A keystone predator at risk? Density and distribution of the spotted hyena (Crocuta crocuta) in the Etosha National Park, Namibia

Article *in* Canadian Journal of Zoology · September 2009

DOI: 10.1139/Z09-082

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A keystone predator at risk? Density and distribution of the spotted hyena (*Crocuta crocuta*) in the Etosha National Park, Namibia

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Abstract: For wildlife management and conservation biology, it is important to be able to estimate the status and distribution of animals and to monitor their population trends. In the Etosha National Park, Namibia, there is a lack of knowledge about numbers and distribution of spotted hyenas (*Crocuta crocuta* (Erxleben, 1777)) and factors regulating their population. To estimate hyena density and distribution, tape-recorded vocalizations (call-ups) were performed to attract hyenas in the central and eastern parts of Etosha. Eighty-five adult and subadult hyenas responded to the calls, with most of them responding in an area with high density of migratory ungulates, principally springbok (*Antidorcas marsupialis* (Zimmermann, 1780)), wildebeest (*Connochaetes taurinus* (Burchell, 1823)), and Burchell's zebra (*Equus burchelli* (Gray, 1824)). These migratory species are the main prey of spotted hyenas in Etosha. There was a strong spatial relationship between hyena density and migratory prey biomass. Based on this mathematical correlation, I estimated 203 ± 79 hyenas, i.e., 2.7 ± 1.1 hyenas/100 km^2, in the central and eastern parts of Etosha. Applying this correlation to the western part of the park, it was possible to estimate 339 ± 176 spotted hyenas, corresponding to an overall density of 2.1 ± 1.0 hyenas/100 km^2, in the whole Etosha National Park.

Résumé : En gestion de la faune sauvage et en biologie de la conservation, il est important d'être capable d'estimer le statut et la répartition des animaux et de suivre leurs tendances démographiques. Au parc national d'Etosha, en Namibie, on a peu d'information sur les nombres et la répartition des hyènes tachetées (*Crocuta crocuta* (Erxleben, 1777)) et sur les facteurs qui contrôlent leur population. Afin d'estimer la densité et la répartition des hyènes dans le centre et l'est d'Etosha, des enregistrements de vocalisations (des appels sur bande magnétique) ont été diffusés afin d'attirer les hyènes. Quatre-vingt-cinq hyènes adultes et subadultes ont répondu aux appels, la plupart dans une région de forte densité de migration d'ongulés, particulièrement de springboks (*Antidorcas marsupialis* (Zimmerman, 1780)), de gnous bleus (*Connochaetes taurinus* (Burchell, 1823)) et de zèbres de Burchell (*Equus burchelli* (Gray, 1824)). Ces espèces migratrices constituent les proies principales des hyènes tachetées à Etosha. Il existe une forte relation spatiale entre la densité des hyènes et la biomasse des proies migratrices. Cette corrélation mathématique a permis d'estimer le nombre de hyènes à 203 ± 79, c'est-à-dire 2,7 ± 1,1 hyènes/100 km^2, dans le centre et l'est d'Etosha. En appliquant cette corrélation à l'ouest du parc, il est possible d'estimer le nombre de hyènes tachetées à 339 ± 176, ce qui correspond à une densité globale de 2,1 ± 1,0 hyènes/100 km^2, dans l'ensemble du parc national d'Etosha.

[Traduit par la Rédaction]

Introduction

Large carnivores in sub-Saharan Africa have shown a marked decrease in their numbers and distribution since the 1950s. This decline has been attributed to a gradual reduction of suitable habitat owing to increasing conflict with human development (Nowell and Jackson 1996; Mills and Hofer 1998).

Through its influence on foraging rate and hunting success, food dispersion is an important selective force on the social and spatial organizations of predators in that it may modulate group and territory sizes (resource dispersion hypothesis; Macdonald 1983). In semi-desert areas, the low densities of large predators has generally been associated with low prey densities (Stander 1991; Mills 1994). However, animals living at low densities may be susceptible to threats that face small populations, including demographic and environmental stochasticity (Caughley and Gunn 1996) and reduced genetic variability that could lead to social instability or extinction (Trinkel et al. 2008). Spotted hyenas (*Crocuta crocuta* (Erxleben, 1977)), similar to lions (*Panthera leo* (L., 1758)) (Stander 1991) and African wild dogs (*Lycaon pictus* (Temminck, 1820)) (Gusset et al. 2008), are strongly dependent on protected areas or zones of low human density with sufficient numbers of suitable prey (Mills and Hofer 1998). Thus, the future of these species lies inside rather than outside large conservation areas.

