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Anthropogenic influences on spotted hyaenas in a protected area, the Kruger National Park

by

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Summary

Human population growth generally causes carnivore declines. The rapid expansion of urban landscapes creates both biotic and abiotic changes that are known to negatively impact carnivore populations (Šálek, Drahníková & Tkadlec, 2015). Carnivores are considered particularly sensitive to human population growth and urbanisation due to persecution, large home range requirements and slow population growth (Woodroffe, 2000). This can cause local extinctions or active avoidance of humans by carnivores (Ordeñana et al., 2010; Schuette et al., 2013). However, some carnivore species are attracted to areas with high human population densities due to the benefits associated with the use of human based resources such as food and shelter. The spotted hyaena (*Crocuta crocuta*) is the most social of all hyaena species. Clans vary in size from three in the Kalahari up to 80 in East Africa. Spotted hyaenas typically eat prey of medium to large body size. The spotted hyaena is known for its opportunistic scavenging and the species will readily exploit anthropogenic food. In contrast to many species associated with anthropogenic food use, spotted hyaenas are large carnivores that often hunt larger prey. In this study I tested how life-history characteristics influenced visitation at known human resource sites, how the amount of anthropogenic material in scat samples varied in relation to human habitation, and how anthropogenic activity and infrastructure modified the behaviour of a large carnivore, the spotted hyena, in the Kruger National Park. I found that subadults and juveniles were the most frequent visitors at known anthropogenic sites, and I suggest that hyaenas were not visiting the anthropogenic sites in a need of food. Analysis of scats taken from the whole range of the southern section of the park showed that anthropogenic use was quite low, but also that the use was higher in the dry than in the wet season. However, anthropogenic

material did not seem to have been included in hyaena diets in proportion to its availability. Instead, anthropogenic resources appear to have been utilised only by certain hyaenas or cohorts. Despite a presumed low value of anthropogenic resources, human activity and infrastructure were still altering spotted hyaena behaviour. A collared hyaena living in an area with large amounts of anthropogenic activity and infrastructure had a smaller home range that was used less evenly than another collared female living with less contact with humans. Home range size and use also exhibited seasonal variation, with larger areas used in the dry season. Spotted hyaenas inhabiting areas with higher human activity and infrastructure exhibited lower social network density and longer path lengths than those living away from human activity. However, my results did not fully follow those predicted by variations in resource abundance. We predicted that hyaena clans in areas with denser infrastructure and more human activity would show less group cohesiveness and hence both less dense and less complex social networks, caused by a greater access to anthropogenic food and therefore a decreased need for group related foraging.To conclude, my results suggests that anthropogenic resources in the Kruger National Park were of limited nutritional value for or not preferred by spotted hyaenas, but that they were still utilised and influenced spotted hyaena space use and social interactions. These observations are perplexing, and I suggest that further work is needed to improve our understanding of the impact of human activity and infrastructure inside protected areas on native wildlife populations.

I, Lydia Belton declare that the thesis/dissertation, which I hereby submit for the degree Doctor of Philosophy at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

Signature:

Date: 21st April 2017

Note on the Text

In this thesis I investigate the influences of human infrastructure, activity and associated resources on varying aspects of spotted hyaena biology inside one of the largest protected areas in southern Africa, the Kruger National Park. The thesis consists of this general introduction, four data chapters, and a final chapter containing overall conclusions from the work. Each data chapter has been submitted for publication, including chapter four which has already been published. Therefore, each data chapter is written in the format for an intended journal, so that differences in style and some repetition, particularly of method and study area description, may exist.

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Contents

Chapter 1: Introduction

General Background

Human habitation takes many forms, from the world's largest concrete jungles to semi-nomadic hunter gatherers. Over the last two centuries human population growth has been coupled with a continuing global trend of urbanisation (Cohen 2003). Over half of the world's human population currently lives in urban areas with the global urban population predicted to grow by 1.84% per year between 2015 and 2020 (WHO 2014). This urbanisation is recognised as a major risk to biodiversity (McKinney 2006). Urbanisation results in the replacement of existing habitat with man-made infrastructure and with subsequent habitat fragmentation (Sol et al. 2013; Widdows and Downs 2015). However, human infrastructure does provide opportunities to utilise new resources, and the often predictable nature of anthropogenic food sources in urban areas makes them a reliable alternative to the often seasonal changes of native resources (Widdows and Downs 2015). Therefore, urban environments can be regarded as a distinct wildlife habitat (Šálek et al. 2015), and urban ecology is subsequently becoming a rapidly expanding field of research (Magle et al. 2012).

Most research in urban ecology focusses on towns and cities in highly modified environments. However, urbanization occurs in other areas as well. Modern conservation practice emphasises the importance of public support of conservation. Tourism raises funds and gives people a greater appreciation for the need to protect conservation areas. As a result conservation areas frequently contain sites of high human activity and carnivore

presence is tolerated by local people (Naughton-Treves et al. 2003). Concentrated human activity creates pockets of urbanisation in a landscape of protected wildlife populations, thus creating an urban setting that can be exploited by protected opportunistic carnivores. Within conservation areas, concentrated human activity integrated in a landscape of protected wildlife populations often leads to close contact between humans and non-human animals (hereafter animals). This situation could potentially lead to conflict, which may be difficult to resolve because of the elevated protection status of the animals in question, and the relative importance of visitors into parks and protected areas.

The order Carnivora has a suite of traits that allow them to adapt to a variety of habitats across the globe. There are an estimated 230+ species globally (Boitani and Powell 2012), inhabiting all continents and they occur in all habitats. They colonise elevations from sea level to greater than 5000m and range in size from 50g - 600kg (Boitani and Powell 2012). Carnivores can be solitary, social or exist in more flexible social groupings, such as species that are only social during the mating season (Dalerum 2007). The position of carnivores at the top of the food chain gives them a strong influence over ecosystems as a whole (Dalerum 2013), but makes them vulnerable to extinction in an increasingly urbanised world (Woodroffe 2000).

Carnivores are particularly sensitive to human population growth and urbanisation due to persecution by humans, large home range requirements and slow population growth (Woodroffe 2000). Consequently, human population growth is often associated with the decline and local extirpation of carnivore populations (Woodroffe 2000). Their large home

range requirements make carnivores vulnerable to habitat modification and increased encounter rates with humans (Treves et al. 2004). Historically their diet has also put them in direct competition with humans for resources (Treves and Karanth 2003), which often has led to conflict and may contribute to persecution. These conflicts have in turn resulted in the local extinctions of carnivore populations or active avoidance of humans by carnivores (Ordeñana et al. 2010; Schuette et al. 2013). Even with changing attitudes towards wildlife in some societies, the persecution of carnivores continues (Kellert et al. 1996; Bunnefeld et al. 2006). The rapid expansion of urban landscapes creates both biotic (habitat loss and fragementaion) and abiotic (shelter) changes that are known to have further negative impacts on carnivore populations (Šálek et al. 2015).

Despite potential disturbances and the generally negative impacts of humans, many carnivore species do successfully live in close proximity to humans. Urban landscapes offer beneficial resources, such as access to predictable anthropogenic food, water and shelter (Bateman and Fleming 2012; Laver 2013; Newsome et al 2014), for those animals capable of successfully exploiting these resources.

Generalist mesocarnivores and omnivores such as coyotes (*Canis latrans*) and raccoons (*Procyon lotor*) have been able to fill this niche and successfully colonise urban areas. Within urban areas, anthropogenic resources such as food and shelter are often abundant, while the risks associated with their exploitation are presumably reduced (Prange et al. 2004; Gerht and Riley 2010). The success or persistence of a carnivore species is therefore dependent on its ability to adapt to these environments (Ditchkoff et al. 2006; McKinney 2006). The perceived potential to directly endanger human life is also an important factor in

successful colonisation of human areas in order to avoid persecution (Gibeau 1998; Burns and Howard 2003), with smaller carnivores perceived as less of a risk.

Carnivore synanthropy (wild animals gaining benefit from living in close association with humans) has been recorded across six of the seven continents (Newsome et al. 2015). Carnivore species recorded to live in close association with humans range in size from the mongooses (Herpestidae) (Laver 2013), to bears (Ursidae) (Beckmann and Berger 2003a; Beckmann and Berger 2003b). However, synanthropy raises management concerns. Disease transmission (Bradley and Altizer 2007), deliberate feeding (Timm et al. 2004; Lukasik and Alexander 2011), damage to property, the killing of domestic animals (Pedersen 2004), and, whilst rare, aggression towards humans (Burns and Howard 2003; Timm et al. 2004) are frequently perceived as problems that need to be addressed. Additionally, some carnivore species are protected, thereby preventing unregulated disturbance, removals or lethal control. This dichotomy between protecting carnivores and finding solutions towards conflicts caused by their presence becomes especially apparent when the conflict arises within a protected area.

Use of anthropogenic food by carnivores has been documented worldwide, including in North American black bears (*Ursus americanus*) (Beckmann and Berger 2003b), South American maned wolves (*Chrysocyon brachyurus*) (Aragona and Setz 2001), red foxes (*Vulpes vulpes*) (Contesse et al. 2004) and Australian dingoes (*Canis dingo*) (Newsome et al. 2013). In addition to the use of anthropogenic food itself, associated changes in behaviour and ecology have been documented. For example, reductions in home range and

increases in population density have been observed in American black bears (Beckmann and Berger 2003b), reduction in dietary breadth has been observed in brown hyaenas (*Hyaena brunnea*) (Maude 2005), and increases in population density and subsequent elevations in the probability of disease transmission has been observed in red foxes that carry the zoonotic *Echinococcus multilocularis* (Hegglin 2003; Mackenstedt et al. 2015). However, since seasonal fluctuations in food supply may alter carnivore behaviour and ecology, seasonal fluctuations in native resources likely influence the relative effects of anthropogenic resources on carnivore behaviour and ecology.

Anthropogenic Influences on Spotted Hyaenas in the Kruger National Park

In this thesis I investigate the influences of human infrastructure, activity and associated resources on varying aspects of spotted hyaena biology inside one of the largest protected areas in southern Africa, the Kruger National Park. My study can be divided into two sections. In the first part (chapters 2 and 3) I evaluate how anthropogenic material is being utilized by spotted hyaenas in the Kruger National park, either through direct observation of visitation at anthropogenic sites (chapter 2) or by quantifying the amount of anthropogenic material in hyaena diet through scat analysis (chapter 3). In the second part (chapters 4 and 5) I continue to evaluate the effects of this potential utilization on two central aspects of spotted hyaena biology, their home range use (chapter 4) and their social interactions (chapter 5). For the purposes of this thesis, the term 'anthropogenic food' will be used to define organic matter that has been discarded by humans and is available for exploitation by carnivores. 'Anthropogenic material' will refer to man-made matter (e.g. plastic or paper) that is found in the scat of animals utilising anthropogenic food. ‘Anthropogenic activity’

refers to the presence of humans and associated infrastructure. The thesis consists of this general introduction, four data chapters, and a final chapter containing overall conclusions from the work.

In chapter two, I set out to test if specific age, rank or sex categories of hyaenas visited anthropogenic sites more than others. This work was done at two sites where deliberate feeding occurred and over two seasons to investigate the role of fluctuations of native prey on visitation at anthropogenic resources. In chapter three, I used analyses of seasonally collected scats to evaluate if hyaenas in close proximity to centres of human activity differed in their diet compared to hyaenas that were less influenced by humans. In chapter four I investigated the role of exposure to human infrastructure on home range size, movement patterns and habitat selection using GPS positioning data. Finally in chapter five I used behavioural data collected on four clans to evaluate the influences of human infrastructure and activity on spotted hyaena social behaviour. Each of these clans had different exposure to human activity and infrastructure. Network analyses based on mathematical graph theory was then applied to see if these differences in human exposure altered patterns of social interactions and dynamics within clans.

Study species: the spotted hyaena

The spotted hyaena is the most social of all hyaena species. Clans vary in size from three in the Kalahari (Mills 1990) up to 80 in East Africa (Boydston et al. 2003). Spotted hyaenas are found across almost all of sub-Saharan Africa in a wide range of habitat types (Figure 1), from the Kalahari Desert (Mills 1984), to a peri-urban existence in Ethiopia (Abay et al.

2010). However, the distribution is patchy with populations concentrated in protected areas (IUCN 2015). Total population size is estimated between 27,000 - 47,000 individuals (Mills and Hofer 1998; IUCN 2015). The continued decline of populations outside of reserves is attributed to habitat transformation and persecution by humans (Mills and Hofer 1998; IUCN 2015). Spotted hyaenas typically eat prey of medium to large body size (Mills and Harvey 2001). They do not exhibit particular prey preferences and avoid only some of the larger herbivores at the species specific level (Hayward 2006). However site specific preferences in prey have been reported (Cooper et al. 1999; Di Silvestre et al. 2000). The spotted hyaena is known for its opportunistic scavenging (Mills and Hofer 1998), and the species will readily exploit anthropogenic food (Yirga et al. 2015). In contrast to many species associated with anthropogenic food use, spotted hyaenas are large carnivores that often hunt larger prey (Cooper et al. 1999). Within South Africa spotted hyaenas are almost entirely confined to protected areas, with an estimated population of 1680 – 5100 individuals (Mills & Hofer, 1998).

Spotted hyaena clans consist of related females and unrelated adult males. Male offspring usually disperse at maturity (Kruuk 1972). A strict matrilineal social structure is maintained through social interactions (Frank 1986). They exhibit high levels of behavioural plasticity, including dietary plasticity (Hayward 2006; Holekamp and Dloniak 2010). Once considered mere scavengers, hyaenas are successful hunters. Working as a team, they are capable of bringing down adult Cape buffalo (*Syncerus caffer*) (Cooper et al. 1999) and gemsbok (*Oryx gazella*) (Trinkel 2009). Other dietary items include rodents, plants, birds and reptiles (Henschel and Skinner 1990; Holmern et al. 2007). One hyaena can eat at least 14.5kg of meat in one sitting (Kruuk 1972), and can digest bone and skin (Kingdon 1988).

Consumption of bone is aided by a high bite force relative to its body size (Christiansen and Wroe 2007). Considering its high behavioural plasticity including frequent opportunistic scavenging (Holekamp and Dloniak 2010), it is not surprising that this species often exploits anthropogenic resources (Mills and Hofer 1998). Whilst scavenging anthropogenic food initially was reported anecdotally (Henschel 1986; Mills and Hofer 1998), it has in more recent years become the focus of scientific studies (Ryan 2007; Fourie 2008; Kolowski and Holekamp 2008; Abay et al. 2010). As with other species, diet switches based on availability of anthropogenic food has been recorded (Yirga et al. 2012), and access to anthropogenic food has caused changes in other aspects of hyaena behavioural ecology. For instance, Kolowski and Holekamp (2008) showed changes to home range size, home range utilisation and a seasonal effect of anthropogenic food utilisation in response to direct access to an anthropogenic food source. In addition, the amount of anthropogenic material found in collected scats in South Africa have differed both between seasons and areas with contrasting levels of human impact (Ryan 2007; Fourie 2008).

Study area: The Kruger National Park

This study took place in the 5000 km^2 Southern section of the Kruger National Park (KNP). KNP is situated in the lowveld of South Africa. It shares boundaries with Mozambique along its eastern side and Zimbabwe in the North. The park covers 2 million hectares. The park is 350 km from North to South but has an average width of 60 km. Field work for this study was carried out in the South of KNP (24-25°S, 31-32°E) below the Tshokwane ranger section and the adjacent Sabie Park private reserve (24°59'S, 31°27'E) which borders southern KNP (Figure 1). Southern KNP falls within the lowveld bushveld zone. Rainfall is

strongly seasonal with the majority falling during the hot summer months (October – March) (Figure 2). Average annual rainfall in this region of the KNP is approximately 650 mm (Venter and Gertenbach 1986). Winters tend to be cool and dry for the southern section of the park. The majority of the southern KNP area is based on granite bedrock (Venter et al. 2003). Southern Kruger has a variety of vegetation types, but the study area is characterised by woodland with basalt soils dominated by *Clerocarya caffra* and *Acacia nigrescens*, with *Combretum* species on granite soils (Ogutu and Owen-Smith 2003). In southern Africa, the wet season is typically associated with increased prey availability related to the reproduction of prey species (Pereira, Owen-Smith & Moleón, 2013), while the dry season in contrast is associated with drought and elevated animal mortality partially caused by disease (Owen-Smith 1990; Pereira et al. 2013).

KNP hosts a diverse array of herbivorous and carnivorous mammals. Prey available for spotted hyaenas in the southern section of the park include, along with small mammals; impala *(Aepyceros melampus),* blue wildebeest *(Connochaetes* taurinus), Burchell's zebra (*Equus burchelli*), greater kudu *(Tragelaphus strepsiceros*), common warthog *(Phacochoerus africanus*), imbabala bushbuck (*Tragelaphus sylvaticus*), nyala (*Nyala angasii*), common reedbuck (*Redunca arundinum*), waterbuck (*Kobus ellipsiprymnus*), steenbok (*Raphicerus campestris*), common duiker (*Sylvicapra grimmia*) and Cape buffalo (*Syncerus caffer*). Other megaherbivores such as African elephant (*Loxodonta africana*), white rhinoceros (*Ceratotherium simum*), black rhinoceros (*Diceros bicornis*), and giraffe (*Giraffa camelopardalis*) are also available, but are presumably only utilized by hyaenas as carrion. Impala in particular constitutes a large part of the hyaena diet in KNP (Henschel and Skinner 1990; Ryan 2007). Four large carnivores live sympatrically with hyaenas in

KNP: African lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), and African wild dog (*Lycaon pictus*).

Chapter 2: Visitation at anthropogenic sites

Individual variation in resource use is often ignored in ecological studies (Bolnick et al. 2003). The assumption is that such variation is limited or plays a minor role in determining ecological processes (Bolnick et al. 2003). Studies have reported that association with human areas and use of anthropogenic resources often varies according to factors such as sex, age and reproductive status (Beckmann and Berger 2003b). A previous study on anthropogenic food use in spotted hyaenas also showed that cohort specific variation existed (Kolowski and Holekamp 2008).

Since carnivore populations tend to be food limited (Beckmann and Berger 2003a), asymmetries in competitive ability may result in contrasting levels of access to a resource, especially when distribution is patchy and supply is predictable (Parker 1974). Such attributes are often characteristic of anthropogenic resources. The benefits associated with obtaining these resources may differ between individuals (Enquist and Leimar 1987). This effect is obvious in sexually dimorphic species such as the Iberian lynx (*Lynx Pardinus*) (López-Bao et al. 2009); older larger males are able to exclude the smaller females and younger males from a resource. These asymmetries are known to influence the way in which various bear species also utilize anthropogenic resources (Beckmann and Berger 2003a). Use of such resources is also often found to be greater during times of natural resource scarcity (Mattson 1990; Fedriani and Kohn 2001; Contesse et al. 2004; López-Bao

et al. 2011).

Within hyaena societies, socially dominant females exclude lower ranking hyaenas from kills and take food from subordinates (Frank 1986). Along with the densely populated urban environment other forms of human habitation exist. Outside the central urban zone, residential and peri-urban areas create a matrix and gradient of human density for wildlife to occupy. Whilst the majority of the scientific studies have focussed on carnivores living in these environments, pockets of high human presence also occur inside protected areas (e.g. Gilchrist and Otali 2002; Quinn and Whisson 2005). I hypothesised that hyaenas with limited access to native food, either because of rank-related access to carcasses or because of limited hunting abilities, would visit anthropogenic sites more often than hyaenas that could sustain themselves on native prey. In addition, I expected that visits at anthropogenic sites would be more frequent in the season with low availability of native prey, and that this seasonal variation would be more pronounced for hyaenas with limited access to native food. I carried out this research by observing individually identified hyaneas from two clans as they visited sites that offered a predictable supply of anthropogenic food.

Chapter 3: Influences of anthropogenic resources on spotted hyaena diet

The effects of anthropogenic food availability on overall diet have been studied in a number of species, for example coyotes and red foxes (Contesse et al. 2004; Grigione et al. 2011; Lukasik and Alexander 2012). Different types and levels of urbanisation will produce contrasting challenges and opportunities for carnivores. In general, however, studies on anthropogenic food use within protected areas are scarce compared to data focusing on

urban and suburban landscapes. Conflicting results between the two environments also suggest that the utilisation of anthropogenic food use inside of natural areas by carnivores would merit more research. In addition, seasonal availability of native prey may also play a role in the utilisation of anthropogenic resources. For example, the maned wolf and coyotes have been observed to switch from native prey to anthropogenic resources during periods of prey scarcity or when anthropogenic resources become more easily available (Aragona and Setz 2001; Morey et al. 2007). Conversely, a reduction in the utilisation of anthropogenic resources have been associated with an increased use of native prey in red foxes (Panek and Budny 2016). As a consequence, the year-round availability of anthropogenic food may produce different dietary patterns in hyaenas living in close proximity to humans compared to those living away from them. For this chapter I collected scats from along the roads of KNP in both wet and dry season. Anthropogenic litter was also tallied in the wet season to see how it varied across the park. The role of sites of high human activity and infrastructure were accounted for by making an 8 km diameter buffer around each site and comparing the amount of anthropogenic material found in scat either inside or outside the buffers.

Chapter 4: Influences of human infrastructure on spotted hyaena home range and spatial use

An increase in anthropogenic food use is frequently associated with a contraction in home range and core area (Kolowski and Holekamp 2008; Newsome et al. 2013; Šálek et al. 2015). However, home range size and utilisation is also dependent on a number of factors, for example seasonal variation and distribution of native resources (Prange et al. 2004). This includes prey density (Herfindal et al. 2005), appropriate shelter (Fisher 2000) and

water (Gerht and Fritzell 1998), and the spatial distribution of prey (Hofer and East 1993). A reduction in home range size has been associated to the availability of anthropogenic resources in for example spotted hyaenas (Kolowski and Holekamp 2008), urban raccoons (Prange et al. 2004), and American black bears (*Ursus americanus*) (Beckmann and Berger 2003a). In addition, Indian mongoose (*Herpestes javanicus*) and red foxes have both been found to use areas with anthropogenic food significantly more often than other areas within their home range (Cavallini 1992; Quinn and Whisson 2005). In this study I compared home range size and space use of two dominant female spotted hyaenas. One was living in a clan on a quiet road far away from any human habitation and the second one was living in the vicinity of the largest area of human infrastructure in the park, the Skukuza rest camp and staff village. Cell phone linked GPS collars took locations at eleven hour intervals to ensure that positions were recorded for both resting and active periods. I used these data to create seasonal home range estimates, evaluate the relative use of space within home ranges during active and resting time periods, and to do a simple habitat selection model within the Skukuza area, to evaluate if there were spatial preference or avoidance for different types of infrastructure within this urban patch.

Chapter 5: The effects of human infrastructure and activity on social interactions

There are strong associations between resource availability and the sociality of carnivores. For example, times of abundant food resources have been associated with a strengthening of social ties in spotted hyaenas (Holekamp et al. 2012), and a weakening of ties when resources are less abundant (Holekamp et al. 2012). However, the effects of anthropogenic activity and related resources on social interactions in group living carnivores has yet only

received limited attention, but they appear to be important. For instance, banded mongooses (M*ungus mungo*) have showed heightened levels of aggression between conspecifics around garbage sites (Flint et al. 2016). Social network analysis provides a powerful framework for quantifying social interactions. The analyses of social interaction networks have, for instance, been used to identify key individuals in social groups, the resilience of social groups to external perturbations, and the effects of social interactions on disease transmission (Wey et al. 2008). In this chapter, I used behavioural data combined with social network analyses to evaluate anthropogenic influences on spotted hyaena social behaviour. Each hyaena clan experienced contrasting levels of human infrastructure and activity, and I contrasted both global network metrics among the clans as well as the relative roles of individuals of varying age, sex and rank classes among the social networks.

References

Abay GY, Bauer H, Gebrihiwot K, Deckers J (2010) Peri-urban spotted hyena (Crocuta crocuta) in Northern Ethiopia: diet, economic impact, and abundance. Eur J Wildl Res 57:759–765.

Aragona M, Setz EZF (2001) Diet of the maned wolf, Chrysocyon brachyurus (Mammalia: Canidae), during wet and dry seasons at Ibitipoca State Park, Brazil. J Zool 254:131–136.

Bateman PW, Fleming PA (2012) Big city life: carnivores in urban environments. J Zool 287:1–23.

Beckmann JP, Berger J (2003a) Using Black Bears to Test Ideal-Free Distribution Models Experimentally. J Mammal 84:594–606.

Beckmann JP, Berger J (2003b) Rapid ecological and behavioural changes in carnivores: the responses of black bears (Ursus americanus) to altered food. J Zool 261:207–212.

Boitani L, Powell RA (2012) Carnivore Ecology and Conservation: A Handbook of Techniques. OUP Oxford

Bolnick DI, Svanbäck R, Fordyce JA, et al (2003) The ecology of individuals: incidence and

implications of individual specialization. Am Nat 161:1–28.

Bowyer RT, McKenna SA, Shea ME (1983) Seasonal Changes in Coyote Food Habits as Determined by Fecal Analysis. Am Midl Nat 109:266.

Boydston EE, Kapheim KM, Szykman M, Holekamp KE (2003) Individual variation in space use by female spotted hyenas. J Mammal 84:1006–1018.

Bradley CA, Altizer S (2007) Urbanization and the ecology of wildlife diseases. Trends Ecol Evol 22:95–102.

Bunnefeld N, Linnell JDC, Odden J, et al (2006) Risk taking by Eurasian lynx (Lynx lynx) in a human-dominated landscape: effects of sex and reproductive status. J Zool 270:31–39.

Burns GL, Howard P (2003) When wildlife tourism goes wrong: a case study of stakeholder and management issues regarding Dingoes on Fraser Island, Australia. Tour Manag 24:699–712.

Cavallini P (1992) Ranging Behavior of the Red Fox (Vulpes vulpes) in Rural Southern Japan. J Mammal 73:321–325.

Christiansen P, Wroe S (2007) Bite forces and evolutionary adaptations to feeding ecology in carnivores. Ecology 88:347–358.

Cohen JE (2003) Human Population: The Next Half Century. Science 302:1172–1175.

Contesse P, Hegglin D, Gloor S, et al (2004) The diet of urban foxes (Vulpes vulpes) and the availablity of anthropogenic food in the city of Zurich, Switzerland. Mamm Biol 69:81–95.

Cooper SM, Holekamp KE, Smale L (1999) A seasonal feast: long-term analysis of feeding behaviour in the spotted hyaena (Crocuta crocuta). Afr J Ecol 37:149–160.

Craig PS, Rogan MT, Campos-Ponce M (2003) Echinococcosis: disease, detection and transmission. Parasitology 127:S1–S16.

Dalerum F (2007) Phylogenetic reconstruction of carnivore social organizations. J Zool 273:90–97.

Dalerum F (2013) Phylogenetic and functional diversity in large carnivore assemblages. Proc R Soc Lond B Biol Sci 280:20130049.

Dell'Arte GL, Laaksonen T, Norrdahl K, Korpimäki E (2007) Variation in the diet composition of a generalist predator, the red fox, in relation to season and density of main prey. Acta Oecologica 31:276–281.

Di Silvestre I, Novelli O, Bogliani G (2000) Feeding habits of the spotted hyaena in the Niokolo Koba National Park, Senegal. Afr J Ecol 38:102–107.

Ditchkoff SS, Saalfeld ST, Gibson CJ (2006) Animal behavior in urban ecosystems:

Modifications due to human-induced stress. Urban Ecosyst 9:5–12.

Enquist M, Leimar O (1987) Evolution of fighting behaviour: the effect of variation in resource value. J Theor Biol 127:187–205.

Fedriani JM, Kohn MH (2001) Genotyping faeces links individuals to their diet. Ecol Lett 4:477–483.

Fisher D o. (2000) Effects of vegetation structure, food and shelter on the home range and habitat use of an endangered wallaby. J Appl Ecol 37:660–671.

Flint BF, Hawley DM, Alexander KA (2016) Do not feed the wildlife: associations between garbage use, aggression, and disease in banded mongooses (Mungos mungo). Ecol Evol 6:5932-5939.

Fourie C (2008) The influence of seasons and human density on anthropogenic food consumption in the spotted hyaena Crocuta crocuta in Kruger National Park M.Sc. thesis. Honours Thesis, University of Pretoria

Frank LG (1986) Social organization of the spotted hyaena Crocuta crocuta. II. Dominance and reproduction. Anim Behav 34:1510–1527.

Gerht S., Riley SP. (2010) Coyotes (Canis latrans). In: Gerht S., Riley SP., Cypher BL (eds) Urban carnivores: ecology, conflict and conservation. John Hopkins University press, Baltimore,

Gerht SD, Fritzell EK (1998) Resource distribution, female home range dispersion and male spatial interactions: group structure in a solitary carnivore. Anim Behav 55:1211–1227.

Gibeau ML (1998) Use of urban habitats by coyotes in the vicinityof Banff Alberta. Urban Ecosyst 2:129-139

Gilchrist JS, Otali E (2002) The effects of refuse-feeding on home-range use, group size, and intergroup encounters in the banded mongoose. Can J Zool 80:1795–1802.

Grigione MM, Burman P, Clavio S, et al (2011) Diet of Florida coyotes in a protected wildland and suburban habitat. Urban Ecosyst 14:655–663.

Hayward MW (2006) Prey preferences of the spotted hyaena (Crocuta crocuta) and degree of dietary overlap with the lion (Panthera leo). J Zool 270:606–614.

