Heterogeneity in the density of spotted hyaenas in Hluhluwe-iMfolozi Park, South Africa

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Animal population sizes and trends, as well as their distributions, are essential information to the understanding and conservation of ecosystems. During this study in Hluhluwe-iMfolozi Park, South Africa, a spotted hyaena *Crocuta crocuta* Erxleben, 1777 (Hyaenidae) population was surveyed by attracting individuals with pre-recorded sounds. The hyaena population (excluding cubs) is substantially larger (321 individuals) than the previous estimate of 200 and this population is the second largest protected population in South Africa. Average hyaena density, at 0.357 individuals/km^2, was relatively high compared to other southern African conservation areas, and range from 0 to 1.25 individuals/km^2 across sampling stations. For short periods, spatial heterogeneity in density was marked at small and large spatial scales, but decreased when averaged over a longer period. This heterogeneity may be important in promoting the coexistence of other large and mobile carnivores in Hluhluwe-iMfolozi Park by creating potential dynamic competition refugia in space and time. Furthermore, heterogeneity of hyaena density at smaller scales should influence studies investigating the avoidance of hyaenas by competitively inferior carnivores.

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Introduction

Animal population sizes and trends, as well as their distributions, are essential information to the understanding and conservation of ecosystems. This is particularly relevant to carnivores which generally occur at low densities, but which may impact on the coexistence of other carnivores (Palomares and Caro 1999), the population dynamics of their prey (Messier 1994, White and Garrott 2005), and even species at lower trophic levels (Ripple *et al.* 2001, Terborgh *et al.*, 2001, Ripple and Beschta 2004, Beschta 2005, Croll *et al.* 2005).

Spotted hyaenas *Crocuta crocuta* Erxleben, 1777 (Hyaenidae) are large African carnivores, and are generally the most numerous within the African large carnivore guild. Previous studies from various ecosystems have shown spotted hyaenas as important interference competitors and/or predators of sympatric large carnivores such as cheetahs *Acinonyx jubatus* (Bertram 1979, Laurenson 1994, 1995, Durant 1998, 2000a, b), lions *Panthera leo* (Cooper 1991), brown hyaenas *Hyaena brunnea* (Mills 1990), and African wild dogs *Lycaon pictus* [Estes and Goddard 1967, Kruuk and Turner 1967, Fanshawe and FitzGibbon 1993, Carbone *et al.* 2005; but see Hayward and Kerley (2008)]. For example, it has been argued that such an interference relationship is partly responsible for the negative correlation between spotted hyaena and wild dog densities across several African ecosystems (Creel and Creel 1996, 2002). According to the 2004 IUCN Red List of Threatened Species all of the abovementioned carnivore species are classified as either "endangered", "vulnerable", or "near threatened". Consequently, the combination of the ecological role of hyaenas within the African large carnivore guild, as well as its own conservation status and that of the other guild members (excluding leopard *Panthera pardus*), poses a multifaceted challenge to the management of large carnivore diversity within protected areas.

An example of one such protected area is Hluhluwe-iMfolozi Park (HiP), in KwaZulu-Natal Province, South Africa. Reintroductions of locally extinct large carnivores including wild dog, cheetah and brown hyaena have been undertaken in HiP, of which only the former two have resulted in remaining, small populations (Whateley and Brooks 1985, Rowe-Rowe 1992, Maddock 1999, Gusset *et al.* 2006, Somers *et al.* 2008). The population and feeding ecology of spotted hyaenas (hereafter referred to as "hyaenas") in HiP was studied in the late 1970s, but there have been no investigations into the potential interference interactions amongst hyaenas and the abovementioned carnivores. For carnivore species locked into such interactions, spatial and temporal heterogeneity may be an important factor for their continued co-existence via

the creation of dynamic refugia (Durant 1998, Saleni *et al.* 2007). Durant (1998) further argued that the distribution of a species averaged over long periods might exhibit very little spatial heterogeneity, but at any given moment may show significant heterogeneity in distribution, with areas of low density or utilization correlating to such refugia. In light of the small size of the reintroduced and threatened large carnivore populations (principally wild dogs) in HiP, we investigated whether any short term spatial and temporal variation of spotted hyaena density existed, in order to determine the presence (or absence) of any short term dynamic interference from hyaenas in HiP. This density mapping was done by combining a well-established density estimation method, the audio playback, with GIS interpolation techniques.

