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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 the presence of human infrastructure and associated human activity on the space use of two spotted hyaena clans within one of the largest protected areas in South Africa, the Kruger National Park. Home range size was smaller for a clan living in close proximity to humans, and this clan also used their home range less evenly while active than a clan without direct access to human infrastructure. They also preferred the village area during their active time but not while resting. Within the village area, the least modified areas were preferred and administration and highly modified areas avoided. While resting, however, there were no preference or avoidance of the village area, but all habitats except unmodified habitats were avoided. We suggest that human infrastructure and associated activity influenced hyaena space use, primarily through alterations in the spatial distribution of food. However, our observations suggest that these effects were indirectly caused by habitat modification that generated favourable hunting habitat, rather than a direct effect of 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.

Spotted hyaena space use in relation to human activity inside 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 the presence of human infrastructure and associated human activity on the space use of two spotted hyaena clans within one of the largest protected areas in South Africa, the Kruger National Park. Home range size was smaller for a clan living in close proximity to humans, and this clan also used their home range less evenly while active than a clan without direct access to human infrastructure. They also preferred the village area during their active time but not while resting. Within the village area, the least modified areas were preferred and administration and highly modified areas avoided. While resting, however, there were no preference or avoidance of the village area, but all habitats except unmodified habitats were avoided. We suggest that human infrastructure and associated activity influenced hyaena space use, primarily through alterations in the spatial distribution of food. However, our observations suggest that these effects were indirectly caused by habitat modification that generated favourable hunting habitat, rather than a direct effect of 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 is frequently associated with a contraction in home range and core area (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 least abundance of native food coincides 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 is scarce compared to data focusing on urban and suburban landscapes.

The spotted hyaena (*Crocuta crocuta*) is a large, nocturnal carnivore that lives in social groups (clans), which consist of related females and their offspring, and unrelated adult males (Kruuk, 1972). The range of the spotted hyaena covers much of sub-Saharan Africa, from the Kalahari desert (Mills, 1984), to a 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 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 anthropogenic resource use.

In this study we monitored the space use of two hyaena clans inside the Kruger National Park, South Africa, one inhabiting an area with high levels of permanent human activity and hence with direct access to anthropogenic resources. The other clan inhabited an area with very limited human activity and hence relied almost entirely on native resources. We predicted that (i) hyaenas living in an environment with high levels of human activity would have a smaller home range and use it less evenly that hyaenas living without direct access to anthropogenic resources, and (ii) the difference between the clans in terms of space use would be higher in the food limited dry season compared to the wet season, and (iii) hyaenas would show either a distinct avoidance or preference of areas with human infrastructure.

MATERIALS AND METHODS

Study Area

The Kruger National Park (KNP) is situated in the north eastern corner of South Africa and covers almost two million hectares. This study took place between May 2007 and December 2009 in a 5000 km^2 southern portion of the park (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*). 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 was 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 4.3km^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 skips 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. Animals 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 20km away that had limited levels of human activity and the only permanent infrastructure was a building that occasionally is used for short stays by park staff or guests.

Study animals and instrumentation

Each area (e.g., Skukuza and Doispane) was inhabited by one spotted hyaena clan. We fitted one animal 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 animals were immobilised from a vehicle by a veterinarian from South Africa National Parks'

Veterinary Wildlife Service department. Both animals were first baited with three pieces of meat, each containing 2 x 15mg midazolam tablets. A combination of 4mg medetomidine hydrochloride and 60mg zolazepam hydrochloride 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 animals 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. This collar could not be removed. The collar on the female in Doispane was fitted on the 20th November 2007 and removed July 2011. 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 active, resting or den. We classed points as active if they occurred between one hour before sunset and one hour after sunrise. Points collected outside of these hours were classified as resting. Data on sunrise and sunset times for the local area was retrieved from a weather service internet site (http://www.timeanddate.com). However, any relocation that occurred within 30m of an identified den site were labelled as den points regardless of the time of day. The location of the dens was monitored throughout the study by visiting the clan. When a den was not located within sight of a road, GPS clusters of points at dawn and dusk that were likely to correspond to a den were identified and investigated on foot. A den at a particular cluster was confirmed by the presence of a suitable burrow or hole for juvenile hyaenas with fresh spoor of adolescent and adult animals present. Other signs such as fresh bone fragments or scat were often also present. In addition to these three classes of activity, 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 (MCPs: Mohr, 1947) to estimate home range sizes for each animal. We used MCP's to characterize home range sizes because they are relatively robust to possible temporal autocorrelation among data (Swihart & Slade, 1985). MCP estimates are also repeatable across different software analysis 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. We have therefore treated these two areas as separate home ranges. Due to their highly clustered nature, we removed den site locations from all home range size estimations. 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 used two metrics to evaluate the spatial patterns of utilization within each home range. First, we quantified the utilization when animals where 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. 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. We then calculated the index H' as:

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

where N is the total number of cells in each home range and P_i is the proportion of relocations in each given cell. 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 resting locations (Clarke & Evans 1954). The nearest neighbour index (*R*) ranges form 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. For each of these data sets, we calculated the index values. We then compared the observed values to the corresponding distributions generated form the random data sets using a z-score transformation (Baddeley, Rubak & Turner 2015). As a heuristic way of comparing the spatial distribution of active and resting 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 clan and each of the Doispane home ranges using tw-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 urbanized village area in Skukuza at two separate scales. First, we outlined the whole human-modified area (village area) using satellite images retrieved from Google Earth (www.google.com/earth/), supplemented with GPS data collected in the field. We quantified both the number of active and 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, administration areas, intermediately modified areas, and unmodified areas (Table 1). 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 or not areas were preferred or avoided while being active or resting. Following Manly et al. (1993), we calculated the selection indices β_i as

$$B_i = \frac{w_i}{\sum_{\iota=1}^{H} w_i}$$

were w_i is the selection ratios for each land use class (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 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 clans, with the Skukuza clan having a smaller home range than the Doispane clan both annually as well as within each season (Table 2). The home ranges were not utilized evenly, and all home ranges had more uneven distributions of active points and more clustered patterns of resting locations than expected by random expectations (Table 3). The Skukuza clan had a different spatial distribution of their active and resting locations compared to the Doispane home ranges, 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 clan utilized its home range more evenly that the utilization in Doispae b on an annual basis, it utilized its home range less evenly that the use of both Doispane ranges within each season (Table 3). Simlarly, the distribution of resting locations differed between the Skukuza clan and both Doispane home ranges (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 Doispane b during the wet season ($Z < 0.01$, $p = 0.998$). The resting points in the Skukuza range was more clustered than both Doispane home ranges for both seasons combined as well as for the dry season, but was only more clustered than one of the two Doispane home ranges during the wet season (Table 3).

For the Skukuza clan, more active locations were found inside the village area than what could be expected based on its proportion within the home range (Table 4), 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 4). During resting hours, 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 $\chi^2 = 0.48$, df = 1, $p = 0.488$). Within the village area, however, resting locations were not found based on the proportion of different land use types (both seasons combined $\chi^2 = 17.9$, df = 3, $p < 0.001$; dry season $\chi^2 = 7.27$, df = 3, $p < 0.063$; wet season $\chi^2 = 8.88$, df = 3, $p = 0.031$), with the unmodified habitat generally being preferred (Table 4).

DISCUSSION

Annual and seasonal home range sizes for the Skukuza clan were consistently smaller than both of the Doispane clan's home ranges. These observations agree with previous studies and highlight that access to an anthropogenic area can often reduce carnivore home range sizes (Šálek, Drahníková & Tkadlec, 2015). In addition, the Skukuza clan utilized its home range less evenly than the Doispane clan, which emphasize that human infrastructure and associated activity not only influenced the total home range sizes, but also how hyaenas used space within these areas. We suggest that human infrastructure and activity influenced spotted hyaena space use by altering resource distributions, primarily caused by the availability of anthropogenic resource. Increased availability of resources may reduce the need for a maintaining large home ranges, 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).

Space use was aggregated for both active and resting locations, which agrees with previous observations of spotted hyaenas (Henschel, 1986; Boydston et al., 2003). However, for both seasons the Skuzuza clan used its home range less evenly than the Doispane one. Variation in space use often depends on resource distributions, with patchy resource distributions often leading to uneven space use (Macdonald, 1983; Gilchrist & Otali, 2002). We suggest that the less even space use exhibited by the Skukuza clan was influenced by more spatially concentrated food resources associated with the village area. Although the resting points similarly were more clustered than random expectations, the resting locations in Skukuza were only more clustered than one of the Doispane home ranges, but not the other. This further supports an interpretation where food resources has influenced spotted hyaena space use, since food resource distribution should have little influence on the locations where hyaenas spend their resting hours (Kruuk, 1972).

In agreement with other studies (Quinn & Whisson, 2005; e.g. Bozek, Prange & Gehrt, 2007), the Skukuza clan showed a preference for the village area when active. Within the village areas, hyaenas preferred intermediately modified habitat the most, followed by unmodified habitat. Administrative and high impact areas were both avoided when active. 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 for resting locations, and within the village area all other habitat classes but the undisturbed habitat were avoided. We 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 easy hunting grounds caused by artificially created open areas. Our interpretation that resource distribution may have driven the habitat associations during active hours is further supported by the lack of habitat preferences for any but the unmodified habitat during resting hours, since areas of 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).

To conclude, although this study was only based on observations on 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 associated activity influenced hyaena space use, that these influences at least to some extent may have been related to resource supply, but only indirectly by generating easy hunting areas. We highlight that further work is needed to explore how humans influence large carnivores and associated ecosystem processes within protected areas.