Hegglin D (2003) The Fox Tapeworm (Echinococcus Multilocularis) and the Red Fox (Vulpus Vulpus) in the Urban Habitat: Ecological and Epidemiological Aspects and an Evaluation of an Intervention Strategy. Zürich

Henschel JR (1986) The Socio-Ecology Of A Spotted Hyaena (Crocuta Crocuta) Clan In The Kruger National Park. Dissertation, University of Pretoria

Henschel JR, Skinner JD (1990) The diet of the spotted hyaenas Crocuta crocuta in Kruger

National Park. Afr J Ecol 28:69–82.

Herfindal I, Linnell JD., Odden J, et al (2005) Prey density, environmental productivity and home-range size in the Eurasian lynx (Lynx lynx). J Zool 265:63–71.

Hofer H, East ML (1993) The commuting system of Serengeti spotted hyaenas: how a predator copes with migratory prey. III. Attendance and maternal care. Anim Behav 46:575–589.

Holekamp KE, Dloniak SM (2010) Intraspecific variation in the behavioral ecology of a tropical carnivore, the spotted hyaena. Advaces Study Behav 42:189–229.

Holekamp KE, Smith JE, Strelioff CC, et al (2012) Society, demography and genetic structure in the spotted hyena. Mol Ecol 21:613–632.

Holmern T, Nyahongo J, Røskaft E (2007) Livestock loss caused by predators outside the Serengeti National Park, Tanzania. Biol Conserv 135:518–526.

IUCN (2015) IUCN 2015. The IUCN Red List of Threatened Species. Version 2015.1. <http://www.iucnredlist.org>. Downloaded on 22nd June 2015.

Kellert SR, Black M, Rush CR, Bath AJ (1996) Human Culture and Large Carnivore Conservation in North America. Conserv Biol 10:977–990.

Kingdon J (1988) East African mammals: an atlas of evolution in Africa. University of Chicago Press

Kolowski JM, Holekamp KE (2008) Effects of an open refuse pit on space use patterns of spotted hyenas. Afr J Ecol 46:341–349.

Kruuk H (1972) The spotted hyena: a study of predation and social behavior. Dissertation, University of Chicago

Laver PN (2013) The foraging ecology of banded mongooses (Mungos mungo): Epidemiological and human-wildlife conflict implications. Virginia Polytechnic Institute and State University

López-Bao JV, Palomares F, Rodríguez A, Ferreras P (2011) Intraspecific interference influences the use of prey hotspots. Oikos 120:1489–1496.

López-Bao JV, Rodrigues A, Palomares F (2009) Competitive asymmetries in the use of supplementary food by the endangered Iberian lynx. Plos One 4:1–10.

Lucherini M, Crema G (1994) Seasonal variation in diet and trophic niche of the red fox in an alpine habitat. Z Für Säugetierkd 59:1–8.

Lukasik V, Alexander S (2012) Spatial and Temporal Variation of Coyote (Canis latrans) Diet in Calgary, Alberta. Cities and the Environment (CATE) 4:8.

Lukasik VM, Alexander SM (2011) Human–Coyote Interactions in Calgary, Alberta. Hum Dimens Wildl 16:114–127.

Mackenstedt U, Jenkins D, Romig T (2015) The role of wildlife in the transmission of parasitic zoonoses in peri-urban and urban areas. Int J Parasitol Parasites Wildl 4:71–79.

Magle SB, Hunt VM, Vernon M, Crooks KR (2012) Urban wildlife research: Past, present, and future. Biol Conserv 155:23–32.

Mattson DJ (1990) Human impacts on bear habitat use. In: Bears: their biology and management, a selection of papers from the eighth international conference on bear research and management. International Association of Bear Research and Management, Victoria, British Columbia, Canada, pp 33–56

Maude G (2005) The Comparative Ecology of the Brown Hyaena (Hyaena brunnea) in Makgadikgadi National Park amd a Neighbouring Commumity Cattle Are in Botswana. MSc, University of Pretoria

McKinney ML (2006) Urbanization as a major cause of biotic homogenization. Biol Conserv 127:247–260.

Mills MGL (1990) Kalahari hyaenas. Unwin Hyman

Mills MGL (1984) The comparative behavioural ecology of the brown hyaena Hyeana brunnea and the spotted hyaena Crocuta crocuta in the southern Kalahari. Koedoe Suppl 27:237–247.

Mills MGL, Harvey M (2001) African predators. Smithsonian Institution Press

Mills MGL, Hofer H (1998) Hyaenas. Status survey and conservation action plan. IUCN/SSC Hyaena Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK

Morey PS, Gese EM, Gehrt S (2007) Spatial and temporal variation in the diet of coyotes in the Chicago Metropolitan Area. Am Midl Nat 158:147–161.

Naughton-Treves L, Grossberg R, Treves A (2003) Paying for Tolerance: Rural Citizens' Attitudes toward Wolf Depredation and Compensation. Conserv Biol 17:1500–1511.

Newsome TM, Ballard G-A, Dickman CR, et al (2013) Home range, activity and sociality of a top predator, the dingo: a test of the Resource Dispersion Hypothesis. Ecography 36:914–925.

Newsome TM, Dellinger JA, Pavey CR, et al (2015) The ecological effects of providing resource subsidies to predators. Glob Ecol Biogeogr 24:1–11.

Ogutu JO, Owen-Smith N (2003) ENSO, rainfall and temperature influences on extreme population declines among African savanna ungulates. Ecol Lett 6:412–419.

Ordeñana MA, Crooks KR, Boydston EE, et al (2010) Effects of urbanization on carnivore

species distribution and richness. J Mammal 91:1322–1331.

Owen-Smith N (1990) Demography of a Large Herbivore, the Greater Kudu Tragelaphus strepsiceros, in Relation to Rainfall. J Anim Ecol 59:893–913.

Panek M, Budny M (2016) Variation in the feeding pattern of red foxes in relation to changes in anthropogenic resource availability in a rural habitat of western Poland. Mamm Biol - Z Für Säugetierkd 82:1–7.

Parker GA (1974) Assessment strategy and the evolution of fighting behaviour. J Theor Biol 47:223–243.

Pedersen SE (2004) Urban Coyotes: Preparing residents of the Greater Washington Metropolitan Area for potential conflicts. Virginia Polytechnic Institute and State University.

Pereira LM, Owen-Smith N, Moleón M (2013) Facultative predation and scavenging by mammalian carnivores: seasonal, regional and intra-guild comparisons. Mammal Rev 44:1–12.

Prange S, Gerht S., Wiggers E. (2004) Influences of anthropogenic resources on raccoon (Procyon lotor) movements and spatial distribution. J Mammal 85:483.

Quinn JH, Whisson DA (2005) The effects of anthropogenic food on the spatial behaviour of small Indian mongooses (Herpestes javanicus) in a subtropical rainforest. J Zool 267:339–350.

Ryan B (2007) Effects of anthropogenic food sources on diet and parasite loads in spotted hyaena, Crocuta crocuta (Erxleben, 1777) in Kruger National Park,. Dissertation, University of Pretoria

Šálek M, Drahníková L, Tkadlec E (2015) Changes in home range sizes and population densities of carnivore species along the natural to urban habitat gradient. Mammal Rev 45:1–14.

Schuette P, Wagner AP, Wagner ME, Creel S (2013) Occupancy patterns and niche partitioning within a diverse carnivore community exposed to anthropogenic pressures. Biol Conserv 158:301–312.

Sol D, Lapiedra O, González-Lagos C (2013) Behavioural adjustments for a life in the city. Anim Behav 85:1101–1112.

Tao Y, Borger L, Hastings A (2016) Dynamic Range Size Analysis of Territorial Animals: An Optimality Approach. Am Nat 188:460–474.

Timm RM, Baker RO, Bennett JR, Coolahan CC (2004) Coyote Attacks: An Increasing Suburban Problem.

Treves A, Karanth KU (2003) Human-carnivore conflict and perspectives on carnivore management worldwide. Conserv Biol 17:1491–1499.

Treves A, Naughton-Treves L, Harper EK, et al (2004) Predicting Human-Carnivore Conflict: a Spatial Model Derived from 25 Years of Data on Wolf Predation on Livestock. Conserv Biol 18:114–125.

Trinkel M (2009) Prey selection and prey preferences of spotted hyenas Crocuta crocuta in the Etosha National Park, Namibia. Ecol Res 25:413–417.

Trinkel M, Fleischmann PH, Steindorfer AF, Kastberger G (2004) Spotted hyenas (Crocuta crocuta) follow migratory prey. Seasonal expansion of a clan territory in Etosha, Namibia. J Zool 264:125–133.

Venter FJ, Gertenbach WPD (1986) A Cursory Review of the Climate and Vegetation of the Kruger National Park. Koedoe 29:139–148.

Venter FJ, Scholes RJ, Eckhardt HC (2003) The abiotic template and its associated vegetation patterns. In: Du Toit JT, Rogers KH, Biggs HC (eds) The Kruger Experience: Ecology and Management of Savanna Heterogeneity. Island Press, Washington DC, USA, pp 83–129

Wey T, Blumstein DT, Shen W, Jordán F (2008) Social network analysis of animal behaviour: a promising tool for the study of sociality. Anim Behav 75:333–344.

WHO (2014) http://www.who.int/gho/urban_health/situation_trends/urban_population_growth_text/en/. Acessed 2016/10/30.

Widdows CD, Downs CT (2015) A genet drive-through: are large spotted genets using urban areas for “fast food”? a dietary analysis. Urban Ecosyst 1–14.

Woodroffe R (2000) Predators and people: using human densities to interpret declines of large carnivores. Anim Conserv 3:165–173.

Yirga G, De Iongh HH, Leirs H, et al (2012) Adaptability of large carnivores to changing anthropogenic food sources: diet change of spotted hyena (Crocuta crocuta) during Christian fasting period in northern Ethiopia. J Anim Ecol 81:1052–1055.

Yirga G, Leirs H, De Iongh HH, et al (2015) Spotted hyena (Crocuta crocuta) concentrate around urban waste dumps across Tigray, northern Ethiopia. Wildl Res 42:563.

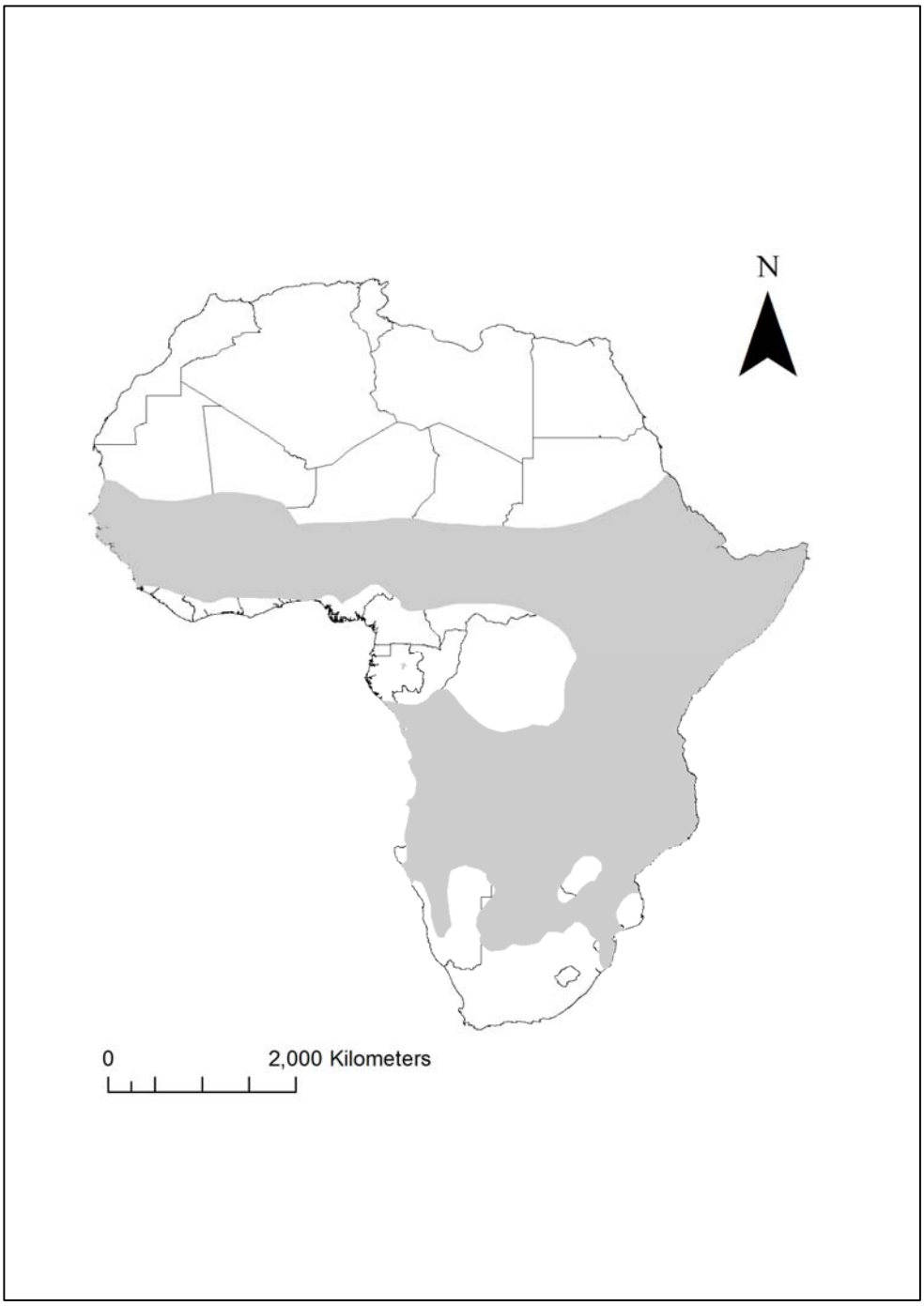

Figure 1. Extent of the spotted hyaena (*Crocuta crocuta*) across sub-Saharan Africa (shaded grey area)

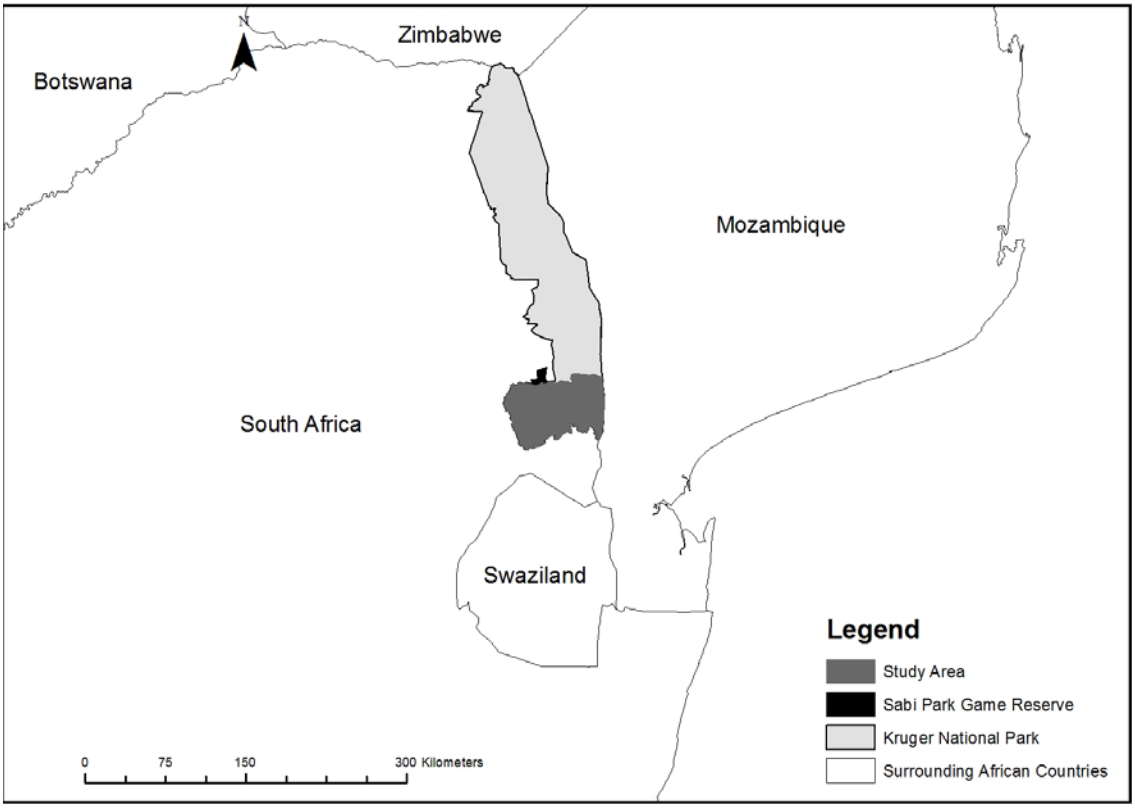

Figure 2. The position of Kruger National Park within Southern Africa showing the research area and the adjoining Sabi Game Reserve

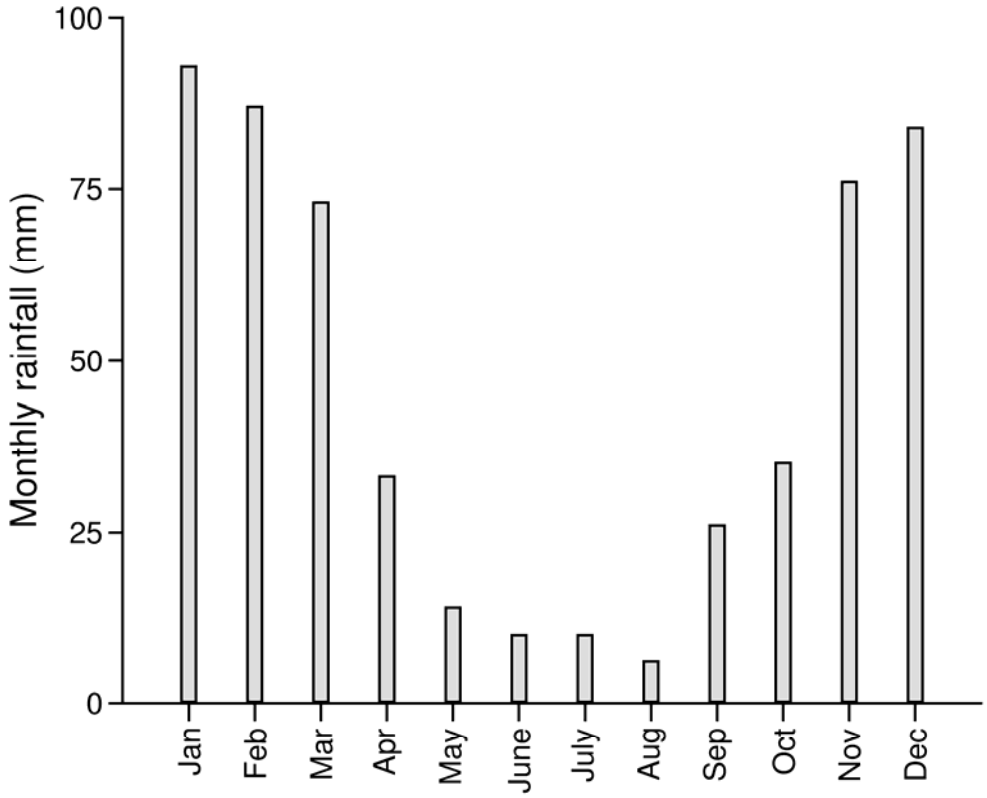

Figure 3. Average monthly rainfall data for Southern Kruger, (Venter, Scholes & Eckhardt, 2003)

Chapter 2: Spotted hyaena visitation at anthropogenic sites in the Kruger National Park, South Africa

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Abstract

Some carnivore species are attracted to areas with high human activity due to the benefits associated with anthropogenic, or human based, resources. However, using anthropogenic resources may also be risky, as it may be related to elevated levels of persecution and disturbance. Within protected areas, such risks are largely eliminated, so that the use of anthropogenic resources largely is determined by the relative value between different resource types. We tested how state-dependent life-history characteristics in a large carnivore, the spotted hyena (*Crocuta crocuta*), influenced seasonal visitation rates at sites with elevated human activity and infrastructure within the Kruger National Park, South Africa. We predicted that spotted hyaenas with restricted ability to procure native food would be the most frequent visitors, and that the sites would be more visited during the dry season, which has lower prey abundance than the wet season. Contrary to these predictions, there was no effect of social rank on visitation rates. Moreover, although seasons influenced the effect of age on visitation, juveniles had higher visitation rates than some other age classes during the wet season. In general, visitation rates were not consistently higher during the dry season, nor was there more pronounced differences between age classes in the dry season. We suggest that these results indicate that the anthropogenic sites were visited as part of exploratory behaviour coupled with occasional rewards. Our study suggests that management action that limits any rewards from hyaena visits at anthropogenic sites, coupled with deterrents that may increase the perceived risk of visitation may be effective in minimizing human-hyaena conflict inside of this protected area.

Keywords: Anthropogenic resources; Carnivora; behaviour; *Crocuta crocuta*

Introduction

Carnivores often avoid areas with high population densities to reduce the risks associated with close proximity to humans (Boydston *et al.* 2003; Mattson 1990). However, this pattern is not universal, with some carnivores surviving well in close proximity to humans, or even being attracted to anthropogenic areas (Fedriani *et al.* 2001). Some carnivores, notably generalist mesocarnivores and omnivores, frequently use anthropogenic resources such as waste, shelter or water, if they are sufficiently abundant and the risks associated with their exploitation are low (Beckmann & Berger 2003; Fedriani *et al.* 2001; Herr *et al.* 2010; Quinn & Whisson 2005; Rode *et al.* 2006).

While many studies have focused on how carnivores utilise anthropogenic resources outside protected areas, such as farming communities and urban areas (Abay *et al.* 2010; Holmern *et al.* 2007; Kolowski & Holekamp 2009; Yirga *et al.* 2015), anthropogenic environments may also occur within conservation areas. Here, areas with concentrated human activity can create pockets of urbanisation in a landscape of protected wildlife populations. Outside of protected areas, there is normally a risk associated with the utilisation of anthropogenic resources, as these typically are located in close association to areas with an elevated risk of disturbance or persecution (e.g., Swanepoel *et al.* 2015). However, inside of protected areas persecution is often limited relative to unprotected land, so that the relative value of anthropogenic versus native resources are among the primary determinants of their use. Therefore, protected areas provide interesting model systems for evaluating how environmental factors influence the utilisation of anthropogenic resources in an environment with reduced risk.

The relative intrinsic value of any resource can vary between individuals depending on state dependent factors related to the cost and benefits associated with its utilisation. For instance, asymmetries in competitive ability between individuals may result in

contrasting levels of access to limited resources. Such asymmetries often get accentuated by a patchy distribution and predictable supply (Parker 1974). Different cohorts of animals can also vary in their nutritional requirements (López-Bao *et al.* 2009; Rode *et al.* 2006), or require different amounts of energy to obtain and utilise a resource (Bonanni *et al.* 2007). Individual variation in the ability to acquire resources and the relative net benefits to different cohorts have been observed in a wide range of carnivores, such as the Iberian lynx (*Lynx pardinus,* López-Bao *et al.* 2009), feral cats (*Felis silvestris catus*, Bonanni *et al.* 2007), black bears (*Ursus americanus*, Beckmann & Berger 2003), and brown bears (*Ursus arctos,* Rode *et al.* 2006).

The spotted hyaena (*Crocuta crocuta*) is a large communally breeding carnivore which is often persecuted outside of protected areas (Holmern *et al.* 2007; Pangle & Holekamp 2010). However, because of their highly adaptable generalist feeding strategy (Kruuk 1972), spotted hyaenas also frequently exploit anthropogenic resources (Abay *et al.* 2010; Kolowski & Holekamp 2008; Yirga *et al.* 2010; Yirga *et al.* 2015). Within spotted hyaena clans, high ranked females have greater access to food than hyaenass of lower social rank, and may exclude low ranked clan members entirely (Frank 1986; Henschel 1986). Independent of rank, age can also be influential in an spotted hyaena's ability to acquire food. For instance, juveniles and sub-adults have their nutritional needs largely met by their mothers, both by lactation (Boydston *et al.* 2005) and by their mothers giving them access at kills (Frank 1986; Watts *et al.* 2009). Young adults are however independent of their mother but are often still ineffective hunters (Holekamp & Smale 1998), partly because of undeveloped skull morphology (Tanner *et al.* 2010).

We investigated the effects of social rank, age and sex on seasonal visitation rates by spotted hyaenas at two sites of elevated human activity (anthropogenic sites) in Kruger National Park, South Africa. In the park, spotted hyaenas frequently raid litter bins and beg for food at cars and along camp fences. Anthropogenic material (e.g. plastic, glass and foil) has been recorded in up to 54% of spotted hyaena scats at one major

anthropogenic site (Ryan 2007). These observations suggest that the hyaenas in the park have easy access to anthropogenic resources and utilise them regularly. We therefore predicted that spotted hyaenas visited anthropogenic sites in order to procure food. Based on this assumption, we hypothesised that hyanenas with limited access to native food, either because of rank-related access to carcasses or because of limited hunting abilities, would visit anthropogenic sites more often than hyaenas that could sustain themselves on native prey. In addition, we expected that visits at anthropogenic sites would be more frequent in seasons of low availability of native prey, specifically the dry season when preferred less young prey are available (Kruuk 1972) and that this seasonal variation would be more pronounced for hyaenas with limited access to native food. Based on these hypotheses, we tested the following specific predictions: (i) young adults and low ranked hyaenas would be observed at anthropogenic sites more often than adults and high ranked hyaenas, (ii) juveniles and sub-adults would be observed at anthropogenic sites less often than other hyaenas since they get their resources supplied by their mother, and (iii) seasonal variation in visitation would be the greatest for young adults and low ranked hyaenas.

Research methods and design

Study site

Kruger National Park (KNP) is situated in the north eastern corner of South Africa and covers almost 20,000 km^2. Our study focused on two sites, the Skukuza tourist camp and staff village (31°35'34.323"E, 24°59'43.625"S) and the Afsaal picnic site (31°32'0.15"E, 25°17'24.217"S). Both sites lie in the southern section of the KNP (figure 1). Southern KNP falls within the lowveld bioregion (Mucina and Rutherford 2006). Vegetation is dominated by *Clerocarya caffra* and *Acacia nigrescens*, with *Combretum* species dominating on granite based soils. Rainfall is seasonal with the majority falling between October and March, with a peak in January and February (Venter *et al.* 2003). Average

annual rainfall is approximately 550 mm and the mean monthly temperatures range from 7 to 32 ºC (http://www.worldclim.org). KNP hosts a diverse array of herbivorous and carnivorous mammals which for the southern section of the park include impala (*Aepyceros melampus*), blue wildebeest (*Connochaetes taurinus*), zebra (*Equus burchelli*), kudu (*Tragelaphus strepsiceros*), warthog (*Phacochoerus aethiopicus*), imbabala bushbuck (*Tragelaphus sylvaticus*), nyala (*Tragelaphus angasii*), common reedbuck (*Redunca arundinum*), waterbuck (*Kobus ellipsiprymnus*), steenbok (*Raphicerus campestris*), common duiker (*Sylvicapra grimmia*) and Cape buffalo (*Syncerus caffer*). The section also contains megaherbivores such as elephant (*Loxodonta africana*), white rhinoceros (*Ceratotherium simum*), black rhinoceros (*Diceros bicornis*), and giraffe (*Giraffa camelopardalis*), as well as the large carnivores lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), and African wild dog (*Lycaon pictus*).

Study animals and data collection

We conducted the study between May 2007 and December 2009 on two spotted hyaena clans. The "SK" clan was located in the vicinity of Skukuza tourist camp and the "AF" clan at the Afsaal picnic site. The SK clan had free access to the unfenced staff village consisting of 250 houses, an enclosed staff compound, a golf course, a shop, communal areas, as well as administrative buildings beside an enclosed area with tourist accommodation (rest camp). The staff area combined with the rest camp covers 4.3 km^2 and houses approximately 2300 staff (Foxcroft *et al.* 2008). Fences around both individual houses and the compound prevented easy access to household rubbish bins. However, rubbish bins in communal areas and larger waste collection sites were unfenced. The number of larger waste collection sites varied over time. Open gates and damaged fencing also allowed for opportunistic access to other rubbish bins. SK hyaenas also had access to the unfenced car park of a picnic site which contained rubbish bins and they were able to walk along the perimeter fence of the tourist rest camp. The Afsaal picnic site consists of a shop, a cafeteria and a picnic area, all of which are unfenced, with

an adjoining fenced residence typically housing four to five staff. Permanent water sources exist in the vicinity of both sites. Visitors are required to return to a camp or leave the park by a specific time that varies throughout the year to coincide with sunset, and members of staff do not walk in unfenced areas after dark. Hyaenas were therefore able to visit unfenced anthropogenic areas after dark with minimal disturbance.

We observed clans at communal den sites identified along the edges of public roads for assessing clan size and composition, as well as recording state dependent characteristics of each hyaena such as sex, age and social rank. These observations were augmented with observations of the clans whenever they were encountered opportunistically. All individuals in both clans were individually recognizable by their unique spot patterns and each individual was sexed based on the shape of the phallic glans following observations (Frank *et al.* 1990). Hyaenas were categorised into four age classes: juvenile (< 14 months), sub-adult (14-24 months), young adult (25-48 months) and adult (> 48 months). For hyaenas with unknown birth dates we based the age estimation on pelage and size. This age approximation was confirmed retrospectively by comparing photos of hyaneas with unknown age to those with a known birth date. We used the average weaning age recorded for east African spotted hyaenas, 14 months (Boydston *et al*. 2005; Holekamp *et al.* 1996), since we did not get sufficient data to make reliable estimates in the KNP. We classed juveniles and sub-adults separately to facilitate an evaluation of any effects of lactation and lower hunting success on the utilisation of anthropogenic resources. Since spotted hyaenas are born at a natal den and typically move to a communal den at an age of 0-4 weeks (Holekamp *et al.* 1997), our age estimates of birth dates are accurate to within a month. Rank was defined from the outcomes of dyadic interactions (Holekamp & Smale 1993) and leg lifting during ritualised greeting displays (Kruuk 1972). Following Kolowski & Holekamp (2008) females and natal males (juveniles, sub-adults and young adults) were classed as high or low ranked. We assigned all adult males to a separate immigrant class which we regarded to be subordinate to females. We excluded juveniles that were only observed at the den from the rank estimations, as well as any

individuals that were never sighted at the natal den or were only recorded once within each home range. In both clans 20 hyaenas moved between age groups, whilst no hyaenas were observed to move between the broad rank categories high and low.

