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Martina Trinkel
University of KwaZulu-Natal

Paul H Fleischmann
Karl-Franzens-Universität Graz

Gerald Kastberger
Karl-Franzens-Universität Graz

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Spotted hyenas (*Crocuta crocuta*) follow migratory prey. Seasonal expansion of a clan territory in Etosha, Namibia

Martina Trinkel*, Paul H. Fleischmann, Albert F. Steindorfer and Gerald Kastberger

Institute of Zoology, University of Graz, Universitätsplatz 2, A-8010 Graz, Austria

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Abstract

The spatial organization of one clan of spotted hyenas *Crocuta crocuta* in the centre of the Etosha National Park, Namibia, is described during the dry and the wet seasons. The clan comprised 11 adults and sub-adults and occupied a territory of 160 km^2 in the dry season and 320 km^2 in the wet season. The dry season territory contained a low density (one animal/km^2) of resident herbivores, such as gemsbok *Oryx gazella*, kudu *Tragelaphus strepsiceros*, giraffe *Giraffa camelopardis*, steenbok *Raphicerus campestris* and ostrich *Struthio camelus*, and a higher density of migratory species (12 animals/km^2), principally springbok *Antidorcas marsupialis*, zebra *Equus burchelli* and wildebeest *Connochaetes taurinus*. These migratory species were the main prey of clan members. At the start of the wet season, the migratory herbivores migrated to the north-west, resulting in a considerable decline in the density of prey in the area used by clan members during the dry season. In response to this decline in prey, clan members followed the migratory herds and shifted the focus of their activities to an area grazed by migratory herbivores during the wet season. There existed a strong spatial relationship between the hyena density and the migratory prey density in both the dry and wet season. We postulate that the considerable enlargement of the clan territory in the wet season is a response to both the migratory movements of prey and an increase in the dispersion of prey during the wet season.

Key words: spotted hyena, Etosha, territory, 100% minimum convex polygon, *Crocuta crocuta*

INTRODUCTION

Food dispersion, through its influence on foraging rate and hunting success, is an important selective force on the social and spatial organization of predators in that it may modulate group and territory sizes (resource dispersion hypothesis: Macdonald, 1983). The social and spatial organization of carnivores has been postulated to be linked to resource characteristics (Macdonald, 1983; Moehlman, 1986, 1989), but few studies have quantitatively demonstrated such a link (Packer, 1986; Hofer, 1988; Baker *et al.*, 2000).

Here, we present results from a 1-year study on spotted hyenas *Crocuta crocuta*, a group-living carnivore, in the Etosha National Park, Namibia. This ecosystem is dominated by migratory herbivores whose seasonal movements produce fluctuations in local prey abundance. Compared to the Serengeti, an ecosystem dominated by large movements of migratory herds, the density of both migratory and resident prey in Etosha is much lower. In the Serengeti, hyenas cope with the fluctuations in prey abundance by defending exclusive clan territories and additionally, by undertaking frequent long-distance trips outside their territory to feed on the nearest large herds of migratory herbivores (Hofer & East, 1993*a*,*b*,*c*, 1995). In contrast, some ecosystems are characterized by stable, abundant and relatively uniformly distributed herds of herbivores. In these areas, such as the Ngorongoro Crater and Masai Mara (East Africa) or the Kruger (South Africa), spotted hyenas were found to have stable clans that maintained permanent territories. These territories were stable with only slight shifts in boundary positions (Kruuk, 1972; Bearder, 1977; Whateley & Brooks, 1978; Frank, 1986; Henschel, 1986; Cooper, 1989; Sillero-Zubiri & Gottelli, 1992; Frank, Holecamp & Smale, 1995).

In this paper, we analyse some aspects of the spatial organization of the Nebrownii clan in the central district of the Etosha National Park and compare its characteristics with those of the same species living in other savannah and woodland environments of East and South Africa. We demonstrate that spotted hyenas in Etosha expanded their territory enormously from the dry to the wet season to follow the migratory patterns of important prey species.

*All correspondence to: M. Trinkel, Breitenweg 17, A-8042 Graz, Austria
E-mail: martina_trinkel@yahoo.com

