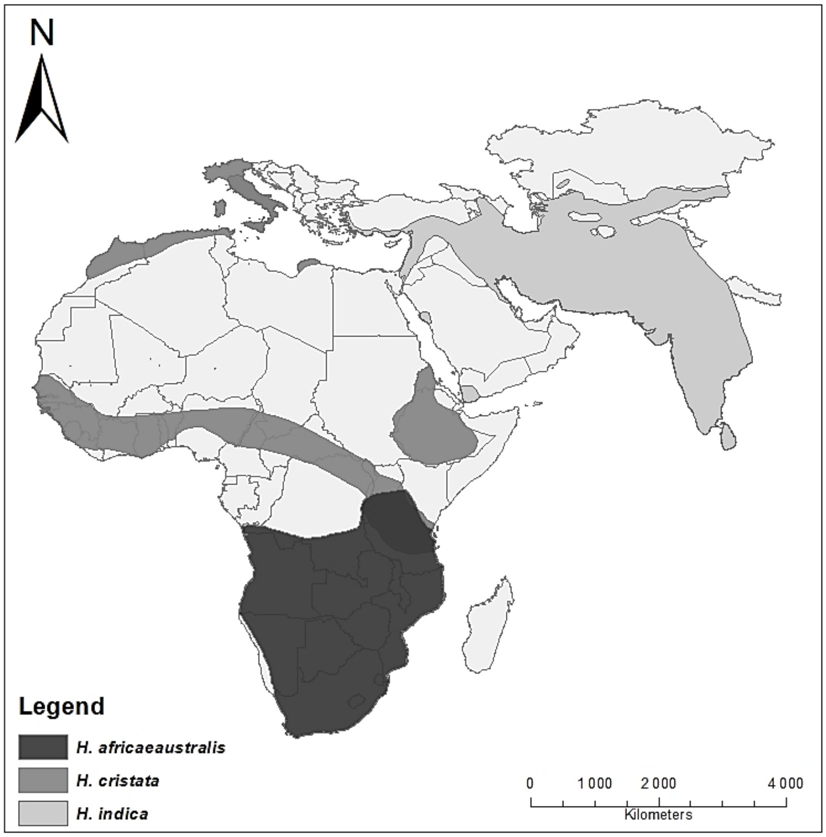

Fig. 1.1. Geographic distribution of the sub-genus *Hystrix* along Africa and southwest Asia. *Hystrix africaeaustralis* (Cassola 2016), *Hystrix cristata* (Amori and De Smet 2016), and *Hystrix indica* (Amori et al. 2016).

Cape porcupine ecological description

Cape porcupines are hystricomorphic, nocturnal and robust rodents, with a size range of 10 - 24.1 kg (Corbet and van Aarde 1996). Cape porcupines are monogamous and there is no sexual dimorphism between sexes (Mori and Lovari 2014). Their habitat preferences have been described as being broad and diverse, including both wildlands and human-modified habitats (Skinner and Chimimba 2005). They occur in most vegetation types found in the sub-region including the Namib Desert coastal areas (Skinner and Chimimba 2005), as well as within croplands and suburban gardens (Child et al. 2016). Cape porcupines can be found at elevations ranging from sea level to approximately 2000 m (de Graaff 1981).

Since Cape porcupines are nocturnal animals, they normally rest during the day in burrows they either dug themselves or modified from other species (e.g. the aardvark - *Orycteropus afer*) (Child et al. 2016). They also use rock crevices, caves or anthropogenic resources (drainage pipeline – pers. Obs.) for shelter (Skinner and Chimimba 2005). The burrow system which Cape porcupines inhabit are shared among many other species (Corbet 1991). Cape porcupines are also considered as ecosystem engineers because, in addition to their burrows providing shelter for other species, their digging for food disturbs the soil and creates sites for seedling recruitment, and as such influences vegetation dynamics (Bragg et al. 2005).

Cape porcupines are generalist herbivores that dig up and feed on almost all herbaceous material, including roots, tubers, and geophytes (Corbet 1991; Bragg et al. 2005). They also feed on fruits, seed pods and remove the bark of certain trees and feed on the inner bark (phloem, cambium, and/or xylem) (de Villiers and van Aarde 1994). Seasonal agricultural crops such as maize, potatoes, sweet potatoes, butternut, melons and ground nuts, are also consumed by Cape porcupines (Skinner and Chimimba 2005). According to Pillay et al. (2015), Cape porcupines can feed on approximately 1.5 kg – 3 kg of sweet potato, potato, and butternut per night, if not limited by foraging time. That, as well as their destructive feeding habits, have led to their persecution in farming communities (Monadjem et al. 2015).

Cape porcupines are becoming a problem also in suburban areas, due to their feeding on vegetables or vegetation in people's gardens (Lovari et al. 2017). This may be a contributing factor to porcupine-human conflict especially in areas whereby Cape porcupines come into direct contact with human habitation, i.e. farms and suburbia. We suspect this conflict will only increase with the expansion of these human-modified habitats. As a result, with the increase in human-modified land uses (urbanisation and agriculture) it is important to study how this expansion is influencing Cape porcupine spatial behaviour within these landscapes.

Previous studies on Cape porcupines

The most recent study on Cape porcupine ecology was conducted by Bragg (2003) - density, burrow ecology and space use. Other studies are quite dated and includes work done by Corbet and van Aarde (1996) - social organisation and space use, de Villiers and van Aarde (1994) – habitat disturbance, De Villiers et al. (1994) – habitat utilisation, Corbet (1991) – social organisation and group living, Thomson (1974) - tree damage. Besides Corbet (1991) and Corbet and van Aarde (1996), no other study has estimated Cape porcupine home ranges. As a result, very little information exists on Cape porcupine ranging patterns, especially within the context of anthropogenic land-use change.

Study aims and thesis structure

The present study aims to aid in addressing the gap in our knowledge with regards to Cape porcupine space use, particularly regarding their home ranges, movements, and habitat use within farmlands and urban areas. Agriculture and urbanisation are two of the most prominent land-use types that are projected to increase globally, so we need to assess how these changes are likely to influence species dynamics in order to ensure their survival within the projected increase in human-induced environmental change. The objectives of this study were to 1) investigate home ranges of Cape porcupines on farmland, peri-urban and suburban areas in KwaZulu-Natal, South Africa, 2) to determine how Cape porcupines use their habitats along a farmland-suburban gradient in KwaZulu-Natal, South Africa. In order to achieve the study aims and objectives, Cape porcupines were fitted with GPS transmitter collars and the information obtained was used to determine aspects of the spatial and movement ecology of the species.

The thesis is structured with each data chapter written in a manuscript format for submission to an international peer review journal. Any repetition was unavoidable.

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CHAPTER 2

Home ranges of Cape porcupines on farmland, peri-urban and suburban areas in KwaZulu-Natal, South Africa

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Running header: Home ranges of Cape porcupines

ABSTRACT

Cape porcupines, *Hystrix africaeaustralis*, are one of the South African mammalian species that are increasing their range and abundance with changing land-use. Knowledge of the spatial movement of this species can provide important ecological information and provide possible reasons why this species is capable of adapting and surviving in a range of habitats. We investigated the home ranges of 15 radio-tagged Cape porcupines on farmlands, peri-urban and suburban areas in KwaZulu-Natal, South Africa. The Kernel Density Estimate (KDE) revealed an overall estimated mean home range of 39.37 ± 6.33 ha (n = 9) which ranged from 13.19 ha - 67.19 ha. When compared with other *Hystrix* species, Cape porcupines had the lowest estimated home range size. Individuals on farmlands had the smallest estimated home range area (24.57 ha), relative to the suburban area. The largest home range area was found in the suburban area, Simbithi (45.18 ha). Our results suggest that Cape porcupine ranging ecology is influenced by food resource distribution and availability, with suitable agricultural crops generally available all year round on farmlands. Therefore, we conclude that the variation in home range of Cape porcupines within different land-use types shows their behavioural flexibility in response to forage availability.

Keywords: *Hystrix africaeaustralis*, Land-use change, Kernel Density Estimator (KDE), GPS telemetry, Forage distribution

INTRODUCTION

A home range was traditionally defined as an area used by an individual animal in search for resources that will ultimately increase their fitness, including searching for food, acquiring a mate, caring for offspring, and avoiding predators (Burt 1943; Kaunda 2001; Powell 2012). However, Powell (2012b) and others (Powell and Mitchell 2012; Spencer 2012) have criticised this definition as being vague and difficult to quantify. As a result, numerous attempts have been made to modify this home range concept (Powell 2012b; Spencer 2012).

Recently, the home range definition has been updated to include what is termed a cognitive map (Spencer 1992; Spencer 2012). A cognitive map enables an animal to learn and memorise information of specific areas of value within a habitat as it explores its environment (Spencer 1992; Schiller et al. 2015). This information can be stored and updated regularly by an animal depending on the frequency of use of the specific area (Moorcroft 2012; Powell 2012). So, as the animal uses a habitat more frequently, the accuracy of its stored information increases, ultimately enabling the animal to make informed decisions about its habitat (Spencer 2012). This will cause an animal to routinely return to preferred sites within its habitat, thus establishing its home range within preferred sites and ignoring other sites (Spencer 2012). As a result, a home range can thus be defined as an area that is used and updated regularly by an animal (Powell 2012b; Powell and Mitchell 2012; Spencer 2012). This leads an animal to constantly change its behaviour within its environment as specific resources change throughout the animal's lifetime (Mitchell and Powell 2004; Goldingay 2015). Due to seasonal changes in resources availability and distribution, individual animals will respond by shifting their resource use to other parts of their environment, resulting in a change in both the location and size of an animal's home range (Valeix et al. 2012; Clapp and Beck 2015). However, a home range is only just a small part of an animal's space use which is used on a daily routine, it is not inclusive of the entire range that the animal utilises during its entire lifetime (Powell 2012).

Animals have home ranges because of the need to fulfil their fitness (reproduction and or survival) requirements, through resource acquisition and exploitation (Börger et al. 2008; Powell 2012). Another reason for maintaining a home range, is to gather and store knowledge about where and when to locate resources within its habitat (Van Moorter et al. 2009; Spencer 2012). Hence, those animals who are familiar with their habitats, will have a competitive advantage over those that do not, due to their ability to locate resources more efficiently (Powell 2012b; Fagan et al. 2013).

Within a home range, animals learn and recognise areas of importance, with regards to locating resources an individual animal requires (Powell 2012; Powell and Mitchell 2012). Resources are not only limited to food and shelter, but also includes areas of cover for protection from predators, finding mates, and areas of avoiding competition from conspecifics (Powell 2012; Powell and Mitchell 2012). Animal movement and space use is dependent on previous experience within a particular habitat patch, with regards to preferred resources and how they are distributed within that habitat, in space and time (Merkle et al. 2014). Basically, the more an animal uses a habitat, the greater the accuracy and information obtained and stored, thus increasing the efficiency of use to locate resources within a specific patch site (Fagan et al. 2013; Wang 2016). The more regularly an animal traverses preferred sites within a habitat, the more defined its home range becomes (Fronhofer et al. 2013). Therefore, for a home range to exist, animals need to explore patches within their habitats, learn and gain information on suitable and unsuitable sites, and then establish a home range within suitable areas, if possible (Mitchell and Hubblewhite 2012; Spencer

2012). This, in turn affects where and how home ranges of individuals are distributed within the landscape (Powell 2012b).