We recorded visitation from direct observations at either the Skukuza rest camp or the Afsaal picnic site. Visitation at Skukuza was recorded as animals present along the montitored section of fence line. At Afsaal visitation occurred when hyaenas entered the unfenced picnic are Observations were made with the aid of hand-held torches at Skukuza and a spot light at Afsaal. At the Skuzuza site, many camp sites also had illuminated the area along the fence line. All animals were well know and easily identified. Hyaenas did not appear to disturbed by the lighting. Only three hyaenas were not identified during these study session (see below). Afsaal hyaenas were regularly observed at the den with a spotlight and similarly did not appear to be perturbed by its use. Due to the more open setting of Afsaal, once within the complex all animals were easily identified. The data were restricted to the presence or absence of each clan member at each observation session, since dense vegetation in Skukuza and the layout of Afsaal did not allow us to reliably record times of arrival or departure, or to make detailed and meaningful observations of individual behaviour. We conducted 24 observation sessions in Skukuza between September 2007- December 2009 and 21 observation sessions in Afsaal between June 2008 – September 2009. To allow for temporal independence between observations we allowed a minimum of one week between each observation period at each site. At Skukuza, a 400 metre section of the camp fence perimeter adjacent to a camping area was selected for observation. We selected this site since most hyaenas that we opportunistically observed within the Skukuza village also utilized this site, probably because it provided easily accessible food in the form of food remains and garbage thrown over the fence by tourists. We therefore believe that it provides a representative sample of hyaena activity within Skukuza, since the complex structure of the village prevented us from monitoring the whole area. In Afsaal, we simultaneously monitored the picnic site and staff residences. Observations in Skukuza lasted for two

hours, beginning 30 minutes after the closing of rest camp gates at sunset. This period was chosen to coincide with visitors having returned to the camp and beginning to prepare food. Observations in Afsaal commenced at dusk and continued for one hour. At each observation session, all hyaenas observed were recorded as present. Data from a pilot study suggested that hyaenas mainly used these sites at dusk. In addition, we repeatedly visited the Afsaal site during other times of the night, but none of these visits revealed other hyaneas at the site than those recorded at dusk. Therefore, we believe that our observation periods gave a representative sample of visitation at each site, despite the different observation times. On three occasions individuals were seen at the Skukuza site but could not be identified with any certainty. These individuals were not included in the analysis.

Statistical Analysis

The probabilities that individual hyaenas were present at anthropogenic sites were analysed using a generalised linear mixed model (glmm) with a binomial error structure and logit link function. The model used the proportion of observation nights for which a given individual was present at the anthropogenic resource point as the response variable. We calculated this proportion as the number of observation nights a given clan member was observed at a resource site divided by the total number of possible nights that individual could have been at the resource. Total number of possible observation nights was defined as all observation events during which a hyaena was confirmed as alive and a clan member of a specific age or rank category. An animal was defined as dead or dispersed if it had not been seen for a minimum of three months before the end of the study, but we used the last date it was observed alive to define its clan membership. Rank, sex, age, and season were included as categorical fixed effects, as well as two way interactions between season and rank, sex and age. We included individual nested within clan as a random effect structure. Fixed terms were evaluated using sequential likelihood ratio tests using a type II sum of squares approach (Hector *et al.* 2010). Multiple

comparisons of means were carried out using pair wise contrasts on predicted marginal means with the alpha error adjusted for multiple comparisons following Benjamini & Hochberg (1995). Statistical analyses were conducted using R version 3.3.0 (http://www.r-project.org), and the user contributed packages lme4 (version 1.1-7; Bates *et al.* 2015) and lsmeans (Lenth 2016).

Results

In total, we identified 29 hyaenas in the SK and 25 in the AF clan (table 1). At SK, 16 different individuals were recorded at anthropogenic resource sites, and 9 were recorded at AF. There was a significant interaction effect of age and season on the probability that individual clan members would be observed at anthropogenic resource sites ($\chi^2 = 7.94$, df = 3, P = 0.05), but no significant interactions between season and either sex ($\chi^2 = 2.28$, df = 1, P = 0.13) or rank ($\chi^2 = 0.10$, df = 2, P = 0.95). There were no significant main effects of either sex ($\chi^2 = 1.81$, df = 1, P = 0.18) or rank ($\chi^2 = 1.13$, df = 1, P = 0.57) on visitation rates. Juveniles were observed significantly more at anthropogenic resource sites than young adults during the wet season (table 2), and there were tendencies for juveniles and sub-adults to be observed more often than young adults and adults (figure 2).

Discussion

The observed patterns of visitation at anthropogenic resource sites in KNP did not follow predictions from age and rank related ability to hunt and procure food, nor predictions based on seasonal variation in resource supply. We suggest that these observations indicate that the anthropogenic sites were not primarily visited for foraging purposes. Instead, we suggest that the sites may have been visited as part of exploratory behaviour. Such behaviour may have been reinforced by occasional rewards with little direct associated risk. Exploratory behaviour is common among carnivores (Bekoff 1989), and

is typically most prevalent among younger cohorts. In spotted hyaenas, exploratory behaviour has been positively linked to innovation ability in adults (Benson-Amram & Holekamp 2012), and similar observations have been made both in other carnivores and in non-mammalian predators (Biondi *et al.* 2010, Thornton & Samson 2012). It may therefore serve as a fitness enhancing behaviour in rapidly changing or unpredictable environments.

Our data points to a limited nutritional importance of any potential food resources available at the observed anthropogenic sites. Such an interpretation contrasts previous observations in Kenya, where visitation rates at an open refuse pit were directly linked to low social rank and to periods of low prey availability (Kolowski & Holekamp 2008). Studies on other carnivore species suggest that anthropogenic resources may be under-utilised (Morey *et al.* 2007) or that native resources are more preferred (Fedriani *et al.* 2001). We highlight that the motivation for visiting anthropogenic sites likely is highly context dependent, and influenced by the relative risk that is associated with visitation as well as by the relative value of any potential resources available at the sites. While motivation may be directly related to state dependent factors such as age and sex, extrinsic factors such as availability of native resources could also be important. We therefore highlight that motivation to visit anthropogenic sites likely is a complex interaction between exploratory behaviour, perceived risk, and the value of potential resources relative to resources available from other sources, e.g. native prey.

Because close contact between large carnivores and humans may lead to conflict also inside of protected areas, incentives for these hyaenas to visit anthropogenic sites should be minimized. Since our results suggest that spotted hyaenas may not have visited these sites because of any nutritional need for alternative food, we suggest that removing occasional rewards may be effective in preventing the sites from being visited. This could, for instance, be achieved by strict garbage control, and by strict enforcement of appropriate visitor behaviour. In addition, since the direct benefits of visiting these sites

may be low, increasing the appeared risk of visiting them may also be effective. Several mechanisms have been suggested for such deterrent effects, ranging from sensory deterrents to technologically advanced methods of real time virtual fences (Jachowski *et al.* 2014). While our data show limited visitation to sites where humans are present, it is important to minimize the risks assocoiated with a close association. In 2016 a visitor was severely injured by a hyaena that had gained access to a camp. We suggest that ethical and efficient mechanisms are developed for KNP, as these likely will be efficient in preventing conflict between hyaenas and people inside the park.

Conclusion

Visitation rates by spotted hyaenas at anthropogenic resource sites in Kruger National Park, South Africa, did not suggest that hyaenas were visiting anthropogenic sites because of nutritional need for easy food. Instead, we suggest that the anthropogenic sites were visited by young hyaenas as part of exploratory behaviour that was reinforced by occasional rewards. We suggest that management action limiting any occasional rewards in combination with an increased deterrent at anthropogenic sites may provide effective in minimizing human-hyaena conflict inside the KNP.

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References

Abay, G.Y., Bauer, H., Gebrihiwot, K. & Deckers, J., 2010, 'Peri-urban spotted hyena (Crocuta crocuta) in Northern Ethiopia: diet, economic impact, and abundance.' European Journal of Wildlife Research, 57, 759–765.

Bates, D., Maechler, M., Bolker, B.M. & Walker S.C, 2011, 'Fitting linear mixed effect models using lme4.' Journal of Statistical Software, 67, 1-48.

Beckmann, J.P. & Berger, J., 2003, 'Using Black Bears to Test Ideal-Free Distribution Models Experimentally.' Journal of Mammalogy, 84, 594–606.

Benjamini, Y. & Hochberg, Y., 1995, 'Controlling the false discovery rate: a practical and apowerful approach to multiple hypothesis testing.' Journal of the Royal Statistical Society, Series B, 57, 289-300.

Bekoff, M., 1989, 'Behavioural development of terrestrial carnivores.' In J.L. Gittleman (Ed.), Carnivore behaviour, ecology and evolution, Volume 1, pp. 89-124. Cornell University Press, New York.

Benson-Amram, S. & Holekamp, K.E., 2012, 'Innovative problem solving by wild spotted hyenas' Proceedings of the Royal Society Series B Biology 279, 4087–4095.

Biondi, L.M., Bó, M.S. & Vasallo, A.I., 2010, 'Inter-individual and age differences in exploration, neophobia and problem-solving in ability in a Neotropical raptor (Milvago chimango).' Animal Cognition, 13, 701-710.

Bonanni, R., Cafazzo, S., Fantini, C., Pontier, D. & Natoli, E., 2007, 'Feeding-order in an urban feral domestic cat colony: relationship to dominance rank, sex and age.' Animal Behaviour, 74, 1369–1379.

Boydston, E.E., Kapheim, K.M., Van Horn, R.C., Smale, L. & Holekamp, K.E., 2005, 'Sexually dimorphic patterns of space use throughout ontogeny in the spotted hyena (Crocuta crocuta).' Journal of Zoology, 267, 271–281.

Boydston, E.E., Kapheim, K.M., Watts, H.E., Szykman, M. & Holekamp, K.E., 2003, 'Altered behaviour in spotted hyenas associated with increased human activity.' Animal Conservation, 6, 207–219.

Fedriani, J.M., Fuller, T.K. & Sauvajot, R.M., 2001, 'Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California.' Ecography, 24, 325–331.

Foxcroft, L.C., Richardson, D.M. & Wilson, J.R.U, 2008, 'Ornamental plants as invasive

aliens: problems and solutions in Kruger National Park, South Africa.' Environmental Management, 41, 32–51.

Frank, L.G., 1986, 'Social organization of the spotted hyaena Crocuta crocuta. II. Dominance and reproduction.' Animal Behaviour 34, 1510–1527.

Frank, L.G., Glickman, S.E., Powch, I., 1990, 'Sexual dimorphism in the spotted hyaena (Crocuta crocuta).' Journal of Zoology 221, 308–313.

Hector, A., von Felten, S. & Schmid, B., 2010, 'Analysis of variance with unbalanced data: an update for ecology & evolution.' Journal of Animal Ecology, 79, 308–316.

Henschel, J.R., 1986, 'The socio-ecology of a spotted hyaena (Crocuta crocuta) clan in the Kruger National Park.' BSc thesis, University of Pretoria, Pretoria, South Africa.

Herr, J., Schley, L., Engel, E. & Roper, T.J., 2010, 'Den preferences and denning behaviour in urban stone martens (Martes foina).' Mammalian Biology - Zeitschrift fur Saugetierkunde, 75, 138–145.

Holekamp, K.E. & Smale, L., 1993, 'Ontogeny of dominance in free-living spotted hyaenas: juvenile rank relations with other immature individuals.' Animal Behaviour 46, 451–466

Holekamp, K.E. & Smale, L., 1998, 'Behavioral development in the spotted hyena.' Bioscience, 48, 997–1005.

Holekamp, K.E., Smale, L., Berg, R. & Cooper, S.M., 1997, 'Hunting rates and hunting success in the spotted hyena (Crocuta crocuta).' Journal of Zoology, 242, 1–15.

Holekamp, K.E., Smale, L. & Szykman, M., 1996, 'Rank and reproduction in the female spotted hyaena.' Journal of Reproduction and Fertility, 108, 229–237.

Holmern, T., Nyahongo, J. & Røskaft, E., 2007, 'Livestock loss caused by predators outside the Serengeti National Park, Tanzania.' Biological conservation, 135, 518–526.

Jachowski, D.S., Slotow, R. & Millspaugh, J.J., 2014, 'Good virtual fences make good neighbors: opportunities for conservation.' Animal Conservation, 17, 187-196.

Kolowski, J.M. & Holekamp, K.E., 2008, 'Effects of an open refuse pit on space use patterns of spotted hyenas.' African Journal of Ecology, 46, 341–349.

Kolowski, J.M. & Holekamp, K.E., 2009, 'Ecological and anthropogenic influences on space use by spotted hyaenas.' Journal of Zoology 277, 23–36.

Kruuk, H., 1972, The spotted hyena: a study of predation and social behavior. University

of Chicago Press, Chicago, USA.

Lenth, R.V., 2016, 'Least square means: The R package lsmeans.' Journal of Statistical Software, 69, 1-33.

López-Bao, J.V., Rodrigues, A. & Palomares, F., 2009, 'Competitive asymmetries in the use of supplementary food by the endangered Iberian lynx.' Plos One, 4, 1–10.

Mattson, D.J., 1990, 'Human impacts on bear habitat use.' International Conference on Bear Research and Management, 8, 33–56.

Morey, P.S., Gese, E.M. & Gehrt, S., 2007, 'Spatial and temporal variation in the diet of coyotes in the Chicago Metropolitan Area.' American Midland Naturalist, 158, 147–161.

Mucina, L. & Rutherford, M.C., 2006, The vegetation of South Africa, Lesotho and Swaziland. SANBI, Pretoria, South Africa.

Pangle, W.M. & Holekamp, K.E., 2010, 'Lethal and nonlethal anthropogenic effects on spotted hyenas in the Masai Mara National Reserve.' Journal of Mammalogy, 91, 154–164.

Parker, G.A., 1974, 'Assessment strategy and the evolution of fighting behaviour.' Journal of Theoretical Biology, 47, 223–243.

Quinn, J.H. & Whisson, D.A., 2005, 'The effects of anthropogenic food on the spatial behaviour of small Indian mongooses (Herpestes javanicus) in a subtropical rainforest.' Journal of Zoology, 267, 339–350.

Rode, K.D., Farley, S.D. & Robbins, C.T., 2006, 'Sexual dimorphism, reproductive strategy, and human activities determine resource use by brown bears.' Ecology, 87, 2636–2646.

Ryan, B., 2007, 'Effects of anthropogenic food sources on diet and parasite loads in spotted hyaena, Crocuta crocuta (Erxleben, 1777) in Kruger National Park.' MSc Thesis, University of Pretoria.

Swanepoel, L., Somers, M.J., Van Hoven, W., Scheiss-Mejier, M., Owen, C., Snyman, A., Martins, Q., Camacho, G., Boshoff, W. & Dalerum, F., 2015, 'Survival in southern African leopard populations.' Oryx, 49, 595-603.

Tanner, J.B., Zelditch, M.L., Lundrigan, B.L. & Holekamp, K.E., 2010, 'Ontogenetic change in skull morphology and mechanical advantage in the spotted hyena (Crocuta crocuta).' Journal of Morphology, 271, 353-365.

Thornton, A. & Samson, J., 2012, 'Innovative problem solving in wild meerkats' Animal

Behaviour, 83, 1459-1468.

Venter, F. J., Scholes, R. J., and Eckhardt, H. C., 2003, 'The abiotic template and its associated vegetation patterns.' In J.T. Du Toit, K.H. Rogers, & H.C. Biggs (Eds.), The Kruger experience: ecology and management of savanna heterogeneity, pp. 83–129. Island Press, Washington DC, USA.

Watts, H.E., Tanner, J.B., Lundrigan, B.L. & Holekamp, K.E., 2009, 'Post-weaning maternal effects and the evolution of female dominance in the spotted hyena.' Proceedings of the Royal Society of London B: Biological Sciences, 276, 2291–2298.

Yirga, G., De Iongh, H.H., Leirs, H., Gebrihiwot, K., Deckers, J. & Bauer, H., 2010, 'Adaptability of large carnivores to changing anthropogenic food sources: diet change of spotted hyena (Crocuta crocuta) during Christian fasting period in northern Ethiopia.' Journal of Animal Ecology, 81, 1052-1055.

Yirga, G., Leirs, H., De Iongh, H.H., Asmelash, T., Gebrehiwot, K., Deckers, J. & Bauer, H., 2015, 'Spotted hyena (Crocuta crocuta) concentrate around urban waste dumps across Tigray, northern Ethiopia.' Wildlife Research, 42, 563-569.

Table 1. Total number of spotted hyaenas (*Crocuta crocuta*) in each age, sex and rank class present in the Afsaal and Skukuza hyaena clans during the study.

	Afsaal			Skukuza		
	Low rank	High rank	Immigrant	Low rank	High rank	Immigrant
Females						
Juveniles	2	5		2	2	
Sub-adults	2	0		3	6	
Young adults	4	4		2	10	
Adults	6	7		5	8	
Males						
Juveniles	3	1		2	6	
Sub-adults	5	0		4	5	
Young adults	4	0		8	5	
Adults			6			8

Table 2. Results of pair wise comparisons of the proportion of time spotted hyaenas (*Crocuta crocuta*) of different age classes were observed at the anthropogenic resource sites during the dry and the wet season. Results are based on pair wise contrasts on predicted marginal means based on a generalized linear mixed model with a binomial error and logit link.

	Dry season			Wet season		
Contrast	Difference[a]	*Z*	P_{adj} [b]	Difference[a]	*Z*	P_{adj} [b]
Juveniles – Sub-adults	-0.17 ± 0.47	0.36	0.72	1.50 ± 0.82	1.83	0.13
Juveniles – Young adults	0.74 ± 0.49	1.52	0.19	2.85 ± 0.89	3.20	**0.01**
Juveniles – Adults	1.69 ± 0.95	1.78	0.15	2.40 ± 1.21	1.98	0.13
Sub-adults – Young adults	0.91 ± 0.47	1.93	0.15	1.35 ± 0.88	1.54	0.19
Sub-adults – Adults	1.86 ± 0.95	1.97	0.15	0.90 ± 1.21	0.75	0.55
Young adults – Adults	0.95 ± 0.94	1.01	0.37	-0.45 ± 1.01	0.44	0.66

[a] Differences are given on a logit scale ± 1 SE

[b] The alpha error was adjusted for multiple comparisons by controlling for the false discovery rate (Benjamini and Hochberg, 1995)

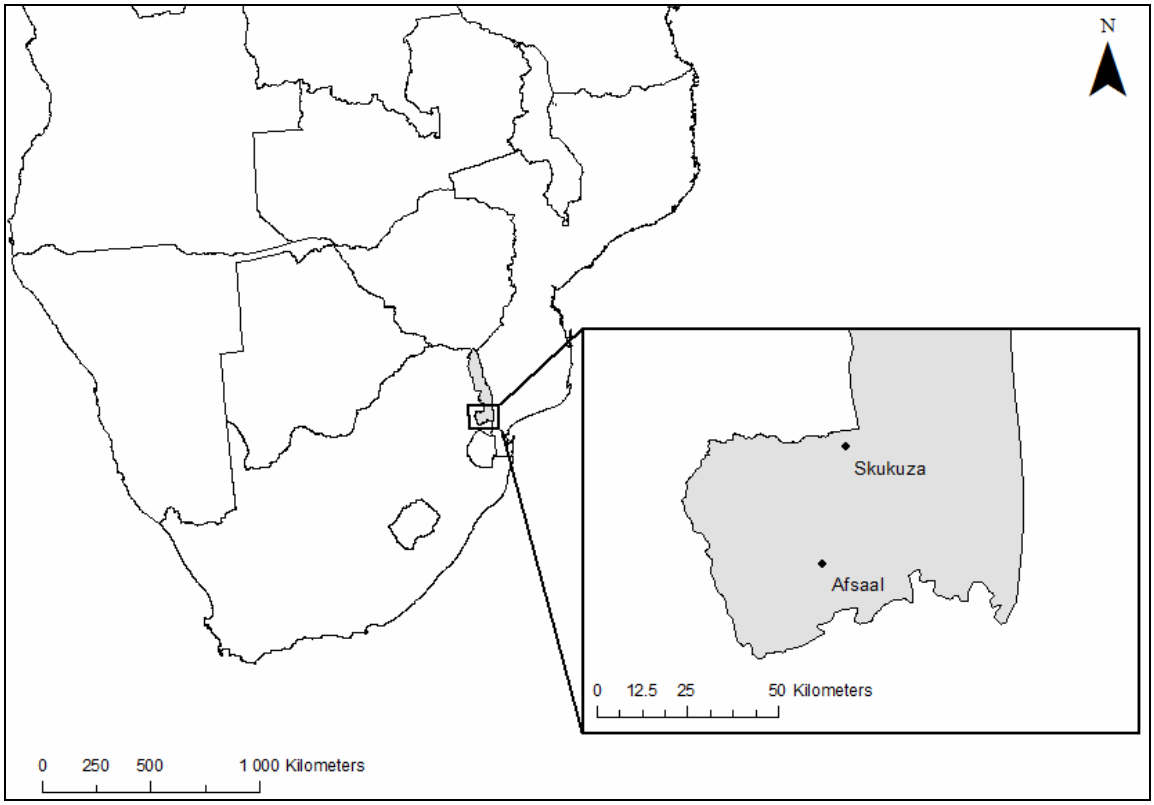

Figure 1. Location of the Afsaal (AF) and Skukuza (SK) spotted hyaena (*Crocuta crocuta*) clans and associated anthropogenic resource sites in Kruger National Park, South Africa.

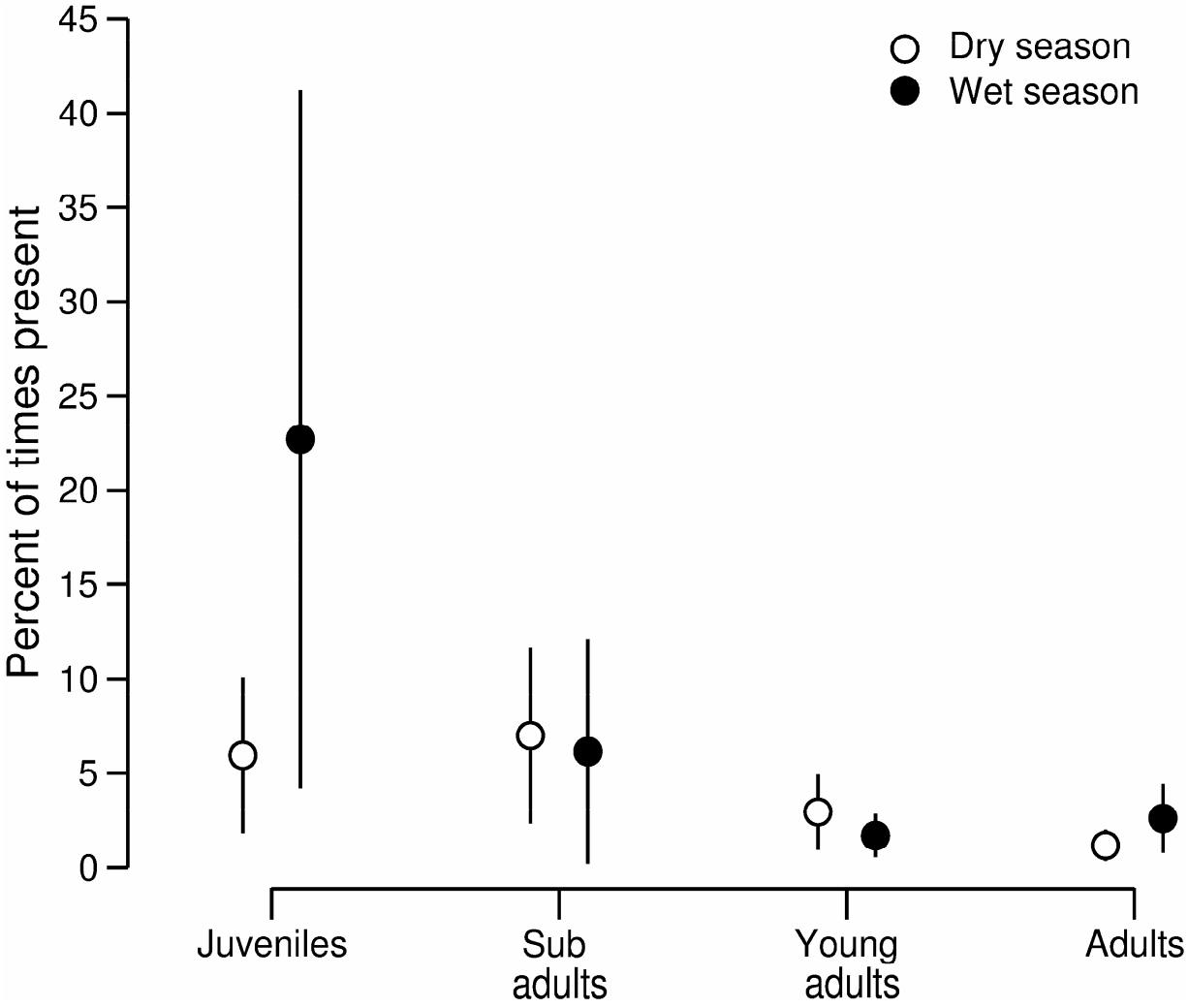

Figure 2. Percentage of nights spotted hyaenas (*Crocuta crocuta*) of different age classes were observed at anthropogenic resource sites during the dry and the wet seaon in the Kruger National Park, South Africa. The percentages were based on number of observation events an animal was observed at a resource site divided by the total number of observation events that each individual could have been observed as a member of that age and rank class. The figure presents mean ± SE.

Chapter 3: Anthropogenic influences on spotted hyaena diet in the Kruger National Park, South Africa

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Abstract

Rapid expansion of urban landscapes has led to an increase in carnivores that live close to human dominated environments. Some carnivore species have successfully adapted to these novel conditions and taken advantage of opportunities associated with human habitation. Whilst many studies have compared carnivores living in protected areas to those in an urban setting, few have looked at the relationships between carnivores and human habitation within protected areas. In this study we examined the effects human habitation on the diet of spotted hyaenas (*Crocuta crocuta*) in the Kruger National Park, South Africa. Proximity to human habitation influenced spotted hyaena diet composition, but these effects were stronger in the wet compared to the dry season. However, despite a positive association between the amount of roadside anthropogenic litter and the proximity to and size of the nearest human habitation, neither of these variables influenced the amount of anthropogenic material in spotted hyaena diet. Instead, there were near significant seasonal differences, with a higher amount of anthropogenic material suggested for the dry season. Our results indicate that spotted hyaenas in the Kruger National Park did not use anthropogenic food in relation to its abundance, but that proximity to human habitations nonetheless influenced diet composition. We suggest that these effects of human habitation may have been indirect, and related to human influences on prey demography and behaviour.

Key words: *Crocuta crocuta*, Carnivora, anthropogenic resources, protected areas

Introduction

Human population growth is often correlated with the decline and local extinction of carnivore populations (Woodroffe 2000). The rapidly expanding extent of urban landscapes creates both biotic and abiotic challenges that are known to negatively impact carnivores (Šálek et al. 2015). Carnivores are considered particularly sensitive to human population growth and urbanisation due to persecution, large home range requirements and slow population growth (Woodroffe 2000). However, urban landscapes also offer alternative resources, such as access to predictable food waste, water and shelter (Bateman and Fleming 2012; Laver 2013).

Some carnivore species not only co-exist with humans, but thrive in urban environments (Bateman and Fleming 2012). Carnivore synanthropy (wild animals gaining benefit from living in close association with humans) has been recorded across six of the seven continents (Newsome et al. 2015). Species recorded to live in close association with humans range in size from the mongooses (Herpestidae) (Laver 2013), to bears (Ursidae) (Beckmann and Berger 2003a; Beckmann and Berger 2003b). The often predictable nature of the anthropogenic food resources makes urban areas a reliable alternative to the often seasonal changes of natural resources (Widdows and Downs 2015). Therefore, urban environments can be regarded as a distinct wildlife habitat (Šálek et al. 2015), and urban ecology is subsequently becoming a rapidly expanding field of research (Magle et

al. 2012).

The effects of anthropogenic food availability on overall diet have been studied in a number of species. A seasonal change in anthropogenic food use was, for instance observed in coyotes (*Canis latrans*), with a greater use during the dispersal season and greater use by transient animals (Grigione et al. 2011; Lukasik and Alexander 2012). A preference for anthropogenic food during the winter months has also been observed in large spotted genets (*Genetta tigrina*) (Widdows and Downs 2015). Reductions in natural resources or the ability to procure them has been suggested as the cause of a switch to anthropogenic food in red (*Vulpes vulpes*) and Arctic foxes (*Vulpes lagopus*) (Savory et al. 2014), as well as in spotted hyenas (*Crocuta crocuta*) (Kolowski and Holekamp 2008). These findings indicate that anthropogenic food may be less preferred to natural foods, and only utilised by animals in poor health that need food that is easy to procure (Murray et al. 2015), or by animals that experience periods of food scarcity. Throughout this manuscript, we will use the term 'anthropogenic food' for organic matter that has been discarded by humans and is available for exploitation by carnivores and 'anthropogenic material' for man-made matter (e.g. plastic or paper) that is found in the scat of animals utilising anthropogenic food.