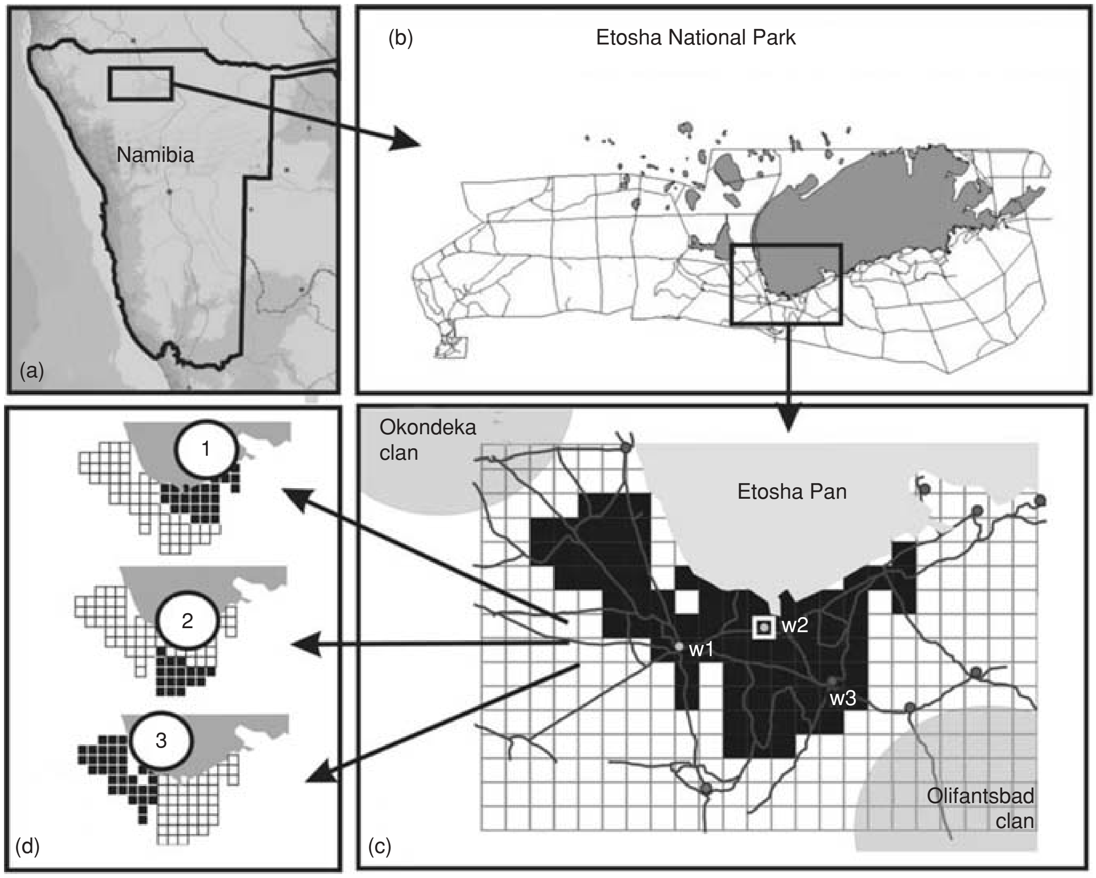

Fig. 1. Map of Namibia. (a) The Etosha National Park. (b) The study area in the centre of Etosha. (c) Two clans (Olifantsbad, Okondeka) neighboured the Nebrownii clan. W1, W2 and W3 are permanent waterholes within the study area. The waterholes outside this area are also registered as shaded circles. The lines are gravel roads. (d) Shows three zones (1, 2, 3) of the study area.

METHODS

Study area

The Etosha National Park (Fig. 1) is situated between three major biotic zones: the southern savannah woodland, the south-west arid, and the Namib desert (Smithers, 1983) with its coordinates centred at 19° S, 16° E. Etosha occupies an area of 22 270 km^2, with a mean annual rainfall of 351 mm. There is a wet season from January to May and a dry season from June to December. The Etosha pan is a saline desert surrounded by short-grass plains (Le Roux *et al.*, 1988) and comprises less than 10% of Etoshas surface area. This study was conducted in a 600 km^2 area in the centre of the Etosha National Park. This area, displayed in Fig. 1c, is part of the Etosha pan and contains grassy plains and adjacent woodlands with *Colophospermum mopane* in tree or scrub form (Du Preez, 1974). To correlate hyena density with prey density, we divided the study area into three zones (zone 1, 2 and 3; Fig. 1d) based on the road network and vegetation type.

Clan size and composition

The study focused on one group of spotted hyenas, the Nebrownii clan, living in the centre of the Etosha National Park. Spotted hyenas live in social groups, or clans, comprising several matrilines. Females are philopatric (i.e. remain in their natal groups), while most males disperse (Kruuk, 1972; Frank, 1986; Henschel & Skinner, 1991; Mills, 1994; East & Hofer, 2001). Observations began in June 2000 and continued until June 2001. They include 650 observation hours of identified clan members. Data were collected by following the hyenas in a vehicle throughout the night, usually between 18:00 in the evening and 8:00 in the morning. Within a few weeks of daily field observation members of the Nebrownii clan were habituated to our research vehicle and artificial light.