Spotted hyenas are keystone predators (Paine 1969) in many African ecosystems, and their presence is a useful indicator of ecosystem health. Hyenas can survive in environments from which other large predators such as cheetahs (*Acinonyx jubatus* (Schreber, 1775)), lions, and wild dogs have been extirpated; if hyenas also vanish, a particular habitat may have become degraded (Mills and Hofer 1998). The Etosha National Park, a semi-desert area, contains the larg-

Received 27 April 2009. Accepted 9 July 2009. Published on the NRC Research Press Web site at cjz.nrc.ca on 30 September 2009.

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est spotted hyena population in Namibia. A recent study on one hyena clan in Etosha showed that there existed a strong spatial relationship between hyena density and migratory prey density (Trinkel et al. 2004). However, there were concerns that this group might be too small to be viable, because of high adult mortality (Trinkel 2003). An essential prerequisite for both wildlife management and conservation biology is the knowledge of the status, distribution, and population trends of species.

The objective of the present study is to provide estimates of the number of hyenas, their density and distribution, and the factors regulating their population in Etosha. As Etosha is a semi-desert area with low prey densities, I predict that (*i*) spotted hyena densities will be low compared with other ecosystems. Furthermore, I will test the hypothesis of Trinkel et al. (2004) who studied only one spotted hyena clan in Etosha. I predict that (*ii*) there will be a strong spatial relationship between hyena density and distribution and the density and distribution of migratory ungulates, i.e., the main prey of hyenas, and consequently, that (*iii*) migratory prey is the limiting factor of the spotted hyena population in Etosha.

Materials and methods

Study area

The Etosha National Park is situated between three major biotic zones (the southern savannah woodland, the southwest arid zone, and the Namib desert (Smithers 1983) in northern Namibia) with Etosha's coordinates centered at 19°S, 16°E. Etosha occupies an area of 22 270 km^2, with a mean annual rainfall of 351 mm. The Etosha pan is a saline desert surrounded by short-grass plains (Le Roux et al. 1988) and comprises <10% of Etosha's surface area. There is a wet season from January to April and a dry season from May to December. Artificial water points and natural springs are the only permanently available water during the dry season (Fig. 1). This study covered 7950 km^2 in the central and eastern parts of the Etosha National Park (blocks 1–6; Fig. 1), excluding the 4590 km^2 Etosha pan with no resident hyenas. The vegetation in the central and eastern parts (blocks 1–6), as well as in the western part of the park (blocks 7–17), are similar, containing grassy plains and adjacent woodland with *Colophosperum mopane* (Kirk ex Benth.) Kirk ex J. Leonard, acacia (*Acacia* P. Mill.), *Combretum* Loefl., and tropical almond (*Terminalia* L.) as the dominant tree species (Le Roux et al. 1988). Ungulate species commonly preyed on by hyenas in this area include mostly migratory herbivores, i.e., springbok (*Antidorcas marsupialis* (Zimmermann, 1780)), wildebeest (*Connochaetes taurinus* (Burchell, 1823)), and Burchell's zebra (*Equus burchelli* (Gray, 1824)) (Trinkel et al. 2004). To correlate hyena density with prey biomass, the study area was divided into six blocks (Fig. 1). The entire perimeter of the Etosha National Park is fenced and borders on rural communities in the north and on commercial farmland in the east and south.

The call-up experiment

Tape-recorded vocalizations were used to attract spotted hyenas and other predators, such as lions. Vocalizations used included the interaction between spotted hyenas and lions, an interclan fight between spotted hyenas, hyenas competing on a kill, and the distress call of a warthog. This combination of vocalizations was shown to attract hyenas when they are hungry, but also when social circumstances would attract them to the sounds (Mills 1994). The vocalizations were played on a MP3 player connected to a 8 Ω amplifier (380 W GXV 376 TC; Gelhard, Oer-Erkenschwick, Germany) powered by a 12 V car battery. Vocalisations were broadcast from four horn speakers (375 mm × 222 mm × 300 mm SK-159; Monacor International, Bremen, Germany) powered by four horn driver units (75 Watt, 16 Ω KU-516; Monacor International, Bremen, Germany) mounted on the top of the roof of the vehicle, and fixed in such a way that 180° were covered when playing the sound.