Different types and levels of urbanisation will produce contrasting challenges and opportunities for carnivores. Whilst the majority of the scientific studies have focussed on carnivores living in non-protected environments, pockets of high human presence also occur inside protected areas (e.g. Gilchrist and Otali 2002; Quinn and Whisson 2005).

Many of the features associated with different anthropogenic zones therefore also occur in protected areas, with resources provided as a predictable but patchy resource. However, despite the obvious conservation and management implications of the utilisation of anthropogenic food by large predators inside conservation areas, studies on anthropogenic food use within protected areas is scarce compared to data focusing on urban and suburban landscapes.

The spotted hyaena is a large carnivore that lives in social groups known as clans, which consist of related females and their offspring and unrelated adult males. Male offspring usually disperse at maturity (Kruuk 1972). A strict matrilineal social structure is maintained through social interactions (Frank 1986). The range of the spotted hyaena covers much of sub Saharan Africa, from the Kalahari Desert (Mills 1984), to a peri-urban existence in Ethiopia (Abay et al. 2010), although distribution is patchy (IUCN 2015). Spotted hyaenas exhibit high levels of behavioural plasticity, including dietary plasticity (Hayward 2006; Holekamp and Dloniak 2010). Once considered mere scavengers, spotted hyaenas are successful hunters, capable of bringing down adult Cape buffalo (*Syncerus caffer*) (Cooper et al. 1999) and gemsbok (*Oryx gazella*) (Trinkel 2009). Other dietary items include rodents, plants, birds and reptiles and livestock (Henschel and Skinner 1990; Holmern et al. 2007). Considering its high behavioural plasticity, including frequent opportunistic scavenging (Holekamp and Dloniak 2010), it is not surprising that this species often exploits anthropogenic resources (Mills and Hofer 1998). Whilst scavenging anthropogenic food has previously been reported anecdotally

(Henschel 1986; Mills and Hofer 1998), it is only in more recent years that this has become the focus of scientific studies (Ryan 2007; Kolowski and Holekamp 2008; Fourie 2008; Abay et al. 2010). As with other species, a diet switch based on availability of anthropogenic food has been recorded (Yirga et al. 2012), and access to anthropogenic food has also been related to other aspects of spotted hyaena behavioural ecology such as space use (Kolowski and Holekamp 2008).

In this study, we investigated the effects of human habitation and of availability of anthropogenic resources on spotted hyaena diet in one of the largest protected areas in southern Africa, the Kruger National Park (KNP). KNP is situated in the North Eastern corner of South Africa (31°37'38.513"E, 25°10'18.804"S) and covers 19 485 km^2. KNP is open to the public, it attracts over one million visitors per year, and it has numerous facilities for tourists along with staff accommodation (SANParks 2011). The park is also home to an estimated 2500 spotted hyaenas (Mills et al. 2001). We predicted that anthropogenic material found in scat would be higher in the dry season when other food sources are limited. Sites of high human habitation vary in size inside the park. We therefore predicted that the size of these sites would be positively related to the amount of available anthropogenic food, and subsequently that spotted hyaenas close to large sites would utilise more anthropogenic food compared to spotted hyaenas close to small ones. Finally, we predicted that there would be a negative relationship between the amount of anthropogenic food utilised by spotted hyaenas and their distance to the nearest site of high human habitation.

Materials and methods

Study area

Our study focused on the southern section of the KNP, which covers 5000 km^2. Vegetation in this area of the park is characterised by woodland. Basalt soils are dominated by *Clerocarya caffra* and *Acacia nigrescens*, with *Combretum* species on granite soils (Ogutu and Owen-Smith 2003). Rainfall is seasonal with the majority falling between October and March, with a peak in January and February (Venter et al. 2003). Average annual rainfall is approximately 650 mm for the Southern section (Venter and Gertenbach 1986). Mean monthly temperatures range from 7 to 32 ºC for this area (Venter and Gertenbach 1986). KNP hosts a diverse array of herbivorous and carnivorous mammals. Prey available for spotted hyaenas in the Southern section of the park include, along with small mammals; impala (*Aepyceros melampus*), blue wildebeest (*Connochaetes* taurinus), zebra (*Equus burchelli*), kudu (*Tragelaphus strepsiceros*), warthog (*Phacochoerus aethiopicus*), imbabala bushbuck (*Tragelaphus sylvaticus*), nyala (*Nyala angasii*), common reedbuck (*Redunca arundinum*), waterbuck (*Kobus ellipsiprymnus*), steenbok (*Raphicerus campestris*), common duiker (*Sylvicapra grimmia*) and Cape buffalo (*Syncerus caffer*). Other megaherbivores; elephant (*Loxodonta africana*), white rhinoceros (*Ceratotherium simum*), black rhinoceros (*Diceros bicornis*), and giraffe (*Giraffa camelopardalis*), are also available presumably most often as carrion. Impala constitutes a large part of the spotted hyaena diet in KNP (Henschel and Skinner

1990; Ryan 2007). Four large carnivores live sympatrically with spotted hyaenas in KNP; African lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), and African wild dog (*Lycaon pictus*).

Anthropogenic litter survey

We estimated the impact of human activity on the amount of anthropogenic food available using road side surveys of litter as a proxy. During the 2010 wet season, we recorded litter observed by the road sides whilst carrying out scat collection (described below). We recorded all litter within one metre of the edges of the road for all the roads covered in the scat collection (see below). Litter was classed as fabric, paper, plastic, glass, anthropogenic organic (for example discarded food), metal or miscellaneous, and for each observation a spatial coordinate was taken.We quantified litter intensity as number of occurrences per 1 km of road by splitting all roads into 1 km segments using ArcGIS (www.esri.com) and counted the number of litter occurrences within each segment.

Defining anthropogenic sites

We used fixed sites of elevated human activity to evaluate anthropogenic effects on spotted hyaena diet. Throughout the manuscript, we will use the collective term 'anthropogenic sites' for these locations. Within KNP there are amenities for visitors in the form of rest camps and picnic sites. A rest camp was defined as a fenced area used for

guests staying overnight in the park, along with associated staff accommodation and administrative buildings. Picnic sites were defined as unfenced areas with a shop used by visitors during park opening hours. Skukuza is the largest rest camp in KNP and is the administrative centre of the park. In addition to the rest camp, the site also includes an unfenced staff village, administrative buildings and additional fenced staff accommodation. Skukuza is the only site that contains both a picnic site and a rest camp. However, due to the size of this site and its associated infrastructure the picnic site was regarded as part of the Skukuza complex. Smaller private rest camps exist but were not included in the study due to their small size and limited access to the roads surrounding them.

We used satellite images from Google Earth (http://earth.google.com/) to create polygons that outlined each anthropogenic site, and used these polygons to quantify the area of each site in km^2. We then calculated the geographic centre of each polygon, and created a circular buffer around this centre with a diameter of 8 km, which corresponds to the mean estimated diameter of the spotted hyaena home ranges estimated from data on two spotted hyaena females that were fitted with GPS collars during the study (chapter 4).

Scat collection and diet estimation

Scat samples were collected from August to September 2009 (dry season) and during the beginning of April 2010 (end of the wet season). Scats were opportunistically located

while slowly driving public roads as well as the private roads surrounding each anthropogenic site's accommodation and administrative areas. While driving, two observers scanned the roadsides for samples. Spotted hyaena scats were identified by their white colouring, their size, and the tendency of the hyaenas to make use of latrines. All samples were put into paper bags, and stored in a cool dry place until further analysis. Severely degraded samples, where it was obvious that hair had already broken down in the matrix were excluded from analysis.Spotted hyaena scats are typically comprised of animal matter, for example bone shards and hair, some plant matter and faecal matrix (Henschel and Skinner 1990; Fourie 2008). To remove as much faecal matrix as possible, samples were crushed in a pestle with a mortar, sewn into individual cloth bags, soaked overnight and then put through two cold wash cycles of a washing machine. Samples were then sieved, before being dried for 48 hours in an oven at 55 ºC.

Each scat was classed as collected either inside or outside an anthropogenic site buffer zone. For each season, we randomly selected 154 washed samples for each category, i.e. inside or outside of buffer zones, for further diet analyses. Each of these samples were, once dried, spread out on a sheet of white paper and diet components were recorded into seven broad categories; mammal, reptile and bird (pooled), invertebrate, plant, anthropogenic material and matrix. For anthropogenic material, we also recorded the type of material, e.g. plastic or metal. Since the volume of particular items in scat does not accurately depict the amount of each item consumed (Henschel and Skinner 1990), items were recorded as either present or absent.

Data analyses

To evaluate the effects of size and the distance to the nearest anthropogenic site on the abundance of road side litter, we used a generalised linear mixed model with a Poisson distribution and a log link function. Litter counts per 1 km of road was used as the response variable, distance to nearest anthropogenic site, size of the nearest anthropogenic site and the two-way interaction as fixed effects. Because not all road segments were exactly 1 km in length, each data point was weighted by segment length.

We similarly used a generalised linear mixed model with a Poisson error structure and log link function to evaluate the effects of distance to anthropogenic sites and season on spotted hyaena diet composition. For this model, we grouped scat samples by their nearest anthropogenic site. With this grouping we used the frequencies of scats containing remains from each diet category as the dependent variable and diet category, season, and distance to anthropogenic sites, described as a binary factor depending on whether or not a scat was collected inside or outside of anthropogenic site buffer zones and all interactions as fixed effects.

To evaluate the effect of distance to anthropogenic sites on the probability that hyena scats would contain anthropogenic material, we used a generalised linear mixed model with binomial error structure and a logit link function. In this model, we used the presence or absence of anthropogenic material in each scat as a binary response variable,

and distance to anthropogenic sites (inside or outside of a buffer), season and their two-way interaction as fixed effects.

To evaluate the effects of the size of anthropogenic sites on the probability that hyena scats would contain anthropogenic material, we fitted a generalised linear mixed model only to samples that were located closer than 8 km to the nearest anthropogenic site. The model had a binomial error structure and a logit link function. We used the presence or absence of anthropogenic material in each scat as a binary response variable, and area of the anthropogenic site was treated as a continuous variable, and season as fixed. The two-way interactions were analysed.

For all models, we fitted the identity of the nearest anthropogenic site as a random term to account for inherent differences between each of the locations. We evaluated fixed effects by sequentially removing them in order of complexity using likelihood ratio tests (Crawley 2007), analogously to type II sums of square tests (e.g. Hector et al. 2010). Data wereanalysed with the statistical package R using the lme4 library (Bates et al. 2011).

Results

Anthropogenic Litter Density

We surveyed 883.86 km of roads and recorded 1276 individual pieces of litter, although the majority of road sections surveyed were litter free. The most abundant forms of litter

observed were plastic (51 %) and paper (36 %). Organic material (i.e. discarded food) contributed little (0.9%) to the total amount of litter observed (Fig. 1). There was a significant interaction effect of the size of and distance to the nearest anthropogenic site on litter abundance: (χ^2 = 45.84, *df* = 1, *P* < 0.01), with a stronger negative effect of distance at larger sites (β = -0.10, *t* = 71.9, *df* = 1, *P* < 0.01).

Overall diet content

There was a significant three way interaction between diet category, distance to anthropogenic sites (i.e. inside or outside buffers), and season on frequency of occurrences in spotted hyaena scats (χ^2 = 17.30, *df* = 5, *P*< 0.01). Primarily for mammals, the main prey for spotted hyaenas, there was a more pronounced difference between scats collected close to and far from anthropogenic sites during the wet compared to the dry season (Fig. 2).

Anthropogenic content of scats

The presence of anthropogenic material in scats was low, with on average 10.6 % of samples containing anthropogenic material. Only three types of anthropogenic material were recorded: plastic, paper and metal. Plastic was the most commonly found type of anthropogenic material, found in 77.0% of samples that contained anthropogenic material (Fig. 3). There was no significant effect of distance to anthropogenic sites (inside versus outside buffers) on the proportion of samples found to contain anthropogenic material,

nor a significant interaction between season and distance to anthropogenic sites ($\chi^2 = 1.08$, $df = 1$, $P = 0.30$). There was however a near significant effect of season on the probability of finding anthropogenic material in scats ($\chi^2 = 3.41$, $df = 1$, $P = 0.06$), with a higher probability in the dry compared to the wet season (Fig. 3).Within anthropogenic buffer zones, there was no significant effect of the size of the nearest anthropogenic site ($\chi^2 = 0.89$, $df = 1$, $P = 0.35$) nor a significant interaction between size and season ($\chi^2 < 0.01$, $df = 1$, $P = 0.98$) on the probability of scats containing anthropogenic material.

Discussion

We found that the proximity of sites with elevated human habitation influenced spotted hyaena diet, and that these effects differed between seasons. Overall diet content concurred with other studies on spotted hyaenas, with the majority component being mammal hair, and to lesser extent reptilian and invertebrate remains (Henschel and Skinner 1990). However, the amount of anthropogenic material in scats was relatively low, only 10 %. Coyotes living in urban areas have been shown to exhibit a lower dietary diversity when compared to non-urban coyotes, which has only partly been attributed to an increased reliance on anthropogenic food (Grigione et al. 2011). We suggest that our results similarly point to indirect effect of human habitation on spotted hyaena diet and resource use, potentially related to human influences on prey demography and behaviour.

Previous studies on other carnivore species have consistently found a higher use of

anthropogenic resources in areas with high levels of human habitation (Fedriani et al. 2001; Newsome et al. 2010; e.g. Grigione et al. 2011). In our study, spotted hyaena scats collected within one home range radius of anthropogenic sites of 8 km were not more likely to contain anthropogenic material than scats collected outside of this zone. In addition, we found no effect of the size of anthropogenic sites on the probability of finding anthropogenic material in scats collected close to them. Considering that both size and distance influenced the frequency of anthropogenic material found along roads, these results suggest that spotted hyaenas in the southern section of the KNP do not necessarily feed on anthropogenic food in relation to its abundance. Such an interpretation would imply that use of anthropogenic food is not opportunistic. Instead, these results suggest that anthropogenic food is used either by specialised individuals within the population, or that it is used opportunistically but only by a sub-set of the hyaenas, which may mute any effects of litter abundance on the frequency of anthropogenic materials in scats.

We observed a near significant difference between seasons in the occurrence of anthropogenic material, with a higher occurrence in scats collected in the dry compared to the wet season. Similar patterns of use have been documented in coyotes, Arctic and red foxes and brown bears (*Ursus arctos*) (Morey et al. 2007; Savory et al. 2014; Kavčič et al. 2015), as well as in spotted hyaenas (Kolowski and Holekamp 2008). Lower rainfall received during the dry season is associated with lower survival in prey such as kudu (Owen-Smith 1990), and the wet season has an abundance of young prey which

spotted hyaenas preferentially prey on (Kruuk 1972). We therefore suggest that our observations of higher levels of anthropogenic material in the dry compared to the wet season may indicate that anthropogenic food is of relatively low quality (Lukasik and Alexander 2012; Savory et al. 2014; Murray et al. 2015), and subsequently used as an alternative food source primarily during periods of relative food scarcity (Lukasik and Alexander 2012; Kavčič et al. 2015). If this assumption is correct, we may regard anthropogenic food as an allochthonous resource that could sustain spotted hyaena and possibly other omnivorous predator populations through periods of food scarcity, and hence influence the predator prey dynamics within this and similar protected areas.

It is important to note, however, that our findings are a conservative estimate of anthropogenic food use in KNP. Anthropogenic material in scats may not accurately reflect the actual amount of anthropogenic food consumed. Digestible foods, such as processed carbohydrates and meat are not quantifiable through scat analysis. This has been highlighted through studies of the San Joaquin kit fox (*Vulpes macrotis mutica*), where isotope analysis revealed a heavier reliance on anthropogenic food than suggested by traditional scat analysis (Newsome et al. 2010).

It is unsurprising that litter density declined with increasing distances from anthropogenic areas, and that the sizes of anthropogenic areas influenced litter density. Due to plastic's resilient nature it is also not surprising that it was the most frequently recorded litter type recorded on the roads of KNP. Organic anthropogenic material was, by contrast, the least recorded litter type. This is probably due to two reasons. First, food items decompose

relatively quickly, and second, edible waste would be quickly consumed by any number of opportunistic species, including spotted hyaenas.

In conclusion our study suggested that the proximity to sites of human habitation influenced spotted hyaena diet as could be determined by using non digestible remains in scat, but that there were seasonal differences in these effects. However, these effects were not caused by differences in the use of anthropogenic food, since the probability of finding anthropogenic material in spotted hyaena scats was not related to either the proximity to sites with high human habitation or the size of the nearest site with human habitation. We found near significant differences between seasons, with higher presence of anthropogenic material in scats collected in the dry compared to the wet season. We suggest that any effect of human habitation on spotted hyaena diet may be indirect effects related to prey demography and behaviour. We further suggest that anthropogenic food may be regarded as an allochthonous resource which may aid in maintaining populations through periods of food scarcity.

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Committee (protocol number EC010-07) and the Kruger National Park Animal Use and Care Committee.

References

Abay GY, Bauer H, Gebrihiwot K, Deckers J (2010) Peri-urban spotted hyena (*Crocuta crocuta*) in Northern Ethiopia: diet, economic impact, and abundance. Eur J Wildl Res 57:759–765

Bateman PW, Fleming PA (2012). Big city life: carnivores in urban environments. J Zool 287:1–23

Bates D, Maechler M, Bolker B (2011) lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-39. http://CRAN.R-project.org/package=lme4.

Beckmann JP, Berger J (2003)a Rapid ecological and behavioural changes in carnivores: the responses of black bears (*Ursus americanus*) to altered food. J Zool 261:207–212

Beckmann JP, Berger J (2003)b Using black bears to test ideal-free distribution models experimentally. J Mamm 84:594–606

Cooper SM, Holekamp KE, Smale L (1999) A seasonal feast: long-term analysis of feeding behaviour in the spotted hyaena (*Crocuta crocuta*). Afr J Ecol 37:149–160

Crawley MJ (2007) The R book. John Wiley & Sons, Chichester

Fedriani JM, Fuller TK, Sauvajot RM (2001) Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. Ecography 24:325–331

Fourie C (2008) The influence of seasons and human density on anthropogenic food consumption in the spotted hyaena Crocuta crocuta in Kruger National Park M.Sc. thesis. Honours Thesis, University of Pretoria South Africa.

Frank LG (1986) Social organization of the spotted hyaena Crocuta crocuta. II. Dominance and reproduction. Anim Behav 34:1510–1527

Gilchrist JS, Otali E (2002) The effects of refuse-feeding on home-range use, group size,

and intergroup encounters in the banded mongoose. Can J Zool 80:1795–1802

Grigione MM, Burman P, Clavio S, Harper SJ, Manning D, Sarno RJ (2011) Diet of Florida coyotes in a protected wildland and suburban habitat. Urb Ecosyst 14:655–663

Hayward MW (2006) Prey preferences of the spotted hyaena (*Crocuta crocuta*) and degree of dietary overlap with the lion (*Panthera leo*) J Zool 270:606–614

Hector A, von Felten S, Schmid B (2010) Analysis of variance with unbalanced data: an update for ecology & evolution. J Anim Ecol 79:308–316

Henschel JR (1986) The socio-ecology of a spotted hyaena (*Crocuta crocuta*) clan in the Kruger National Park. Dissertation, University of Pretoria.

Henschel JR, Skinner JD (1990) The diet of the spotted hyaenas *Crocuta crocuta* in Kruger National Park. Afr J Ecol 28:69–82

Holekamp KE, Dloniak SM (2010) Intraspecific variation in the behavioral ecology of a tropical carnivore, the spotted hyaena. Adv Stud Behav 42:189–229

Holmern T, Nyahongo J, Røskaft E (2007) Livestock loss caused by predators outside the Serengeti National Park, Tanzania. Biol Cons 135:518–526

IUCN (2015) IUCN 2015. The IUCN Red List of Threatened Species. Version 2015.1. <http://www.iucnredlist.org>. Downloaded on 22nd June 2015.

Kavčič I, Adamič M, Kaczensky P, Krofel M, Kobal M, Jerina K (2015) Fast food bears: brown bear diet in a human-dominated landscape with intensive supplemental feeding. Wildl Biol 21:1–8

Kolowski JM, Holekamp KE (2008) Effects of an open refuse pit on space use patterns of spotted hyenas. Afr J Ecol 46:341–349

Kruuk H (1972) The spotted hyena: a study of predation and social behavior. Dissertation, University of Chicago.

Laver PN (2013) The foraging ecology of banded mongooses (*Mungos mungo*): Epidemiological and human-wildlife conflict implications. Virginia Polytechnic Institute and State University Blacksburg, Virginia. Available at: http://vtechworks.lib.vt.edu/handle/10919/50973 [Verified 18 April 2015]

Lukasik V, Alexander S (2012) Spatial and temporal variation of coyote (*Canis latrans*) diet in Calgary, Alberta. Cities and the environment (CATE) 4. Available at: http://digitalcommons.lmu.edu/cate/vol4/iss1/8

Magle SB, Hunt VM, Vernon M, Crooks, KR (2012) Urban wildlife research: Past, present, and future. Biol Cons 155:23–32

Mills MGL (1984) The comparative behavioural ecology of the brown hyaena Hyeana brunnea and the spotted hyaena *Crocuta crocuta* in the southern Kalahari. Koedoe 27:237–247

Mills MGL, Hofer H (1998) Hyaenas. Status survey and conservation action plan. Gland, IUCN

Mills MGL, Juritz JM, Zucchini W (2001) Estimating the size of spotted hyaena (Crocuta crocuta) populations through playback recordings allowing for non-response. Anim Cons 4:335–343

Morey PS, Gese EM, Gehrt S (2007) Spatial and temporal variation in the diet of coyotes in the Chicago Metropolitan Area. Am Midl Nat 158:147–161

Murray M, Edwards MA, Abercrombie B, Clair CCS (2015) Poor health is associated with use of anthropogenic resources in an urban carnivore. Proc Roy Soc B 282:20150009

Newsome SD, Garbe HM, Wilson EC, Gehrt SD (2015) Individual variation in anthropogenic resource use in an urban carnivore. Oecologia 178:115-128

Newsome SD, Ralls K, Job CVH, Fogel ML, Cypher BL (2010) Stable isotopes evaluate exploitation of anthropogenic foods by the endangered San Joaquin kit fox (*Vulpes macrotis mutica*). J Mamm 91:1313–1321

Ogutu JO, Owen-Smith N (2003) ENSO, rainfall and temperature influences on extreme population declines among African savanna ungulates. Ecol Lett 6:412–419

Owen-Smith N (1990) Demography of a large herbivore, the greater kudu *Tragelaphus strepsiceros*, in relation to rainfall. J Anim Ecol 59:893–913

Quinn JH, Whisson DA (2005) The effects of anthropogenic food on the spatial behaviour of small Indian mongooses (*Herpestes javanicus*) in a subtropical rainforest. J Zool 267:339–350

Ryan B (2007) Effects of anthropogenic food sources on diet and parasite loads in spotted hyaena, *Crocuta crocuta* (Erxleben, 1777) in Kruger National Park. Dissertation, University of Pretoria South Africa

Šálek M, Drahníková L, Tkadlec E (2015) Changes in home range sizes and population densities of carnivore species along the natural to urban habitat gradient. Mamm Rev 45:1–14

SANParks (2011) South African National Parks Annual Report 2010/11. Available at: http://www.sanparks.co.za/assets/docs/general/annual-report-2011.pdf

Savory GA, Hunter CM, Wooller MJ, O'Brien DM (2014) Anthropogenic food use and diet overlap between red foxes (*Vulpes vulpes*) and arctic foxes (*Vulpes lagopus*) in Prudhoe Bay, Alaska. Can J Zool 92:657–663

Trinkel M (2009) Prey selection and prey preferences of spotted hyenas *Crocuta crocuta* in the Etosha National Park, Namibia. Ecol Res 25:413–417

Venter FJ, Gertenbach WPD (1986) A Cursory Review of the Climate and Vegetation of the Kruger National Park. Koedoe 29:139-148

Venter FJ, Scholes RJ, Eckhardt HC (2003) The abiotic template and its associated vegetation patterns. In: Du Toit JT, Rogers KH, Biggs HC (eds) The Kruger experience: ecology and management of savanna heterogeneity'. Island Press, Washington DC, pp. 83–129

Widdows CD, Downs CT (2015) A genet drive-through: are large spotted genets using urban areas for 'fast food'? a dietary analysis. Urb Ecosyst 18:907-920

Woodroffe R (2000) Predators and people: using human densities to interpret declines of large carnivores. Anim Cons 3:165–173

Yirga G., De Iongh HH, Leirs H, Gebrihiwot K, Deckers J, Bauer H (2012) Adaptability of large carnivores to changing anthropogenic food sources: diet change of spotted hyena (*Crocuta crocuta*) during Christian fasting period in northern Ethiopia. J Anim Ecol 81:1052–1055

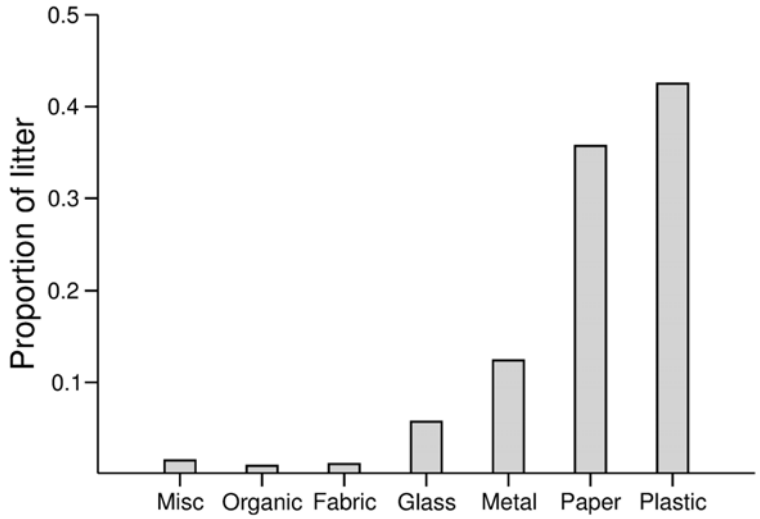

Figure 1. Total counts of different types of litter observed on the roads of KNP

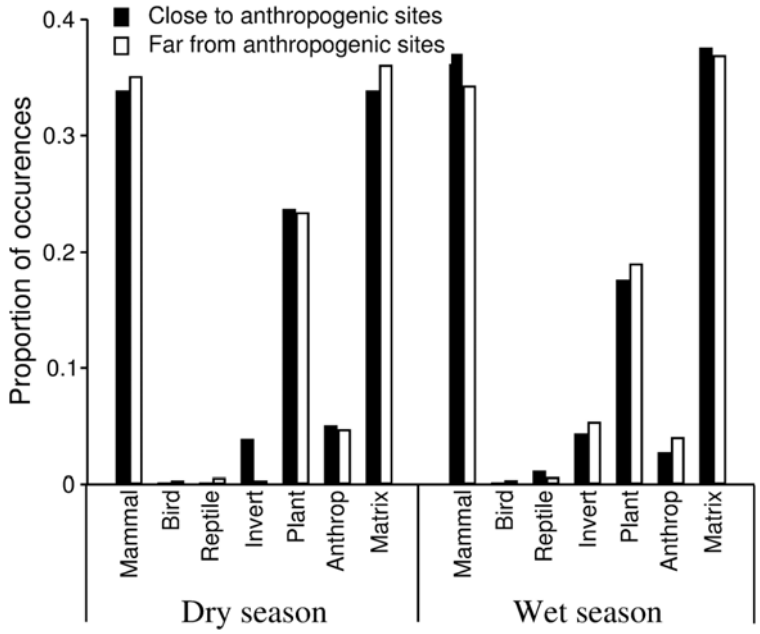

Figure 2. Diet composition estimated from scats collected close to and from anthropogenic sites, quantified as whether or not a scat was collected inside (close) or outside (far) of 1 home range diameter wide buffer zones around the centre of anthropogenic sites. Diet composition was estimated as frequency of occurrence of different diet categories in the dry and the wet season.

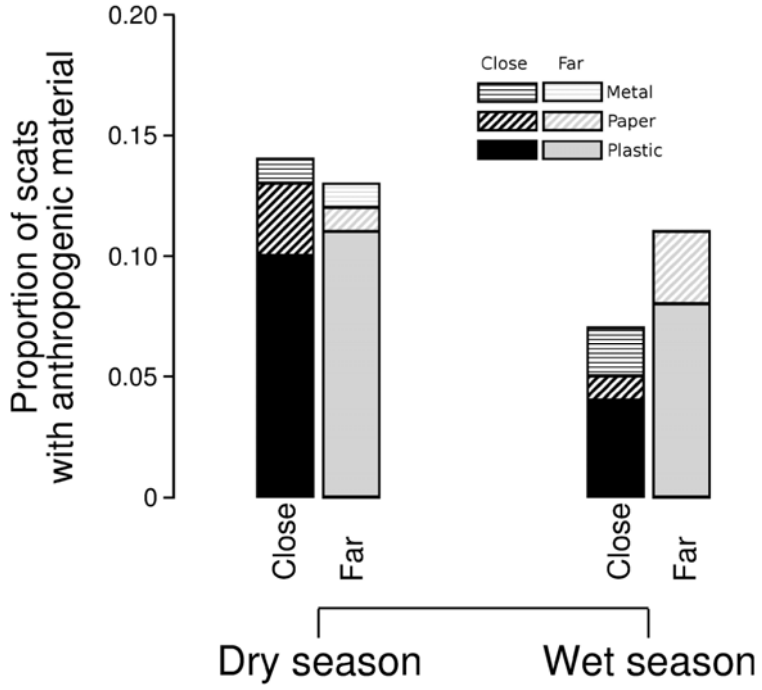

Figure 3. Different types of anthropogenic material identified in scats collected close to and from anthropogenic sites, quantified as whether or not a scat was collected inside (close) or outside (far) of 1 home range diameter wide buffer zones around the centre of anthropogenic sites.