The first objective of this study was to provide an updated estimate of total population size of hyaenas for HiP. The second objective was to determine the mean hyaena density across HiP and the magnitude of heterogeneity in hyaena density. The third objective was to produce a map of hyaena density across the surface of the park for the relevant sampling periods. The results are discussed with regards to previous studies using the same census technique, earlier hyaena population estimates for HiP, potential mechanism creating heterogeneity in hyaena density, the co-existence of hyaenas with other large carnivores, and the relevance of scale when evaluating potentially competitive, interspecific spatial relationships involving hyaenas. Finally we consider aspects of the hyaena's existence in and around HiP, and it's bearing on the conservation status of this species in South Africa.

Study area

This survey was conducted in HiP (previously Hluhluwe-Umfolozi Park) (28°00'–28°26'S, 31°41'–32°09'E), KwaZulu-Natal Province, South Africa. HiP covers an area of approximately 900 km², with altitudes ranging from 40–590 m a.s.l. Fencing of the reserve was started in the 1940's and completed during the late 1970's. Although the reserve is fenced, the fence is not 100% secure and large carnivores, including lions and wild dogs regularly leave (Ezemvelo KZN Wildlife, unpubl.) and the fence is not considered a

barrier to dispersing individuals. The landscape is broken by numerous valleys and hills, especially in the north-eastern part of the park. HiP is completely surrounded by community owned, subsistence agricultural land with high human and livestock densities (Infield 1988). Human attitudes around HiP are often negative towards large carnivores (Gusset *et al.* 2008).

HiP comprises a diverse range of habitats and lies within the Zululand thornveld subcategory of coastal tropical forest types and the lowveld subcategory of tropical bush and savannah types (Acocks 1988). Most species of the African large carnivore guild, including wild dogs, cheetahs, lions, and leopards *Panthera pardus* are present. A wide range of ungulate species with mostly sedentary or non-migratory habits is present (Bourquin *et al.* 1971, Brooks and Macdonald 1983).

Material and methods

Response distance and probability

To census the hyaena population in HiP we used the broadcasting of pre-recorded sounds (ie "playbacks", "call-ups", or "call-ins") since it is an inexpensive and rapid technique and has been extensively used for this species in various conservation areas across Africa (Kruuk 1972, Whateley and Brooks 1978, Whateley 1981, Mills 1985, Sillero-Zubiri and Gottelli 1992, Creel and Creel 1996, 2002, Ogutu and Dublin 1998, Mills *et al.* 2001, Maddox 2003, Salnicki 2004, Ogutu *et al.* 2005). Independent trials were conducted to determine the maximum response distance and the response probability in order to calibrate the observed results with these parameters, which then allows the calculation of the hyaena density and population size (Ogutu and Dublin 1998, Mills *et al.* 2001, Ogutu *et al.* 2005).

Locating stationary hyaenas in HiP in order to conduct these response trials proved to be problematic for several reasons. Although hyaenas were seen regularly, these animals were mostly moving, and searching for hyaenas was restricted to the tourist road and management track network. This was further complicated by limited visibility away from roads and tracks due to the dense vegetation of HiP. In order to circumvent this problem, hyaenas were called to a station by playback where identification footage was taken by video of as many as possible of the responding hyaenas. Following this, a subsequent playback was done at a set distance away. This method was conducted at six different distances across a range of locations spread over HiP (Table 1). In this regard, a positive response was defined as when any of the previously identified animals arrived within view of the second playback location. From the response distance, a circular census area around each playback station was calculated. The response probability was determined by the ratio of responding identified hyaenas to total indentified hyaenas within the response distance. Response distance testing was also conducted following the Mills *et al.* (2001) method on a single radio-collared adult female hyaena (with her two *ca*. 11 month old cubs) after she was located by radio telemetry.

Table 1. The number of adult and sub-adult hyaenas of which identification footage was taken at the first playback station and the number of these individuals subsequently responding at a second station for various distances between playback stations during response calibration testing in HiP. * – represents radio-collared adult female.