In many instances, home range sizes have been shown to be directly influenced by the spatial location and distribution of resources relative to the consumer (Barraquand and Murrell 2013; Goldingay 2015) and habitat quality (Moorcroft 2012; Powell and Mitchell 2012; Spencer, 2012). In addition, other factors include competition (intraspecific), whereby individuals consume and deplete available resources, thus structuring the way animals are distributed in space and time (Powell 2012). Also, home range size is influenced by the individual's behaviour, in terms of resource search ability, maturity, experience, nutritional or physiological condition, social status, sex, and resting site location, among others (Burt 1943; Kaunda 2001; Powell 2012b; Powell and Mitchell 2012).

Home range sizes in mammals have been shown to be directly influenced by body mass, with diet type and physical environment playing an additional influence (Haskell et al. 2002; Tucker et al. 2014). In comparing home range sizes among mammal groups within the terrestrial and marine biomes, Tucker et al. (2014) found that mammal body mass explained the majority of variation within mammal home range sizes. For example, mammals with a larger body mass occupied a larger home range size. This is mainly due to their energetic requirements (locomotion and metabolic), with large mammals having higher energetic demands, and range widely in order to meet these energetic demands (Tamburello et al. 2015). Additionally, diet also influences the sizes of mammal home ranges, in that carnivores appear to have the largest home range sizes relative to both omnivores and herbivores (Haskell et al. 2002; Barraquand and Murrell 2012; Tucker et al. 2014). This is mainly due to the carnivore diet having lower density resource compared with the herbivorous diet (Haskell et al. 2002). This is the same in both the terrestrial and marine environments, with some exceptions (Tucker et al. 2014). Similar trends of the effect of body mass and diet on home range sizes have also been observed in birds (Schoener 1968).

Ranging patterns of wildlife are also determined by their environment. Expanding agricultural, urban and intermediate anthropogenic landscapes through conversion of natural habitats mediates species distributions and space use (Viana et al. 2018). The effect of anthropogenic land-use changes on movement and ranging patterns of wildlife varies according to the species involved. This is due to the challenges (high levels of disturbance, and/or increased traffic- risk of mortality from vehicle collisions or direct persecution) and the opportunities (anthropogenic resources- food, water, shelter, and/or protection from predators) that wildlife may come across within these landscapes. Generally, this leads to home range contraction as a consequence of increased anthropogenic resources (food, water and shelter). As result, species tend to respond by concentrating their activities in the smallest area possible for them to meet their minimum energetic requirements (Baker et al. 2017). For example, when compared with their rural conspecifics, species inhabiting human-dominated landscapes have smaller home ranges (Vangestel et al. 2010; Sprent and Nicol 2012; Wright et al. 2012; Adams et al. 2014; Walton et al. 2017). In fact, home range seems to be influenced to a great extent by habitats which are highly productive or are rich in resources (Walton et al. 2017).

For Cape porcupines, (*Hystrix africaeaustralis*), there is very little information on their home ranges (Corbet 1991; Corbet and van Aarde 1996). Most of the home range research has been conducted on other closely related *Hystrix* porcupines, the crested porcupine (*H. cristata*- Sonnino 1988; Lovari et al. 2013; Mori et al. 2014) and Indian crested porcupines (*H. indica* - Salts and Alkon 1989; Sever and Mendelssohn 1991). Food availability (Saltz and Alkon 1989), habitat richness (Lovari et al. 2013), and seasonal variation (Corbet and Van Aarde 1996; Mori et al. 2014; Sonnino, 1988), all influenced porcupine ranging patterns. Contrary, sex and size have not been revealed to influence porcupine ranging patterns (Lovari et al. 2013; Mori et al. 2014). Also, because of the porcupine's wide ecological tolerance, they have adapted well to most habitats (De Villiers et al. 1994). In recent years, they have expanded their range and abundance closely into human modified environments. This is regardless of the fact that land-use changes generally negatively affect biodiversity (Chapin et al. 2000; Cardinale et al. 2012; McGill 2015). However, Cape porcupines seem to be thriving in human modified habitats, such as in croplands and suburban areas. As such, we wish to find out what enables Cape porcupines to survive in these human-modified landscapes, starting with their ranging behaviour. Since there is little information on Cape porcupines, we aimed to investigate their home ranges in the two most dominant land-use practices, agricultural (farmlands) and urbanised (suburban) areas. No work to date has been conducted on Cape porcupines in urban settings. This is the first study of its kind to compare Cape porcupine home ranges between farmlands and suburban areas. Therefore, we hypothesised that home-range size will vary along a suburban/farmland gradient. We predicted that home range size would become smaller with predictable food resources (i.e. croplands).

METHODS

Study site description

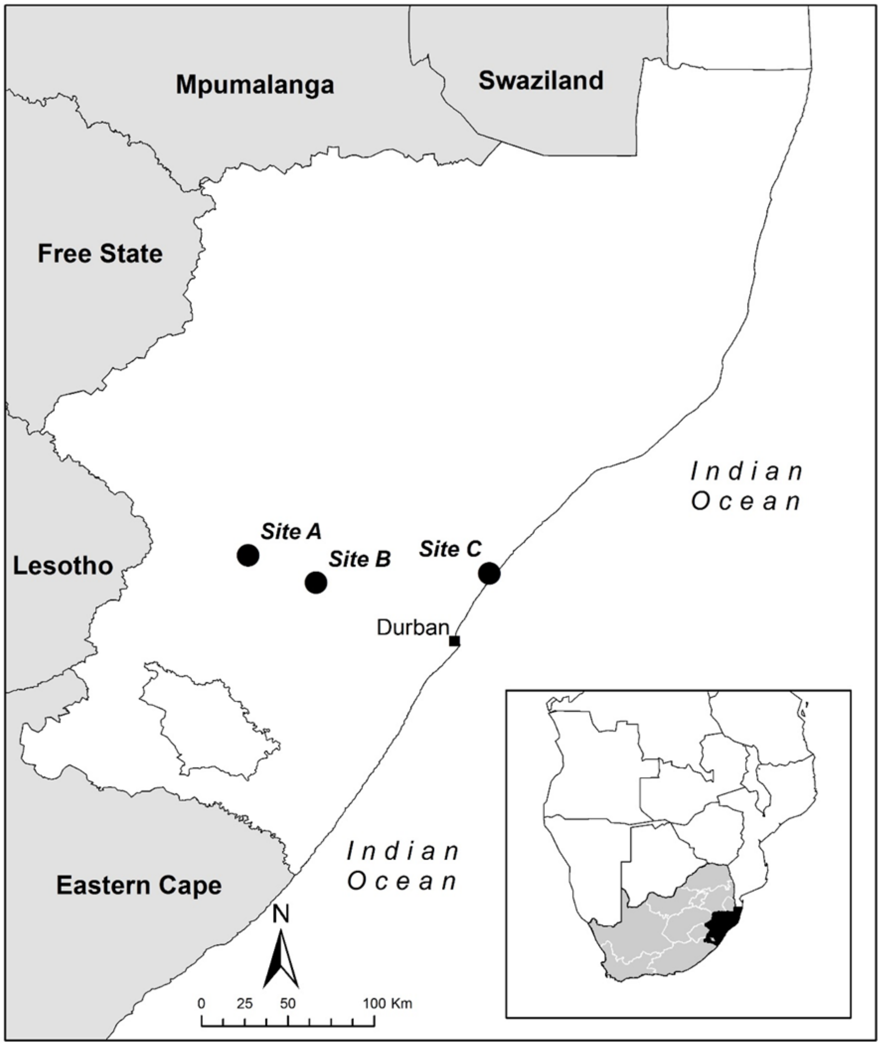

Fig. 2.1. Location of study sites in KwaZulu-Natal, South Africa. Site A is located in Fort Nottingham (farmlands), Site B is at Howick (peri-urban), Site C is at Ballito (suburban).

Site A: Farmlands (Fort Nottingham)

This study site included five privately owned commercial farmland areas along Nottingham Road, KwaZulu-Natal (KZN), South Africa (Table 1). It is situated along the low lying area of the

Drakensberg Midlands. High levels of agricultural disturbance practices occur, which includes areas of intensively farmed lands. Primary land-use types include crop production (maize, seed potatoes), livestock farming (meat and dairy production), plantation and natural forest (Ramesh et al. 2015). Livestock farms dedicate large areas to pasture and indigenous grasslands which is then utilised for livestock grazing. Vegetation types that dominate include highland sourveld grassland, natural occurring indigenous forests bush clumps (Killick 1990; Mucina and Rutherford 2006), as well as exotic plantation forests of *Pinus patula* and *Eucalyptus* spp. (Ramesh and Downs 2013), including scattered patches of invasive black wattle (*Acacia meansii*) bush clumps occurring in low lying regions and hilly slopes. The area has a combination of private and government-owned land, but a greater percentage of land is privately owned. The farms are distinctly separated with fence lines that demarcate farmland boundaries, but are easily accessible to wildlife for moving in and out (i.e. no restriction to wildlife movement). Fort Nottingham receives rainfall during the summer season, with frost occurring at least 4 months of a year, and snow occurring at least twice a year. The region has an undulating to rugged hilly terrain, with valleys occupied by rivers and wetlands (Ramesh and Downs 2013). In addition to domestic livestock (cattle, sheep), are numerous naturally occurring wildlife in the region (refer to Ramesh and Downs 2015).

Site B: Peri-urban (Howick)

KwaWula Game Estate, near Howick KZN, is a 225 ha gated residential estate with 51 freestanding residential plots (Table 2.1). KwaWula Game Estate has other residential estates, on the one side, and timber plantation forests on the other. The vegetation description in Howick is classified as the Moist Midlands Mistbelt Grassland (Mucina and Rutherford 2006). This area has cool, dry winters and warm, wet summers. The relative humidity level is 65% p.a. It receives a moderate amount of frost when the nearby Drakensberg Mountains become snow laden (when snow falls). The area has a hilly and rolling landscape. There are numerous wildlife species found at the KwaWula Estate, including ungulates, meso-predators, and small mammals.

Site C: Suburban (Ballito)

This site is located along the North Coastline of KZN, between the old town centres of Ballito and Salt Rock (Table 2.1). It is a secure, gated residential estate, with an area of approximately 430 ha. The region of Ballito was historically dominated by sugar cane farming, until the late 1990s, when residential and commercial urban developments were accelerated (Bundy 2004). The estate is bordered by a thin inland strip of sugarcane farming (Duminy 2007). The entire estate is fenced off with an electrified palisade security fence and wildlife are unable to move in or out of the estate. The housing density of the estate is approximately 2063 residences. Of the 430 ha of land, Simbithi boast approximately 133.97 ha of natural vegetation which is inclusive of coastal and swamp forest, wetlands and grasslands. It has a humid-subtropical climate that receives a summer rainfall. The highest rainfall occurs during the month of January, and about 70% occurs between October and March. Relative humidity (RH) in this area is 78%. The topography that is gentle and undulating. The estate comprises a number of naturally occurring wildlife in addition to domestic animals (dogs, cats, caged birds, etc.).