Individual hyenas of the Nebrownii clan and adjacent clans of spotted hyenas were characterized by visual identification of spot patterns, scars and natural ear-notches, and catalogued by digital photographs. The animals were sexed using differences in body outline (Frank, 1986), reproductive status (large teats), and from their third month onwards using the shape of their phallic glans (Frank, Glickman & Powch, 1990). The approximate age of hyenas was determined by visual inspection of caught animals and by digital photographs of their teeth. Five age classes were distinguished based on tooth eruption and wear, in particular with regard to the third premolar in the lower jaw (Kruuk, 1972). Individual

Table 1. Minimum convex polygon (MCP) (95% and 100%) areas of all adult and sub-adult clan members for the dry and the wet season

	Dry season	Wet season
Number of fixes	250	145
Territory (km^2) 100% MCP	160	320
Number of fixes	228	133
Territory (km^2) 95% MCP	130	287

hyenas were considered to be clan members if they have repeatedly visited the communal den.

Determination of territories

A territory of a clan is defined as that area which is advertised and defended by the clan members (Wilson, 1975; Davies & Houston, 1978; Kaufmann, 1983; Boydston, Morelli & Holekamp, 2001). The extent of the territory of spotted hyenas can be estimated on the basis of territorial clashes, scent-marking activities and defended kills (Hofer & East, 1993*a*). One adult female hyena of the Nebrownii clan was attracted with strange hyena sound and bait to fit her with a radio-collar (149 MHz, Advanced Telemetry Systems, USA), after immobilization with Zoletil. The ranges of the Nebrownii clan were delineated from direct observations during aerial and ground tracking of the radio-collared and focal hyenas (240 fixes of known adult and sub-adult individuals during the dry season from July to November 2000; 155 fixes of known adult and sub-adult individuals during the wet season from February to May 2001). An observer-bound Global Positioning System (GPS) was used to record the position of individuals and to map their movements. The home-range areas were estimated by fitting a 95% and 100% minimum convex polygon MCP (Mohr, 1947) by using the Animal Movement Analysis Extension of ArcView 3.2 (ESRI 1996; Hooge & Eichenlaub, 1997), whereby the outer locations were connected to form a polygon. The 95% MCP was calculated according the method proposed by White & Garrott (1990). This simple and easy method allows comparison with other studies (Harris *et al.*, 1990). We confirmed range sizes to be asymptotic by plotting range size against increasing number of fixes. (See Table 1.)

Determination of prey density

The distributions and densities of various prey species were estimated from censuses based on road counts during the day covering the dry and wet season territory of the Nebrownii clan. Three counts were made both in the dry (August, September, October 2000) and in the wet seasons (February, March, April 2001). Dasman & Mossman (1962) and Hirst (1969) considered road counts as an ungulate census technique that is inexpensive and reasonably accurate. Counts were carried out along a 157 km road circuit across the study area. Species included in the total count were the migratory prey with zebra, wildebeest and springbok as well as the resident woodland herbivores with gemsbok, kudu, giraffe, steenbok and ostrich. A strip of ~800 m wide on either side of the road was considered as every animal present in this strip could be identified using 7 × 42 binoculars. We verified that the resulting density estimates were unbiased by randomly performing transects perpendicular to the road and comparing results. Additionally, the survey area is an open habitat where sightability bias is low.

RESULTS

Structure of the Nebrownii clan

In July 2000, the Nebrownii clan consisted of five adult females (age class 3), one sub-adult female (age class 2), one female cub of 8 months (age class 1), three adult males (age class 3), two sub-adult males (age class 2) and three male cubs (12-month-old twins and one singleton of 6 months; age class 1). The radio-collared female was the mother of the twins. The female cub was last seen at the end of August 2000 and is assumed to have died at the age of 10 months. No cubs were born and none of the females was known to be pregnant during this 1 year of the study.

Territories of the Nebrownii clan

The clan members occupied territories that differed between the dry and the wet seasons. Dry season observations were recorded from July to November 2000 and wet season observations from February to May 2001. The territory of all clan members was 160 km^2 during the dry season and 320 km^2 during the wet season.

Territorial defence included defecations at latrines, scent marking (pasting) and vocal displays ('whooping', East & Hofer, 1991*a*,*b*) in both the dry and the wet seasons. Clan members scent marked inside their territory, typically around kills and at the communal den ('hinterland marking' Mills & Gorman, 1987), but they were not observed marking the territory boundaries. During the dry season we occasionally encountered individually known members of other clans in two different border areas of the Nebrownii clan: members of the Okondeka clan in the north-west and the Olifantsbad clan in the south-east (Fig. 1). We never observed any territorial conflicts between these three clans in the centre of Etosha, even when the Nebrownii clan enlarged its territory in the wet season and moved closer to the neighbouring Okondeka clan. We assume that hyena territories in the centre of Etosha are separated by areas where no resident hyenas live.