The study was performed between August and October 2008 on 32 nights starting at sunset when hyenas become active. Each night of the survey, a route of 80–110 km was driven. At approximately 10 km intervals along the route, the vehicle was stopped and the tape was played. Depending on the conditions of the roads, the drive between two calling stations took between 20 and 80 min. Thirty to 45 min were spent at each calling station. After about 5 min of playing into one direction, the car was turned through 180° and the vocalizations were played for 5 min into the other direction. Approximately 5 min after the end of the first playing, the tape was replayed and the car again turned 180° after 5 min. In total, the tape was broadcast at 99 calling stations. Thirty-five to 65% of each block within the study area were sampled (Table 1). A red-filtered spotlight was used to scan the area for responding predators. Hyenas are easy to see with a spotlight, as the light is reflected in their eyes and their characteristic gait can quickly be identified. Hyenas that responded were recorded with a digital video camera and identified by visual identification of their spot patterns and natural ear notches (Kruuk 1972; Frank 1986; East et al. 1993). As calling stations were about 10 km apart and hyenas were individually identified, the chances of double-counting were practically excluded. Wind conditions were held as constant as possible and call-ups were not performed when the wind exceeded 2 on the Beauford wind scale.

The maximum distance to vocalizations at which hyenas responded and the hyenas response probability were estimated from 15 calibration experiments. These tests were conducted by filming a group of hyenas and playing the vocalizations starting at 3.8 km from the group. The sound with the speakers directed towards the hyenas was played in the same way as in the survey. Responding hyenas were filmed, and the number of hyenas responding were recorded. Calibration experiments indicated that the range hyenas would respond is 3.4 km. Therefore, taking 3.4 km as the radius of a circle, the sampled area per station was 36.3 km^2. As described by Mills et al. (2001), hyenas responded in a group, i.e., either all of them responded or none of them did. The hyena's response probability was 72%. The response behavior of hyenas with regard to the number of responses by time of the day was uniformly distributed.

Determination of prey density and distribution

Aerial surveys were conducted by the Ministry of Envi-

Fig. 1. (*a*) Map of Namibia. (*b*) Study area within the Etosha National Park. Spotted hyena (*Crocuta crocuta*) call-ups were preformed in blocks 1–6. Prey densities were determined in all blocks (blocks 1–17). ●, waterholes.