Distance between stations (km)	Identified hyaenas	Responding hyaenas
2.2	1	0
2.5	1*	0
2.8	3	3
2.9	2	0
3.4	2	0
4.3	5	0
4.4	3	0

Playbacks

Playback procedures in the field mainly followed Mills *et al.* (2001) and Creel and Creel (2002). Playbacks were conducted between the hours of 18:00 (starting range 18:00–18:43h) and 02:00 (finishing range 22:00–01:54h), depending on the number of playback stations (hereafter referred to as "stations") visited per night. Response calibration trials indicated a response distance of 2.8 km. Thus adjacent stations were located at least 5.6 km apart, although the majority were substantially further apart. Given this minimum distance of 5.6 km between stations, positions for stations were located on roads and management tracks from a GIS road map of HiP. To obtain maximum visibility as open an area as possible was selected for each station, and these were either on or within 50 m of a road or management track. A median of four stations (range 3–5) were visited per night, each night covering a different and non-overlapping area, and driving between stations taking on average 26 min (range 15–40 min; excluding a single non-standard event of 62 min).

Upon arrival at a station, an audiotape containing sounds known to attract hyaenas, was played through a mobile 12 V amplifier and cassette tape player attached to two, 12 Ω, horn speakers. This tape included recordings of whooping hyaenas, hyaenas fighting over a kill, an inter-clan fight between hyaenas and hyaenas mobbing lions. The speakers were mounted on the roof of a small truck and faced in opposite directions. The tape was played for 6 min, with the speakers turned 90° after three min, followed by 5 min of silence. This playing procedure was repeated three times at each station. The tape was played a fourth time if hyaenas were heard in the vicinity of the station but did not come into view.

Two observers with spotlights, stood on the open back of the truck, and scanned the vicinity occasionally. A third observer recorded identification footage of hyaenas with a digital video camera. A fourth person recorded all data, and if

present a fifth observer equipped with a pair of 10×42 binoculars recorded detailed observations. A fixed core of two observers was present at all playbacks conducted, in order to reduce observer bias. So as to prevent double counting at stations, all hyaenas that appeared were carefully observed (spot patterns, or other individually characteristic features were noted where possible). The data recorded included the number of hyaenas, age class, and geographical coordinates of the station. The three age classes used, cub (< 12 months), sub-adult ($12–24$ months) and adult (> 24 months) were estimated from body size.

Two series were conducted, the first comprising 5 nights on 13, 14, 15, 21 and 22 October 2003, and the second 6 nights on 27, 30 and 31 August and 13, 14 and 15 September 2004. As recommended by Mills *et al.* (2001), the effects of habituation on response were minimized through the lapse of 10 months between the two series. The numbers of stations visited during the two series were 20 and 24 respectively. The second series included a re-sampling of 19 stations of the first series. An additional five stations were added during the 2004 series to sample the south-western area of HiP (Fig. 1). The 2003 and 2004 series respectively covered 46.3% and 53.3% of the total area of the park.