Dry season territory

From July to November 2000, Nebrownii hyenas were observed to spend most of their time in a small area

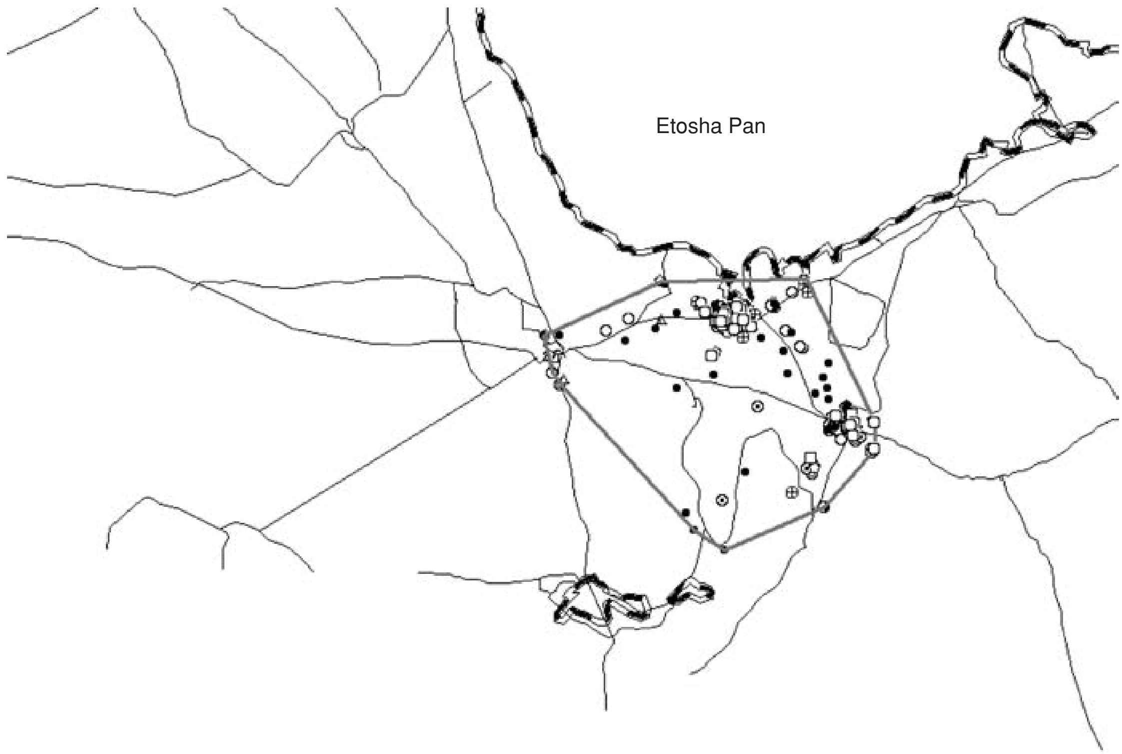

Fig. 2. Minimum convex polygon (100%) area for all adult and sub-adult clan members during the dry season. Individual animal sightings are depicted by the different symbols. The black circles represent the radio-collared female.

of their 160 km^2 dry season territory (Figs 2 & 3). The focus of activity of all clan members displayed as the 50% Kernel area was in the north-eastern part (zone 1) of their territory (Figs 2 & 3). The radio-collared female spent 82% and the other clan members spent 92% of the time observed in zone 1, and most meals (87%, 15 observations) were obtained here (Figs 2 & 3). Nebrownii hyenas mostly fed on migratory prey: of all kills the clan members made (24 observations), 12 were springbok, seven wildebeest, four zebra and one oryx. The north-eastern part of the clan's territory (zone 1) was characterized by the short-grass plains with a high level of migratory prey (such as springbok, zebra and wildebeest), two waterholes (the Nebrownii and the Gemsbokvlakte waterhole), and the location of the communal den near the Nebrownii waterhole (Fig. 1c). The clan frequently used both waterholes. The Okaukuejo waterhole, next to the main tourist camp, was floodlit throughout the night. There, we had observed only seven visits of hyenas during the dry season.

Wet season territory

During the wet season, i.e. from February to May 2001, the Nebrownii clan expanded its territory from 160 to 320 km^2 to the north-west, an area where no resident hyena clan was observed during the dry season before (Figs 4 & 5). The focus of activity of all clan members was in the north-western part (zone 3) of their territory (Figs 4 & 5). Sixty-three per cent of the fixes of the radio-collared individual and 61% the other clan members were observed in zone 3. This area was characterized by a high abundance of migratory herbivores. During the wet season, hyenas as well as prey animals were rarely seen at the waterholes, because water stood practically everywhere and animals were not dependent on waterholes as much as in the dry season. The communal den, which was used by Nebrownii hyenas during the dry season, was flooded; we were not aware of any alternative den during the wet season. We assume that there was no need for a den as the cubs were already old enough and independent from any den and also, no further cubs had been born.