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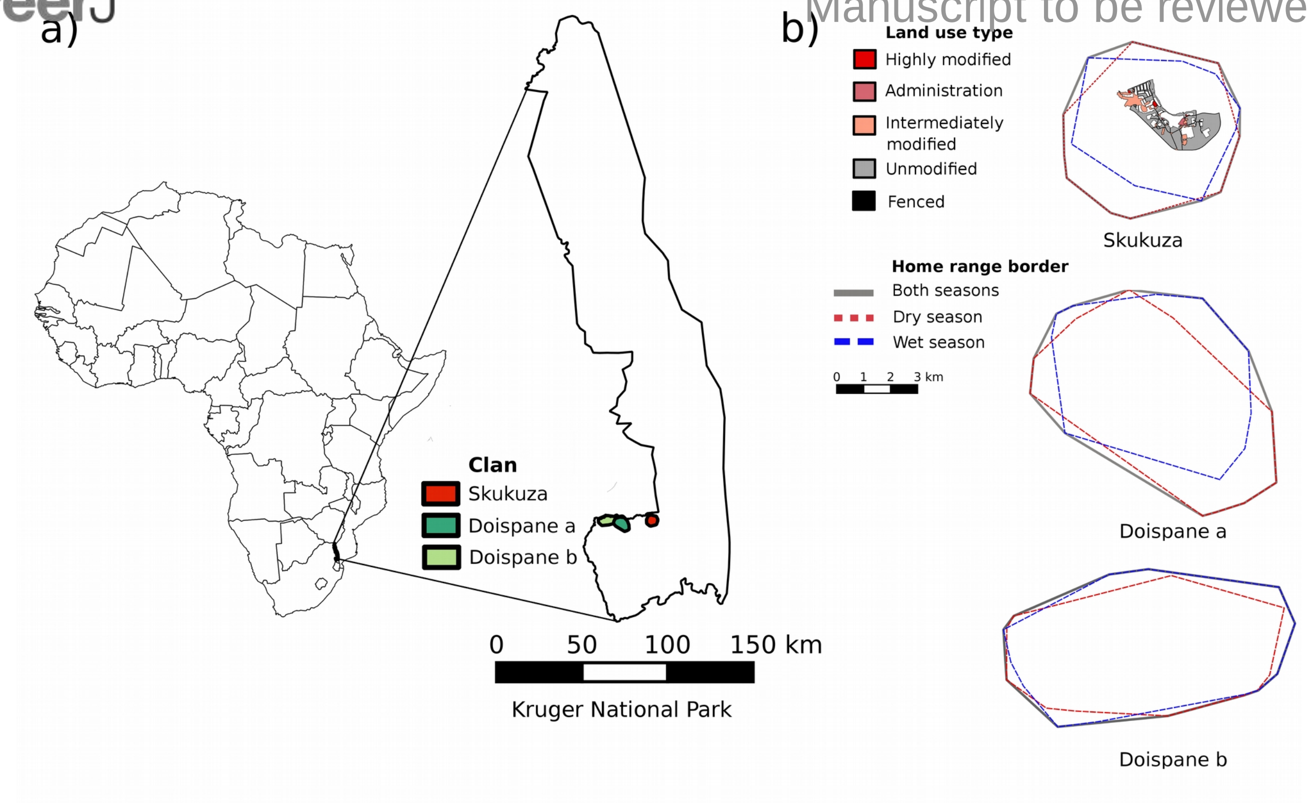

Locations of the three home ranges within the Kruger National Park as well as the annual and seasonal borders for these home ranges. The Skukuza clan had access to a village area with four unfenced land use types, highly modified, administration, intermediately modified and unmodified areas.

Table 1: Description of four unfenced land use types within the village area in Skukuza.

Habitat Type	Description
Highly modified	Unfenced area with high levels of human use that are unfenced
Administration	Unfenced areas containing business buildings and their surrounding car parks with no fences
Intermediately modified	Areas that have been altered from their natural state but are without buildings or facilities, e.g. golf course and a cricket pitch
Unmodified	Unaltered habitat inside the village boundary

Table 2: Sizes (km^2) of seasonal and annual 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	20.7
Low human activity (a)	53.1	44.4	39.7
Low human activity (b)	47.9	41.0	45.6

Table 3. Spatial distributions of spotted hyaena active and resting 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 form 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.

		Active				**Resting**			
Clan	**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 4. Spotted hyaena utilization of a village area and of different land 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 type refer to the percent of locations within the village area. Beta coefficients describes relative selection for the different land types within the village area, scaled so that values < 0 indicates that types are used less than availability (i.e. avoided) and values > 0 indicates that they are used more than availability (preferred).

	Active						**Resting**					
	Annual		**Dry season**		**Wet season**		**Annual**		**Dry season**		**Wet season**	
Landtype	***% 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