Data analysis

All spatial exercises and calculations were conducted in the program ArcMap 8.3 (ESRI 2003). Data layers of the
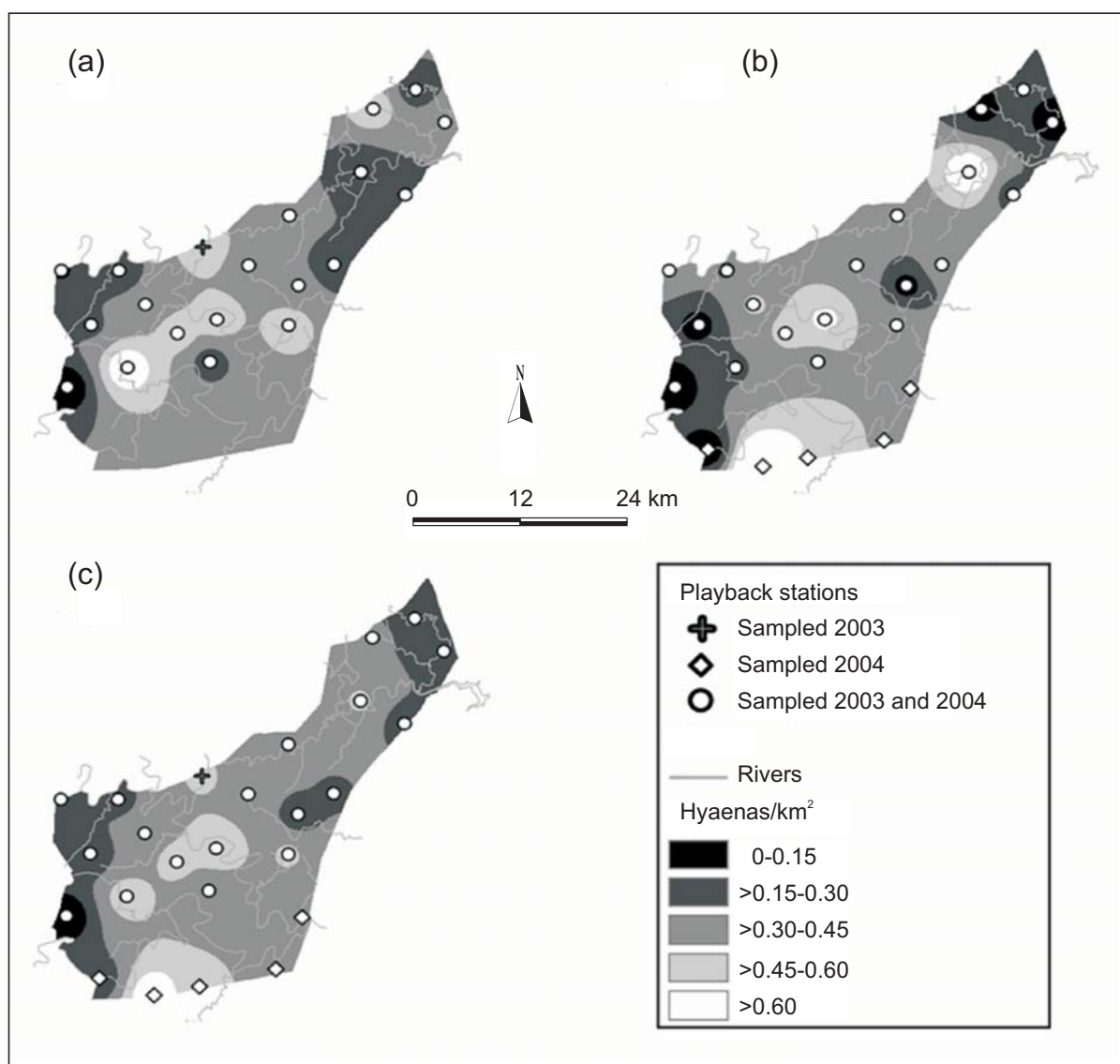

Fig. 1. Density (hyaenas/km^2) distribution maps of hyaenas in HiP illustrating spatial heterogeneity in hyaena density across the park for (a) 2003, (b) 2004, and (c) average of 2003 and 2004.

station locations and the HiP boundary were created. Another data layer containing circular response areas with radius equal to the response distance (2.8 km) for each playback station was created. As some stations had response areas overlapping with the HiP boundary these external areas were removed to yield adjusted response areas. A single station with response area overlapping the boundary was excluded from this procedure for the following reasons: approximately two-thirds of this station's response area lay outside the park boundary, and during both series hyaenas with snares were recorded at this station indicating that these hyaenas probably had been foraging outside the park, as snaring inside the park is effectively absent. This behaviour was only apparent in the clan adjacent to this single area.

The sizes of all the response areas (adjusted and unchanged) were calculated in km^2. Assuming equivalent response probability across stations the numbers of observed hyaenas at each station were adjusted with the response probability (in our instance 0.6) to derive expected numbers for each station (Ogutu and Dublin 1998, Mills *et al.* 2001). Hyaena densities (individuals/km^2) were then calculated for each station by dividing the expected number of hyaenas by the size of the adjusted or unchanged response area. Means and confidence intervals for the expected number and density of hyaenas per station for the 2003 and 2004 series were calculated following Ogutu *et al.* (2005) using the non-parametric bootstrap method based on 10000 replications with replacement in the program R 2.5.0 (R Development Core Team 2007). Population size (adults and sub-adults) was estimated by multiplying density estimates (mean, plus lower and upper 95% bootstrap confidence limits) with the surface size of HiP. The percentage of cubs responding to playbacks was very small, as also noted by Mills *et al.* (2001), and this was not incorporated into density and population size estimates. All statistical analysis other than bootstrapping was performed in STATISTICA 6.1 (Statsoft 2003).

Spatial interpolation through the inverse distance weighted method was performed on the individual station densities in order to produce a continuous hyaena density map of HiP for the periods covered by both series. For this procedure power was set at 2, search radius type as variable, number of points set at $n-1$ (n – number of stations), and output cell size at 100 m. A composite density distribution map was calculated representing the average of the two maps for the 2003 and 2004 series. All layers were projected with UTM 36S and WGS84 map datum.