Prey density within the territory of the Nebrownii clan

There were large fluctuations in herbivore abundance within the hyena's territory. The number of resident herbivores changed little during the dry and the wet season compared with the larger changes in the numbers and distribution of migratory herbivores. The overall mean density of resident herbivores was one animal/km^2 during the dry and the wet seasons, while that of the migratory herbivores was 12 animals/km^2 during the dry season and 5 animals/km^2 during the wet season. Prey animals concentrated in different areas within the hyena's territory: during the dry season, most prey animals were observed in the north-east (zone 1), whereas during the wet season, most of the herbivores concentrated in the north-west (zone 3).

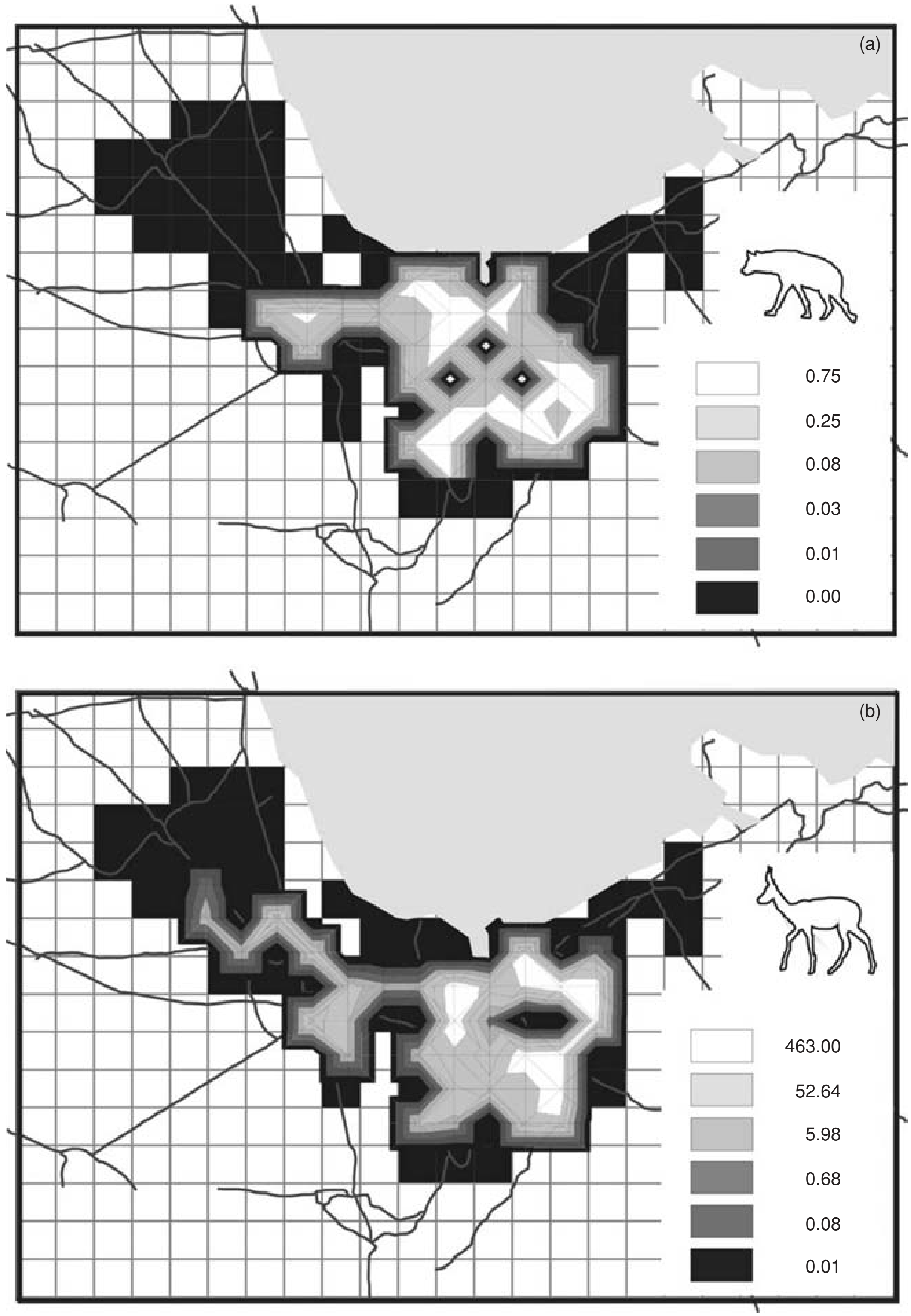

Fig. 3. Hyena (a) and prey (b) densities in the centre of Etosha in the dry season. The different hyena and prey densities (shaded) are log scaled. Black areas refer to the grids which had been periodically surveyed. The white areas refer to densities of > 0.750 hyenas (a) and > 463 prey animals (a) per survey and grid (2.5 × 2.5 km). The black zones refer to densities of < 0.007 hyenas (a) and < 0.042 prey animals (b) per survey and grid.