Chapter 4: Spotted hyaena space use in relation to infrastructure in a protected area

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Abstract

Increasing human population growth has led to elevated levels of human-carnivore conflict. However, some carnivore populations have adapted to urban environments and the resources they supply. Such associations may influence carnivore ecology, behaviour and life-history. Pockets of urbanisation sometimes occur within protected areas, so that anthropogenic influences on carnivore biology are not necessarily confined to unprotected areas. In this study we evaluated associations between human infrastructure and related activity and space use of spotted hyaenas within one of the largest protected areas in South Africa, the Kruger National Park. Home range size was smaller for the dominant female of a clan living in close proximity to humans than that of the dominant female of a clan without direct access to human infrastructure. The home range including human infrastructure was also used less evenly during the night, presumably when the hyaenas were active. Within this home range, the village area was preferred during the night, where the least modified areas within the village were preferred and administration and highly modified areas were avoided. During the day, however, there were no preference or avoidance of the village area, but all habitats except unmodified habitats within the village area were avoided. We suggest that human infrastructure and associated activity influenced hyaena space use, primarily through alterations in the spatial distribution of food. However, these effects may have been indirectly caused by habitat modification that generated favourable hunting habitat rather than a direct effect caused by access to human food such as garbage. Because of the often pivotal effects of apex predators in terrestrial ecosystems, we encourage further work aimed to quantify how human presence influences large carnivores and associated ecosystem processes within protected areas.

Introduction

Human population growth is bringing people into conflict with carnivores at higher frequencies than ever before (Woodroffe, 2000). Carnivores are considered particularly sensitive to human population growth and urbanisation due to persecution, large home range requirements and slow population growth (Cardillo et al., 2004). The rapid expansion of urban landscapes creates both biotic and abiotic changes that negatively impact carnivore populations (Šálek, Drahníková & Tkadlec, 2015). This can cause local extinctions or active avoidance of humans by carnivores (Ordeñana et al., 2010; Schuette et al., 2013).

However, whilst anthropogenic disturbance is classically known for causing population declines (Woodroffe, 2000), some carnivores have adapted to live in close proximity to humans and may directly benefit from the association (e.g. Fedriani, Fuller & Sauvajot, 2001; Contesse et al., 2004; Bozek, Prange & Gehrt, 2007). For carnivores living in close association with humans, several demographic and behavioural changes have been noted, such as alterations in population density (Fedriani, Fuller & Sauvajot, 2001), home range size (Quinn & Whisson, 2005), diet (Newsome et al., 2014), and space utilisation (Gilchrist & Otali, 2002). Such changes are often attributed to anthropogenic food supplementing the diet.

An increase in use of anthropogenic food has frequently been associated with a

contraction in home range and core area size (Kolowski & Holekamp, 2008; Newsome et al., 2014; Šálek, Drahníková & Tkadlec, 2015). However, home range size and use is also dependent on other factors, such as seasonal variation in native food sources. Typically, the season with a lower abundance of native food has coincided with more frequent anthropogenic food use (Lucherini & Crema, 1994; Kolowski & Holekamp, 2008; Pereira, Owen-Smith & Moleón, 2013). In addition, behavioural and physiological differences related to sex (Beckmann & Berger, 2003) and social status (Boydston et al., 2003) may also influence space use and resource exploitation.

Most research on anthropogenic influences on carnivore biology has been conducted in urban environments (reviewed in Bateman & Fleming, 2012). However, areas of elevated human activity also occur inside protected areas (e.g. Gilchrist & Otali, 2002; Quinn & Whisson, 2005), and many anthropogenic factors influencing carnivore space use may also exist inside protected areas. Despite the obvious management implications of the influence of human activities on carnivore space use inside protected areas, studies on anthropogenic influences on carnivores within protected areas are scarce compared to data focusing on urban and suburban landscapes.

The spotted hyaena (*Crocuta crocuta*) is a large, primarily nocturnal carnivore that lives in social groups (clans) with fission-fusion social dynamics, meaning that clan members are not always spatially co-located at all times. A clan consists of related females and their offspring as well as unrelated adult males (Kruuk, 1972; Mills, 1984; Henschel,

1986).Within a clan the hyaenas are organized by a strict social hierarchy where females are dominant to adult males, and ranks are temporally consistent (Kruuk 1972). The range of the spotted hyaena covers much of sub-Saharan Africa, from the Kalahari Desert (Mills, 1984) to peri-urban areas in Ethiopia (Abay et al., 2010), although distribution is patchy (IUCN, 2015). The spotted hyaena is known for its opportunistic scavenging (Mills & Hofer, 1998), and the species will readily exploit anthropogenic food (Yirga et al., 2015). In contrast to many species associated with anthropogenic food use, spotted hyaenas are large carnivores that often hunt large prey (Cooper, Holekamp & Smale, 1999). However, their food is often seasonally variable, a trait associated with anthropogenic food use in other species. In southern Africa, the wet season is typically associated with increased prey availability related to the reproduction of prey species (Pereira, Owen-Smith & Moleón, 2013), while the dry season in contrast is associated with drought and elevated animal mortality partially caused by disease (Owen-Smith, 1990; Pereira, Owen-Smith & Moleón, 2013). Hence, environmental factors could influence need for anthropogenic resource use in this species.

To date, there is very scant information on the effects of anthropogenic resources on spotted hyaena space use, and all accounts we are aware of come from east Africa and Ethiopia (Kolowski & Holekamp, 2008; Yirga et al. 2015). For instance, a single source of anthropogenic food associated with a small human settlement had a marked impact on hyaena space use patterns in the Masai Mara National Reserve in Kenya (Kolowski & Holekamp, 2008). Here, we aimed to test if a larger but less concentrated source of

anthropogenic resources would have a similar influence on hyaena space use patterns. We monitored the space use of two spotted hyaena females belonging to separate clans inside the Kruger National Park (KNP), South Africa, one inhabiting an area with high levels of permanent human activity and extensive and complex infrastructure. Hence, this clan had direct access to anthropogenic resources, although those resources were spread out spatially rather than located at a single source. The other clan inhabited an area with very limited human activity and almost no permanent infrastructure. The hyaenas in this clan therefore relied almost entirely on native resources.

Because the often clustered distribution of human resources frequently cause carnivore range contraction (Šálek, Drahníková & Tkadlec, 2015), an observation that is related to the general importance of the distribution of critical resources for carnivore space use (Sandell, 1989), we predicted that hyaenas living in an environment with high levels of human resources would have a smaller home range and use it less evenly than hyaenas living without direct access to anthropogenic resources. We also predicted that human influence on space use would be higher in the food limited dry season compared to the wet season. Extensive human settlements may be beneficial in that that they provide more resources which are reliably available, yet they often represent sites that have higher rates of disturbance and potential risks. We therefore predicted that hyaenas would use areas close to human residential infrastructure in relation to the relative trade-off between the resource value and the cost of disturbance. Such trade-offs could lead to temporal avoidance or preference of areas with human infrastructure, where the use of

anthropogenic resources is higher during periods of low levels of human activity.

Materials and methods

Study area

The KNP is situated in the north eastern corner of South Africa and covers almost two million hectares (Fig. 1). This study took place between May 2007 and March 2010 in a 5000 km^2 southern portion of the park. Vegetation in the study area is characterised by woodland with basalt soils dominated by *Clerocarya caffra* and *Acacia nigrescens*, with *Combretum* species on granite soils (Ogutu & Owen-Smith, 2003). Rainfall is seasonal with the majority falling between October and March, with a peak in January and February (Venter, Scholes & Eckhardt, 2003). Average annual rainfall is approximately 650 mm for the Southern section (Venter & Gertenbach, 1986). Mean monthly temperatures range from 7 to 32ºC for this area (Venter & Gertenbach, 1986). KNP hosts a diverse array of herbivorous and carnivorous mammals. Prey available for hyaenas in the Southern section of the park include, along with small mammals; impala (*Aepyceros melampus*), blue wildebeest (*Connochaetes* taurinus), Burchell's zebra (*Equus burchelli*), greater kudu (*Tragelaphus strepsiceros*), common warthog (*Phacochoerus africanus*), imbabala bushbuck (*Tragelaphus sylvaticus*), nyala (*Nyala angasii*), common reedbuck (*Redunca arundinum*), waterbuck (*Kobus ellipsiprymnus*), steenbok (*Raphicerus campestris*), common duiker (*Sylvicapra grimmia*) and Cape buffalo (*Syncerus caffer*). Other megaherbivores such as African elephant (*Loxodonta africana*), white rhinoceros

(*Ceratotherium simum*), black rhinoceros (*Diceros bicornis*), and giraffe (*Giraffa camelopardalis*) are also available, presumably most often as carrion. Impala in particular constitutes a large part of the hyaena diet in KNP (Henschel & Skinner, 1990; Ryan, 2007). Four large carnivores live sympatrically with hyaenas in KNP; African lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), and African wild dog (*Lycaon pictus*).

Data were collected in two areas with contrasting levels of human activity. The Skukuza area included the Skukuza rest camp and staff village area (31°59'E, 25°00'S). Skukuza is the largest rest camp in KNP and hosts up to 300 visitors. It is also the administrative hub for the whole of KNP with a large staff village. In Skukuza, hyaenas had free access to the unfenced staff village consisting of 250 houses, an enclosed staff compound, a golf course, a shop, communal areas, and administrative buildings beside an enclosed area with tourist accommodation (rest camp). The staff area combined with the rest camp covers 4.3 km^2 and houses approximately 2300 staff (Foxcroft, Richardson & Wilson, 2008). Fences around both individual houses and the compound prevented easy access to household rubbish bins. However rubbish bins in communal areas and larger waste collection sites were unfenced. Open gates and damaged fencing also allowed for opportunistic access to other rubbish bins. Hyaenas also had access to the unfenced car park of a picnic site, which contained rubbish bins and they were able to walk along the perimeter fence of the tourist rest camp. Visitors are required to return to a camp or leave the park by a specific time that varies throughout the year to coincide with sunset and

members of staff do not walk in unfenced areas after dark. Hyaenas were therefore able to use unfenced anthropogenic areas after dark with minimal disturbance. In contrast, we also collected data in a neighbouring area (Doispane; 31°25'E, 25°01'S) approximately 20 km away that had limited levels of human activity and the only permanent infrastructure was a building that occasionally was used for short stays by park staff or guests. The Doispane area was at the border of the park and had, similar to the Skukuza area, access to permanent water. Vegetation in this region of the Kruger National Park is homogeneous (Rutherford et al., 2006). Water access, which is one of the main drivers behind herbivore distribution within the park (Redfern et al., 2003; Smit et al., 2007), was similar between the two areas and prey densities are relatively homogeneous throughout this southern section of the Kruger National Park (Seydack et al., 2012). Therefore, the main differences between the two areas in terms of resource availability for spotted hyaenas are likely related to the elevated human presence in Skukuza caused by the Skukuza village complex.

Study animals and instrumentation

Each area (e.g., Skukuza and Doispane) was inhabited by one spotted hyaena clan. The clan in Skukuza consisted of five adult females, one adult male and up to nine subadult or young adult males and seven subadult or young adult females. The Doispane clan was substantially smaller and consisted of three adult females, two adult males and up to two subadult or young adult males and one subadult or young adult female. Both clans had

juveniles present during the duration of the time they were monitored. We monitored the clan in Skukuza from May 2007 to December 2009 and the one at Doispane from May 2007 until August 2008. Monitoring was primarily done at the den locations but also when hyaenas were opportunistically encountered. Observations were partly done for a concurrent study on the influence of human activity on hyaena behaviour and ecology. We monitored the locations of den sites throughout the study by visiting the clans. These visits varied in frequency from daily to once every second week. When a den was not located within sight of a road, we used clusters of relocations from marked hyaenas (see below) at dawn and dusk to identified likely den locations, which were confirmed by direct visitations. In each clan we had all hyaenas individually recognized based on general characteristics and spot patterns. We scored rank relationships from the outcome of pair-wise interactions.

We fitted one hyaena in each clan with a collar mounted GPS unit that was tasked to download data through the GSM network (African Wildlife Tracking, Pretoria, South Africa). We selected the dominant female from each clan to create a reliable comparison (Boydston et al., 2003). The social rank was confirmed through behavioural observations of aggressive interactions between clan members. The hyaenas were immobilised from a vehicle by a veterinarian from South Africa National Parks' Veterinary Wildlife Service department. Both hyaenas were first baited with three pieces of meat, each containing 2 x 15 mg midazolam tablets to enable safer darting. A combination of 4 mg medetomidine hydrochloride and 60 mg Zoletil was then delivered via a CO_2-powered dart rifle. An

intramuscular injection of atipamezole was administered to reverse the effects of the medetomidine and hyaenas were kept under observation whilst recovering. The female in Skukuza was fitted with her first collar on the 20th October 2007. This stopped working 5th July 2008 and was replaced 24th April 2009. The second collar stopped working on the 19th November 2009 and could not be removed. The collar on the female in Doispane was fitted on the 20th November 2007 and removed July 2011, although we only had access to data from this collar until 6 March 2010. We therefore collected spatial data on the female in Skukuza during the periods October 2007 – 5 July 2008 and 24 April – 19 November 2009 and on the female in Doispane during the period 20 November 2007 – 6 March 2010. Hence, we collected data on both clans simultaneously for the majority of the time the Skukuza clan had an active collar, and we additionally collected data on an extended time period for the Doispane clan. Although sample size may bias home range size estimates, we have retained our full data record in the analyses to improve the accuracy of the estimated home ranges for Doispane. With the complete set of locations we had sufficient samples sizes in both Skukuza and Doispane to accurately estimate seasonal home range sizes (Supplementary Information 1), so that the uneven sample sizes should not influence any differences between the clans in terms of home range size. Both females were nursing during the time for which each clan was observed, i.e. May 2007 to December 2009 for Skukuza and May 2007 to August 2008 for Doispane.

Research was approved by the University of Pretoria Animal Use and Care Committee (protocol number EC010-07) and the Kruger National Park Animal Use and Care

Committee, and was additionally carried out under a research permit from the South African National Parks Board for the project "Impact of human habitation on population dynamics of spotted hyaenas".

Data collection, classification and analyses

The collars were set to take readings on an 11 hour schedule. This schedule provided temporally independent points that covered all hours of the day. Each relocation point was classed as night, day or den. We regarded the time between one hour before sunset and one hour after sunrise as night time and times outside of these hours as day time as it correspond to spotted hyaena activity patterns (Henschel, 1986; Kolowski et al., 2007). Although we acknowledge that we did not have direct measurement of activity during each of these time periods, our observations confirmed that activity within both clans were principally nocturnal, suggesting that most locations during the night were of active hyaenas and locations during the day were resting locations. Data on sunrise and sunset times for the local area were retrieved from a weather service internet site (http://www.timeanddate.com). However, any relocation that occurred within 30 m of an identified den site was labelled as den points regardless of the time of day. In addition to these three classes of locations, we also grouped relocations by season. Following Venter et al (2003), we defined all relocations between October and March as having occurred during the wet season and the other relocations as having occurred during the dry season.

We used 95% Minimum Convex Polygons (MCP's: Mohr, 1947) to estimate home range sizes for each hyaena. We used MCP's to quantify home range sizes because they are relatively robust to possible temporal autocorrelation among data and they do not rely on arbitrarily chosen smoothing parameters or spatial resolutions of the underlying reference grid, which could influence the resulting space use estimates (Swihart & Slade, 1985; Row & Blouin-Demers, 2006; Boyle et al., 2009). MCP estimates are also repeatable across different software programs and therefore provide results that are directly comparable with those of other studies (Harris et al., 1990; Larkin & Halkin, 1994; Lawson & Rodgers, 1997). During October 2008, the clan at Doispane shifted its home range to the west with only a small overlap with the previous home-range. This shift included a shift in den locations, and our observations confirmed that all clan members appear to have shifted their movement patterns along with the marked female. We have therefore treated these two areas as separate home ranges for our analyses. Due to their highly clustered nature, we removed den site locations from all home range size estimations, but we have included them in the visual representation of the home ranges because den location potentially can influence home range patterns. For each home range, we created three size estimates, one including all relocations, one for the wet season and one for the dry season. We based our home range estimates on 745 locations (470 in the dry and 275 in the wet season) for the Skukuza female, 269 locations (138 dry and 131 wet season) for the Doispane female in the initial home range and 558 (195 dry and 363 wet season) locations in the subsequent home range.

We used two metrics to evaluate the spatial patterns of utilization within each home range. First, we quantified the utilization of the home ranges during the night, i.e. when we regarded the hyaenas to have been active, using a normalized Shannon spatial diversity index (Payne et al., 2005). This index provides a measure of the evenness of home range utilization and varies from 0, which indicates a completely clustered utilization, to 1, which indicates a completely even utilization of the home range. The index is a quantification of continuous use of space, albeit sampled at discrete points in time. We selected this index for the night time locations because we regard them to be instantaneous point samples of a continuous movement process, and hence this index to be more appropriate than indices that explicitly evaluate patterns of discrete spatial points. To calculate this index, we first created a grid where the cells corresponded to 1% of respective home range, and calculated the number of relocations within each cell. The grid was confined within each respective estimated home range border. We selected this grid resolution as it provided a sufficient number of cells for calculations while avoiding an excessive number of empty cells. We calculated the index H' as:

$$H' = \frac{\sum_{i=1}^{N} P_i \times \ln(P_i)}{L \ln(N)}$$

where N is the total number of cells in each home range and P_i is the proportion of relocations in each given cell i. We calculated indices for all relocations combined as well as one index for each season. Second, we used the nearest neighbour index to quantify the spatial distributions of day time locations, i.e. when we regarded hyaenas to

have been resting (Clarke & Evans 1954). We opted for a separate index for the day time locations because it is explicitly quantifying the spatial distribution of discrete spatial events, which we believe was appropriate for the distribution of locations when hyaenas were assumed to have been stationary. The nearest neighbour index (R) ranges from 0 (totally clustered distribution) to 2.15 (completely even distribution), and is scaled so that a value of 1 indicates a random distribution, values > 1 indicates an over-dispersed distribution and values < 1 indicates a clustered distribution. For both indices, we evaluated if the observed values deviated from expectations based on a random spatial distribution of points by generating 1000 random point data sets for each home range, each constrained within the home range border and with the same number of locations as the real datasets, and then calculated the index values for each of these random data sets. A random utilization is a sensible expectation to have under the null hypothesis of no preference for features or areas within a home range (Samuel, Pierce & Garton 1985). We evaluated how likely the observed index values were under random expectations using a z-score transformation based on values from the randomly generated data (Baddeley, Rubak & Turner 2015). As a heuristic way of comparing the spatial distribution of night and day time locations between the Skukuza and the Doispane clans, we subtracted the observed value from those calculated from the random data sets (Manly 1997), and used these deviations from random expectations to compare the Shannon and nearest neighbour index between the Skukuza and each of the Doispane home ranges using two-sample permutation tests. We did one comparison for each pair of home ranges (i.e. Skukuza and each of the two Doispane ranges) for both seasons combined as well as one

for each season.

We evaluated the utilization of the urban village area in Skukuza at two separate scales. First, we outlined the whole village area using satellite images retrieved from Google Earth (www.google.com/earth/), supplemented with GPS data collected in the field. We quantified the number of night time (i.e. active) and day time (resting) locations within and outside this area. Second, we described the utilization of different land use types within the village area. For this quantification, we similarly created a map that delineated four different types of land use in the area; highly modified areas - unfenced area with high levels of human use that are unfenced, administration areas - unfenced areas containing business buildings and their surrounding car parks with no fences, intermediately modified areas - areas that have been altered from their natural state but are without buildings or facilities, e.g. golf course and a cricket pitch, and unmodified areas - unaltered habitat inside the village boundary. We then scored each location in the village area to belong to each of these four classes. For both scales, we used a simple resource selection function to determine whether areas were preferred or avoided during night and day, i.e. while active or resting. Following Manly et al. (1993), we calculated the selection indices β_i as:

$$\beta_i = \frac{w_i}{\sum_{i=1}^{H} w_i}$$

where w_i is the selection ratios for each land use class i (i.e. the proportion of locations within each class divided by the proportion of available land that each class was covering)

and *H* is the total number of land use classes. For ease of interpretation, we scaled each index so that a value of zero indicates that a class has been used in relation to its availability, a negative value suggests avoidance and a positive value suggests selection (Dalerum, Boutin & Dunford, 2007). We evaluated whether the utilization of the different habitat classes (i.e. within or outside of the village area or the four land use types within the village area) deviated significantly from a utilization based on availability using chi-square tests.

Results

Home range sizes varied both seasonally as well as between the two females. Despite being part of a larger clan, the female in Skukuza had a smaller home range than the Doispane one both annually as well as within each season (Table 1). The home ranges were not utilized evenly, and all home ranges were less evenly used by night and had more clustered patterns of daytime locations than expected by random distributions (Table 2). The Skukuza female had a different spatial distribution of locations during the night compared to the Doispane female, for both seasons combined (Skukuza vs. Doispane a, $Z = 43.8$, $p < 0.001$, Skukuza vs. Doispane b, $Z = 44.1$, $p < 0.001$), for the dry season (Skukuza vs. Doispane a, $Z = 13.1$, $p < 0.001$, Skukuza vs. Doispane b, $Z = 43.2$, $p < 0.001$), and for the wet season (Skukuza vs. Doispane a, $Z = 43.4$, $p < 0.001$, Skukuza vs. Doispane b, $Z = 41.2$, $p < 0.001$). Although the Skukuza female utilized its home range more evenly than the utilization in the second Doispane range on an annual

basis, it utilized its home range less evenly than both Doispane ranges within each season (Table 2). Similarly, the distribution of day time locations differed between the Skukuza and the Doispane females (both seasons combined: Skukuza vs. Doispane a, $Z = 6.69$, $p < 0.001$, Skukuza vs. Doispane b, $Z = 13.2$, $p < 0.001$; Dry season: Skukuza vs. Doispane a, $Z = 32.2$, $p < 0.001$, Skukuza vs. Doispane b, $Z = 15.1$, $p < 0.001$; Wet season: Skukuza vs. Doispane b, $Z = 33.0$, $p < 0.001$), with the exception of differences between Skukuza and the second Doispane home range during the wet season ($Z < 0.01$, $p = 0.998$). The day time points in the Skukuza home range were more clustered than both Doispane ranges for both seasons combined as well as for the dry season, but were more clustered than only one of the two Doispane home ranges during the wet season (Table 2).

For the Skukuza female, more locations during the night were found inside the village area than what could be expected based on its proportion within the home range (Table 3), for both seasons combined ($\chi^2 = 67.4$, $df = 1$, $p < 0.001$) as well as for both the dry ($\chi^2 = 21.9$, $df = 1$, $p < 0.001$) and the wet season ($\chi^2 = 50.7$, $df = 1$, $p < 0.001$). Within the village area, the utilization of the different land use types also differed from their availability (both seasons combined $\chi^2 = 86.3$, $df = 1$, $p < 0.001$; dry season $\chi^2 = 48.4$, $df = 1$, $p < 0.001$; wet season $\chi^2 = 47.6$, $df = 1$, $p < 0.001$), with the intermediately modified and unmodified areas being preferred and the highly modified and administration areas avoided (Table 3). During the day, the village area was neither preferred nor avoided (Table 3; both seasons combined $\chi^2 = 0.59$, $df = 1$, $p = 0.443$; dry season $\chi^2 = 3.44$, $df = 1$,

p = 0.063; wet season χ^2 = 0.48, df = 1, p = 0.488). Within the village area, however, unmodified habitat was generally being preferred during the day (both seasons combined χ^2 = 17.9, df = 3, p < 0.001; dry season χ^2 = 7.27, df = 3, p < 0.063; wet season χ^2 = 8.88, df = 3, p = 0.031, Table 3).

Discussion

Annual and seasonal home range sizes for the Skukuza female were consistently smaller than both of the Doispane female's home ranges. These observations suggest that human activity and infrastructure were associated with spotted hyaena home range sizes according to our first prediction, i.e. that human infrastructure and activity would be associated with smaller home ranges. Such an interpretation of our results would agree with previous studies that have highlighted that access to anthropogenic areas may reduce carnivore home range sizes (e.g., Šálek, Drahníková & Tkadlec, 2015). Increased availability of resources may reduce home range sizes, especially for larger carnivores that often need to use large areas in search of prey (Kolowski & Holekamp, 2008; Gerht & Riley, 2010; Newsome et al., 2013). Our comparison included two females of equal rank that inhabited areas of similar habitat with comparable prey densities, and therefore we suggest that human infrastructure and activity were associated with spotted hyaena space use by altering resource distributions. We highlight that this interpretation is further supported both by the differences in clan sizes and in number of re-locations for each seasonal home range. The clan with the larger size would be predicted to have a larger

home range because of an increased metabolic need (Gittleman & Harvey, 1982), and any potential sample size effect would cause a positive relation between number of re-locations and estimated home range size (Boyle et al., 2009). Instead, we observed the opposite. The clan with the smallest home range was both the largest and had the most number of relocations for home range estimation. We interpret these observations as further support for an association between human activity and infrastructure and the observed home range sizes.

In addition, the Skukuza female utilized its home range less evenly than the Doispane one, which emphasizes that human infrastructure and related activity may not only have been associated with total home range sizes, but also with how hyaenas used space within these areas. Space use was aggregated during both night and day time, which agrees with previous observations of spotted hyaenas (Henschel, 1986; Boydston et al., 2003). For both seasons the Skuzuza female used its home range less evenly than the Doispane one. Patchy resource distributions have often led to uneven space use (Macdonald, 1983; Gilchrist & Otali, 2002). We therefore suggest that the less even space use in Skukuza supported our second prediction, i.e. that spatially concentrated resources associated with the village area would cause a less even home range utilization. Although the day time locations, presumably when hyaenas were resting, similarly were more clustered than random expectations, day time locations in Skukuza were more clustered than only one of the Doispane home ranges, but not the other. This supports an interpretation where resources associated with anthropogenic food influenced spotted hyaena space use,

because food distribution should have little influence on the locations where hyaenas spend their resting hours. However, we note that there was only marginal seasonal variation in the differences between clans in terms of home range size and use. This observation contradicts our third prediction, and instead suggests that temporal variation in native food did not alter the association between anthropogenic areas and spotted hyaena space use.

In agreement with other studies (Quinn & Whisson, 2005; e.g. Bozek, Prange & Gehrt, 2007), the Skukuza female showed a preference for the village area during the night, i.e. presumably when active. Within the village area, hyaenas preferred intermediately modified habitat the most, followed by unmodified habitat. Administrative and high impact areas were both avoided during the night. The intermediately modified habitat primarily consisted of open areas such as a golf course, a cricket pitch and various patches of disturbed but un-built land. Contrarily, there was no significant preference for or avoidance of the village area during the day, and within the village area all other habitat classes but the undisturbed habitat were avoided. We suggest that these observations supported also our final prediction, that resources would be utilized according to a trade-off between potential benefits and expected risks. Although we do not have information on direct access to anthropogenic resources, such resources would have been more available in the highly modified areas which were consistently selected against. The unmodified and particularly the intermediately modified habitat instead presented artificial open habitat patches. In particular, the golf course attracted several

prey species such as impala and warthog because of its artificially watered vegetation. We believe that this could have generated a habitat patch with aggregations of native prey that additionally was more favourable for hunting than the surrounding woodlands (Mills & Funston, 2003). We therefore suggest that the village area may not have been utilized to gain direct access to anthropogenic resources, but that the preference for the village area was driven by an indirect access to aggregations of native prey that existed in favourable hunting habitat. Such an interpretation is further supported by the lack of habitat preferences for any but the unmodified habitat during resting hours, because areas close to infrastructure that may represent elevated human activity probably were avoided if they were not associated to direct or indirect benefits (e.g. Gerht & Riley, 2010; Riley et al., 2010).

We acknowledge several shortcomings with our study. Our study is preliminary because we have an effective sample size of only one clan. This limits broader conclusions of our results, but none the less provides some insights into further directions for research. Additionally, we compared two clans over somewhat different time periods. This could have biased the results in four principal ways. First, because sample size is related to estimated home range size until an asymptote in number of relocations has been reached, we could have biased our home range size estimates simply because we used different number of relocations for each clan. However, it appears that we had reached an asymptote for all seasonal ranges. Additionally, we had lower sample sizes for the home ranges that were estimated to have been the biggest. Hence, any potential effect of sample

size should have strengthened rather than weakened our conclusions. Second, because we collected data in Doispane during periods when we did not collect data in Skukuza, environmental conditions could have caused additional biases in the results. We can not rule out that such biases influenced our data. However, environmental conditions are relatively consistent in the study area, and we did monitor both clans simultaneously during the majority of the time. We therefore regard it unlikely that temporal variation in environmental conditions had a large influence on our results. Third, the two groups differed in both group size and composition. However, as group size generally is expected to cause increased home range sizes in group living carnivores, and we observed a negative relationship between group size and home range size, we interpret also this potential bias to strengthen rather than weaken our data interpretation. Finally, we collected data on only a single female in each clan. Although we attempted to minimize potential biases by marking the dominant female, state dependent differences such as pregnancy and lactation may still have influenced our comparison (Boydston et al., 2003). However, when observed, both females were nursing. We interpret these observations that both females had similar reproductive states throughout the study, although we cannot confirm this with direct observations.