Table 2.1: Summary of the climate at each study site in KwaZulu-Natal, South Africa

Climate	**Fort Nottingham**	**Howick**	**Ballito**
Average Annual Rainfall (mm)	975.4	861	985
Average Annual Temperature (°C)	20.5	16.4	20.7
Altitude (m)	1514	1066	116
Co-ordinates	29°26’43’’ S	29°27’08’’ S	29°31’37’’ S
	29°52’41’’ E	30°15’33’’ E	31°14’23’’ E
Dominant land-use type	Farmland	Peri-urban	Suburban

https://en.climate-data.org/location/27052/ (Howick), https://en.climate-data.org/location/13476/ (Ballito), Ramesh et al. 2013 (Fort Nottingham)

Data collection

Fifteen Cape porcupines were captured using steel walk-in cage traps (70 cm x 60 cm x 120 cm) baited with butternut, sweet potatoes and potatoes. Cage traps were left near Cape porcupine burrows that showed signs of being active as a result of the presence of quills, scats and paw prints. Traps were baited in the evening, and checked the next morning. If no porcupine was caught, the baited cage trap was left and checked daily until a Cape porcupine was caught.

Captured Cape porcupines were chemically immobilised by a veterinarian using a drug combination of Medetomidine (0.1 mg/kg) and Anaket (10 mg/kg) injected intramuscularly. This drug combination was effective in initiating anaesthesia and ensuring good muscle relaxation in a short space of time (3-5 min). Under sedation, individuals were handled and the following procedures undertaken: sexing, weighing, body measurements taken, and radio-collars fitted. Cape porcupines were kept under sedation for less than 25 min per occasion. Sedated individuals were then injected intramuscularly with the reversal drug Atipamezole (0.1 mg/kg), with individuals recovering within 3-7 min. After individuals recovered from anaesthesia, they were then released back to their burrows.

Cape porcupines were fitted with global position system (GPS)UHF transmitters (Animal Trackem, Pietermaritzburg and Wireless Wildlife, Pretoria, South Africa) while anaesthetised. Transmitters and collars weighed 70 g each, which was less than the recommended 5% of body mass (Kenward 2001). Care was taken to avoid restricting movement by placing the transmitter collars around the neck area of Cape porcupines with a two-finger distance was left between the collar and the neck of the individual.

GPS location data were scheduled at 2 h intervals and fixes were concentrated during the dark hours (19h00 – 04h00) due to the consistent nocturnal behaviour of Cape porcupines (Ramesh and Downs 2015). GPS transmitters were programmed to emit four GPS fixes per day. Re-location data were collected from radio-tagged individuals from the first day of capture. GPS locations were downloaded from the GPS transmitters using a solar-powered GPS/UHF receiver (base station). When the individual was within a 5 to 10 km radius of the base station, data would be downloaded and then sent via a cell phone network. The data were accessed and downloaded from the wireless wildlife website (http://wirelesswildlife-wildife.co.za/), where all the GPS location data were stored and accessed.

Home range estimator criteria

We only attempted to estimate the home range size for individuals which had a sample size of >30 locations, according to recommendations by Seaman et al. (1999). In addition, we only reported home range estimates for individuals who reached site fidelity, as recommended by Laver and Kelly (2008). The reproducible home range (rhr) package (Signer and Balkenhol, 2015) in the

RStudio programme (RStudio Team, 2015) in R (R Core Development Team 2015) was used to estimate home ranges. The Kernel Density Estimator (KDE) was used as the home range estimator method of choice (Worton 1989). Since home range sizes estimated using KDE are greatly influenced by bandwidth choice (Seaman and Powell 1999; Powell 2000; Laver and Kelly 2008), we used the least-squares cross-validation (LSCV) bandwidth. As part of our home range analyses using KDE_{lscv}, the 50 % and 95 % isopleths, as well as the core home range for each individual were reported (Laver and Kelly 2008). Since there is no "one-size-fits-all" bandwidth choice, because all have their own limitations, the LSCV bandwidth that was chosen was sufficient for our data. This is because LSCV works well for moderate sample sizes, which was the case for our data (Heidenreich et al. 2013).

Statistical analyses

All statistical analyses were performed using SPSS version 25 (IBM SPSS 2017). In order to confirm the sexual monomorphism found in Cape porcupines, we tested for correlation in mean body mass of males and females using the Person correlation. This was confirmed due to lack of significant differences between male and female body mass. We used the one-way Analysis of Variance (ANOVA) to statistically analyse the estimated home range sizes. We also used the one-way ANOVA to test for differences in home ranges as affected by body mass, sex, months and site. The assumptions of the one-way ANOVA were tested before all analyses were performed on the home range estimates.

Table 2.2: Summary information of the Cape porcupines captured and fitted with GPS transmitters along a land-use gradient at the three sites, Fort Nottingham, KwaWula and Simbithi

Individual ID	Study site	Sex	Start Date	End Date	Number of days deployed	Pre-screened GPS fixes	Screened GPS fixes	Body mass (kg)
PNF6	Fort Nottingham	F	2016-08-10	2016-08-26	17	113	26	14
PNM7	Fort Nottingham	M	2016-08-10	2016-09-15	37	129	100	15
PNM8	Fort Nottingham	M	2016-09-07	2016-09-07	1	42	15	17
PNF10	Fort Nottingham	M	2016-08-01	2016-12-01	123	125	98	21
PNM11	Fort Nottingham	F	2016-10-13	2016-10-13	1	0	0	15
PKM1	KwaWula	M	2015-09-04	2016-01-25	144	101	87	9
PKM2	KwaWula	M	2015-10-09	2016-01-07	120	114	30	20
PKM3	KwaWula	M	2015-10-10	2016-11-30	418	122	44	18
PKF4	KwaWula	F	2015-11-02	2016-03-17	137	121	114	8
PKF5	KwaWula	F	2015-11-02	2016-02-22	113	42	35	27
PSF1	Simbithi	F	2016-10-13	2016-12-06	80	59	57	18
PSF2	Simbithi	F	2016-07-14	2016-11-28	138	183	108	14
PSM3	Simbithi	M	2016-07-06	2016-11-30	148	254	202	18
PSM4	Simbithi	M	2016-07-15	2016-10-03	81	113	94	13
PSM5	Simbithi	M	2016-07-21	2016-11-20	123	74	57	22

RESULTS

Of the five Cape porcupines captured and tagged on the farmland sites, four individuals provided some data. However, porcupines were snared and eaten on the farmland sites, and cage traps were stolen. Due to the short duration these animals were tracked, three were subsequently discarded from our analyses.

Although a total of 15 Cape porcupines were fitted with GPS transmitters, only nine had sufficient data to be analysed. These included six males (PKM1, PKM2, PKM3, PSM3, PSM4, and PSM5) and three females (PNF10, PSF1, and PSF2). These individuals had GPS relocation data ranging from 30 – 202 GPS fixes. A total of six Cape porcupines had GPS transmitter malfunctions and/or battery failures. This resulted in a number of limitations within this study such as 1) a reduced sample size (9 of 15 functional GPS transmitters), 2) low GPS fix frequency (with only 4 fixes per day, some were no location fixes), and 3) a reduced study duration (3 – 5 months' worth of data out of 12 months planned). Although they have higher frequency of relocations, they also tend to have short duration (limited by battery life) and a low sample size (fewer individuals collared) due to their cost.

Body mass (kg)

Cape porcupine body mass ranged from 8 kg (male) to 27 kg (female) (Table 2.2). Mean (± SE) male body mass (16.67 ± 1.96 kg, n = 6) did not differ significantly from mean (± SE) female body mass (15.67 ± 1.20 kg, n = 3) (Independent sample t-test, $t_{(1,7)} = -0.336$, P = 0.747). However, there was no significant correlation between mass and sex (Pearson Correlation = 0.126, P = 0.0.747).

Home range estimation (variation according to gender)

There was also a variation in estimated home range size for both the males and females (Fig. 2.2). Mean (± SE) estimated home range size was larger for males (44.64 ± 8.82 ha; 95% KDE_{lscv} and 36.22 ± 7.27 ha; core area KDE_{lscv}) compared with females (28.81 ± 2.72 ha; 95% KDE_{lscv} and 28.29 ± 5.74 ha; core area KDE_{lscv}). However, estimated mean home ranges between males and females did not differ significantly for both the 95% KDE_{lscv} (One-way ANOVA, $F_{(1.7)} = 1.475$, $P = 0.264$) and the core area KDE_{lscv} (One-way ANOVA, $F_{(1.7)} = 0.494$, $P = 0.505$).

Monthly home range estimation

Due to a low GPS fix rate, all home ranges for Cape porcupines at each site were pooled to estimate mean monthly home ranges. Monthly home ranges varied within and along the land-use gradient. On the farmland, October had the lowest estimated Cape porcupine home range (11.72 ha) and November had the highest (24.07 ha) (Fig. 2.3). At KwaWula (peri-urban area), November had the lowest estimated Cape porcupine home range (13.70 ha) and September had the highest home range (28.84 ha) (Fig. 2.4). At Simbithi (suburban area), July had the lowest estimated home range size (23.21 ha) and September had the highest home range (53.84 ha) (Fig. 2.5). However, results revealed a non-significant difference in the ***overall*** monthly home ranges among sites for both 95% KDE_{lscv} (One-way ANOVA, $F_{(4,20)} = 0.861$, $P = 0.519$) and core area KDE (One-way ANOVA, $F_{(4,20)} = 1.428$, $P = 0.294$).

Home range estimation

We estimated the home range sizes of a total of 9 individuals (6 males, 3 females). All these individuals showed variation in their estimated home range sizes (Fig. 2.1). Mean (± SE) home range size for the 95% KDE_{lscv} was 39.37 ± 6.33 ha (range 13.96 - 67.19 ha) and was 33.57 ± 5.15 ha (range 13.61 – 64.42 ha) for the core area KDE_{lscv}. We compared the estimated home ranges among study sites with varying land use practices (Fig 2.6). The farmland area had the lowest estimated home range (24.57 ha, 95% KDE_{lscv}) relative to the peri-urban (34.61 ha, 95% KDE_{lscv}) and suburban areas (45.18 ha, 95% KDE_{lscv}). The suburban area (Simbithi) had the highest mean (± SE) estimated home range (45.18 ± 6.31 ha; 95% KDE_{lscv} and 35.49 – 4.05 ha; core KDE_{lscv}) which ranged from 27.99 – 62.89 ha. However, no significant differences among study sites were found for both 95% KDE_{lscv} (One-way ANOVA, $F_{(2.6)} = 0.564$, $P = 0.597$) and core area KDE_{lscv} (One-way ANOVA, $F_{(2.6)} = 0.186$, $P = 0.835$).