Prey density during the dry season

According to the three censuses during the dry season (August, September and October 2000) the migratory prey density was 12 animals/km^2 with a mean number of 2154 ± 395 (SD) migratory ungulates in the dry season territory of the Nebrownii clan. Migratory prey animals were concentrated in zone 1 (68%; 1475 ± 272

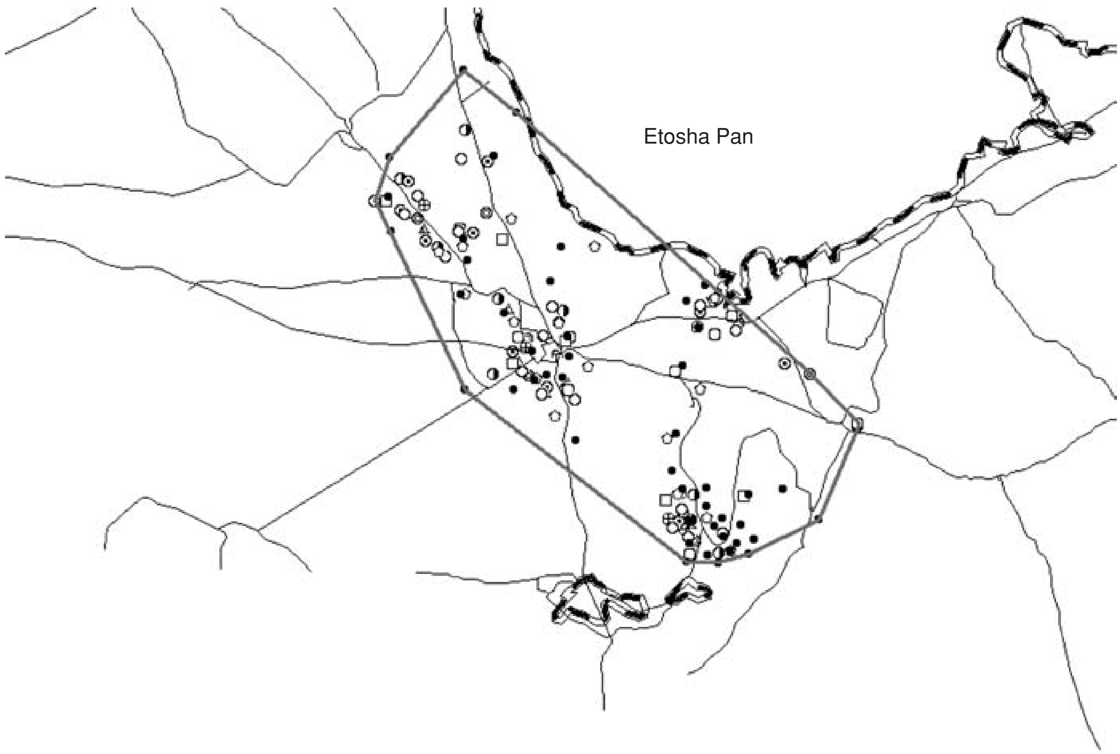

Fig. 4. Minimum convex polygon (100%) area for all adult and sub-adult clan members during the wet season. Individual animal sightings are depicted by the different symbols. The black circles represent the radio-collared female.

animals). Zone 2 contained 22% (477 ± 85 animals) of the migratory prey and only 10% (202 ± 38 animals) of the migratory herbivores were observed in zone 3 (Fig. 3).

Prey density during the wet season

According to the three censuses during the wet season (February, March and April 2001) the total migratory ungulate density in the wet season territory was five animals/km^2 with a total mean number of 1497 ± 293 (SD) migrants. Migratory prey animals concentrated on the short grass plains in zone 3 (89%, 1337 ± 251 animals). Zone 2 had 103 ± 26 migratory animals (7%) and only 57 ± 16 migrants (4%) were observed in zone 1 (Fig. 5).