Results

Response distance and probability

We tested seven different response distances for 17 identified hyaenas of which only one test produced a positive response (Table 1). No hyaenas responded beyond a distance of 2.8 km. The absence of hyaena response above 2.8 km between testing stations underscored our confidence that the re-sampling of individuals (at least within one night's playbacks) was highly unlikely during the actual survey. The ratio of responding hyaenas to total hyaenas for the three trials within the response distance of 2.8 km yielded a response probability of 0.60.

Hyaena numbers, density and distribution

Hyaenas were seen at 19 of 20 (95.0%) and 22 of 24 (91.7%) stations for the 2003 and 2004 series respectively. Both sexes and all age classes were recorded, but only 2.7% of the total number of aged individuals were judged to be < 12 months old. Four hyaenas with wire or cable snares around their neck or head were recorded at three stations during the two series. Lions were recorded at five of 44 stations, with spotted hyaenas being present on four (80%) of these occasions. There was no evidence that lion presence influenced spotted hyaena response (Fischer exact test: $p = 0.31$).

Observed numbers of hyaenas per station ranged from 0–12 individuals for both series. There was no significant difference between the number of observed hyaenas responding per station for 2003 and 2004 ($F = 0.02$, $p = 0.88$), and thus these estimates were combined to give a

Table 2. The total number of hyenas responding (n), estimates of the mean and the associated 95% bootstrap confidence limits (lower, upper) for, the expected number of individuals within the response range of a station, the population density (numbers/km^2), and population size (number) for the 2003 and 2004 playback series in HiP.

Year	Playback stations	Area (km^2)	n	Expected number			Density			Size		
				Mean	Lower	Upper	Mean	Lower	Upper	Mean	Lower	Upper
2003	20	417.3	92	7.670	5.750	9.830	0.350	0.268	0.438	315.0	241.2	394.2
2004	24	480.4	107	7.421	5.347	9.583	0.363	0.259	0.481	326.7	233.1	432.9

mean density of 0.357 hyaenas/km^2 (lower: 0.259 and upper: 0.481, range = 0.0 − 1.25) and a mean adult and sub-adult population estimate of 321 hyaenas (lower: 233, upper: 433) (Table 2). Spatial interpolation of the station densities for 2003 and 2004 series produced a map of hyaena density across the park for the two play-back periods (Fig 1a, b). Average hyaena density across HiP can bee seen in Fig 1c.

Discussion

Previous hyaena playback studies across several African ecosystems have found a range of response distances including 2.5 km in Serengeti National Park (Maddox 2003), 3.0 km in Ngorongoro Crater and Lower Zambezi National Park (Kruuk 1972, Leigh 2005), 3.2 km in Kruger National Park (Mills *et al.* 2001), 3.7 km in Selous Game Reserve (Creel and Creel 1996, 2002), and 4 km in Masai Mara National Reserve (Ogutu *et al.* 2005). Some of the above studies also quantified response probability, and results of 0.61 (Mills *et al.* 2001), 0.88 (Maddox 2003), and 0.583 were determined (Ogutu *et al.* 2005). Our response parameters (distance and probability) are well within the range found in the above ecosystems, and although they were based on a small sample size, we believe that these response parameters represent realistic estimates. The statistical similarity between the two series in our survey in the number of hyaenas responding per station would indicate the precision of this survey technique. We suggest that surveys within HiP are continued at regular intervals (every 3–4 years) to monitor population trends.

The first detailed population study on hyaenas in HiP from 1975 to 1981, where playbacks were combined with the Lincoln Index, indicated densities of 0.46 and 0.36 hyaenas/km^2 (adult and sub-adult) for the respective study areas in Hluhluwe and iMfolozi (Whateley and Brooks 1978, Whateley 1981). In Hluhluwe the total study area, from which the density was derived, included the minimum territory sizes of the three study clans plus peripheral areas between these territories and the HiP and study area boundary. Subsequently a forested area representing one quarter of the total study area was subtracted as it was thought to be "little-used", although two of the study clan territories included tracts of forest (Whateley and Brooks 1978). In iMfolozi, the minimum territory size of the single study clan was used without the addition of peripheral areas (Whateley 1981). Potentially both, but most probably the Hluhluwe calculation, resulted in the overestimation of hyaena densities with later extrapolations across HiP resulting in the probable overestimation of total population size (350 adults and sub-adults) (Whateley and Brooks 1985).