To conclude, although this study was based on observations on only two individuals within two clans, it provided valuable insights into the effects of anthropogenic areas on the space use of a large carnivore inside a protected area. Our observations supported that human infrastructure and related activity were associated with hyaena space use, and that

these associations at least to some extent may have been related to resource supply, but only indirectly by generating favourable hunting areas. We highlight that further work is needed to explore associations between humans and large carnivores and their related ecosystem processes within protected areas. In particular, we argue that we need to quantify the relative effects of direct provision of food through anthropogenic resources versus indirect provision of food through the creation of favourable hunting habitats, and if such effects alter large carnivore ecosystem function in protected areas.

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References

Abay GY., Bauer H., Gebrihiwot K., Deckers J. 2010. Peri-urban spotted hyena (Crocuta crocuta) in Northern Ethiopia: diet, economic impact, and abundance. European Journal of Wildlife Research 57:759–765. DOI: 10.1007/s10344-010-0484-8.

Baddeley A, Rubak E, Turner R. 2015. Spatial point patterns: Methodology and applications with R. London: Chapman and Hall.

Bateman PW., Fleming PA. 2012. Big city life: carnivores in urban environments. Journal of Zoology 287:1–23. DOI: 10.1111/j.1469-7998.2011.00887.x.

Beckmann JP., Berger J. 2003. Rapid ecological and behavioural changes in carnivores:the responses of black bears (Ursus americanus) to altered food. Journal of

Zoology 261:207–212. DOI: 10.1017/S0952836903004126.

Boydston EE., Kapheim KM., Szykman M., Holekamp KE. 2003. Individual variation in space use by female spotted hyenas. Journal of Mammalogy 84:1006–1018. DOI: 10.1644/BOS-038.

Boyle SA., Laurenco WC., da Silva LR., Smith AT. 2009. Home range size vary with sample size and methods. Folia Primatologia 80:33-42. DOI: 101159/000201092.

Bozek CK., Prange S., Gehrt SD. 2007. The influence of anthropogenic resources on multi-scale habitat selection by raccoons. Urban Ecosystems 10:413–425. DOI: 10.1007/s11252-007-0033-8.

Cardillo M., Purvis A., Sechrest W., Gittleman JL., Bielby JL., Mace GM. 2004. Human population density and extinction risk in the worlds carnivores. PloS Biology 2:0909-0914. DOI: 10.1371/journal.pbio.0020197.

Clark PJ., Evans FC. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology, 35:445–453. DOI: 10.2307/1931034.

Contesse P., Hegglin D., Gloor S., Bontadina F., Deplazes P. 2004. The diet of urban foxes (Vulpes vulpes) and the availablity of anthropogenic food in the city of Zurich, Switzerland. Mammalian Biology 69:81–95. DOI: 10.1078/1616-5047-00123.

Cooper SM., Holekamp KE., Smale L. 1999. A seasonal feast: long-term analysis of feeding behaviour in the spotted hyaena (Crocuta crocuta). African Journal of Ecology 37:149–160. DOI: 10.1046/j.1365-2028.1999.00161.x.

Dalerum F., Boutin S., Dunford JS. 2007. Wildfire effects on home range size and fidelity of boreal caribou in Alberta, Canada. Canadian Journal of Zoology 85:26–32. DOI: 10.1139/z06-186.

Fedriani JM., Fuller TK., Sauvajot RM. 2001. Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. Ecography 24:325–331. DOI: 10.1034/j.1600-0587.2001.240310.x.

Foxcroft LC., Richardson DM., Wilson JRU. 2008. Ornamental plants as invasive aliens: problems and solutions in Kruger National Park, South Africa. Environmental Management 41:32–51. DOI: 10.1007/s00267-007-9027-9.

Gerht S., Riley SP. 2010. Coyotes (Canis latrans). In: Gerht S., Riley SP., Cypher BL eds. Urban carnivores: ecology, conflict and conservation. Baltimore: John Hopkins University press, 79-96.

Gilchrist JS., Otali E. 2002. The effects of refuse-feeding on home-range use, group size,

and intergroup encounters in the banded mongoose. Canadian Journal of Zoology 80:1795–1802. DOI: 10.1644/BRG-021 491-497.

Gittleman JL., HarveyPH. 1982. Carnivore home-range size, metabolic needs, and ecology. Behavioral Ecology and Sociobiology 10:57-63. DOI:10.1007/BF00296396.

Harris S., Cresswell WJ., Forde PG., Trewhella WJ., Woollard T., Wray S. 1990. Home-range analysis using radio-tracking data–a review of problems and techniques particularly as applied to the study of mammals. Mammal Review 20:97–123. DOI: 10.1111/j.1365-2907.1990.tb00106.x.

Henschel JR. 1986. The socio-ecology of a spotted hyaena (Crocuta crocuta) clan in The Kruger National Park. MSc Thesis. Pretoria: University of Pretoria.

Henschel JR., Skinner JD. 1990. The diet of the spotted hyaenas Crocuta crocuta in Kruger National Park. African Journal of Ecology 28:69–82. DOI: 10.1111/j.1365-2028.1990.tb01138.x.

IUCN. 2015. The IUCN Red List of Threatened Species. Version 2015.1. <http://www.iucnredlist.org>. Downloaded on 22nd June 2015.

Kolowski JM., Katan D., Theis KR., Holekamp KE. 2007. Daily patterns of activity in the spotted hyena. Journal of Mammalogy 88:1017–1028. DOI: 10.1644/06-MAMM-A-143R.1.

Kolowski JM., Holekamp KE. 2008. Effects of an open refuse pit on space use patterns of spotted hyenas. African Journal of Ecology 46:341–349. DOI: 10.1111/j.1365-2028.2007.00846.x.

Kruuk H. 1972. The spotted hyena: a study of predation and social behavior. Chicago: University of Chicago Press.

Larkin RP., Halkin D. 1994. A review of software packages for estimating animal home ranges. Wildlife Society Bulletin (1973-2006) 22:274–287.

Lawson EJG., Rodgers AR. 1997. Differences in home-range size computed in commonly used software programs. Wildlife Society Bulletin (1973-2006) 25:721–729.

Lucherini M., Crema G. 1994. Seasonal variation in diet and trophic niche of the red fox in an alpine habitat. Zeitschrift für Säugetierkunde 59:1–8.

Macdonald DW. 1983. The ecology of carnivore social behaviour. Nature 301:379–384. DOI: 10.1038/301379a0.

Manly BFJ. 2007. Randomization, bootstrap, and Monte Carlo methods in biology. 2nd

ed. London: Chapman and Hall.

Manly BJF., McDonald L., Thomas D. 1993. Resource selection by animals: statistical design and analysis for field studies. London: Chapman and Hall.

Mills MGL. 1984. The comparative behavioural ecology of the brown hyaena Hyeana brunnea and the spotted hyaena Crocuta crocuta in the southern Kalahari. Koedoe (Suppl) 27:237–247.

Mills MGL., Funston PJ. 2003. Large carnivores and savanna heterogeneity. In: Du Toit JT., Rogers KH., Biggs CH. eds. The Kruger experience. Ecology and management of savanna heterogeneity. Washington DC: Island Press.

Mills MGL, Hofer H. 1998. Hyaenas. Status survey and conservation action plan. Gland, Switzerland and Cambridge, UK: IUCN/SSC Hyaena Specialist Group.

Mohr CO. 1947. Table of equivalent populations of North American small mammals. American Midland Naturalist 37:223–249. DOI:10.1371/journal.pone.0100764.

Newsome TM., Ballard GA., Dickman CR., Fleming PJS., van de Ven R. 2013. Home range, activity and sociality of a top predator, the dingo: a test of the Resource Dispersion Hypothesis. Ecography 36:914–925. DOI: 10.1111/j.1600-0587.2013.00056.x.

Newsome TM., Ballard GA., Fleming PJS., Ven R van de., Story GL., Dickman CR. 2014. Human-resource subsidies alter the dietary preferences of a mammalian top predator. Oecologia 175:139–150. DOI: 10.1007/s00442-014-2889-7.

Ogutu JO., Owen-Smith N. 2003. ENSO, rainfall and temperature influences on extreme population declines among African savanna ungulates. Ecology Letters 6:412–419. DOI 10.1046/j.1461-0248.2003.00447.x.

Ordeñana MA., Crooks KR., Boydston EE., Fisher RN., Lyren LM., Siudyla S., Haas CD., Harris S., Hathaway SA., Turschak GM., Miles AK., Van Vuren DH. 2010. Effects of urbanization on carnivore species distribution and richness. Journal of Mammalogy 91:1322–1331. DOI: 10.1644/09-MAMM-A-312.1.

Owen-Smith N. 1990. Demography of a large herbivore, the greater kudu Tragelaphus strepsiceros, in relation to rainfall. Journal of Animal Ecology 59:893–913. DOI: 10.2307/5021.

Payne LX., Schindler DE., Parrish JK., Temple SA. 2005. Quantifying spatial pattern with evenness indices. Ecological Applications 15:507–520. DOI: 10.1890/03-5029.

Pereira LM., Owen-Smith N., Moleón M. 2013. Facultative predation and scavenging by mammalian carnivores: seasonal, regional and intra-guild comparisons. Mammal Review

44:1-12. DOI: 10.1111/mam.12005.

Quinn JH., Whisson DA. 2005. The effects of anthropogenic food on the spatial behaviour of small Indian mongooses (Herpestes javanicus) in a subtropical rainforest. Journal of Zoology 267:339–350. DOI: 10.1017/S0952836905007491.

Redfern JV., Grant R., Biggs H., Getz WM. 2003. Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. Ecology 84:1092-2107. DOI:10.1890/01-0625

Riley SP., Boydston EE., Crooks KR., Lyren LM. 2010. Bobcats (Lynx rufus). In: Gerht S., Riley SP., Cypher BL eds. Urban carnivores: ecology, conflict and conservation. Baltimore: John Hopkins University press, 121-140.

Row JR., Blouin-Demers G. 2006. Kernels are not accurate home range size estimators for herpetofauna. Copeia 4:797-802. DOI: 10.1643/0045-8511.

Rutherford MC., Mucina L., Lötter MC., Bredenkamp GJ., Smit JHL., Scott-Whaw RC., Hoare DB., Goodman PS., Bezuidenhoit H., Scott L., Ellis F., Powrie LW., Siebert F., Mostert TH., Henning BJ., Venter CE., Camp KGT., Siebert SJ., Mathwes WS., Burrows JE., Bodson L., van Rooyen N., Schmidt E., Winter PJD., du Preez PJ., Ward RA., Williamson S., Hurter PJH. 2006. Savanna biome. In: Mucina L., Rutherford MC eds. The vegetation of South Africa, Lesotho and Swaziland. Strelitza 19. Pretoria: South Africa National Biodiversity Institute, 438-539.

Ryan B. 2007. Effects of anthropogenic food sources on diet and parasite loads in spotted hyaena, Crocuta crocuta (Erxleben, 1777) in Kruger National Park,. MSc. Thesis. Pretoria: University of Pretoria.

Šálek M., Drahníková L., Tkadlec E. 2015. Changes in home range sizes and population densities of carnivore species along the natural to urban habitat gradient. Mammal Review 45:1–14. DOI: 10.1111/mam.12027.

Sandell M.1989. The mating tactics and spacing patterns of solitary carnivores. In: Gittleman JL ed. Carnivore behavior, ecology, and evolution, Ithaca: Cornell University Press, 164–182

Samuel MD., Pierce DJ., Garton EO. 1985. Identifying areas of concentrated use within a home range. Journal of Animal Ecology 54:711-719. DOI: 10.2307/4373.

Schuette P., Wagner AP., Wagner ME., Creel S. 2013. Occupancy patterns and niche partitioning within a diverse carnivore community exposed to anthropogenic pressures. Biological Conservation 158:301–312. DOI: 10.1016/j.biocon.2012.08.008.

Seydack AH., Grant CC., Smit IP., Vermuelen WL., Baard J., Zambatis N. 2012. Large

herbivore population performance and climate in a South African semi-arid savanna. Koedoe 54:1049. DOI: 10.4102/koedoe.v54i1.1047.

Smit IPJ., Grant CC., Devereux BJ. 2007. Do artificial waterholes influence the way herbivores use the landscape? Herbivore distribution patterns around rivers and artificial surface water sources in a large African savanna park. Biological Conservation 136:85-99. DOI: 10.1016/j.biocon.2006.11.009.

Swihart RK., Slade NA. 1985. Testing for independence of observations in animal movements. Ecology 66:1176–1184. DOI: 10.2307/1939170.

Venter FJ., Gertenbach WPD. 1986. A cursory review of the climate and vegetation of the Kruger National Park. Koedoe 29:139-148. DOI: 10.4102/koedoe.v29i1.526.

Venter FJ., Scholes RJ., Eckhardt HC. 2003. The abiotic template and its associated vegetation patterns. In: Du Toit JT., Rogers KH., Biggs HC. eds. The Kruger Experience: Ecology and Management of Savanna Heterogeneity. Washington DC, USA: Island Press, 83–129.

Woodroffe R. 2000. Predators and people: using human densities to interpret declines of large carnivores. Animal Conservation 3:165–173. DOI: 10.1111/j.1469-1795.2000.tb00241.x.

Yirga G., Leirs H., De Iongh HH., Asmelash T., Gebrehiwot K., Deckers J., Bauer H. 2015. Spotted hyena (Crocuta crocuta) concentrate around urban waste dumps across Tigray, northern Ethiopia. Wildlife Research 42:563. DOI: 10.1071/WR14228.

Table 1. Sizes (km^2) of seasonal and annual spotted hyaena (*Crocuta crocuta*) home ranges (95 % MCP) in three areas of different levels of human activity. The low activity sites were inhabited by the same clan that sequentially shifted their home range half way through the study.

Level of human activity	Annual	Dry season	Wet season
High human activity	33.7	31.6	24.5
Low human activity (a)	53.1	44.4	39.7
Low human activity (b)	47.9	41.0	45.6

Table 2. Spatial distributions of spotted hyaena (*Crocuta crocuta*) night and day locations in three home ranges with contrasting levels of human activity. The low activity home ranges were inhabited by the same clan that sequentially shifted their home range half way through the study. The spatial distribution of active points were evaluated with using a normalized Shannon spatial diversity index (*H'*), which range from 0 (completely clustered use of space) to 1 (completely even use of space). The spatial distributions of resting sites were quantified as a nearest neighbour index (*R*), which ranges from 0 (totally clustered distribution) to 2.15 (completely even distribution). A value of 1 indicates a random distribution, values > 1 indicates an overdispersed distribution and values < 1 indicates a clustered distribution.

		Night				Day			
Home range	Human activity	H'_{Obs}	H'_{Exp}	Z	P	R_{Obs}	R_{Exp}	Z	P
Both seasons									
Skukuza	High	0.69	0.85	40.3	<**0.001**	0.41	1.03	16.2	<**0.001**
Doispane a	Low	0.71	0.84	14.4	<**0.001**	0.44	1.04	10.4	<**0.001**
Doispane b	Low	0.65	0.77	27.6	<**0.001**	0.39	1.03	15.2	<**0.001**
Dry season									
Skukuza	High	0.63	0.78	30.7	<**0.001**	0.35	1.03	14.5	<**0.001**
Doispane a	Low	0.71	0.91	12.1	<**0.001**	0.52	1.06	6.88	<**0.001**
Doispane b	Low	0.75	0.87	10.6	<**0.001**	0.42	1.05	8.79	<**0.001**
Wet season									
Skukuza	High	0.69	0.85	18.8	<**0.001**	0.52	1.04	7.96	<**0.001**
Doispane a	Low	0.81	0.90	5.90	<**0.001**	0.55	1.07	5.55	<**0.001**
Doispane b	Low	0.70	0.81	16.9	<0.001	0.39	1.04	11.9	<0.001

Table 3. Spotted hyaena (*Crocuta crocuta*) utilization of a village area and of different land use types within this village area in the Kruger National Park. Percent of locations for the non-village and the village area refer to the percent of all locations within the home range, whereas the percent of locations of each land use type refer to the percent of locations within the village area. Beta coefficients describes relative selection for the village area and within the village area also for the different land use types, scaled so that values < 0 indicates avoidance (i.e. that an area is used less than its availability) and values > 0 indicates preference (i.e. that an area is used more than its availability).

	Night						Day					
	Annual		Dry season		Wet season		Annual		Dry season		Wet season	
Land use type	*% of locations*	*β*	*% of locations*	*β*	*% of locations*	*β*	*% of locations*	*β*	*% of locations*	*β*	*% of locations*	*β*
Non-village area	64.1	-0.29	72	-0.21	53.4	-0.27	89.9	0.1	94.1	0.21	82.2	0.05
Village area	35.9	0.29	28.0	0.21	46.6	0.27	10.1	-0.1	5.9	-0.21	17.8	-0.05
Administration area	0	-0.25	0	-0.24	33.3	-0.21	0	-0.25	0	-0.25	0	-0.25
High impact area	2.27	-0.22	2.2	-0.25	0	-0.25	0	-0.25	0	-0.25	0	-0.25
Intermediately modified habitat	50.0	0.30	50.0	0.14	64.4	0.44	4.8	-0.19	0	-0.25	7.7	-0.16
Unmodified habitat	46.2	0.16	46.0	0.34	32.2	0.03	95.2	0.69	100	0.75	92.3	0.66

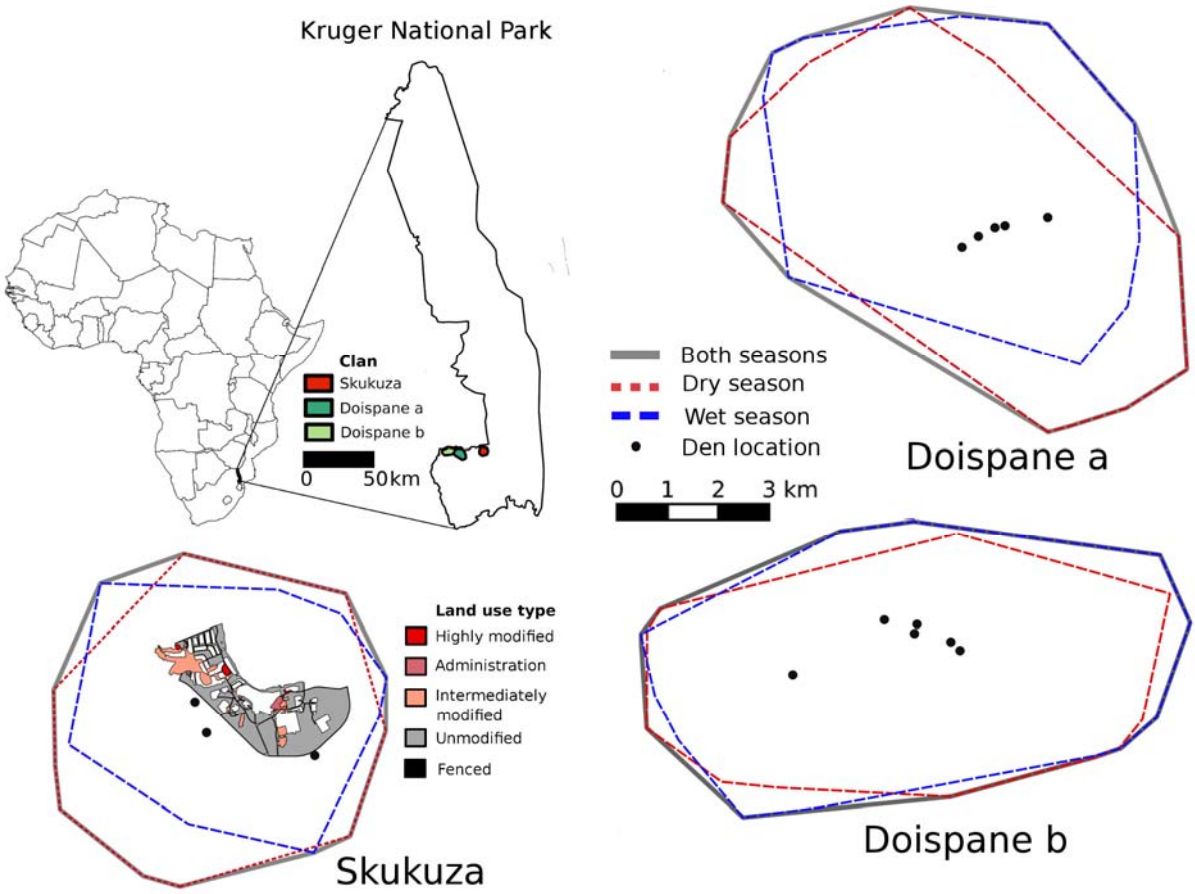

Figure 1. Locations of the three home ranges within the Kruger National Park as well as the annual and seasonal borders for these home ranges. The Skukuza clan had access to a village area with four unfenced land use types; highly modified, administration, intermediately modified and unmodified areas.

Supplementary Information

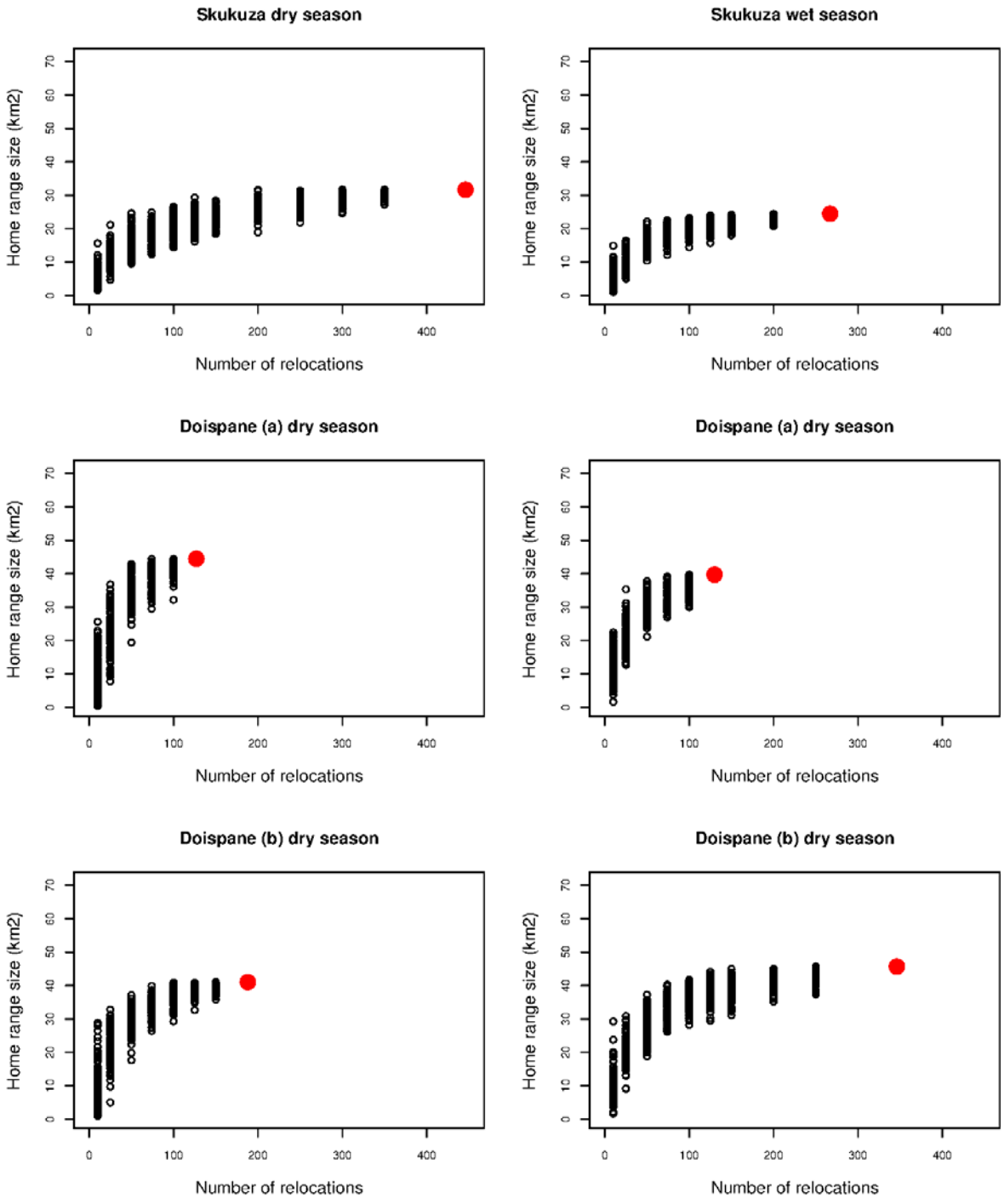

Figure S1. Accumulation curves for home range size for each clan and season. The large red dot marks the estimated home range size given the full set of data that were utilized.

Further supplementary material is available at the PeerJ website (https://peerj.com/articles/2596/#supplemental-information)

Chapter 5: Social networks of spotted hyaenas in areas of contrasting human infrastructure and activity

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Abstract

Group living animals rely on social interactions to maintain the structure and cohesiveness of the social group. Changes in resource abundance can influence social interactions with an expected weakening of social ties during times of resource scarcity. Although human infrastructure and activity often impose a disturbance to animal populations, it can also be a source of reliable resources that are relatively easy to access. We evaluated if the social networks differed among four spotted hyaena clans experiencing contrasting levels of human infrastructure and activity in the Kruger National Park, South Africa. Clans living in areas of limited human infrastructure and activity had denser social networks with shorter path lengths than the social networks of a clan with high levels of human activity. The clan with the lowest level of human activity demonastrated higher cluster coefficients the other clans. Although the clans differed in the relative network roles of hyaenas with different rank and age classes, these differences were not consistently related to variation in human infrastructure and activity. We suggest that anthropogenic resources may have weakened the social bonds of spotted hyaenas, but that the relative importance of individuals of contrasting age, sex and rank for spotted hyaena social networks may be resilient to external perturbations. Finally, our study supported previous suggestions that individual characteristics may have important influences for the relative roles of animals in social networks.

Key words: social interactions, social network, graph theory, large carnivore, Carnivora, anthoropogenic, sociality

Introduction

Group living entails both costs and benefits to individuals, and is therefore predicted when the benefits outweigh the costs. In carnivores, the evolution of sociality is predominantly associated with a need to defend food and territory and the ability to cooperatively hunt larger prey (Creel & Macdonald, 1995; Gittleman, 1989; Macdonald, 1983; but see Dalerum, 2007 for an alternative view). Many group living carnivores rely on complex social interactions among group members to maintain the cohesiveness of the social group. Social interactions among group members can therefore be critically important for the survival and fitness of many group living carnivores (Alexander, 1974). Social network analysis provides a powerful tool for quantifying social interactions, and the analyses of interaction networks has been used to identify key individuals in social groups, and, for example, the resilience of social groups to external perturbations, and the effects of social interactions on disease transmission (Wey et al., 2008).

Resource abundance can influence several aspects of sociality in mammals. For example, more abundant food can lead to larger group sizes (Newsome, Ballard G-A., Dickman CR., Fleming PJS., van de Ven et al., 2013), and limitations in resources can affect intra-group competition and subsequent aggressive encounters (Banks, Piggott, Stow & Taylor, 2007). Social bonding can, however, lead to increased tolerance for group members at patchy food resources, although these bonds are not always strong enough to overcome competition (Marshall, Carter, Ashford, Rowcliffe & Cowlishaw, 2015). Consequently, social ties may be weakened during periods of low resource abundance (Holekamp, Smith, Strelioff, Van Horn & Watts, 2012), although similar weakening of bonds has also been reported with high food abundance (e.g. Henzi, Lusseau, Weingrill, van Schaik & Barrett, 2009). Therefore, resource abundance and distribution can have strong effects on the interactions within social groups.

Whilst human population growth is classically associated with carnivore population declines

(Woodroffe, 2000), some carnivore species successfully utilise anthropogenic resources. Such utilisation has been associated with changes in diet, demography, life history traits, space use and social behaviour (e.g., Beckmann & Berger, 2003a,b; Belton, Cameron & Dalerum, 2016; Contesse, Hegglin, Gloor, Bontadina & Deplazes Contesse, 2004; Prange, Gehrt & Wiggers, 2003). Many species that frequently seem to utilise anthropogenic resources (e.g., banded mongoose *Mungos mungo*: Flint, Hawley & Alexander, 2016; coyotes: Fedriani, Fuller & Sauvajot, 2001; spotted hyaenas: Kolowski & Holekamp, 2008) live in social groups. Anthropogenic resources alter both resource distribution and abundance within a landscape. However, the extent to which anthropogenic food can influence the social interactions of group living species remains relatively poorly understood, and studies so far have been limited to interactions linked to localized anthropogenic food sites such as garbage dumps (Flint et al., 2016).

The spotted hyaena (*Crocuta crocuta*) is a large hyaenid that lives in social groups known as clans (Kruuk, 1972). The clan is dominated by a female matriarch and a strict linear hierarchy is followed by other females in the clan and their sub-adult offspring (Frank, 1986). Young adult males disperse at sexual maturation, which occurs between the ages of two and six years (Holekamp & Dloniak, 2010). Immigrant males follow a linear hierarchy below all females and their offspring, which typically is based on tenure (East & Hofer, 2001). The spotted hyaena has often been reported to exploit anthropogenic food sources (Kolowski & Holekamp, 2008; Yirga et al., 2015). However, although both diet (Yirga et al., 2012) and space use (Kolowski & Holekamp, 2008; Belton et al., 2016) have been associated with access to anthropogenic resources, the influence of anthropogenic resources on social interactions within hyaena clans has received limited attention. This is unfortunate, since social interactions is a central component of spotted hyaena biology.

In this study we quantified the social networks of four spotted hyaena clans with exposure to contrasting levels of human infrastructure and activity inside the Kruger National Park in South

Africa. We hypothesise that these contrasts in infrastructure and activity would lead to a variation in access to anthropogenic food. We predicted that hyaena clans in areas with denser infrastructure and more human activity would show less group cohesiveness and hence both less dense and less complex social networks, associated with greater access to anthropogenic food and therefore a decreased need for group related foraging. In addition, we expected that the effect of human activity and infrastructure would be highest for young hyaenas, since these have been observed to be the predominant users of anthropogenic food resources.