Correlation between hyena density and prey density

The routing of the surveys was chosen to maximize the number of encounters with hyenas. Therefore, on the basis of our experiences, and on the daily information from visitors, we surveyed those grids more often where the hyenas were expected to occur; the other grids, where the chance to meet an animal was exceptionally low, were routinely surveyed at least five times a week. The census of the prey included all grids in the study area (see Fig. 1) and the number of surveys was equal for each grid. The comparison of hyena and prey density therefore depended on the number of surveys according to the equation:

the density of hyenas or prey in the grid q:

$$d_{hp}(q) = M_{hp}(q)/n(q)$$

with d_{hp}, the hyena (h) or prey density (p) in the grid q, M_{hp}, the number of hyenas (h) or prey (p) in the grid q; n (q), the number of surveys in the grid q.

There exists a strong spatial relationship between hyena (d_h) and migratory prey density (d_p) for both the dry and the wet seasons, which can be described according to the equation:

$$d_h = 0.0019 d_p + 0.2341; R = 0.97$$

The regression graph (Fig. 6) reflects a linear correlation between hyena sightings (fixes) per survey (observer effort) and zone (1, 2, 3) and the prey sightings per survey and zone (1, 2, 3).

DISCUSSION

The Nebrownii spotted hyena territory (dry season and wet season territories) was large, distinct and essentially exclusive. The Nebrownii clan coped with the variable resources by using a large dry season territory (160 km^2, Figs 2 & 3) and additionally, by expanding it up to double the size (320 km^2) in the wet season to follow the migratory herds (Figs 4 & 5). The dry season territory of the Nebrownii clan contained a low density (one animal/km^2) of resident herbivores and a higher density