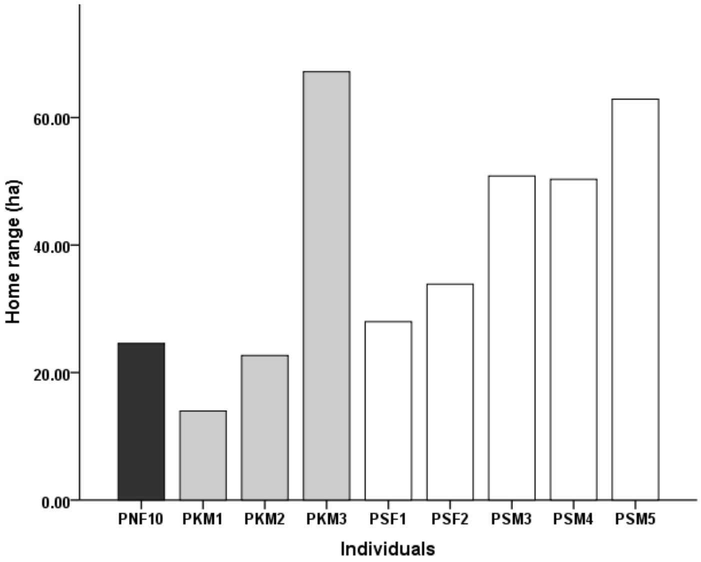

Fig. 2.2. Estimated mean home ranges of individual Cape porcupines on farmland, peri-urban and suburban areas (Dark shaded bar = individual at the farm site, light grey shaded bar = individuals at the KwaWula peri-urban area, white bars = individuals at the Simbithi suburban area)

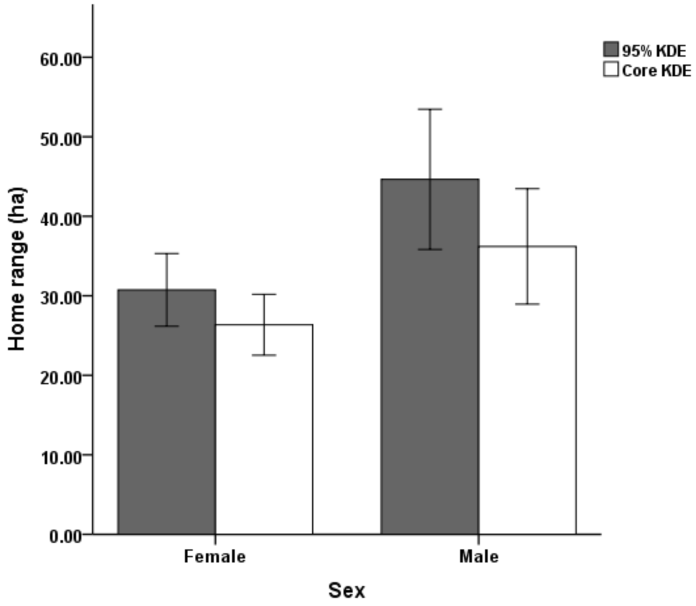

Fig. 2.3. Comparison of the estimated mean home ranges (95% KDE and core KDE home ranges) of male and female Cape porcupines on farmlands, peri-urban and suburban areas

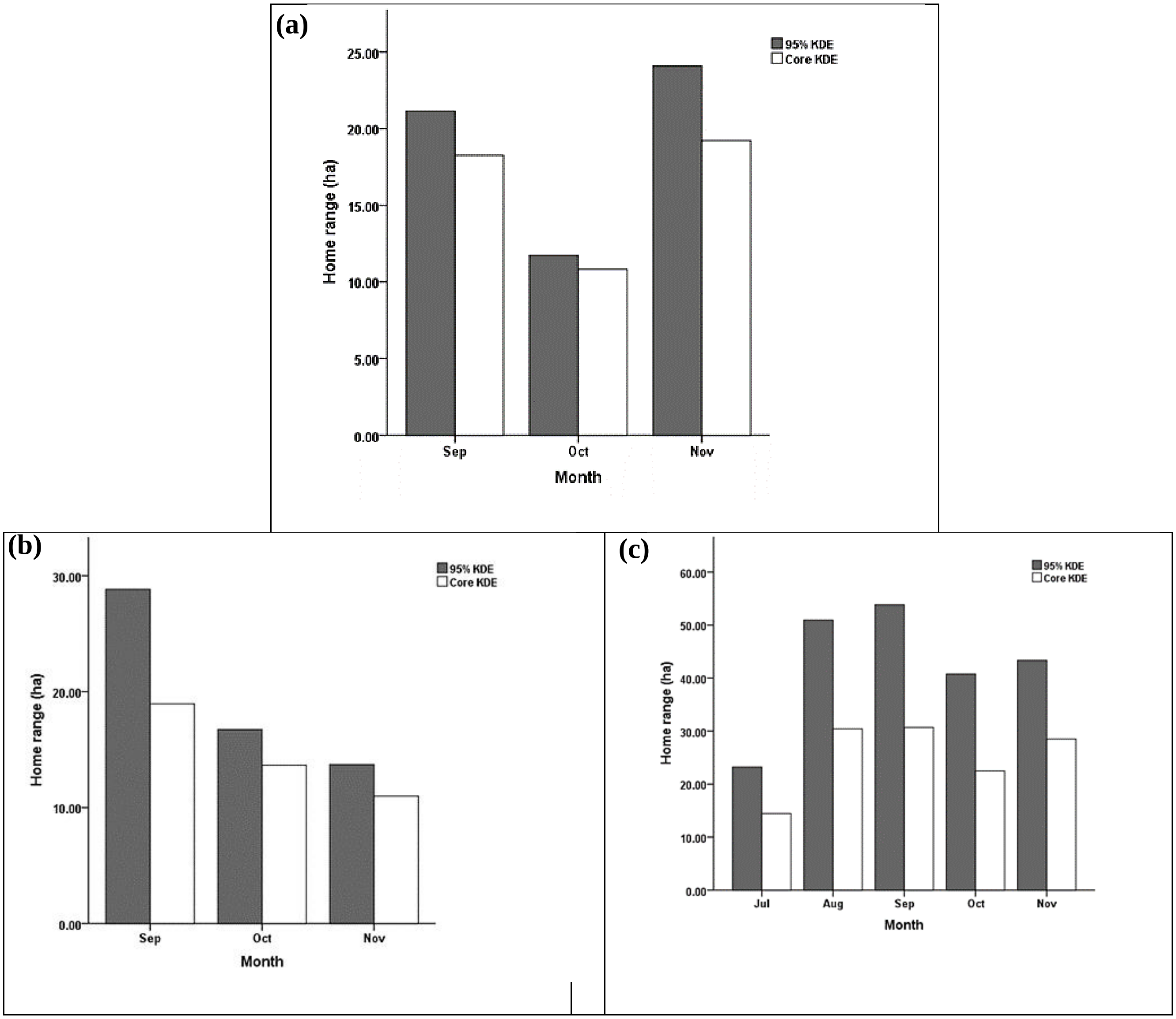

Fig. 2.4. Comparison of Estimated mean monthly home ranges (95% KDE and core KDE) of Cape porcupines on a) farmland areas, b) peri-urban, and c) suburban area.

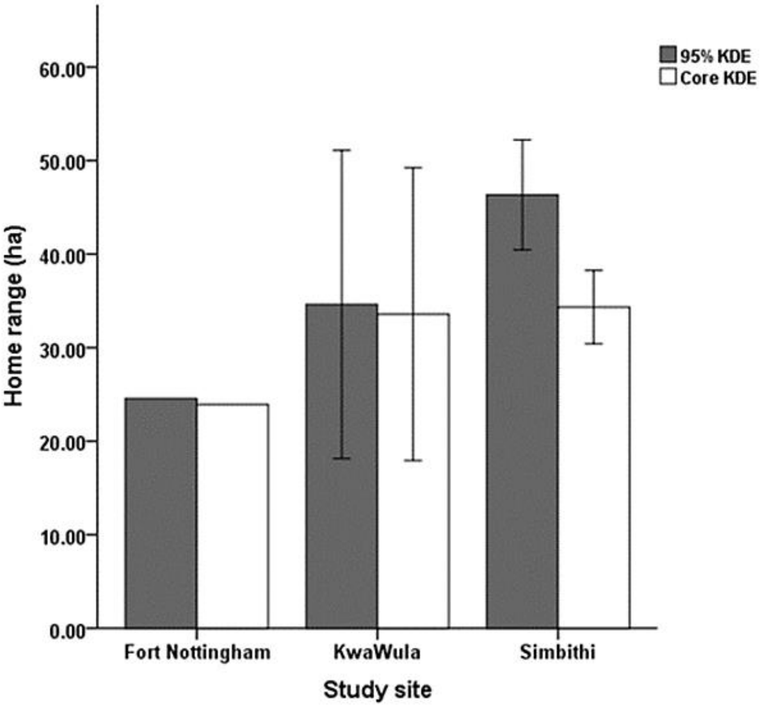

Fig. 2.5. Estimated overall home ranges of Cape porcupines on the farmland, peri-urban and suburban areas where 95% KDE and core KDE home ranges were compared.

DISCUSSION

Although our results were relatively short term (c. 5 months), we consider our estimates to be highly informative, particularly since it is the first of its kind to estimate home ranges of Cape porcupines between differing land use practices, using GPS telemetry. However, in this study, the frequency of GPS fix locations was limited by battery life.

Overall, the Cape porcupine mean 95% KDE_{lscv} home range (± SE) was 39.37 ± 6.33 ha (n = 9), which ranged from 13.96 ha to 67.19 ha. Contrary to general belief, the core KDE home range size was somewhat similar to the 95% KDE_{lscv}, with an overall mean (± SE) home range of 33.57 ± 5.15 ha and ranged from 13.61 ha to 64.42 ha. We found that our estimated home range sizes differed from those previously estimated for other closely related *Hystrix* porcupines (Table

2.3). *Hystrix* porcupines within the humid-subtropical climate had smaller estimated home range sizes (39.37 ha- current study) compared with those in the semi-arid (165.92 ha- Corbet, 1991) and semi-desert climates (155 ha- Salts and Alkon, 1989). This observation seems to be consistent with McNab's (1963) theory, that mammals living in arid areas enlarge their ranging patterns in relation to resource distribution and availability. Hence why there is a discrepancy in home range sizes of porcupines in the subtropical to semi-desert regions.

For instance, within arid habitats, resources needed by organisms seem to be variable and unpredictable throughout the landscape (Shmida et al. 1986, Ward 2008). Rainfall may be one of the primary limiting resource in arid ecosystems and this determines the vegetation and species dynamics within these areas (Holmgren et al. 2006; Golodets et al. 2013). Furthermore, due to rainfall patterns, biomass production and species diversity tend to decrease from humid to arid ecosystems in a non-linear trend (Shmida et al. 1986). Organisms living in desert habitats have higher energetic requirements, because they have to range far to locate resources that are often spatially scattered.