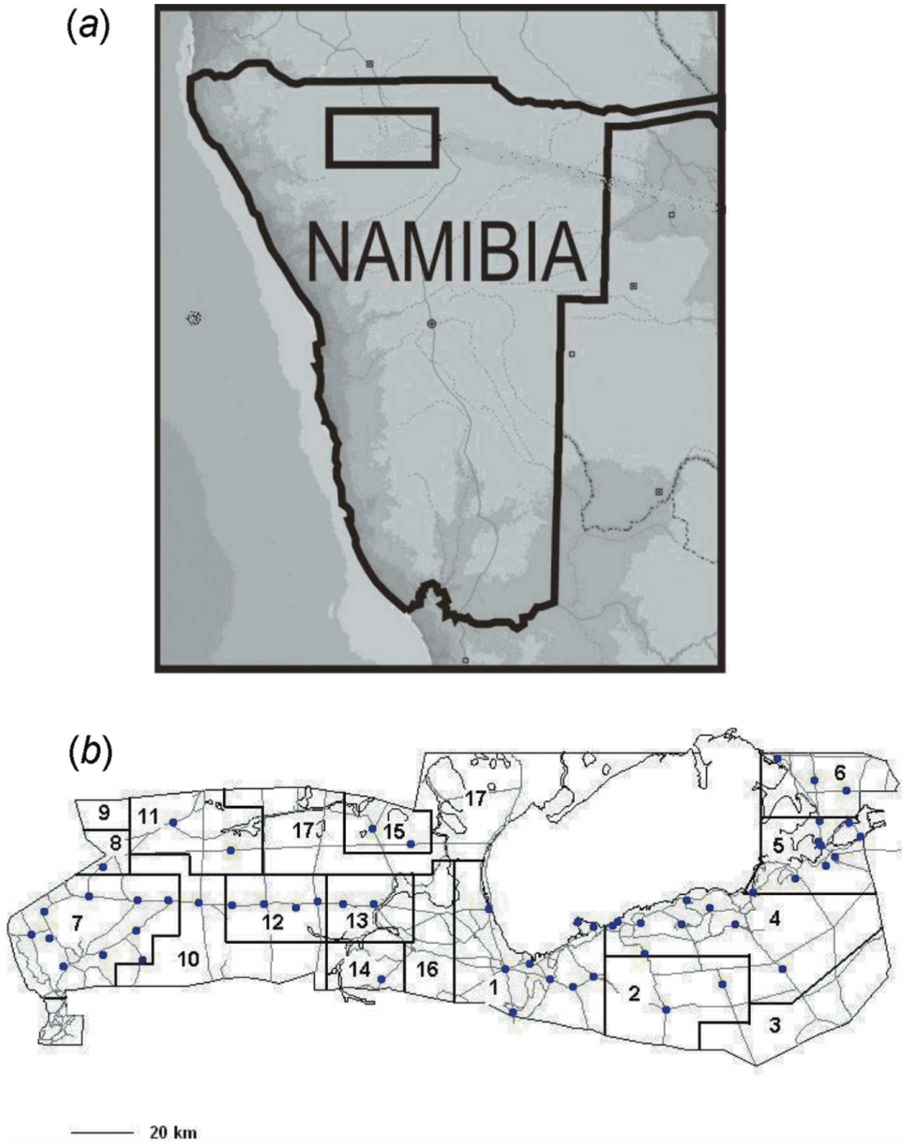


Table 1. Number of calling stations and prey densities in each block (blocks 1–6) within the study area.

Block	Area of block (km^2)	No. of stations	Percentage of blocks	Prey density/km^2 Migratory	Resident
1	1498.4	26	63	3.6	0.8
2	1427.4	15	38	0.7	0.4
3	1145.3	11	35	0.0	0.2
4	2038.2	23	41	2.1	0.3
5	918.1	12	48	4.2	1.1
6	921.1	12	47	1.7	1.6

ronment and Tourism during the dry season in 2005 and covered the whole Etosha National Park, an area of 18 551 km^2, excluding the Etosha pan (Kilian and Kolberg 2005). Two aircraft, a Cessna 206 and a Cessna 182, were used. Ungulates included in the count were migratory species such as springbok, wildebeest, and zebra, as well as resident species such as red hartebeest (*Alcelaphus buselaphus* (Blainville, 1816)), gemsbok (*Oryx gazella* (L., 1758)), giraffe (*Giraffa camelopardalis* (L., 1758)), and eland (*Taurotragus oryx* (Pallas, 1766)). The survey zone was stratified into 17 blocks (Fig. 1) based on the availability of permanent water. Depending on the expected density and distribu-

Fig. 2. Calling stations within the study area (□) and stations at which spotted hyenas (*Crocuta crocuta*) responded to the calls (■).

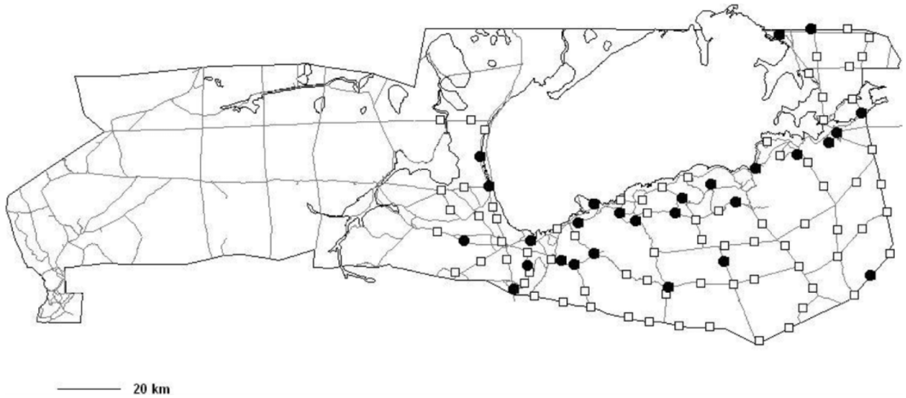


Table 2. Number of spotted hyenas (*Crocuta crocuta*), number of lions (*Panthera leo*), and the group composition of lions at calling stations where both predators responded.