Methods

Study area

This study took place in a 5000 km^2 southern portion of KNP (Fig. 1). Vegetation in the study area is characterised by woodland with basalt soils dominated by *Clerocarya caffra* and *Acacia nigrescens*, with *Combretum* species on granite soils (Ogutu & Owen-Smith, 2003). Rainfall is seasonal with the majority falling between October and March, with a peak in January and February (Venter, Scholes & Eckhardt, 2003). Average annual rainfall is approximately 650 mm for the Southern section (Venter & Gertenbach, 1986). For this study we defined the months October – March as wet season and April – September as dry season. Mean monthly temperatures range from 7 to 32ºC (Venter & Gertenbach, 1986). KNP hosts a diverse array of herbivorous and carnivorous mammals. Prey available for hyaenas in the Southern section of the park include, along with small mammals; impala (*Aepyceros melampus*), blue wildebeest (*Connochaetes* taurinus), Burchell's zebra (*Equus burchelli*), greater kudu (*Tragelaphus strepsiceros*), common warthog (*Phacochoerus africanus*), imbabala bushbuck (*Tragelaphus sylvaticus*), nyala (*Nyala angasii*), common reedbuck (*Redunca arundinum*), waterbuck (*Kobus ellipsiprymnus*), steenbok (*Raphicerus campestris*), common duiker (*Sylvicapra grimmia*) and Cape buffalo (*Syncerus caffer*). Other megaherbivores such as African elephant (*Loxodonta africana*), white rhinoceros (*Ceratotherium simum*), black

rhinoceros (*Diceros bicornis*), and giraffe (*Giraffa camelopardalis*) are also available, but are presumably only utilized by hyaenas as carrion. Impala in particular constitutes a large part of the hyaena diet in KNP (Henschel & Skinner, 1990; Ryan, 2007). Four large carnivores live in sympatry with hyaenas in KNP; African lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), and African wild dog (*Lycaon pictus*).

Study population

We collected data between May 2007 and December 2009 on four clans (Figure 1) that experienced different levels of human activity (Table 1). Clans were frequently visited for behavioural observations, and also opportunistically encountered at other times. All individuals in each clan were individually recognisable by their unique coat spot patterns. A photographic catalogue was created to help with identification, and at the time a clan was observed we counted all present clan members. Based on these records, we calculated monthly values for clan size as well as sex, age and rank ratios. If a hyaena was not seen during a month but was subsequently observed in later months it was added retrospectively to the tally. Mean clan sizes (mean ± sd) were 10 (±1.67) for Doispane,18.67 (±1.37) for Afsaal, 24.56 (± 4.10) for Kruger Gate and for Skukuza 25.1 (±1.10), Sex ratios (M:F, DP = 1 : 1.22, AF = 1 : 1.29, KG = 1 : 0.87, SK = 1 : 1.16) and age ratios (AD : YA : SA, DP = 1 : 0.20 : 0.8, AF = 1 : 0.70 : 1.70, KG = 1 : 0.48 : 1.16, SK = 1 : 1.39 : 1.49) for the clans were similar.

The Doispane clan denned in a remote area. The shortest route between the den areas and the closest rest camp was 27.5 km away on dirt roads and the main gate was 14.5 km away. Phabeni gate, a smaller gate with limited use was situated 18.8 km from the clan. The Doispane clan therefore experienced substantially less human disturbance than the other clans. The Afsaal clan frequently denned by the side of the road within 500m of the Afsaal picnic site. The Afsaal picnic site consists of a shop, a cafeteria and a picnic area, all of which are unfenced, with an adjoining

fenced residence typically housing four to five staff. There was also associated fenced living quarters for staff. This clan was observed to receive deliberate feeding by tourists. The Kruger Gate clan resided in an area that received high levels of activity during daylight hours but with relatively limited amount of infrastructure. The clan denned by the main road midway between Skukuza rest camp and Paul Kruger Gate, a main entrance to the park that is situated 12 km from Skukuza. The home range of the Skukuza clan encompassed the Skukuza rest camp and associated staff village (Belton et al. 2016). Skukuza is the largest rest camp in KNP and hosts up to 300 visitors. It is also the administrative hub for the whole of KNP with a large staff village. Hyaenas in the Skukuza clan had free access to the unfenced staff village consisting of 250 houses, an enclosed staff compound, a golf course, a shop, communal areas, and administrative buildings beside an enclosed area with tourist accommodation. The staff area combined with the rest camp covers 4.3km^2 and houses approximately 2300 staff (Foxcroft, Richardson & Wilson, 2008). The combined area of these two structures creates the largest area of human modified habitat in the park.

Evaluation of human infrastructure and activity

To provide a quantified measure of the amount of human infrastructure and activity associated with each clan, we calculated the road density and the litter density along roads in areas surrounding the locations of behavioural observations for each clan. There areas were estimated as circular areas with a diameter 8 km centered on the spatial centroid of all den sites that were used for observations. The size of this area corresponds approximately to observed spotted hyaena home range sizes within the park (Belton et al., 2016). Road densities were calculated from official park maps, and roadside litter was calculated as part of a concurrent study.

Behavioural observations

We recorded behavioural observations while the hyaenas were aggregated around den sites. This was typically at dawn and dusk. At dusk hyaenas would often stay for a few hours, before leaving to

utilise their home range. In the morning adults would congregate at the den site for a few hours and then leave to go and rest elsewhere. Subadults were often out of the den even when adult hyaenas were not present. For logistic reasons we only conducted behavioural observations when the clans were utilising a den by a road. Monitoring of active den sites was focussed around dawn and dusk. To attempt to capture data on the arrival and departure of each individual, observations began two hours before sunrise or sunset. Observations ended when all adults had left the den. Observation hours varied depending on the presence of hyaenas at the den site. Sessions lasted between one and 4 hours (Doispane: 01:15 ± 00:54; Afsaal: 02:31 ± 01:21; Kruger Gate: 01:16 ± 00:45; Skukuza: 01:50 ± 01:27). The clans were observed over the following periods; Doispane clan (31 visits): 09/04/2008 – 26/07/2008, Kruger Gate clan (17 visits): 18/03/2008 – 23/12/2008, Afsaal clan (32 visits): 17/07/2009 – 29/11/2009, Skukuza clan (41 visits): 06/04/2009 – 06/10/2009. We recorded behaviour for a total of 38 hours at the Doispane clan, for 40 hours at the Afsaal clan, for 40 hours at the Kruger gate clan and for 73 hours at the Skukuza clan.

We recorded the frequency of pair-wise interactions between clan members during each observation period (Altmann, 1974; Holekamp & Smale, 1991). In each interaction the initiator and receiver of the interaction were recorded, if possible. Interactions included approaches, genital greeting, muzzle greeting, aggression and play. Play was defined as interactions between hyaenas that showed no obvious signs of aggression or dominance behavior. A genital greeting consists of two hyaenas standing side to side, nose to tail (Kruuk, 1972). Asymmetries in this greeting point to a dominant and subordinate relationship between the hyaenas. Each hyaena sniffs at the other's genitals and leg lifting can occur. The hyaena that lifts its leg first is most often the subordinate in the pair (East, Hofer & Wickler, 1993). This criterion was used along with aggressive and subordinate classes of age and sex to define dominance between individuals. A muzzle greeting was defined as two hyaenas coming together and sniffing each others muzzle area, as often occurred when a female was lying down nursing cubs was approached by another. Since there is no clear dominance asymmetry

in a muzzle greeting, we did not use this behaviour to determine rank relations. Similarly, we excluded all play behaviour from rank calculations. Aggressive interactions included chasing, lunging, biting or snapping and were further confirmed by submissive and defensive behaviours such as carpal crawl, moving away, giggling and bared teeth from the receiver (Kruuk, 1972).

Age and sex classification

Each individual was sexed based on the shape of the phallic glans (Frank, Glickman & Powch, 1990), and categorised into one of three age classes; sub-adults (0-24 months), young adult (25-48 months) and adult (> 48 months). We based age class determinations on pelage and size for hyaenas with unknown birth dates at the start of the study, the definition of spots on the coat, and length of coat. Age classification was confirmed retrospectively by frequently taking photographs of all young hyaenas and comparing them to hyaenas of known age. Within seasons, we let a hyaena belong to the age class it inhabited for the majority of time within a specific season. Adult males needed to be observed at a den site at least once during the study period to be considered as part of the clan. Males that did not meet this criterion were regarded as transient and excluded from analysis.

Determination of dominance structures

Individuals within spotted hyaena clans live in distinct social dominance hierarchies. We used the outcomes of pair-wise interactions to assign the social rank of each individual. In this study we used a broad classification of social rank relations and classed each hyaena as 'high', 'low', ‘dominant’ or 'immigrant'. We used information from previous studies to assist with assigning ranks due to sparse data for some individuals. Since a female's cubs hold the rank below their mother with all previous offspring following sequentially behind the most recent (Holekamp & Smale, 1991), we could assign some ranks based on the rank of the mother. Conversely, we used interactions between cubs to infer maternal dominance in cases when data between adults were missing (Frank 1986).

Individuals with unknown maternity were included in the hierarchy following the results of interactions with other group members. Immigrants were defined as adult and young adult males that were frequently subordinate to subadult and adult group members. Because the hierarchy amongst immigrant males is based on tenure (East & Hofer, 2001), new immigrant males that joined the clans during the study were added consecutively to the bottom of the hierarchy. However due to low interaction rates between immigrant males they were all classified as immigrants in analysis. Membership to the high and low groups was determined by adding up the total number of non immigrant individuals and dividing that figure in two. The exception was Kruger Gate clan, where a number of young adult males of unknown maternity were dominant over the immigrant males and were assigned to the lower rank.

Quantification of interaction structures

We use methods based on mathematical graph theory to quantify properties of the social networks of the four spotted hyaena clans. Although graph theory is an old branch of discrete mathematics (Euler, 1741), it has only recently seen a wider use in biological sciences (Miranda, Parrini & Dalerum, 2013), including quantifying social structures of animal groups (Wey et al., 2008). Network tools based on graph theory offer a powerful framework for testing the structure of social organisation and structure between animals (Krause, Lusseau & James, 2009). A mathematical graph consists of nodes (or vertices) which are connected by links (edges). In animal social networks, the nodes usually represent individual animals and links some form of social interaction between these animals. Networks are built from interaction matrices, which can either be symmetric, in cases when the directions of the social interactions are not known or of interest, or asymmetric, in which case the directions of the interactions are known.

Based on our observations of social interactions we created one weighted assymetric interaction matrix for each clan based on the total number of interactions between each pair of group members.

From this matrix we created a network describing the structure of the social interactions in each clan (Newman, Watts & Strogatz, 2002). Behaviours were collapsed to a winner/ loser interaction. A 'winner' that showed dominance over another hyaena, and a 'loser' who exhibited subordinate or defensive behavior. There are many metrics and indices available to quantify the structure of interactions in such social networks (e.g. Wey et al., 2008). In this study, we used three indices to quantify the properties of the social networks of each clan. Density (*D*) quantifies the ratio of the number of observed edges to the number of theoretically possible edges. High density scores indicate that a large number of the possible interactions are realised (Wey et al., 2008), and subsequently that many of the individuals in the group are interacting with each other. Conversely a low *D* value suggests that the relations between individuals are weaker with less frequent interactions (Madden, Drewe, Pearce & Clutton-Brock, 2009). Thus, density is an overall measure of group cohesiveness. We used a weighted density index calculated as the sum of all observed interactions divided by the total number of possible links (Darst, Reichman, Ronhovde & Nussinov, 2013). Path length (*L*) quantifies average path length between all pairs of individuals in the group. Path length therefore indicates the network's overall connectedness (Wey et al., 2008). High *L* scores indicate that some group members only interact very indirectly with others. For instance, a high *L* score in a hyaena clan could be caused by a limited amount of interactions between immigrant males and lower ranking females and dominant hyaenas (Frank, 1986). The global clustering coefficient (*C*) of a network describes the degree to which nodes within a network tends to cluster together (Wasserman and Faust 1994). In a social context, the clustering coefficient provides an evaluation of how a group of individuals divide themselves into sub-groups. Here, we used the weighted global clustering coefficient suggested by Opsahl and Panzarasa (2009) to quantify the clustering coefficient for the social network of each hyaena clan.

We used four indices to relate the position and importance of each individual in the four social networks to its age, sex and rank. In- (*ID*) and out-degree (*OD*) quantify the number of incoming

and outgoing interactions for each node. In a social context, *ID* represents the number of interactions that an animal has directed towards it, i.e. when it was not initiating the interaction. Conversely, *OD* refers to the number of social interactions that an individual initiates (Wey et al., 2008; Madden et al., 2009). High *ID* and *OD* scores suggest that a certain individual may be driving the network structure. We used node strength as a measure of ID and OD, which is a weighted metric for the number of in- and out going links to a given node (Barrat, Barthelemy, Pastor-Satorras & Vespignani Barrat, 2004). Betweenness centrality (*BC*) quantifies the importance of an individual's position in the network. It measures the extent to which each individual lies on edges between other pairs of individuals in the network (Wey et al., 2008). *BC* therefore provides a measure of how important an animal is for social connectivity (Wey et al., 2008). We used the weighted betweenness centrality proposed by Brandes (2001) to quantify the betweenness centrality for each individual in the four hyaena clans. The local clustering coefficient (*CI*) of an individual node describes the relationship between this individual and its closest neighbours. It quantifies the probability that adjacent nodes are connected. High *CI* scores indicate that an animal has a strong likelihood of interacting with its nearest neighbours in the network (Wey et al., 2008; Madden et al., 2009). We used the weighted local clustering coefficient proposed by Barrat et al. (2009) to quantify the clustering around each specific node. For all metrics, we used the total number of observed interactions as weights.

Statistical analyses

To evaluate if the social network of each clan differed from expectations based on randomly generated networks, we created 1000 permutated matrices for each clan. In each of these permutations, we kept the network size (i.e. clan size) and both the total number of links (i.e. degree distribution) and the total number of interactions (i.e. link weights) as in the respective original matrix, but we randomly shuffled links and among pairs of group members and weights among the new links (Erdõs and Rényi, 1959, see Bejder, Flecther & Brager, 1998 for implementations in

animal social networks). We selected this null model since it provides an intuitive framework to evaluate topology against, while avoiding making unnecessarily speculative assumptions regarding link distributions. For each of these 1000 permutations we calculated both the path length and the global clustering coefficient, and compared the observed values to the expected ones based on the permutated matrices using Z score transformations. As a heuristic way of comparing the four observed networks in terms of path length and the global clustering coefficient, we calculated *D*-values as the deviations between the observed values and each of the 1000 values from the permutated matrices (Manly, 2007). We used these *D*-values as the response variable in one-way permutation based ANOVAs to evaluate the effect of clan on the deviation in observed path lengths from random expectations. We similarly used permutation based pair-wise tests to compare all the clans among each other. In these pair-wise comparisons, we adjusted the p-values for multiple comparisons using the false discovery method (Benjamini & Hochberg, 1995). We did not conduct evaluations against random expectations for density because our chosen null model made such comparisons trivial.

To evaluate if human activity and infrastructure influenced how hyaenas of different age, sex and rank classes contributed to the social networks, we combined the individual indices (i.e. in- and out-degree, betweenness centrality and clustering coefficient) with data on the sex, age and rank of each hyaena. Three hyaenas in the Kruger Gate clan shifted age class from subadult to young adult during the observation period. For each of these hyaenas, we used the age class at the median point of the observation period as the age class in the analyses. No other hyaena shifted age group and no hyaena shifted rank class during the observations. We used the corresponding index values as response variable in a permutation based factorial ANOVA. We ran one analyses for each index, and used clan, age, sex, rank and all two-way interactions between clan and the other three variables as predictors. We did not include higher-order interactions since the social structure of spotted hyaena clans do not allow for fully resolved high-order interactions among our classes of age, sex

and rank. For instance, there are per definition no immigrant females, nor are there any adult males of high or low rank.

Statistical analyses were carried out using the software environment R version 3.3.0 (http://www.r-project.org). Network quantification and randomizations were conducted using functions in the user contributed packages igraph (Csárdi & Nepusz, 2006) and tnet (Opsahl, 2009). All permutation based tests were carried out using functions in the package lmPerm (Wheeler, 2010).

Results

The Doispane clan had the highest density, Afsaal and Kruger gate clans having lower densities, and the Skukuza clan having the lowest density value (Table 1). There were significant differences among the clans in terms of the deviation from random expectations in path length ($F_{3,3996}$ = 7393, p <0.01, Figure 2), with the Doispane, Afsaal, and Skukuza having shorter path lengths than random expectations (Table 1). Similarly, there were significant differences among the clans in terms of deviations from random expectations in cluster coefficients ($F_{3,3996}$ = 2178, p <0.01), with all clans having lower clustering coefficients than random expectations (Table 1). The deviation between the observed and expected path length was lower for Skukuza than all other clans (Doispane, Z = -40.18, $p_{adj} < 0.01$; Afsaal, Z = -30.50, $p_{adj} < 0.01$; Kruger Gate, Z = -36.54) and higher for the Kruger gate clan than all the other clans (Doispane, Z = 37.60, $p_{adj} < 0.01$; Afsaal, Z = -40.87, $p_{adj} < 0.01$). The Doispane clan had higher deviation between the observed and expected path length than the Afsaal clan (Z = 33.98, $p_{adj} < 0.01$). The deviation between the observed and expected clustering coefficient was higher for Skukuza than all other clans (Doispane, Z = 29.49, $p_{adj} < 0.01$; Afsaal, Z = 35.00, $p_{adj} < 0.01$; Kruger Gate, Z = 41.48) and lower for the Kruger gate clan than all the other clans (Doispane, Z = -27.03, $p_{adj} < 0.01$; Afsaal, Z = -22.81, $p_{adj} < 0.01$). The Doispane clan had higher deviation between the observed and expected path length than the Afsaal clan (Z = 9.26, $p_{adj} < 0.01$).

There was a significant interaction effect between clan and rank for indegree ($F_{9,60}$ = 3,51, $p < 0.01$) and outdegree ($F_{9,60}$ = 2.76, $p < 0.01$) (Figure 3a-d), but not for betweenness centrality ($F_{9,60}$ = 1.63, $p = 0.12$) or the cluster coefficient ($F_{9,60}$ = 0.93, $p = 0.51$) (Figure e-h). For indegree there was also a significant interaction effect of clan and age ($F_{6,60}$ = 3.04, $p = 0.01$) (Figure 3a,b). There were no significant interaction effects of clan and age for outdegree ($F_{6,60}$ = 0.64, $p = 0.70$), betweenness centrality ($F_{6,60,}$ = 0.88, $p = 0.51$) or the clustering coefficient ($F_{6,60}$ = 0.15, $p = 0.99$). Similarly, there were no interaction effects of clan and sex for any of the individual indices (indegree $F_{3,60,}$ = 0.57, $p = 0.63$; outdegree $F_{3,60,}$ = 1.08, $p = 0.36$; betweenness centrality: $F_{3,60,}$ = 1.00, $p = 0.40$; clustering coefficient $F_{3,60,}$ = 0.11, $p = 0.96$). There was a significant effect of sex for outdegree ($F_{1,60,}$ = 5.80, $p = 0.02$), but not for the other indices (indegree $F_{1,60,} < 0.01$, $p = 0.97$; betweenness centrality: $F_{1,60,}$ = 1.08, $p = 0.30$; clustering coefficient $F_{1,60,}$ = 0.67, $p = 0.42$). There were no significant effects of age on either outdegree ($F_{2,60,}$ = 0.23, $p = 0.79$), betweenness centrality ($F_{2,60,}$ = 0.82, $p = 0.44$) or the clustering coefficient ($F_{2,60,}$ = 0.51, $p = 0.63$).

In- and outdegree scores were not higher for dominant females than the other hyaenas except for outdegree in the Kruger Gate clan (Figure 3a-d). However, dominant females in the Doispane, Kruger Gate and Skukuza clans had noticeably higher betweenness centrality than other hyaenas, whereas there were less pronounced differences in the Afsaal clan (Figure 3e). Across all four clans, there were limited variation in the clustering coefficient among sex, age and rank classes (Figure 3g,h).

Both road and anthropogenic litter density generally corresponded to the perceived level of human activity and infrastructure in the four areas. Doispane had 0.25 km of roads / km^2 and 1.34 pieces of litter / km of road, Afsaal had 0.36 km of roads / km^2 and 1.85 pieces / km, Kruger Gate 0.36 km of roads / km^2 and 5.37 pieces / km and Skukuza had 0.95 km of roads / km^2 and 9.42 pieces / km (Table 1).

Discussion

The four clans differed in their overall network properties, and all clans generally differed in cohesiveness compared to randomly generated networks. While it is expected that the interaction patterns among individuals of a highly social species will differ from random interaction structures (Wey et al., 2008), we suggest that at least parts of the differences among clans may have been influencedby the differences in human activity and associated resources. The clans that experienced the least human activity had denser social networks than the clans in areas with more activity, indicating that hyaenas in these clans were interacting with more group members. Conversely, we observed the opposite for path length and global clustering, where the clans with with access to less human infrastructure and activity had shorter path lengths and higher clustering coefficients. Combined these results demonatrate that clans living in areas of elevated human activity, may weaken the social bonds within spotted hyaena clans. Such an interpretation is supported by previous observations of chacma baboons (*Papio hamadryas ursinus*), in which periods of high food abundance have been associated with a weakening of social bonds (Henzi et al., 2009). However, we note that our results contradict previous observations on spotted hyaenas that suggest weaker social bonds when native food supply is low (Holekamp et al., 2012).

Although age and rank classes differed among clans in their role in the social networks, we observed no consistent trends in how these differences related to the human infrastructure and activity. In addition, we observed no differences among clans in the roles of males and females in the social networks. These observations suggests that while human activity seems to have influenced the overall cohesiveness of the observed clans, it did not influence the relative strength of interactions among group members of different sex, age and rank categories. Social interactions have been related to a broad array of individual characteristics, such as relatedness to interaction partner (Wiszniewski et al., 2010; Chiyo et al., 2011; Carter, Seddon, Frère, Carter & Goldizen,

2013), similarity of interaction partner in terms of age, sex and rank (i.e. homophily, McPherson, Smith-Lovin & Cook, 2001), and familiarity with interaction partner (Kurvers et al., 2013). Previous observations suggest that both kinship and age are strong determinants of interaction strength within spotted hyaena clans, and that kinship related effects on social bonds are robust against fluctuations in resource abundance (Holekamp et al., 2012). Our observations support these findings, and further highlight that the relative association patterns among group members within hyaena clans may be resilient to external perturbations.

Across the four clans, there were substantially larger effects of rank than of age or sex on individual social metrics. However, we did not find that the dominant females had more central and connected roles in the respective networks of all the groups. Furthermore, both age and sex are important factors in the spotted hyaena social structure. For instance, males show much lower levels of aggression than females (Frank, 1986), and younger hyaenas tend to have stronger social ties compared to old hyaenas (Holekamp et al., 2012). Yet, we found relatively limited consistent differences among sex and age classes in our study. While our observations agrees with those made by Holekamp et al. (2012) in that dominant females may not necessarily be the most connected individuals, we contradict their findings in that we found no consistent effects of sex or age. Instead, our data may support a strong individual variation in social connectivity. Such an interpretation would re-iterate previous suggestions of the potential importance of individual personalities or behavioural syndromes on the role of individuals in social networks (Sih et al., 2009).

Finally, we recognise some methodological shortcomings of our study. First, it is based on a very low sample size, with only four clans included in the analyses. However, many studies on social networks within animal societies rely on observations of single groups (e.g., spider monkeys *Ateles geoffroyi*: Ramos-Fernandés et al., 2009, chacma baboons: Henzi et al., 2009, spotted hyaenas: Holekamp et al., 2012). Hence, we have very limited information of variation among social groups

in the network properties even in the most well studied species. Second, seasonality plays an important role in resource availability in African savannas (Pereira, Owen-Smith & Moleón, 2013), and can influence the social networks of spotted hyaenas (Holekamp et al., 2012). However, although our data were pooled across both seasons it did not contain any bias in terms of seasonality in the observations among the four groups. Hence, we argue that any seasonal influences on social interactions likely did not strongly affect our group comparisons. Finally, we collected all our interaction data at, or close to active den sites. Social associations have been suggested to be strongly context dependent (Kurvers et al., 2013), and we can not rule out that other interaction structures may be prominent in other social or ecological contexts. However, active dens are central locations for all the clan members, and the lack of direct resource competition (that for instance may be prevalent at kill sites) may generate more neutral and representative association patterns. In addition, by only including data from one social context, we did not introduce potential biases in our observations.

To conclude, our observations suggested that the spotted hyaena clan in an area of elevated human infrastructure and activity had a less dense and less connected social network than clans with lower access to anthropogenic resources. However, we did not find consistent differences in the effects of human infrastructure and activity in the relative roles of individuals of contrasting sex, age and rank classes, supporting that the relative social associations among clan members are robust against external perturbations. Finally, our data indicated an individual variation in the role of hyaneas of different sex, age and rank classes, and we argue that further research is required to evaluate the influences of individual personalities and behavioural syndromes on the role of individuals in animal social networks. Individual personality traits have previously been recorded in hyaenas (Yoshida et al., 2016) which with further research could also be applied to network analysis

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References

Alexander R. D. (1974). The evolution of social behavior. Annual Review of Ecology and Systematics, 5, 325–383.

Altmann J. (1974). Observational study of behavior: Sampling methods. Behaviour, 49, 227–267.

Banks S. C., Piggott M. P., Stow A. J. & Taylor A. C. (2007). Sex and sociality in a disconnected world: a review of the impacts of habitat fragmentation on animal social interactions. Canadian Journal of Zoology, 85, 1065–1079.

Barrat, A., Barthelemy, M., Pastor-Satorras, R. & Vespignani, A., (2004). The architecture of complex weighted networks. Proceedings of the National Academy of Sciences, 101, 3747-3752.

Beckmann J. P. & Berger J. (2003)a. Using Black Bears to Test Ideal-Free Distribution Models Experimentally. Journal of Mammalogy, 84, 594–606.

Beckmann J. P. & Berger J. (2003)b. Rapid ecological and behavioural changes in carnivores: the responses of black bears (Ursus americanus) to altered food. Journal of Zoology, 261, 207–212.

Bejder, L., Fletcher, D. & Brager, S. (1998). A method for testing association patterns of social animals. Animal Behaviour, 56, 719–725.

Belton, L., Cameron, E.Z. & Dalerum, F. 2016. Spotted hyaena space use in relation to human infrastructure inside a protected area. PeerJ, 4, e2596.

Benjamini Y. & Hochberg Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. Journal of the Royal Statistical Society. Series B (Methodological), 57, 289–300.

Brandes U. (2001). A faster algorithm for betweenness centrality. Journal of Mathematical Sociology, 25, 163-177.

Carter, K. D., Seddon, J. M., Frère, C. H., Carter, J. K. & Goldizen, A. W. (2013). Fission-fusion dynamics in wild giraffes may be driven by kinship, spatial overlap and individual social

preferences. Animal Behaviour, 85, 385-394.

Chiyo, P. I., Archie, E. A., Hollister-Smith, J. A., Lee, P. C., Poole, J. H., Moss, C. J. & Alberts, S. C. (2011). Association patterns of African elephants in all-male groups: the role of age and genetic relatedness. Animal Behaviour, 81, 1093-1099.

Contesse, P., Hegglin, D., Gloor, S., Bontadina, F. & Deplazes, P. (2004). The diet of urban foxes (Vulpes vulpes) and the availability of anthropogenic food in the city of Zurich, Switzerland. Mammalian Biology, 69, 81–95.

Creel, S. & Macdonald, D. W. (1995). Sociality, group-size, and reproductive suppression among carnivores. Advances in the Study of Behaviour, 34, 203–257.

Csárdi G. & Nepusz T. (2006). The igraph software package for complex network research. InterJournal Complex Systems, 1695.

Darst, R. K., Reichman, D. R., Ronhovde, P. & Nussinov, Z. (2013). An edge density definition of overlapping and weighted graph communities. arXiv, 1301.3120v1.

Dalerum, F. (2007). Phylogenetic reconstruction of carnivore social organizations. Journal of Zoology, 273, 90–97.

Erdõs, P. & Rényi, A. (1959). On random graphs. Publicationes Mathematicae, 6, 290–297.

East, M. L. & Hofer, H. (2001). Male spotted hyenas (Crocuta crocuta) queue for status in social groups dominated by females. Behavioral Ecology, 12, 558–568.

East, M. L., Hofer, H. & Wickler, W. (1993). The erect “penis” is a flag of submission in a female-dominated society: greetings in Serengeti spotted hyenas. Behavioral Ecology and Sociobiology, 33, 355–370.

Euler, L. (1741). Solutio problematis ad geometriam situs pertinentis. Commentarii Academiae Scientiarum Petropolitanae, 8, 128–140.

Fedriani, J. M., Fuller, T. K. & Sauvajot, R. M. (2001). Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. Ecography, 24, 325–331.

Flint, B. F., Hawley, D. M.. & Alexander, K. A. (2016). Do not feed the wildlife: associations between garbage use, aggression, and disease in banded mongooses (Mungos mungo). Ecology and Evolution, 6, 5932-5939.

Foxcroft, L. C., Richardson, D. M. & Wilson, J. R. U. (2008). Ornamental plants as invasive aliens: problems and solutions in Kruger National Park, South Africa. Environmental Management, 41, 32–51.

Frank, L. G. (1986). Social organization of the spotted hyaena Crocuta crocuta. II. Dominance and reproduction. Animal Behaviour, 34, 1510–1527.