These results emphasised individual variation in space use of Cape porcupines. Regardless of whether individuals inhabit the same area, there was variation in their estimated home range size. This individual variation may be due to numerous factors acting simultaneously to shape an individual's activity within their landscape. For instance, individuals, although being of the same species and population, may differ in their dietary preferences (Alkon and Saltz 1985; Saltz and Alkon 1989), social ability (Corbet and van Aarde 1996), and resource search capability (Verschut et al., 2016). However, there is great emphasis on the influence of forage availability and distribution in shaping porcupine ranging patterns (De Villiers et al. 1994- *H. africaeaustralis*; Hafeez et al. 2014- *H. indica*; Lovari et al. 2017- *H. cristata*). Diet plays a major role in the space use of porcupines, particularly because *Hystrix* porcupines are considered as agricultural pests (Greaves and Khan 1978; Alkon and Saltz 1985- *H. indica*; Barthelmess 2006- *H. africaeaustralis*). In fact, according to Pillay et al. (2015) an individual Cape porcupine can eat up to 2.5 kg per night. Although porcupines have been shown to prefer underground plant storage organs (Bragg et al. 2005), potential threats such as poaching have the ability to influence porcupine feeding activities. For example, Lovari et al. (2017) showed that crested porcupines within a landscape whereby there are high levels of poaching, they shift from feeding on storage organs and select feeding on epigeal plant materials (fruits and stems). Therefore, this shows that porcupines are able to rapidly respond to changing environmental cues and are able to modify their behaviour and adapt as required. This has allowed these species to successfully establish and thrive within human-dominated environments as a result.

Monthly home range variation is a result of individual variation in space use in response to changing environmental patterns. Individual's use the same general home range areas, but either expand or reduce it depending on monthly environmental changes (Corbet and Van Aarde 1996). According to Corbet and Van Aarde (1996), it is beneficial for individuals to minimise their home range size in order to lower energetic demands related to foraging and other activities. This results in shifts in the positions of home range boundaries from month to month in response to short-term changes in resource distribution and availability. In addition, monthly variation may be a result of other factors such as changing denning areas, reproductive cycle, and climatological events (Sonnino 1988). Our results revealed differences in monthly home ranges along a land-use gradient. However, it would have been interesting to test for seasonal differences in Cape porcupine home range, but due to a short study duration caused by GPS transmitter failures, it was not possible. However, other studies revealed seasonal variation in home range sizes of *Hystrix* porcupines. For example, it was shown that summer home ranges were smaller than winter home ranges in the Cape porcupines (Corbet and Van Aarde 1996), and the crested porcupine (Mori et al. 2014). Contrary, with regards to the crested porcupine, Sonnino (1988) found that home range sizes were higher in summer compared with winter.

Our results showed variation in the estimated home range sizes along a land-use gradient. The farmland area had the smallest estimated home range size (24.57 ha) relative to the urban sites. Cape porcupines inhabiting the farmland site were considered as “crop foragers” because of their consistent use of crop areas for feeding and denning (Saltz and Alkon 1989; pers. obs.). Crop foragers are exposed to food resources that are dense and predictable, which enable these porcupines to reduce their range size and permits high population sizes (Alkon and Saltz 1985; Saltz and Alkon 1989; Sever and Mendelssohn 1991). In croplands, porcupines tend to excavate their burrows in close proximity to crops, thus further reducing their movements between denning and feeding sites (Lovari et al. 2013).

In comparing the peri-urban and the suburban area, overall mean estimated home range was 34.61 ha (KwaWula) and 45.18 ha (Simbithi), respectively. Of all the sites, Simbithi had the largest estimated home range size. Cape porcupines within these sites fed solely on natural vegetation found vegetated habitats and resident’s gardens. These Cape porcupines were categorised as “natural foragers” (Saltz and Alkon 1989). In the suburban area, Cape porcupines had larger mean home range size (39.90 ha) due to high environmental heterogeneity within these landscapes (Lovari et al. 2013). Hencewhy, Cape porcupine home ranges were larger. Consequently, our results reveal that the ranging patterns of Cape porcupines are likely an effect of food search as a result of food resource distribution (Lovari et al. 2013; Mori et al. 2014). As with our results revealing that crop foragers had smaller home ranges sizes relative to natural foragers, other studies had similar findings (Saltz and Alkon 1989; Sever and Mendelssohn 1991; Lovari et al. 2013; Mori et al. 2014). However, Corbet and Van Aarde (1996) and Sonnino (1988) revealed the contrary for the Cape porcupine and crested porcupine, respectively.

Conclusions

Our study showed the flexible nature and behaviour of individual Cape porcupines in adapting and tolerating varying levels of anthropogenic habitat modification. Cape porcupines showed varying individual differences in ranging patterns. The Cape porcupine ranging patterns appear to be strongly linked with resource distribution and availability, as in previous porcupine studies. As expected, Cape porcupine home ranges were smaller in areas where resources were dense and predictable (i.e. cropland areas).

Consequently, this study revealed that anthropogenic alteration of natural habitat for agriculture and urban development does not negatively affect Cape porcupine space use and distribution. In addition, the varying ranging patterns of Cape porcupines in response to changing land-use practises shows the incredible plasticity in the behaviour and adaptability of this species. As a result, this gives us one of the main reasons why Cape porcupines appear to be increasing their range and abundance with anthropogenic changing land-use practices. However, Cape porcupine behavioural flexibility and ability to adapt well to human-modified landscapes, can be a potential in causing human-wildlife conflict, especially in areas where they come into direct contact with human habitations, such as in croplands and sub-urban areas.

Table 2.3: Comparison of home range size estimated for the Cape porcupine current study compared with previous estimates from closely related *Hystrix* porcupines

Reference	***Hystrix* species**	**Home range (ha)**	**Climate**	**N**	**Duration**	**Estimation method**
Current study	*H. africaeaustralis*	39.37*	Humid subtropical	9	5 months	KDE
Lovari et al. 2013	*H. cristata*	49.81	Mediterranean	20	14 months	MCP,KDE
Sever & Mendelssohn, 1991	*H. indica*	82.3	Mediterranean	10	21 months	MCP
Sonnino, 1988	*H. cristata*	93.48	Mediterranean	4	15 months	MCP,UD
Mori et al. 2014	*H. cristata*	94.71	Mediterranean	26	12 months	MCP,KDE
Corbet & van Aarde, 1996	*H. africaeaustralis*	140.25	Semi-arid	10	11 months	MCP
Corbet, 1991	*H. africaeaustralis*	165.92*	Semi-arid	14	12 months	MCP
Salts & Alkon, 1989	*H. indica*	155	Semi-desert	6	9 months	UD

* = Smallest and largest estimated home range sizes. KDE = Kernel Density Estimator, MCP = Minimum Convex Polygon, UD = Utilisation Distribution

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CHAPTER 3

Habitat selection of Cape porcupines along a suburban-farmland gradient in KwaZulu-Natal, South Africa

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Running header: Habitat use of Cape porcupines

ABSTRACT

With the conversion of natural lands into human-modified landscapes globally, certain species have taken an advantage and have expanded their ranges within these landscapes. Cape porcupines *Hystrix africaeaustralis* are one of those species who have exploited anthropogenic land-use change. However, this is cause for concern since they are increasingly coming into conflict with humans in areas whereby there is direct interaction, such as in agricultural or suburban landscapes. As a result, with the aid of telemetry data (July 2016- January 2017) from 11 Cape porcupines, habitat use and selection was investigated across a suburban-farmland gradient in KwaZulu-Natal, South Africa. Two levels of selection were determined, at the landscape area scale (2nd order of selection) and at the home range scale (3rd order of selection). Results revealed that there was a variation in habitat selection at the two spatial scales. At both the 2nd and 3rd order of selection scale, all the Cape porcupines selected the forest with bushland habitat. Although they used other habitat types, they did not select the grassland, residential gardens, agroforestry and croplands, at the landscape scale. However, at the home range scale, some individuals selected for the grassland and garden habitat types. Agricultural areas (croplands and agroforestry) were utilised by Cape porcupines, but were not selected. As also confirmed by other studies, Cape porcupine habitat use and selection appear to be largely influenced by forage quality and availability. Also, this showed the importance of determining habitat selection at multiple scales since there is variation in how individuals interact with their environment at varying ecological scales.

Keywords: *Hystrix africaeaustralis*, food availability, individual behavioural plasticity, GPS telemetry, *Hystrix* spp., land-use

INTRODUCTION

With the biosphere becoming increasingly human-dominated (Ellis 2011), it is crucial to establish how species cope with such changes, in order that conservation projects may evolve in these landscapes, instead of focusing on conserving biodiversity within natural ecosystems and protected areas which are fast becoming isolated and fragmented from the surrounding land-use changes (Bailey et al. 2016). Changes of primary habitats into agricultural and urbanising areas is generally accepted as negatively affecting biodiversity (Newbold et al. 2015; Souza et al. 2015). The increase of agriculture and urbanisation is driven to large extent by the need to provide food, shelter and fuel for the growing human population (Foley et al. 2005). However, this comes at a cost to biodiversity, as land conversion is impacting many species negatively due to loss and fragmentation of natural habitats. As a result, some species risk exclusion or extinction as land-use practices become more intensified. This is particularly true for those species that are sensitive to changes in their landscapes. As a result, it is fundamental that conservation strategies should evolve to include human-modified ecosystems, as these are fast becoming dominant within the biosphere (Koh and Gardner 2010). Although some species decline within the agricultural and urban habitats, some species are able to survive and thrive, due mainly to food resources that human-dominated landscapes provide.

Land conversion into monoculture crop production systems and agricultural intensification are major drivers of biodiversity loss globally (Benton et al. 2003; Green et al. 2005; Kleijn et al. 2009). As a result, farmland wildlife are affected by both the direct and indirect impacts of agriculture (Turcotte et al. 2017). Direct impacts being a result of physical agricultural practices such as the usage of fertilizers/ pesticides, changing land-use, tillage versus herbicide, etc. (Turcotte et al. 2017). Indirect impacts including gas emissions and regional climate change, which generally affects vegetation dynamics (Foley et al. 2005). However, different taxonomic groups respond differently to agriculture and at varying environmental scales (Dainese et al. 2015). For example, while Gonthier et al. (2014) investigated the response of different groups to local and landscape complexity, they revealed that plant species richness was influenced more by local factors. This is mainly due to their sessile nature, which makes plants more sensitive to changes in local factors. While, it was revealed that vertebrate species richness was more affected by landscape complexity (because vertebrates move and use different habitats within a landscape, thus sheltering them from local environmental changes). Be that as it may, a number of species still decline within the agricultural landscape due to land-use intensification (Kleijn et al. 2011). As a consequence of land-use intensification (and increased anthropogenic disturbance), fewer species are able to survive and successfully reproduce within the few ecological niches under intensive agriculture (Kleijn et al. 2009).

Urban expansion and intensification irreversibly converts natural lands to be replaced by artificial structures that impact native species at long-term scales (Seto et al. 2012). This conversion leads to the alteration, fragmentation and loss of habitats, which many native species depend upon (McKinney 2002; Elmqvist et al. 2016). Also, as urbanisation intensifies, natural habitats become more fragmented, thus increasing the likelihood of local extinctions of some wildlife from the urban environment. Urbanisation generally leads to loss of biodiversity (Antrop 2004; McKinney 2002; 2006), but some species have been able to survive and thrive in urban areas (Bateman and Fleming 2012; Magle et al. 2012; Sol et al. 2013). Species that thrive in urban areas usually show behavioural flexibility (plasticity), and often-times possess behaviours which differ from their rural counterparts (Ditchkoff et al. 2006; Lowry et al. 2013; Alberti et al. 2017; Miranda 2017). Urban wildlife have adjusted their behaviours to suit urban environments- which present wildlife with novel challenges (Thompson 2017; Birnie-Gauvin et al. 2017). In urban areas, there is a decline of natural habitats and an expansion of anthropogenic disturbances (in terms of development of artificial infrastructure) (Angel et al. 2011; Seto et al. 2012). Thus, species inhabiting urban areas must adjust their behaviours in order to adapt and exploit anthropogenic resources for food and denning preferences. Therefore, behavioural modification seems to be the prerequisite for urban wildlife survival in the novel urban environment (Lowry et al. 2013; Sol et al. 2013; McDonnell and Hahs 2015). Nonetheless, there is an increased likelihood of conflict between urban wildlife and humans associated with the expansion of urbanisation.