No. of hyenas	No. of lions	Group composition of lions
3	1	Adult male (1)
3	4	Adult male (4)
2	2	Adult male (2)
4	2	Adult female (2)
3	2	Adult male (1), adult female (1)
1	1	Adult male (1)
2	6	Adult female (3), subadult male (3)
1	4	Adult male (4)

tion of wildlife known from aerial surveys of previous years, each block was sampled at intensities of 40%, 20%, or 10% (Kilian and Kolberg 2005), and prey numbers and distribution were statistically evaluated based on Jolly's (1969) method for unequal-sized sampling. A spreadsheet was developed to calculate prey population size, 95% confidence limits, and population distribution. Since 1995, aerial counts have been performed by the Ministry of Environment and Tourism and provide comparable estimates and population trends for migratory and resident herbivores. It was shown that since 1995, the population size of springbok, wildebeest, and zebra, which are the hyenas main prey, fluctuated only slightly.

Calculation of hyena numbers and densities

A linear mathematical relationship between hyena densities (hyenas responding (h) per km^2 and block) and migratory prey biomass (pb) per km^2 in blocks 1–6 was used to calculate the total number of hyenas. The number of hyenas responding in each block (h_b) can be calculated by multiplying hyenas responding per km^2 and block (h) with the area of each block (A_b). To accurately calculate the number of hyenas and hyena densities, it is necessary to specify the response radius, which was determined to be 3.4 km in the calibration experiment, and thus each calling station is assumed to cover an area of 36.3 km^2. When A_s is the area sampled around a calling station, n_s is the number of calling stations in the respective block, and A_b is the area of the respective block, then the number of hyenas corrected for the hyenas' response range (h_r) can be calculated using $h_r = h_b \cdot A_s \cdot n_s / A_b$.

Finally, to obtain the total number of hyenas (h_t) in each block, h_r has to be corrected for the hyenas' response probability (72%) using $h_t = h_r \cdot 100/72$.

Minimum and maximum estimates for hyena numbers per block were calculated from the standard deviation (SD) of the linear relationship, followed by correcting for the hyenas' response range and response probability. To predict hyena numbers and densities for the western part of the park (blocks 7–17), the same linear relationship was used. Statistical analyses were performed with MINITAB version 15 (Minitab Inc., State Collage, Pennsylvania, USA). A $p < 0.05$ was considered to be statistically significant.

Validation of hyena numbers and densities

To validate hyena numbers determined from call-ups, I compared these results with the total count of spotted hyenas in an area covering approximately 1500 km^2 (block 1) within the study area. Hyena clan sizes were determined based on individuals identified by visual examination of spot patterns, scars, and natural ear notches, and catalogued by digital photographs. Territory sizes of hyenas were delineated from aerial tracking and ground tracking of radio-collared and individually known clan members. Values are reported as mean ± SD.

Results

Hyenas responding to calls

Spotted hyenas were observed at 27 of the 99 calling stations (27.3%) (Fig. 2). At those stations, 85 adult and subadult hyenas were attracted to the calls. The mean (SD) number of hyenas seen at 27 stations was 3.2 ± 2.9, and in 75% of the observations, hyena numbers were between one and three animals. On one occasion, 16 adult and subadult hyenas were observed together, and all these animals were known to belong to the Klein Namutoni clan that contains 25–30 adults and subadults. It is the only large clan in Etosha and about twice the size compared with other clans in Etosha (Trinkel 2003; Trinkel et al. 2004). Because of the low number of hyenas responding, it was possible to accurately count the hyenas attracted to the sound. During the survey, it was possible to determine the location of some hyena dens: hyena cubs are attached to the den until they are about 1 year old. However, at six stations where hyenas responded, I recorded 18 cubs: at five stations, the number of

Fig. 3. Distribution of calling stations at which spotted hyenas (*Crocuta crocuta*) responded to the calls (●) (blocks 1–6), as well as density and distribution of migratory prey animals, throughout the whole Etosha National Park. Shaded squares indicate areas with migratory prey densities ranging from 0.95 to 9.5 animals/km^2. Open areas indicate areas where migratory prey densities are <0.95 animals/km^2.