Frank, L. G.., Glickman, S. E., Powch, I. (1990). Sexual dimorphism in the spotted hyaena (Crocuta crocuta). Journal of Zoology, 221, 308–313.

Gittleman, J. L. (1989). Carnivore group living: Comparative trends. In: Gittleman JL ed. Carnivore Behavior, Ecology, and Evolution. Springer US, 183–207.

Henschel, J. R. & Skinner, J. D. (1990). The diet of the spotted hyaenas Crocuta crocuta in Kruger National Park. African Journal of Ecology, 28, 69–82.

Henzi, S. P., Lusseau, D., Weingrill, T., van Schaik, C. P. & Barrett L. (2009). Cyclicity in the structure of female baboon social networks. Behavioral Ecology and Sociobiology, 63, 1015–1021.

Holekamp, K. E. & Dloniak, S. M. (2010). Intraspecific variation in the behavioral ecology of a tropical carnivore, the spotted hyaena. Advances in the Study of Behavior, 42, 189–229.

Holekamp, K. E. & Smale, L. (1991). Dominance acquisition during mammalian social development: the "inheritance" of maternal rank. American Zoologist, 31, 306–317.

Holekamp, K. E., Smith, J. E., Strelioff, C. C., Van Horn, R. C. & Watts, H. E. (2012). Society, demography and genetic structure in the spotted hyena. Molecular Ecology, 21, 613–632.

Kolowski, J. M. & Holekamp, K. E. (2008). Effects of an open refuse pit on space use patterns of spotted hyenas. African Journal of Ecology, 46, 341–349.

Krause, J., Lusseau, D. & James, R. (2009) Animal social networks: an introduction. Behavioral Ecology and Sociobiology, 63, 967–973.

Kruuk, H. (1972). The spotted hyena: a study of predation and social behavior. Dissertation Thesis. University of Chicago.

Kurvers, R. H. J. M., Adamczyk, V. M. A. P., Kraus, R. H. S., Hoffman, J. I., van Wieren S. E., van der Jeugd, H. P., Amos, W., Prins, H. H. T. & Jonker, R. M.. (2013). Contrasting context dependence of familiarity and kinship in animal social networks. Animal Behaviour, 86, 993-1001.

Macdonald, D. W. (1983). The ecology of carnivore social behavior. Nature, 301, 379–384.

McPherson, M., Smith-Lovin, L. & Cook, J. M. (2001). Birds of a feather: homophily in social networks. Annual Review in Sociology, 27, 415-444.

Madden, J. R., Drewe, J. A., Pearce, G. P. & Clutton-Brock, T. H. (2009). The social network structure of a wild meerkat population: 2. Intragroup interactions. Behavioral Ecology and Sociobiology, 64, 81–95.

Marshall, H. H., Carter, A. J., Ashford, A., Rowcliffe, J. M. & Cowlishaw, G.. (2015). Social effects on foraging behavior and success depend on local environmental conditions. Ecology and Evolution, 5, 475–492.

Manly, B. F. J. (2007). Randomization, bootstrap, and Monte Carlo methods in biology. 3rd edition. London: Chapman and Hall.

Miranda, M., Parrini, F. & Dalerum, F. (2013). A categorization of recent network approaches to analyse trophic interactions. Methods in Ecology and Evolution, 4, 897-905.

Newman, M. E., Watts, D. J. & Strogatz, S. H. (2002). Random graph models of social networks. Proceedings of the National Academy of Sciences, 99, 2566–2572.

Newsome, T. M., Ballard, G. A., Dickman, C. R., Fleming, P. J. S. & van de Ven, R. (2013). Home range, activity and sociality of a top predator, the dingo: a test of the Resource Dispersion Hypothesis. Ecography, 36, 914–925.

Ogutu, J. O. & Owen-Smith, N. (2003). ENSO, rainfall and temperature influences on extreme

population declines among African savanna ungulates. Ecology Letters, 6, 412–419.

Opsahl, T.. (2009). Structure and evolution of weighted networks. University of London, Queen Mary College.

Opsahl, T. & Panzarasa, P. (2009). Clustering in weighted networks. Social Networks, 31, 155-163.

Pereira, L. M., Owen-Smith, N. & Moleón, M. (2013). Facultative predation and scavenging by mammalian carnivores: seasonal, regional and intra-guild comparisons. Mammal Review, 44, 1–12.

Prange, S., Gehrt, S. D., Wiggers, E. P. (2003). Demographic factors contributing to high raccoon densities in urban landscapes. Journal of Wildlife Management, 67, 324–333.

Ramos-Fernández, G., Boyer, D., Aureli, F. & Vick, L. G. (2009). Association networks in spider monkeys (Ateles geoffroyi). Behavioural Ecology and Sociobiology, 63, 999-1013.

Ryan, B. (2007). Effects of anthropogenic food sources on diet and parasite loads in spotted hyaena, Crocuta crocuta (Erxleben, 1777) in Kruger National Park. MSc. Thesis. South Africa: University of Pretoria.

Sih, A., Hanser, S. F. & McHugh, K. A. (2009). Social network theory: new insights and issues for behavioral ecologists. Behavioural Ecology and Sociobiology, 63, 975-988.

Venter, F. J. & Gertenbach, W. P. D. (1986). A Cursory Review of the Climate and Vegetation of the Kruger National Park. Koedoe, 29, 139-148.

Venter, F. J., Scholes, R. J. & Eckhardt, H. C. (2003). The abiotic template and its associated vegetation patterns. In: Du Toit, J. T., Rogers, K. H. & Biggs, H. C. eds. The Kruger Experience: Ecology and Management of Savanna Heterogeneity. Washington DC, USA: Island Press, 83–129.

Wey, T., Blumstein, D. T.., Shen, W. & Jordán, F. (2008). Social network analysis of animal behaviour: a promising tool for the study of sociality. Animal Behaviour, 75, 333–344.

Wheeler, R. E. (2010). lmPerm. The R project for statistical computing http://www. r-project.org/.

Wiszniewski, J., Lusseau, D. & Möller, L. M. (2010). Female bisexual kinship ties maintain social cohesion in a dolphin network. Animal Behaviour, 80, 895-904.

Woodroffe, R. (2000). Predators and people: using human densities to interpret declines of large carnivores. Animal Conservation, 3, 165–173.

Yirga, G., Leirs, H., De Iongh, H. H., Asmelash, T., Gebrehiwot, K., Deckers, J. & Bauer, H. (2015). Spotted hyena (Crocuta crocuta) concentrate around urban waste dumps across Tigray, northern Ethiopia. Wildlife Research, 42, 563.

Yoshida, K.C.S., Van Meter, P.E. & Holekamp, K.E (2016). Variation among free-living spotted hyenas in three personality traits. Behaviour, 153, 1665-1722.

Table 1. Estimated and measured levels of human infrastructure and activity four hyaena (*Crocuta crocuta*) clans in the Kruger National Park, as well as interaction density, path length and the global clustering coefficient for the social networks of these clans, including deviations from random expectations for path length and clustering coefficients.

	Human activity and infrastructure				Interaction density	Path length				Clustering coefficient			
Clan	Human activity	Infrastructure	Road density[1]	Litter density[2]	Obs	Obs	Exp	Z	P	Obs	Exp	Z	P
Doispane	Low	Low	0.25	1.34	1.11	1.68	1.78	-2.05	**0.02**	0.54	0.37	-1.32	**0.02**
Afsaal	Intermediate	Intermediate	0.36	1.85	0.39	1.87	2.09	-3.07	<**0.01**	0.41	0.25	-5.81	<**0.01**
Kruger Gate	High	Intermediate	0.36	5.37	0.39	1.95	1.93	0.82	0.21	0.36	0.23	-3.53	<**0.01**
Skukuza	High	High	0.95	9.42	0.26	2.08	2.40	-4.16	<**0.01**	0.39	0.17	-6.37	<**0.01**

[1] Km of road / km^2

[2] Number of pieces of litter / km of road

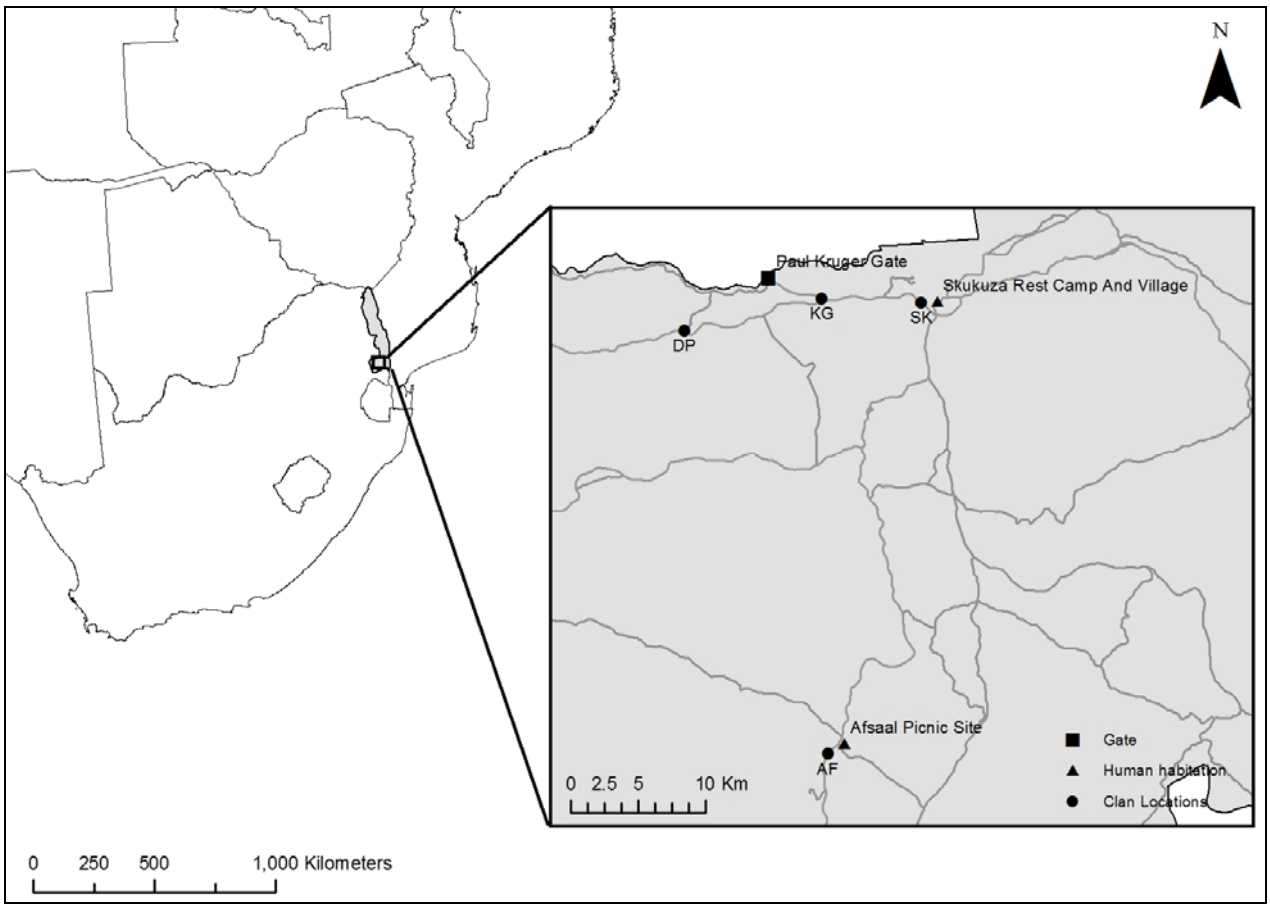

Figure 1. Location of KNP in Southern Africa and the locations of four spotted hyaena (*Crocuta crocuta*) clans living in areas with contrasting amount of human infrastructure and activity. The Doispane clan (DP) lived in an area with very limited human influence, the Afsaal (AF) and Kruger gate (KG) clans lived in areas of intermediate amounts of human infrastructure and activity, and the Skukuza (SK) clan lived close to the largest village complex within the Kruger National Park, Skukuza.

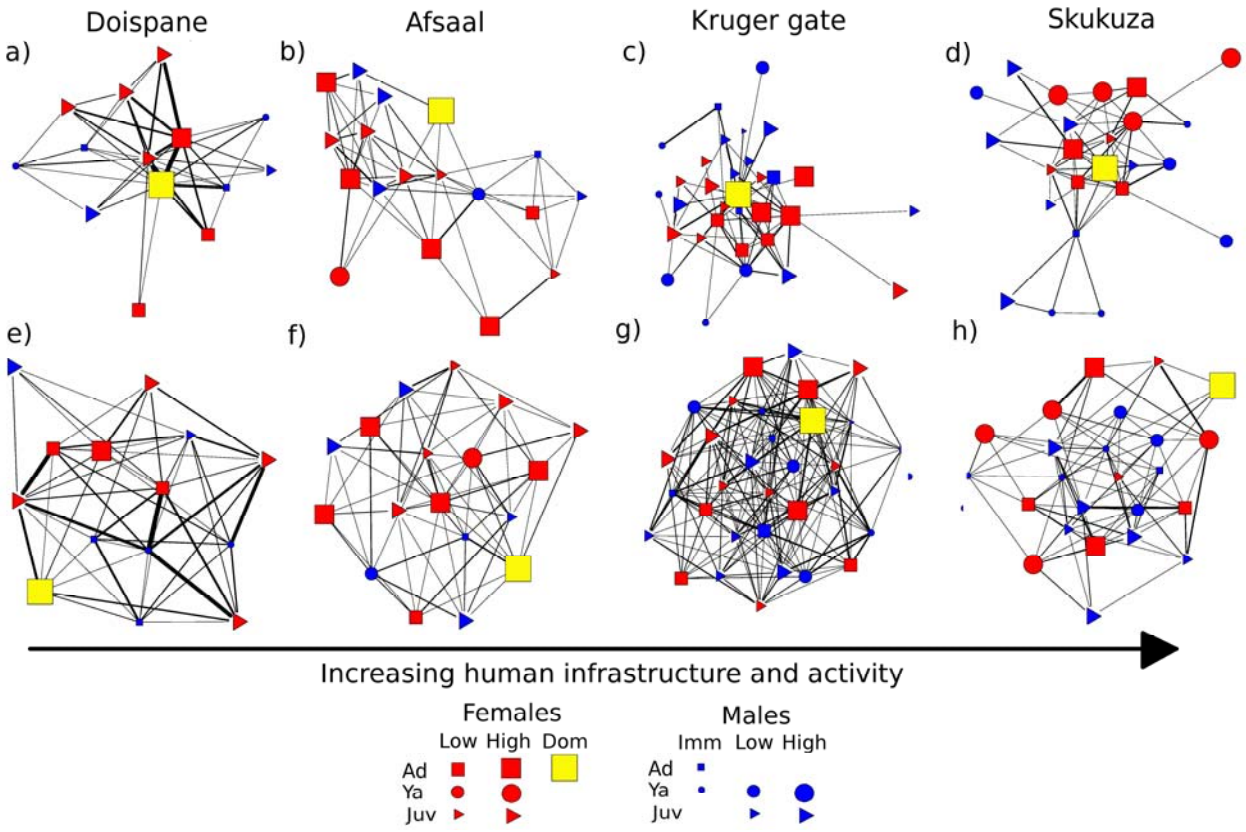

Figure 2. Observed (a-d) and random (e-h) social networks of four spotted hyaena (*Crocuta crocuta*) clans living in areas with contrasting amount of human infrastructure and activity in the Kruger National Park. The Doispane clan lived in an area with very limited human influence, the Afsaal and Kruger gate clans lived in areas of intermediate amounts of human infrastructure and activity, and the Skukuza clan lived close to the largest village complex within the Kruger National Park. Edges are weighted by the number of interactions between a given pair of individuals.

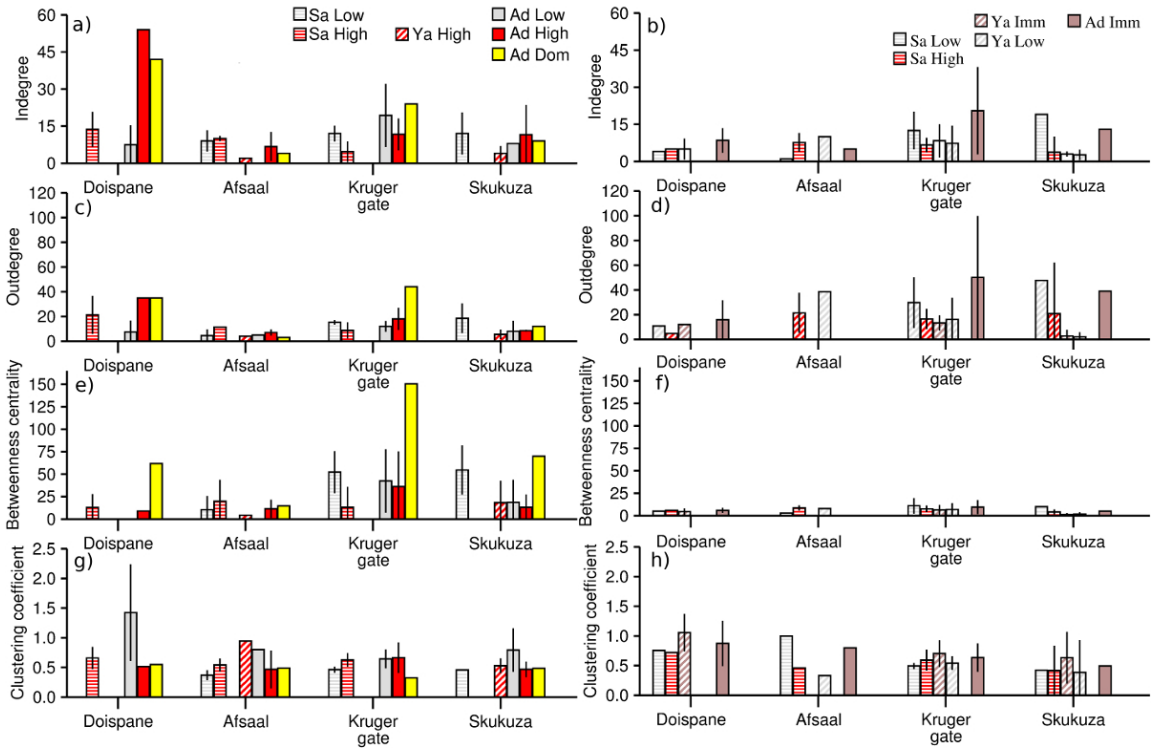

Figure 3. Average (± sd) node values of indegree (a,b), outdegree (c,d), betweenness centrality (d,e) and clustering coefficient (f,g) for female (a,c,d,f) and male (b,d,e,g) spotted hyaenas (*Crocuta crocuta*) of different age (Sa – subadult, Ya – young adult, Ad – adult) and rank (Imm – immigrant, Low, and High) classes in four clans living in areas with contrasting amount of human infrastructure and activity in the Kruger National Park. The Doispane clan lived in an area with very limited human influence, the Kruger Gate and Afsaal clans lived in areas of intermediate amounts of human infrastructure and activity, and the Skukuza clan lived close to the largest village complex within the Kruger National Park. The indices have been calculated from interaction matrices based on behavioural observations.

Chapter 6: Discussion

My observations suggest that anthropogenic resources in the southern section of the Kruger National Park are of low quality or not appropriate for spotted hyaenas, and that hyaenas use these resources opportunistically, albeit to a higher extent in the dry season. I predicted that hyaenas would make greater use of anthropogenic material during the dry season (Aragona and Setz 2001), that hyaenas with a greater need for easily accessible food would more frequently seek access to these resources (Murray et al. 2015), and that hyaneas close to access to anthropogenic resources would utilize these to a higher extent than other hyaenas (Fedriani et al. 2001). Although I observed tourists feeding small bones and scraps to spotted hyaenas at Skukuza rest camp and I observed hyaenas searching for discarded litter and scraps at Afsaal picnic site, at both sites the most frequently observed visitors were young hyaenas, some so young that they were still suckling. I suggest, therefore, that the visits to Skukuza were part of exploratory behaviour, as previously has been seen in this age group (Boydston et al. 2005). I found that anthropogenic material was more common in hyaena scats in the food-limited dry season compared to the wet season, but there was no more anthropogenic material in scats collected close to anthropogenic sites compared to further away.

Despite the suggested limited nutritional importance of anthropogenic resources for spotted hyaenas, human infrastructure and activity did seem to influence spotted hyaena space use and social interactions. The collared female hyaena with direct access to human infrastructure had a smaller home range that was used less evenly, and clans experiencing more human activity had less cohesive social networks than clans living in areas with less human activity. A negative association between human infrastructure and home ranges has also been observed in other carnivore species, for instance raccoons (Prange et al. 2004; reviewed by Šálek et al. 2015). My observations suggested that it was not access to anthropogenic resources *per se*, but rather improved hunting opportunities related to human infrastructure that influenced hyaena space use. My results

contradict previous observations on spotted hyaenas, which suggested strengthened social bonds during times of high food availability (Holekamp et al. 2012). However, similar observations to my own have been made for chacma baboons (*Papio hamadryas ursinus*), where the social bonds were strengthened during periods of low food abundance (Henzi et al. 2009). I did not observe any direct effects of human activity on the social roles of hyaenas of different age, sex and rank (e.g. McPherson et al. 2001).

Large carnivores are important ecosystem components, and most of these ecosystem effects are related to predation (reviewed in Ripple et al 2014). Since my results suggested that anthropogenic resources influenced hyaena diet and space use, I argue that human infrastructure and activity may influence spotted hyaena ecosystem function in the KNP. Such a suggestion would not be entirely novel. For instance, several species, such as coyotes (Fedriani et al. 2001) and raccoons (Prange et al. 2003), live at elevated densities in urban landscapes with the potential for increased disease transmission due to more frequent contact rates (Prange et al. 2003). Frequent avoidance of large carnivores in anthropogenic areas may allow for meso-predator release. Such processes have for instance been found in red foxes and coyotes (Crooks et al. 2010). Seasonal dietary switches to anthropogenic resources can also cause a reduction in trophic niche breadth (Lucherini and Crema 1994; Grigione et al. 2011), and the availability of anthropogenic resources may subsequently alter trophic cascades (Newsome et al. 2014). Furthermore, interspecific competition between lions and spotted hyaenas for food is common (Watts and Holekamp 2008) and lower lion densities may lead to higher rates of reproduction in spotted hyaenas (Watts and Holekamp 2008). Direct predation on hyaena cubs by lions also occurs (Mills and Hofer 1998). Whilst lions are well known for killing livestock (Kissui 2008), they also avoid human settlements (Schuette et al. 2013). Lions were however occasionally recorded in the Skukuza complex. It is possible that KNP's spotted hyaenas gained benefit from less interspecific competition in areas of heightened human activity. In addition, many prey species are known to avoid areas with high predator numbers. Such predator avoidance, coupled with artificially improved forage opportunities (e.g., an artificially watered golf course)

could have caused elevated prey densities inside of the Skukuza area (Sih 2005).

Close contact between humans and a large carnivore involves risk. Habituation has caused problems with dingoes (Burns and Howard 2003), coyotes (Timm et al. 2004) and American black bears (Breck et al. 2009). Many fatal incidents involving carnivore attacks are caused by inappropriate human behaviour (Penteriani et al. 2016), but could be reduced by minimizing incentives for animals to visit anthropogenic sites. The results in my study point to a low reward coming from utilization of anthropogenic resources for hyeanas. Therefore, it could be relatively simple to minimize human-hyaena interactions within the Kruger National Park. Removal of the occasional rewards associated with anthropogenic resources through strict enforcement of appropriate visitor behaviour could be effective. For instance, the litter densities around Skukuza were high and could easily be controlled further. In addition, since the direct benefits of visiting anthropogenic sites was low, increasing the apparent risk of visiting them may also be effective. Several mechanisms have been suggested for such deterrent effects, ranging from sensory deterrents to technologically advanced methods of real time virtual fences (Jachowski et al. 2014). We suggest that a combination of these two approaches, i.e. a stricter enforcement of visitor behaviour coupled with deterrent mechanisms around anthropogenic sites may be effective in eliminating human-hyaena conflict within the KNP.

Conclusions and suggestions for future research

My data suggests that anthropogenic resources were of limited nutritional value or difficult to access for spotted hyaenas in Kruger National Park, but that they were still utilised. The cohort most observed visiting anthropogenic resource sites did not include the hyaenas with the greatest nutritional demands, suggesting that these sites were not visited in relation to nutritional need. Furthermore, scat analysis showed no relationship between proximity to human infrastructure and anthropogenic materials in scats, although season had some influence. Anthropogenic resources

appear to have been utilised only by certain hyaenas or cohorts. However, anthropogenic activity and infrastructure were still altering spotted hyaena behaviour. Home range area and habitat use were altered around an area of human habitation, and social ties within clans were influenced by exposure to human activity and infrastructure. This discrepancy, i.e. an apparent limited value of anthropogenic resources coupled with an obvious effect of them on resource use and social behaviour is perplexing, and requires further attention. In particular, the effects of anthropogenic resources on social interactions are poorly understood. My study also highlighted the importance of individual variation on the roles of hyaenas in social networks, which is a topic that so far has recieved limited attention. Finally, I argue that we need more research evaluating potential effects of anthropogenic resources on the ecosystem roles of spotted hyaenas, and more generally on other large predators as well. For instance, further work could look at the influence of anthropogenic resources on predator-prey dynamics, to see if anthropogenically induced shifts in hyaena densities alter the behaviour and demography of prey species.

References

Aragona M, Setz EZF (2001) Diet of the maned wolf, Chrysocyon brachyurus (Mammalia: Canidae), during wet and dry seasons at Ibitipoca State Park, Brazil. J Zool 254:131–136.

Boydston EE, Kapheim KM, Van Horn RC, et al (2005) Sexually dimorphic patterns of space use throughout ontogeny in the spotted hyena (Crocuta crocuta). J Zool 267:271–281.

Breck SW, Lance N, Seher V (2009) Selective Foraging for Anthropogenic Resources by Black Bears: Minivans in Yosemite National Park. J Mammal 90:1041–1044.

Burns GL, Howard P (2003) When wildlife tourism goes wrong: a case study of stakeholder and management issues regarding Dingoes on Fraser Island, Australia. Tour Manag 24:699–712.

Creel S, Christianson D, Liley S, Winnie JA (2007) Predation Risk Affects Reproductive Physiology and Demography of Elk. Science 315:960–960.

Crooks KR, Riley SP, Gerht S, et al (2010) Community Ecology of Urban Carnivores. In: Urban Carnivores, Ecology, Conflict and Conservation. The Johns Hopkins University Press, Maryland, pp 185–198

Cypher BL (2010) Kit foxes (Vulpes macrotis). In: Urban Carnivores. Johns Hopkins University Press, USA, pp 50–60

Fedriani JM, Fuller TK, Sauvajot RM (2001) Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. Ecography 24:325–331.

Grigione MM, Burman P, Clavio S, et al (2011) Diet of Florida coyotes in a protected wildland and suburban habitat. Urban Ecosyst 14:655–663.

Henzi SP, Lusseau D, Weingrill T, et al (2009) Cyclicity in the structure of female baboon social networks. Behav Ecol Sociobiol 63:1015–1021.

Holekamp KE, Smith JE, Strelioff CC, et al (2012) Society, demography and genetic structure in the spotted hyena: Hyena society, demography and genetics. Molecular Ecology 21:613–632.

Jachowski DS, Slotow R, Millspaugh JJ (2014) Good virtual fences make good neighbors: opportunities for conservation. Anim Conserv 17:187–196.

Kissui BM (2008) Livestock predation by lions, leopards, spotted hyenas, and their vulnerability to retaliatory killing in the Maasai steppe, Tanzania. Anim Conserv 11:422–432.

Lucherini M, Crema G (1994) Seasonal variation in diet and trophic niche of the red fox in an alpine habitat. Z Für Säugetierkd 59:1–8.

McPherson M, Smith-Lovin L, Cook JM (2001) Birds of a Feather: Homophily in Social Networks. Annu Rev Sociol 27:415–444.

Mills MGL, Hofer H (1998) Hyaenas. Status survey and conservation action plan. IUCN/SSC Hyaena Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK

Murray M, Edwards MA, Abercrombie B, Clair CCS (2015) Poor health is associated with use of anthropogenic resources in an urban carnivore. Proc R Soc B 282:20150009.

Newsome TM, Ballard G-A, Fleming PJS, et al (2014) Human-resource subsidies alter the dietary preferences of a mammalian top predator. Oecologia 175:139–150.

Penteriani V, Delgado M del M, Pinchera F, et al (2016) Human behaviour can trigger large carnivore attacks in developed countries. Sci Rep.

Prange S, Gehrt SD, Wiggers EP (2003) Demographic Factors Contributing to High Raccoon Densities in Urban Landscapes. J Wildl Manag 67:324–333.

Prange S, Gerht S., Wiggers E. (2004) Influences of anthropogenic resources on raccoon (Procyon lotor) movements and spatial distribution. J Mammal 85:483.

Ripple WJ, Estes JA, Beschta RL, et al (2014) Status and Ecological Effects of the World's Largest Carnivores. Science 343:1241484.

Šálek M, Drahníková L, Tkadlec E (2015) Changes in home range sizes and population densities of carnivore species along the natural to urban habitat gradient. Mammal Rev 45:1–14.

Schuette P, Creel S, Christianson D (2013) Coexistence of African lions, livestock, and people in a landscape with variable human land use and seasonal movements. Biol Conserv 157:148–154.

Timm RM, Baker RO, Bennett JR, Coolahan CC (2004) Coyote Attacks: An Increasing Suburban Problem.

Watts HE, Holekamp KE (2008) Interspecific competition influences reproduction in spotted hyenas. J Zool 276:402–410.