Cape porcupines *Hystrix africaeaustralis* are a potential problem in suburban areas, due to their feeding on vegetables or vegetation in people's gardens (Pers. Com.). This may be a contributing factor to porcupine-human conflict especially in areas whereby Cape porcupines come into direct contact with human habitation, i.e farms and suburbia. We suspect this conflict will only increase with the expansion of these human-modified habitats. As a result, with the increase in human-modified land uses (urbanisation and agriculture) it is important to study how this expansion is influencing Cape porcupine spatial behaviour, in particular their habitat use within these landscapes.

We therefore investigated habitat selection of Cape porcupines from GPS telemetry data, and using selection scales at two of the four spatial levels defined by Johnson (1980). We determined habitat use and selection of Cape porcupines within the 2nd order of selection (within the landscape area) and 3rd order to selection (within the home range area). This highlights the importance of studying habitat selection at multiple levels because habitat selection is scale-dependent (Mayor et al. 2009). Varying ecological scales provide different habitat components that animals respond to differently (McGarigal et al. 2016). We also aimed to answer three basic questions about Cape porcupine habitat selection: 1) Does habitat selection vary within the landscape (2nd order of selection) and within the home range (3rd order of selection)? 2) Are habitat types used proportionally to their availability? and 3) Are certain habitat types preferred over others?

METHODS

Study site description

Site A: Farmlands (Fort Nottingham)

Five privately owned commercial farms were selected along Fort Nottingham, KwaZulu-Natal (KZN), South Africa (29°26’43’’ S; 29°52’41’’ E). The dominant land-use type within this region is agricultural production including croplands, pastureland (beef and dairy farming), and plantations (Ramesh et al. 2015). Besides agriculture, Fort Nottingham is also dominated by large areas of natural vegetation such as the sourveld grassland and naturally occurring indigenous forest and bush clumps (Killick 1990; Mucina and Rutherford 2006). This area has numerous occurring wildlife species, with an exception of large carnivores and large mammals. Fort Nottingham receives summer rainfall of an average of 975.4 mm annually. Annual temperatures are an average of 20.5 °C, with frost occurring at least 4 months of a year and snow occurring at least twice a year. The region has an altitude of 1514 m above sea level (a.s.l.), and has an undulating to rugged hilly terrain, with valleys occupied by rivers and wetlands (Ramesh and Downs 2013; Ramesh et al. 2015).

Site B: Peri-urban (Howick)

KwaWula Game Estate is a gated residential estate located near Howick, KZN (29°27’08’’ S; 30°15’33’’ E). It has a low housing density of approximately 51 freestanding residential plots and occupies an area of about 225 hectares (ha). KwaWula Game Estate is surrounded by other residential estates on the one side, and timber plantation forests on the other. Mucina and Rutherford (2006) described the vegetation in this region as being dominated by the Moist Midlands Mistbelt Grassland. This region also has isolated patches of forest and clumped bushland. This area has cool, dry winters and warm, wet summers. The average annual rainfall received within this region is 861 mm, with moderate amounts of frost occurring when the nearby Drakensberg Mountain becomes snow laden. Annual temperatures are an average of 16.4 °C. The area has a hilly and rolling landscape, with an altitude of approximately 1066 m a.s.l. Wildlife species occurring at the estate are mostly wild ungulates, medium to small rodents, primates, and small to medium carnivores.

Site C: Suburban (Ballito)

Simbithi Eco-Estate is a suburban area located in Ballito, KZN North coast (29°31’37’’ S; 31°14’23’’ E). It is located between the old town centres of Ballito and Salt Rock. This estate is a secure, gated residential area of approximately 430 ha. The estate is bordered by an electrified palisade security fence, which restricts wildlife movements into or out of the estate. The housing density of this estate is approximately 2063 houses. Although dominated by residential areas, approximately 133.97 ha is dominated by natural vegetation including coastal and swamp forests, wetlands and grasslands. This region receives a summer rainfall of approximately 985 mm on average, annually. The average annual temperature in this region is 20.7 °C. It has a coastal altitude of 116 m a.s.l., with a gentle and undulating topography. The estate comprises numerous naturally occurring wildlife including wild ungulates, primates, rodents, as well as small-bodied carnivores.

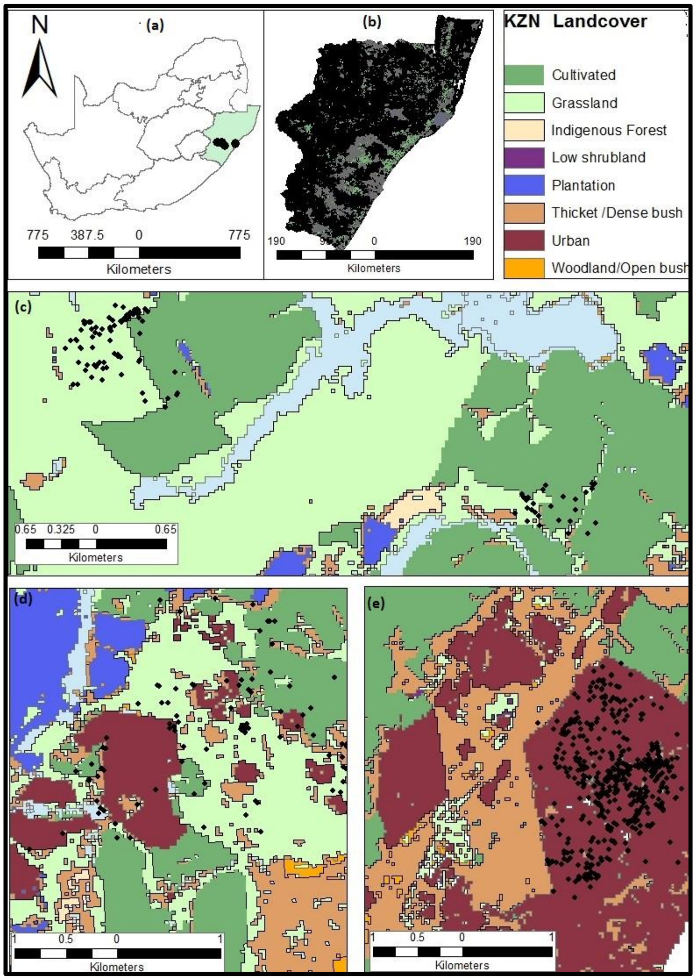

Fig 3.1. Location of study sites in KwaZulu-Natal South Africa (a,b), representing the main land-use types that are found in Fort Nottingham (farmland areas) (c), Howick (peri-urban area) (d) and Ballito (suburban area) (e). Black dots indicate the distribution of GPS points of individual Cape porcupines tagged within each study area.

Data collection

We captured and immobilised a total of 15 Cape porcupines using baited steel walk-in cage traps (70 cm x 60 cm x 120 cm) (Chapter 2). Cape porcupines were captured and collared during the period between September 2015 and August 2016. The baits that were used to lure Cape porcupines into the cage traps were seasonal crops such as butternut, sweet potatoes, maize and potatoes (Pillay et al. 2015). Trap effort was concentrated during the dark hours. Immobilisation ensued once a Cape porcupine was captured. Individuals were injected intramuscularly with a drug combination of Medetomidine (0.1 mg/kg) and Anaket (10 mg/kg) by a veterinarian. The Global Positioning System (GPS) transmitters were then fitted onto the individual. Each procedure would take less than 25 min. per occasion. Atipamezole (0.1 mg/kg), a reversal drug, was then injected intramuscularly into the sedated individual.

The GPS transmitters used in this study were GPS/UHF transmitters (Animal Track-em, Pietermaritzburg and Wireless Wildlife, Pretoria, South Africa). The transmitters and collars weighed approximately 70 g, less than the recommended 5% of body mass (Kenward, 2001). GPS location data were scheduled at 2 h intervals during the dark hours (19h00 – 04h00). GPS transmitters were programmed to receive four GPS fixed per day. We used a solar-powered GPS/UHF receiver (hereafter, base station) to download GPS location data stored on the GPS transmitters. Location data was only downloaded when an individual was within a 5 – 10 km radius of the base station. All downloaded data was then sent via a cell phone network which could be accessed remotely from the wireless wildlife website (http://wireless-wildlife.co.za/) where all the GPS location data were stored. Although GPS transmitters were supposed to stay functional for a minimum of 12 months, all our GPS transmitters experienced battery failures and ultimately ended up working for five months. As a result, study duration was reduced to five months.

Data analyses

GPS fixes from each individual were imported into ArcGIS 10.4.1 (Geographic Information System, Environmental Systems Research Institute, Redlands, California, United States of America) and projected onto the Universal Transverse Mercator (UTM) projection (WGS [World Geodetic System] 1984, UTM Zone 35S). Home Range Tools (HRT version 2.0.20) extension programme (Rogers et al. 2015) for ArcGIS was used to estimate the 100 % Minimum Convex Polygon (MCP) (Hayne 1949). We selected the 100 % MCP in order to create a polygon for all the observed GPS fixes found for each individual. Once that was done, habitat use of Cape porcupines was defined using the South African National Land-cover database (Geoterraimage, 2015). The original 72 land-use categories were compressed and reclassified into five habitat types: forest with bushland, grassland, residential (gardens), agroforestry, and croplands.

The proportional availability of each habitat type and the proportion of GPS locations falling within each habitat type (proportional use) were calculated using Geospatial Modelling Environment (GME, version 0.7.2 for ArcGIS 10.0) (Beyer 2010). To determine whether habitat types were selected, used in proportion or not selected (avoided), we used the Bonferroni *Z*-statistic test (Byers et al. 1984). If a particular habitat type was used above its proportional availability, it was considered “selected”, if it was used below its proportional availability, it was considered to be “not selected” (Johnson 1980). If a habitat type was used in proportion to its availability, this was considered to be random use. The proportion of habitat use against the proportion of habitat availability compared with the Bonferroni confidence interval (CI), was used to determine if there were significant differences for each habitat type (Byers et al. 1984). A significance level of $P < 0.05$ was used to determine significance. Since habitat selection occurs within multiple spatial scales (Johnson 1980), we selected two spatial scales for analyses namely, 2nd-order selection (within the landscape area scale) and 3rd-order selection (within the home range area scale), following recommendations by Johnson (1980).