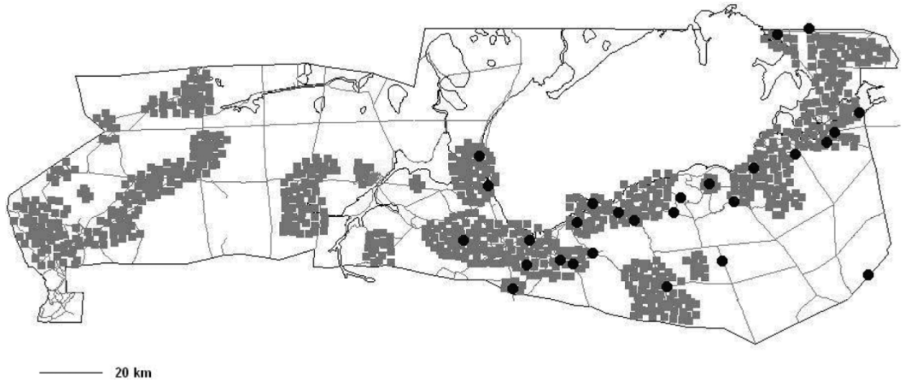
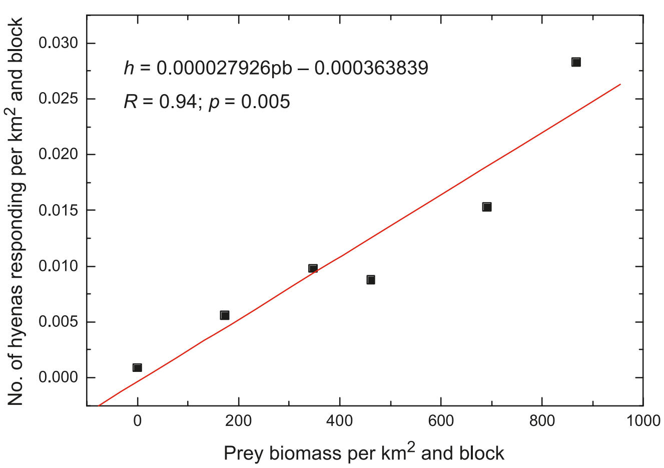


Fig. 4. Hyena (*Crocuta crocuta*) densities (*h*) and prey biomass (pb) in the six blocks within the study area. The regression graph *h* = 0.000027926pb – 0.000362829 (*R* = 0.94) reflects a linear correlation between hyenas responding per square kilometres and block and biomass of migratory prey per square kilometres and block.



cubs was between one and three individuals, and 10 cubs were attracted together with the 16 adult and subadult hyenas of the Klein Namutoni clan. Hyenas were observed at the border between the national park and the adjacent farmland on two occasions: (1) one single hyena and (2) five adult and subadult hyenas accompanied by two cubs. In the latter case, elephants had destroyed the elephant-proof fence over a distance >5 km, and the hyenas, which apparently were moving around outside the park, were attracted to the tape-recorded vocalizations. I presume that these hyenas were primarily living inside Etosha, because they did respond to the calls. In contrast, hyenas that live on farmland permanently are very cautious, because they are heavily persecuted, which makes it unlikely that farmland hyenas would respond to call-ups.

Lions also responded to playbacks of hyena vocalization. The presence of lions, however, did not prevent hyenas from responding. They appeared at 8 of 17 stations where lions were present (47%). At 75% of stations where both hyenas and lions responded, between one and four adult male lions were present (Table 2).

Prey density and distribution

The overall mean density of migratory prey in the whole study area (blocks 1–6) was 2.1 animals/km^2, corresponding to a mean number of 16 036 ± 6 845 migratory ungulates. Migratory herbivores were concentrated in block 5 (4.2 animals/km^2), block 1 (3.6 animals/km^2), block 4 (2.1 animals/km^2), and block 6 (1.7 migrants/km^2). Blocks 2 and 3 contained 0.7 and 0.0 migrants/km^2, respectively. The overall mean density of resident herbivores in the study area was 0.7 ungulates/km^2. Prey densities in each block are given in Table 1.