Post-hoc adjustment on the original Hluhluwe density to include the forested area results in a density of 0.35 individuals/km^2. This adjusted estimate as well as the original estimate for iMfolozi is very similar to the estimates of our survey. This may indicate that the population as a whole has remained fairly constant over this period. However, this interpretation should be treated with caution, as preliminary results indicate that hyaena clan size obtained through individual identification has significantly increased in the same area studied by Whateley and Brooks (1978) in Hluhluwe, with the best estimate of the number of clans at present being 16–20 (J. A. Graf, L. Turelli and M. Szykman, unpubl., 2004).

Relative to other surveyed southern African conservation areas, the average hyaena density in HiP is high, but intermediate if compared to East African areas (see Table 3). Comparing densities on an Africa-wide scale reveals variation of over three orders of magnitude (Table 3). This variability is extended on a smaller scale within an ecosystem such as the Kruger National Park, South Africa, where substantial spatial heterogeneity in density has been recorded across different habitats (Mills *et al.* 2001). Moreover, large temporal changes in hyaena density across seasons have been illustrated for the highly dynamic Serengeti ecosystem of Tanzania as a result of large scale ungulate migration and the resultant commuting system of hyaena (Kruuk 1972, Hofer and East 1993). Significant fluctuations in hyaena density have also been found at longer time scales as docu-

Table 3. Densities of hyaenas in various East and southern African conservation areas.

Region of Africa	Conservation area	Hyaenas/km^2	Source
East Africa	Selous	0.32	Creel and Creel (1996)
	Maasai-Mara	0.404	Ogutu *et al.* (2005)
	Serengeti (source)	0.6	Hofer and East (1995)
	Aberdare	1.3	Sillero-Zubiri and Gottelli (1992)
	Ngorongoro	1.33	Höner *et al.* (2005)
southern Africa	Southern Kalahari	0.008	Mills (1990)
	Etosha	0.05	Gasaway *et al.* (1991)
	Hwange	0.07–0.18	Bowler (1991) in Hofer and Mills (1998), Salnicki (2004)
	Kruger	0.03–0.2	Mills *et al.* (2001)
	Timbavati	< 0.4	Bearder (1977)
	Savuti	< 0.4	Cooper (1989)
	iMfolozi (western)	0.36	Whateley (1981)
	Hluhluwe (north eastern)	0.46	Whateley and Brooks (1978)

mented in the Ngorongoro Crater, Tanzania (Höner *et al.* 2005), as driven by the abundance of key prey species (Höner *et al.* 2005, Hayward *et al.* 2007).

Spatially modelling hyaena density across HiP (Figs 1a, b) indicated that, if measured at small time scales (ie within one night, or the length of each series), hyaena density may be very variable even at relatively small spatial scales (ie between the response areas of two stations). Spatial heterogeneity in density was still maintained if the density maps were averaged over time (ie integrating 2003 and 2004), although the magnitude of density gradients across space appeared to decrease. This homogenisation appeared to be stronger at the smaller (between stations) than at the larger (park wide) scale. If more surveys from consecutive time periods were integrated, this would probably result in a more homogenous spatial distribution of hyaena density, ie density would become more homogenous with increasing temporal scale (Durant 1998). Our data thus expands on the abovementioned spatial and temporal variation in hyaena density at larger scales and demonstrates that hyaena density may be highly variable at small spatial and temporal scales if measured over short periods.

The mechanisms driving this small scale variation in hyaena density in our study site are probably linked to various factors including prey distribution, communal den-site location, vegetation structure and the fission-fusion social system of this species. Within ecosystems with large resident herbivore populations similar to HiP, hyaena distribution has been correlated with small scale variations in prey density even within relatively small clan territories (Boydston *et al.* 2003b, Höner *et al.* 2005, Kolowski and Holekamp 2009). Cromsigt (2006) indicated for the same annual period (August–October) as our survey, significant spatial heterogeneity in the densities of four of the main prey species of hyaena in HiP at an even smaller scale (2.5 × 2.5 km grid) than our survey. This may partly explain the short term spatial variation in hyaena density found during our survey, however this still needs to be investigated.