RESULTS

2nd order of selection (landscape scale)

At the coarse spatial scale all individuals selected forest with bushland habitat type, but did not select residential gardens, agroforestry, or croplands (Fig. 3.2a). The grassland habitat was either selected, used in proportion to its availability or was not selected. All Cape porcupines showed individual variation in their habitat selection within both the landscape scale and the home range scale (Table 3.1). In addition, the majority of the Cape porcupines selected more than one habitat type (Table 3.1). Cape porcupines inhabiting the suburban area (PSF1, PSF2, PSM3, PSM4, and PSM5) selected the forest with bushland habitat and either selected the grassland habitat or was used in proportion (Table 3.1). The garden habitat was not selected by all the Cape porcupines at the suburban area. Cape porcupines inhabiting the peri-urban area (PKM1, PKM2, PKM3, PKF4, and PKF5) all selected the forest with bushland habitat type but all did not select the grassland and garden habitat at the landscape scale (Table 3.1). The porcupine individual (PNF6) at the farmland area, selected for both the forest with bushland and grassland habitats, but did not select the cropland habitat (Table 3.1).

3rd order of selection (home range scale)

At the finer scale, habitat selection differed from the coarse scale as expected, habitat selection became more defined. All Cape porcupines selected the forest with bushland habitat type, but a few individuals used this habitat type in proportion to its availability (Fig. 3.2b). Utilisation of the grassland habitat type was similar to the 2nd order of selection, with some selecting, utilising it in proportion or not selecting this habitat type. Variations between the 2nd and 3rd order of selection were observed within the residential garden and agroforestry habitat types (Fig 3.2). Some individuals were revealed to select or utilise gardens in proportion to their availability at home range scale. Agroforestry were also used in proportion to their availability by some individuals and not selected by the rest (Fig. 3.2). Cape porcupines within the suburban area (PSF1, PSF2, PSM3, PSM4, and PSM5) showed individual variation the selected habitat types (Table 3.2). At the home range scale, the forest with bushland was selected by 4 of 5 individuals, the grassland habitat was selected by 3 of 5 individuals and the garden habitat was selected by 2 of 5 individuals. At the peri-urban landscape (PKM1, PKM2, PKM3, PKF4, and PKF5), all individuals selected the forest with bushland habitat, the grassland habitat was not selected by 4 of 5 individuals, the garden habitat was not selected by all the individuals, and the agroforestry was only used in proportion to its availability by 3 of 5 individuals (Table 3.2). The individual at the farmland area (PNF6) selected all habitat types found within its home range area (Table 3.2).

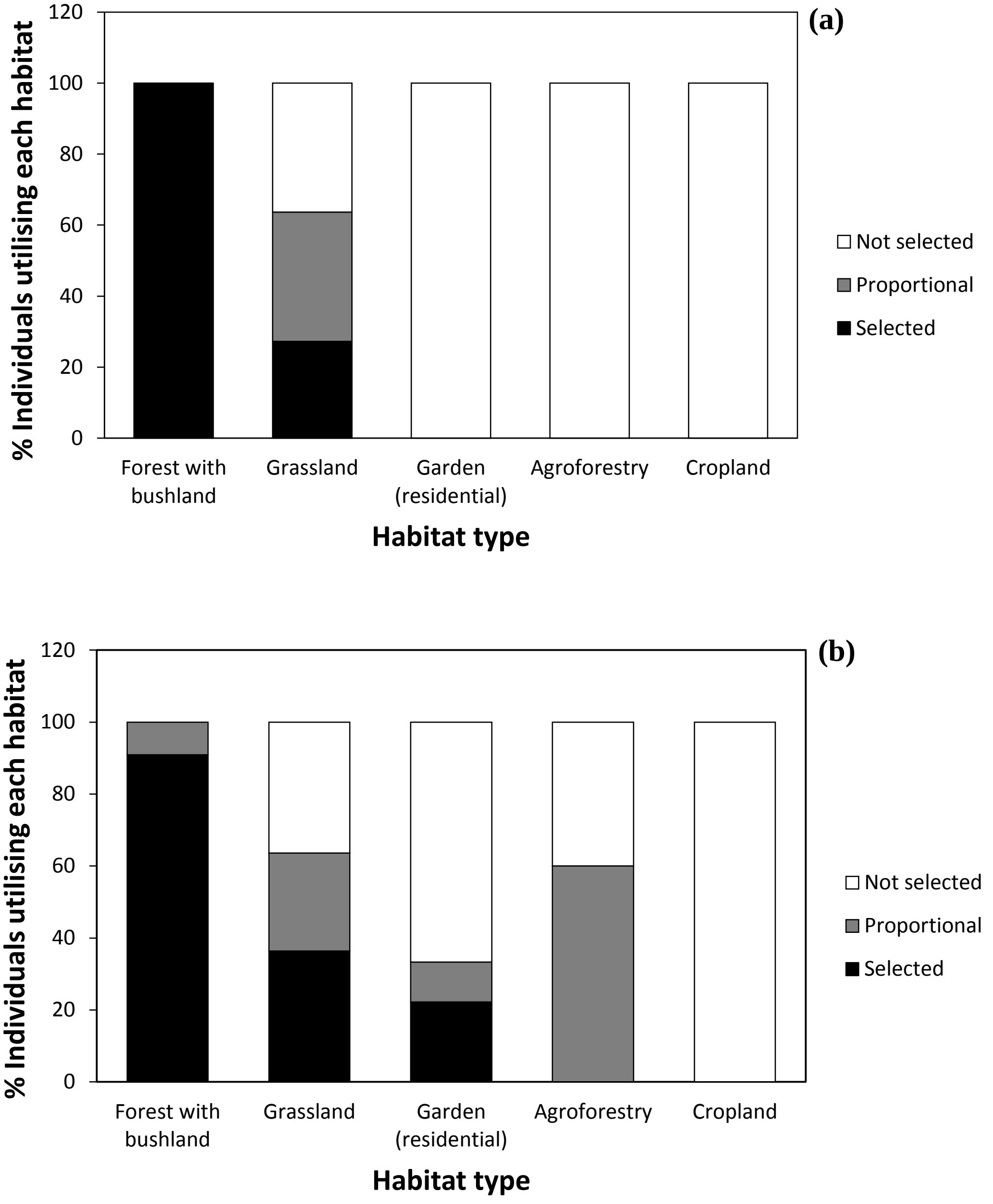

Fig. 3.2. Habitat selection of Cape porcupines in a suburban-farmland gradient in KwaZulu-Natal where (a) shows the second order of habitat selection (within the site scale), and (b) reveals the third order of habitat selection (within the home range scale).

Table 3.1: Within landscape habitat selection (2^{nd} order of selection) by Cape porcupines within the suburban-farmland gradient using Bonferroni confidence intervals at 100% MCP home ranges

	Animal ID										
Habitat type	**PSF1**	**PSF2**	**PSM3**	**PSM4**	**PSM5**	**PKM1**	**PKM2**	**PKM3**	**PKF4**	**PKF5**	**PNF6**
Forest with bushland	+	+	+	+	+	+	+	+	+	+	+
Grassland	+	+	±	±	±	—	±	—	—	—	+
Garden (res)	—	—	—	—	—	—	—	—	—	—	Nil
Agroforestry	Nil	Nil	Nil	Nil	Nil	—	—	—	—	—	Nil
Cropland	Nil	Nil	Nil	Nil	Nil	Nil	Nil	Nil	Nil	Nil	—

+ indicates selected, **-** indicates not selected, **±** indicates that habitat type use was in proportion to its availability (Random use). Suburban area (PSF1, PSF2, PSM3, PSM4, PSM5); peri-urban area (PKM1, PKM2, PKM3, PKF4, PKF5), farmland area (PNF6).

Table 3.2: Within home range habitat selection (3rd order of selection) by Cape porcupines within the suburban-farmland gradient using Bonferroni confidence intervals at 100% MCP home ranges

	Animal ID										
Habitat type	**PSF1**	**PSF2**	**PSM3**	**PSM4**	**PSM5**	**PKM1**	**PKM2**	**PKM3**	**PKF4**	**PKF5**	**PNF6**
Forest with bushland	+	+	+	±	+	+	+	+	+	+	+
Grassland	+	+	+	±	±	—	—	±	—	—	+
Garden (res)	+	—	±	+	—	—	—	—	—	Nil	Nil
Agroforestry	Nil	Nil	Nil	Nil	Nil	—	—	±	±	±	Nil
Cropland	Nil	Nil	Nil	Nil	Nil	Nil	Nil	Nil	Nil	Nil	+

+ indicates selected, **-** indicates not selected, ± indicates that habitat type use was in proportion to its availability (Random use). Habitat selection became more defined within the 3rd (within home range area) order of selection scale. Suburban area (PSF1, PSF2, PSM3, PSM4, PSM5); peri-urban area (PKM1, PKM2, PKM3, PKF4, PKF5), farmland area (PNF6).

DISCUSSION

Investigating animal-habitat interactions is fundamental in understanding animal behavioural ecology and space use, which in turn is useful knowledge for wildlife management and conservation (McLane et al. 2011). Habitat types that are selected or preferred by the subject animal are assumed to be important for their fitness and survival (Manly et al. 2002; Leclerc et al. 2016). This information is especially crucial for threatened/endangered and conflict-causing wildlife, particularly with regards to habitat management (Garshelis 2000). Therefore, conclusions drawn from habitat use studies can be used to manage habitats that would either promote, or conserve the inhabitants (Morris 2003; Grácio et al. 2017).

Wildlife select habitat types that improve their fitness and survivability (Uboni et al. 2017). Such habitats are of high quality resources in terms of food (Dupke et al. 2017), protection from predators (Rehnus et al. 2016), and shelter (Young et al. 2017). The main determinant of habitat selection for Cape porcupines is food distribution (De Villiers et al. 1994; Lovari et al. 2013; Mori et al. 2014a). However, other extrinsic factors may apply, such as predator avoidance (Mori et al. 2014b; Lovari et al. 2017), social status (Lovari et al. 2013; Mori et al. 2014a) and territoriality (de Villiers et al. 1994). For instance, predator avoidance may cause prey species to select habitat types with high cover and protection (Mori et al. 2014b). While for social status (paired versus solitary individual), habitat selection of paired individuals may only be influenced by food search, but those that are solitary may select for habitats that enable food and mate search (Lovari et al. 2013). Finally, with regards to territoriality, individuals may be limited in their habitat selection to habitats located within their territory (De Villiers et al. 1994). Additionally, these individuals have exclusive access to their home ranges and defend the smaller area found within their home range. Individual variation in feeding habits and foraging behaviour (De Villiers et al. 1994) may also explain some individuals preferring habitat types that others do not.

Certain habitat types may be used at large scales, but at finer scales, it may be revealed that certain parts of the most used habitat types are not used because habitat use is scale- dependent (Johnson 1980; Manly et al. 2002; Mayor et al. 2009; McGarigal et al. 2016). For example, although all Cape porcupines selected the forest with bushland habitat at the landscape scale, at the home range scale, we observed that even though a majority of individuals still selected the forest with bushland habitat, a few individuals selected the residential garden and grassland habitat or used these habitats in proportion to their availability.

Furthermore, the majority of Cape porcupine individuals selected for more than one habitat type, emphasising their generalist nature. However, this may be due to variations in diet specialisation exhibited by these individuals (Bolnick et al. 2002). Although Cape porcupines are generalists, each individual has specialised diet preferences that differ from their conspecifics (Fodrie et al. 2015). Individuals differ in their foraging needs for a number of reasons. One reason might be caused by intra-specific competition, which may lead individuals to use less preferred resources or expand their niche to less valuable resources (Araujo et al. 2011). Moreover, with an increase in intra-specific competition, individual diet specialisation tends to increase (Araujo et al. 2011).