Correlation between hyena density and prey biomass

Most of the prey animals and hyenas were concentrated around water holes (Fig. 3). There was a significant difference in hyena response, depending on the proximity of the calling stations to water holes (Fisher's exact test, $p <$ 0.001): 72 hyenas responded at 21 of 36 stations (58.3%) that were <10 km from the nearest water hole, whereas only 13 hyenas were attracted to the sound at 6 of 63 stations (9.5%) that were located >10 km away from water.

There exists a strong spatial relationship between the response of hyenas (*h*) and the migratory prey biomass (pb), which can be described as follows:

$$[1] \quad h = 0.000027926\text{pb} - 0.000362829, \quad R = 0.94$$

The regression graph (Fig. 4) reflects a linear correlation between hyena response per square kilometres and block (1, 2, 3, 4, 5, 6) and migratory prey biomass per square kilometres and block (1, 2, 3, 4, 5, 6).

In the western part of Etosha (blocks 7–17), prey counts were performed; no hyena call-ups were performed. However, as prey biomass is known for the whole park, eq. 1 was used to predict hyena numbers and densities for western Etosha. The numbers of hyenas and hyena densities in each block, calculated from eq. 1, was corrected for the hyena's response range and response probability.

Hyena density (6.6 ± 1.9 hyenas/100 km^2) was highest in block 5, the area with the highest density of migratory prey of the whole park, followed by 3.9 ± 1.3 hyenas/100 km^2 and 2.6 ± 1.2 hyenas/100 km^2 in blocks 1 and 6, respectively (Table 3). In the study area (blocks 1–6), the overall mean density was 2.7 ± 1.1 hyenas/ km^2 with a total number of 203 ± 79 animals.

For the western part of the park, hyena densities (ranging from 2.2 to 3.9 hyenas/100 km^2) are estimated for areas with high prey density, whereas hyena density estimates are low over large parts of the park with low prey density (Table 3). The total number of spotted hyenas in the whole Etosha National Park is estimated at 339 ± 176 spotted hyenas, corresponding to an overall density of 2.1 ± 1.0 hyenas/100 km^2.

Validation of hyena estimates

An area of approximately 1500 km^2 (block 1) is the home of four well-known hyena clans consisting of 15 adults and subadults each (range of clan sizes 11–18 individuals). The total number of 60 hyenas (range 44–72 hyenas) in block 1 practically equals the results of the call-up experiment (mean 59 hyenas; range 41–77 hyenas).

Table 3. Number and density of spotted hyenas (*Crocuta crocuta*) in different areas within the Etosha National Park.

	Hyena number			Hyena density/100 km^2		
Block	Mean	Min.	Max.	Mean	Min.	Max.
1	59	41	77	3.9	2.7	5.2
2	15	4	26	1.0	0.2	1.8
3	0	0	9	0.0	0.0	0.8
4	45	28	62	2.0	1.2	2.8
5	60	43	78	6.6	4.7	8.5
6	24	13	35	2.6	1.4	3.8
7	48	26	69	2.8	1.5	4.0
8	6	2	9	2.2	1.0	3.3
11	16	5	26	1.6	0.5	2.6
12	22	13	31	3.1	1.8	4.4
13	17	9	25	2.9	1.6	4.2
14	11	5	16	2.4	1.2	3.7
15	1	0	10	0.1	0.0	1.5
17	1	0	17	0.0	0.0	0.6
9 + 10 + 16	15	0	25	0.6	0.0	1.0
Sum	339	190	515			
Mean				2.1	0.9	3.1

Note: Hyena numbers were counted in blocks 1–6, whereas hyena numbers were calculated in blocks 7–17. Mean, minimum, and maximum number of hyenas in each block were derived from a linear regression graph that correlates migratory prey biomass and hyenas responding to call-ups.