Communal den-site location may be another factor driving small scale variation in hyaena density. Adult female hyaenas with cubs need to regularly return to the communal den to feed their cubs until these leave the den between 8 and 12 months of age (Kruuk 1972, Boydston *et al.* 2003a). Other clan members also congregate at the communal den which forms the centre of social activity within a clan (Kruuk 1972, Mills 1990). Several authors have hypothesized that these behavioural patterns should influence the spatial distribution of hyaenas within their ter-

ritory, and have shown that the space-use of all hyaena clan members are clumped around these communal den-sites (Boydston 2003a, Kolowski 2007). Communal den-sites are often re-situated within a clan's territory (Kruuk 1972, Mills 1990, Boydston *et al*. 2006) and this could lead to dynamics in hyaena density distribution correlated to the time-scale of these den moves. Interacting with the above two factors, the fission-fusion social system of hyaenas leads to substantial intra-clan group size variation across time and space (Smith *et al*. 2008), and may contribute to density variation across these dimensions within clan territories.

The importance of spatial and temporal heterogeneity in the co-existence of competing species is a well-established concept within community ecology (Polis *et al.* 1989, Holt and Polis 1997, Mills and Funston 2003, Owen-Smith 2004), and as such the temporal and spatial heterogeneity in hyaena density demonstrated in this study may promote the co-existence of other large carnivores with hyaenas in HiP via the creation of dynamic interference competition refugia. Several medium-sized low-density areas were evident for both series in our study and these could function as such refugia. Competitively inferior large carnivores with high mobility, such as wild dogs, may be able to exploit these dynamic refugia as they shift over time, as already demonstrated for cheetah (Durant 1998). Furthermore, this heterogeneity in density at small spatial and temporal scales also has implications for research into the avoidance of hyaenas by competitively-inferior carnivores. Interpretation of our results suggests that measuring and testing for such interactions at several scales (especially small scale) may be important in order to establish the occurrence of this phenomenon. Previous studies in Kruger National Park, South Africa, and Selous Game Reserve (Selous), Tanzania, have found contrasting results regarding the avoidance of hyaenas by wild dogs (Mills and Gorman 1997, Creel and Creel 2002). In Kruger National Park, a negative but non-significant correlation between the ranked habitat preferences of hyaenas (based on hyaena response to playbacks) and wild dog (based on location data) was found (Mills and Gorman 1997). However,

in Selous a significant positive spatial correlation between hyaena density (based on hyaena response to playbacks) and wild dog space use (based on location data) was found (Creel and Creel 2002).

Both above mentioned studies employed wild dog location data grouped over long time periods (several years) and density/distribution relationships between species were necessarily only tested at large spatial scales (habitat scale in Kruger National Park and large grid size [9.26 x 9.26 km] in Selous) as a result of sparse hyaena data (Mills and Gorman 1997, Creel and Creel 2002). Using a different species combination and method in the much more open landscape of the Serengeti plains, Durant (1998) found a significantly negative relationship between cheetah presence and hyaena density during the wet season at a small scale (1–3 km). Further, cheetah avoidance of hyaenas was found at the local scale as well, in a subsequent experimental study where cheetahs were exposed to recorded vocalizations of hyaenas (Durant 2000a). A number of other ecological variables such as prey density, as well as lion density which has been shown to be negatively correlated to wild dog space use in Kruger National Park and Selous (Mills and Gorman 1997, Creel and Creel 2002), may obviously complicate the examination of this interaction (Creel and Creel 2002).

Our data shows that the HiP hyaena population is substantially larger (*ca*. 50%) than the last estimate of 200 individuals (Hofer and Mills 1998) and is the second largest protected population in South Africa following Kruger National Park. In the surrounding Zululand and Maputaland area small populations exist in the Ophathe, Ntshondwe (formerly iThala), and uMkhuze Game Reserves and the Greater St. Lucia Wetlands Park (Pringle 1977, Rowe-Rowe 1992, Skinner *et al*. 1992, Hofer and Mills 1998). Hyaenas are reportedly also present on private game reserves and commercial ranches between these formal reserves (Hunter 1998), which may be either resident or dispersing individuals. Long distance male dispersal, as noted in HiP by Whateley (1980), may allow hyaenas to emigrate to these local populations, and we believe that the HiP population is probably contiguous with

these small populations in an artificial meta-population sense. This extended hyaena population currently constitutes a key population for the continual conservation of this vulnerable species in South Africa (Friedman and Daly 2004).

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