Another reason for Cape porcupine inter-individual variation in habitat use, may be behavioural variation, which influences an individual's ability to locate and defend preferred resources (Bolnick et al. 2002). Individuals may differ in their weighing of factors that contribute to their survival. For instance, some individuals may choose to avoid predators and lose out on foraging opportunity, while others would be less risk-aversive and increase their forage uptake (Giroux et al. 2012; Courbin et al. 2017). Therefore, inter-individual variation in diet preference are driven by phenotypic differences which underlie an individual's resource preference, foraging behaviour, physiological requirements, and or social status (Araujo et al. 2011; Fodrie et al. 2015; Toscano et al. 2016).

Therefore, we can infer that the forest with bushland habitat is important to Cape porcupine spatial behaviour. There are a number of reasons this habitat seems to be important to all Cape porcupines such as fitness benefits in terms of cover and protection from predators (but this is not applicable at all our study areas), shelter for denning and provision of favourable microclimate conditions (Lovari et al. 2017), as well as providing a concentration of preferred feeding areas (De Villiers et al. 1994). There was a lot of de-barked trees within this habitat, and most feeding activity was concentrated on specific tree species that were important to the Cape porcupine diets (feeding on tree roots and bark. pers. obs.). Although this habitat type may cost Cape porcupines with forage quality, which may be low during the winter season, thus may affect fitness. However, the benefits of using this habitat seem to outweigh the costs associated with its use.

We had expected that Cape porcupines would take advantage of the easily accessible food items in residential gardens. However, though residential gardens were utilised for food, this habitat type was not selected by the Cape porcupines. This may be due to the opportunistic foraging nature of Cape porcupines as they feed opportunistically throughout their home range area (De Villiers et al. 1994). Due to the fact that, when not limited by foraging time, Cape porcupines may consume 1.5 - 3 kg of economically important agricultural crops (Pillay et al. 2015), they are able to wipe out an entire patch of preferred garden plants and trees in a night. These individuals may not return to the same garden plot, but utilise it once and finish everything they preferred because of their destructive feeding habits (pers. obs.). However, Cape porcupines may not prefer gardens because not all of them have suitable plants to feed on.

Rejection of croplands by Cape porcupines within farmlands was unexpected, but similar results were obtained by de Villiers et al. (1994), Mori et al. (2014a), and Lovari et al. (2017). Although there is high reward in croplands (in terms of food abundance and availability throughout the year), there is also an associated high risk in these areas due to hunting and persecution risk. However, the most likely explanation that we observed a non-selection of croplands is that we had a low sample size, especially for croplands (one collared individual left), so these results may be inaccurate in this regard.

Habitat selection in Cape porcupines appears largely driven by forage availability (Lovari et al. 2013; Mori et al. 2014a; Lovari et al. 2017). In the forest with bushland habitat type, Cape porcupines find their shelter and food resources within this habitat type. Whereas, in residential and grassland habitats, Cape porcupines dig up and feed on roots and bulbs of grasses and ornamental and wild plants. There were no predators in all our study areas, and because Cape porcupines are nocturnal, they usually avoid humans and are able to exploit all vegetation types. This reveals how flexible Cape porcupines are in their use of their landscapes, although they depend on natural vegetation, they have also made use of anthropogenic resources for food (residential gardens) and shelter (drainage pipes).

Hystrix porcupine feeding ecology is generalist and diverse, and depends on which vegetation type is available within their landscape. However, they do show selective vegetation preference and do not feed on just any plant species. They consume almost all plant materials, including fibrous plant parts and tubers. For example, in forest and woodland habitats, porcupines debark mature trees and feed on the live tissue of the inner bark and uproot young saplings (*H. indica*, Greaves and Khan 1978; Khan et al. 2000; Hafeez et al. 2011; Hafeez et al. 2015; *H. africaeaustralis* – Thomson 1974; De Villiers and van Aarde 1994; De Villiers et al. 1994). In grasslands they feed on wild plant species, including rhizomes, bulbs and geophytes (*H. africaeaustralis* - Bragg et al. 2003; *H. indica* - Mushtaq et al. 2009; *H. cristata* - Santini, 1980). In croplands, they feed on available seasonal crops (*H. africaeaustralis* – Corbet 1991; Corbet and van Aarde 1996; *H. indica* - Alkon and Saltz 1985; Saltz and Alkon 1989; Alkon 1999; Mushtaq et al. 2009; *H. cristata* - Laurenzi et al. 2016, Mori et al. 2017). Moreover, *Hystrix* porcupines do indeed have selective behaviour of certain habitat types over others, as has been found also in other studies (Fattorini and Pokheral 2012 - grassland selected; Mori et al. 2014a – woodland selected, Hafeez et al. 2012 – agricultural areas selected; Lovari et al. 2017 – woodland and shrubwood selected).

Although we were unable to investigate seasonal variation in habitat selection in this study due to the short study duration, other studies found variation in seasonal habitat utilisation (Mori et al. 2014a; Mori et al. 2017). With the reasons for variation in seasonal habitat preferences being attributed to food quality and availability (De Villiers et al. 1994). Thompson (1974) revealed that Cape porcupines de-barked trees more during the dry season, where food resources were scarce. Mori et al. (2014a) found there was seasonal variation in the way crested porcupines used their habitats between the warm and cold periods. Crested porcupines utilised croplands during the warm period in order to supplement food resources where they inhabited poor habitats. Therefore, environmental conditions seem to play a major role in porcupine seasonal variation.

We acknowledge our limitations, especially with regards to the short sampling duration and the low sample size. It is our first attempt at revealing Cape porcupine habitat use within a suburban-farmland context, since these are increasingly dominating land use types globally. Moreover, because Cape porcupines seem to be expanding their range with the increase in human-modified land-use types, it is all the more important to gain knowledge of their habitat use, for conservation and management purposes. Our results need to be interpreted with caution, as further research still needs to be conducted, especially regarding habitat use at multiple scales, both in space and time.

Conclusions

Our results showed the importance of investigating habitat selection at varying spatial scales for a species like the Cape porcupine, from coarse to fine scale- as these will reveal how individuals and ultimately populations change their selection of habitats from large to fine spatial scale. Also, our results revealed that although Cape porcupines still used anthropogenic food resources (residential gardens), they used and selected natural habitat types (forest with bushland and grassland). Furthermore, as revealed by other studies, Cape porcupine habitat use seem to be influenced to a great extent by forage availability. Therefore, we believe that this species success in human-modified landscapes is due to their flexible nature and their wide ecological tolerance.

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CHAPTER 4

CONCLUSIONS

Overview

Relatively little research on the spatial ecology of Cape porcupines *Hystrix africaeaustralis* has been conducted despite their wide distribution, and the few studies that have been done were conducted in natural habitats (Corbet 1991; Corbet and van Aarde 1996). However, with anthropogenic land-use projected to increase in the future (Foley et al. 2005; Alexandratos and Bruinsma 2012; Seto et al. 2012; Fragkias et al. 2013), it is crucial that research efforts be redirected to human-dominated habitats, in order to research species dynamics within these landscapes. This will provide valuable information towards the management and conservation of species in these landscapes.

Research findings

Cape porcupines are generalist rodents, which appear to have come to benefit from the expansion of anthropogenic land-use change. Because of their ability to adapt and exploit anthropogenic resources, their distributions have expanded into these altered anthropogenic landscapes. Our aim was to investigate Cape porcupine home ranges in human dominated landscapes (farmland, peri-urban and suburban areas) in order to assess their ranging patterns (Chapter 2). Our results revealed that Cape porcupine home ranges were influenced by individual, monthly and site variation. We observed inter-individual variability in home range size and distribution. We also observed that Cape porcupines in farmlands had the smallest overall estimated home range size relative to the urban areas.

Habitat selection along a suburban-farmland gradient was also investigated, using two of the four recommended levels of selection (Johnson 1980). The spatial scales that were selected were the landscape scale (2nd order) and home range scale (3rd order). Our results revealed that habitat selection varied at both selection scales (Chapter 3). At the landscape scale, all Cape porcupines selected the forest with bushland habitat, however, individuals behaved differently within their home range scales. Therefore, this emphasises the importance of investigating spatial use at multiple scales, since we could miss valuable information if this is not done.

Limitations of study and further research

The current study was a first attempt at determining the ranging patterns of Cape porcupines under varying anthropogenic land-use types. Our method of choice was global position system (GPS) telemetry monitoring, as this has been a method that is increasingly being used in animal behaviour studies (Handcock et al. 2009). Although GPS telemetry is highly beneficial in 1) their ability to collect baseline location data, 2) tracking of historically elusive/cryptic animals, hence enabling researchers to determine movements, activities, behaviour and diet of subject animals (Hubblewhite and Haydon 2010). However, GPS telemetry has accompanying disadvantages including 1) high cost, 2) short battery life, and 3) regular failures of GPS transmitters (Cagnacci et al. 2010). Consequently, some of our GPS transmitters failed, and that resulted in the reduction of our sampling duration, and ultimately resulted in a low sample size.

Regardless, we consider our results to be highly informative in revealing Cape porcupine ranging patterns and flexibility of behaviour within human-dominated landscapes. These are important findings as they enable us to observe how changing anthropogenic land-use has affected Cape porcupine distribution and behaviour. From our results, it’s clear that Cape porcupines are behaviourally flexible and adaptable, they are able to alter their behaviour in response to changing environmental cues. This has favoured their expansion into human-dominated environments, as well as their ability to exploit anthropogenic resources throughout their range.

Our research showed that, together with previous research, porcupine spatial behaviour is largely influenced by forage availability (De Villiers et al. 1994- *H. africaeaustralis*; Sharma and Prasad 1992- *H. indica*; Lovari et al. 2013- *H. cristata*). We also showed that Cape porcupine habitat selection is dominated by natural habitats (forest with bushland) and anthropogenic food resources (croplands and residential gardens) were used opportunistically depending on their availability (chapter 3). We assume that Cape porcupines use anthropogenic food resources or crops to supplement their diet, since it has been shown that Cape porcupines, if not limited by foraging time, can consume up to 2.5 kg of agricultural crops per night (Pillay et al. 2015). Therefore, there is a potential for conflict in these landscapes as a result.

We therefore suggest the following for future research:

1. A long-term investigation of Cape porcupine movement ecology, with the determination of seasonal and monthly effects, as well as gender effects on home ranges, movement and behavioural activities.

2. To study human-porcupine conflict in farmland and urban areas since Cape porcupines are considered as agricultural pests (Barthelmess 2006), and are increasingly becoming problematic in suburbia (pers. comm.), we require to assess public perceptions and attitudes towards Cape porcupines. To use the data obtained to make informed decisions toward Cape porcupine management and conservation in urban and farmland landscapes
3. To assess the population dynamics of Cape porcupines regardless of the IUCN population status of least-concern (LC). Assessing Cape porcupine populations will enable us to effectively manage these species should need arise, this will enable us to make informed decisions of whether to control or conserve Cape porcupines when dealing with conflict.

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