Discussion

The use of hyena vocalisations to attract spotted hyenas works effectively for monitoring hyena population size and distribution, and seems to be a powerful method to determine population trends. Hyena response varied widely in Etosha with most hyenas occurring in areas where migratory prey density was high. Based on these results, therefore, future call-ups could be performed by park management only in the area with high prey density, making this method even more time and cost effective because of the reduced observer effort. Care has to be taken, however, when counting the animals. Hyenas tend to circle around the vehicle before they lose interest in the sound, thus an inexperienced observer might count the same hyena several times. The hyenas' response range and response probability in Etosha differ only slightly from those observed in the Kruger National Park (Mills et al. 2001). However, I would suggest that the calibration experiment be performed when this technique is used in other areas.

Density estimates (2.1 ± 0.9 hyenas/100 km^2) for the Etosha population are low. In southern and eastern Africa, spotted hyena densities are up to 40 times higher than those observed in Etosha (Kruuk 1972; Mills et al. 2001). Lower hyena density estimates were only reported for the Kahalari, South Africa (Mills 1994), and the Namib desert, Namibia (Tilson and Henschel 1986). However, during a previous study on spotted hyena performed in a small area of Etosha in the 1980s, Gasaway et al. (1989) found that hyena density (5 hyenas/100 km^2) was about 20% higher compared with density estimates in the same area observed during this study, which would suggest that hyena density has been declining.

Differences in carnivore densities, through group and territory sizes, have been attributed to differences in prey abundance and distribution (Macdonald 1983). In Etosha, migratory ungulates constitute most of the prey biomass, and during the dry season, which generally lasts >8 months, the majority of the herbivores are concentrated near water holes. The strong linear relationship between hyenas and migratory herbivores would suggest that the spotted hyena population in Etosha is limited by their main prey. Recently, we obtained similar results for one spotted hyena clan in Etosha, where the hyenas' spatial organization in both the dry and the wet season was strongly related to migratory prey abundance (Trinkel et al. 2004). Trinkel et al. (2004) showed that all members of one clan defended a territory of about 160 km^2 during the dry season, which they enlarged up to double this size during the wet season. Based on the results of Trinkel et al. (2004) and those obtained in this study, it can be concluded that Etosha hyenas will be more dispersed during the wet season, as they enlarge their territory to have access to their main prey.

Spotted hyenas are strongly dependent on protected areas with sufficient numbers of suitable prey (Mills and Hofer 1998). The Etosha National Park with its estimated 340 hyenas is the largest spotted hyena population in Namibia. However, the most important factor affecting population dynamics of spotted hyena outside protected areas seems to be human-caused mortality (Frank et al. 1995; Mills and Hofer 1998). In the Serengeti, about 8% of breeding female spotted hyenas were removed as a result of snaring and poisoning by game-meat hunters; it was argued that interaction between people and wildlife at the periphery may affect wildlife throughout a protected area (Hofer and East 1995). Between 2000 and 2004, an intensive farm survey was performed by the Ministry of Environment and Tourism: every year, at least 45 "problem" hyenas were killed on farms bordering Etosha (B. Kötting, personal communication (2008)), which is >10% of the whole spotted hyena population within Etosha. Thus, besides prey density and distribution, human-caused mortality could lead to a decline of the spotted hyena population in Etosha.

In this study, I provide an estimate of the status and distribution of a keystone predator, the spotted hyena, within the Etosha ecosystem. The call-up technique seems to be a powerful method for monitoring trends in hyena populations. As hyena density is strongly correlated with prey density, future call-ups could be performed only in the area of high prey density, which would make this method even more cost effective. To be able to identify whether the hyena population is stable or whether it is declining, the population should be monitored on a regular basis. A limitation of this method is that spotted hyenas quickly become habituated to the sound, resulting in low repeatability (Mills et al. 2001). Therefore, call-up experiments should not be repeated in the same area more than twice a year. However, because the estimated number and density of hyenas in Etosha is very low, a further decline in the spotted hyena population could have dramatic consequences for the whole ecosystem.

Acknowledgements

The Namibian Ministry of Environment and Tourism is thanked for the permission to conduct this study, Anton Paar GmbH for financial support, and P. Funston and G. Peters for providing hyena calls. N. Brian, W. Handley, F. Iifo, J. Kapner, W. Kilian, H. Kolber, M. du Plessis, and G. Shatumbo performed the aerial survey. N. Berriman, S. Kötting, and all staff members of the Etosha National Park provided assistance, information, and advice throughout the project. G. Kastberger provided logistic support. This paper was improved by the comments of Marion East and two anonymous reviewers.

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