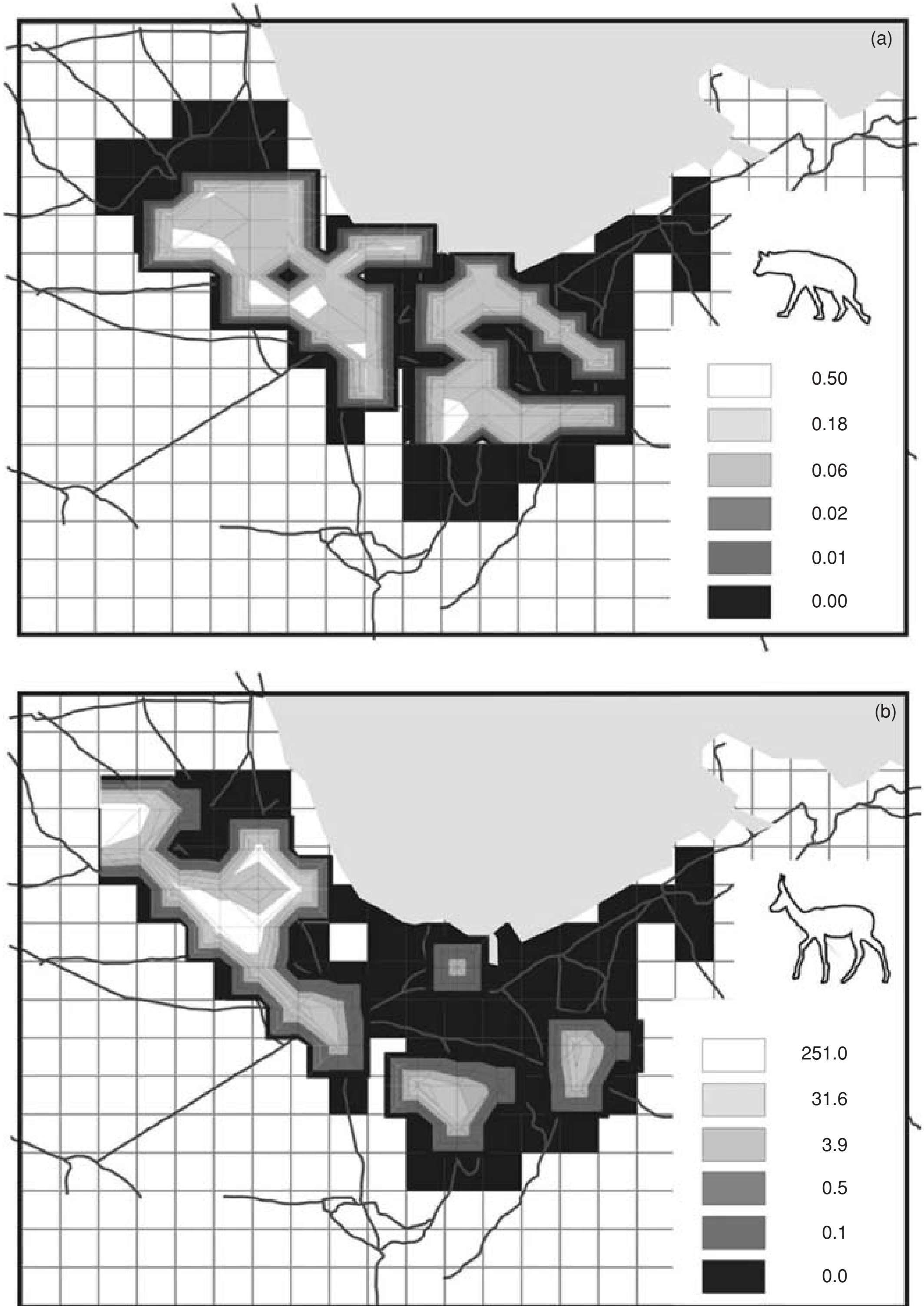

Fig. 5. Hyena (a) and prey (b) densities in the centre of Etosha in the wet season. The white areas refer to densities of > 0.500 hyenas (a), and > 251 prey animals (a) per survey and grid (2.5 × 2.5 km). The black zones refer to densities of < 0.006 hyenas (a) and < 0.035 prey animals (b) per survey and grid.

of migratory species (12 animals/km^2). In Etosha, the seasonal movements of the migratory ungulates produce fluctuations of local prey abundance and result from specific habitat types, in particular by the amount of grass available resulting from erratic rainfall (Berry, 1980, 1981). At the start of the wet season, migratory herbivores migrated to the north-west, causing a considerable decline in the density of prey in the area used by clan members

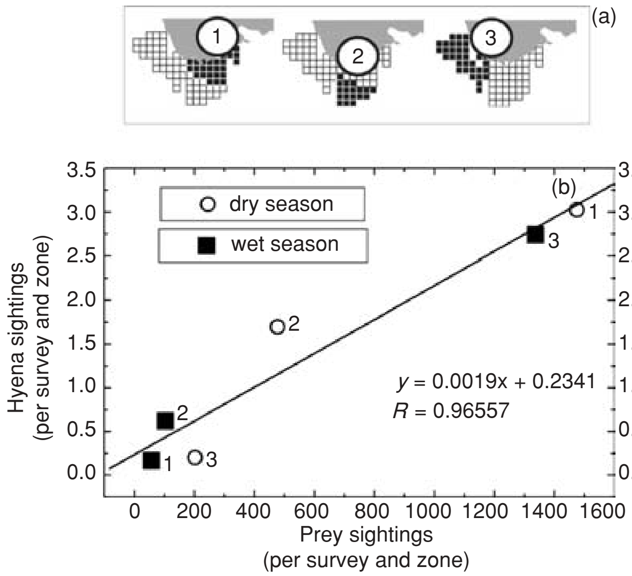

Fig. 6. Prey and hyena densities in the centre of Etosha. (a) The three zones (1, 2, 3) in the study area. (b) The regression graph $d_h = 0.0019\ d_p + 0.2341$; $R = 0.97$, reflects a linear correlation between the migratory prey (p) sightings per survey and zone and hyena sightings (h) per survey and zone in the dry (open circles) and wet season (black squares).

during the dry season. In response to the decline in migratory prey during the wet season, clan members shifted the focus of their main activities to an area grazed by migratory herbivores.

A different strategy to cope with strong fluctuations of migratory herbivores has been described for Serengeti hyenas that maintain permanent territories, and additionally forage outside their territory when their prey base becomes too low (Hofer & East, 1993*a*,*b*,*c*, 1995). This leads to an increase of the hyenas foraging ranges but also to an interference with the territories of adjacent clans. When migratory prey density is high, all hyena clan members forage inside their territories (Hofer & East, 1993*a*, 1995).

The land-use strategy of the Nebrownii clan where all members followed the movements of the migratory prey in the wet season has not been previously described. The reason why the Etosha set up is different from the Serengeti is the year round concentration of migrants. Commuting hyenas in the Serengeti exploit high concentrations of migratory herbivores in the northern woodlands in the dry season and on the southern plains in the wet season. In contrast, in Etosha there is a high concentration of migrants in the dry season, whereas in the wet season migratory animals are widely dispersed. It is thus the lack of concentration of herbivores anywhere in Etosha in the wet season that is the key reason why Etosha hyenas do not commute. If the Etosha ecosystem had high concentrations of migratory herbivores in both the wet and dry seasons, as occurs in the Serengeti, we might expect a mosaic of smaller territories and a commuting system. We suggest that for the Etosha hyena population the dispersed prey conditions in the wet season sets the spatial distribution of clan territories, which can be contracted in the dry season as prey availability increases.

In the Ngorongoro (Kruuk, 1972), Masai Mara (Frank, 1986), Kruger (Henschel, 1986), Hluhluwe (Whateley & Brooks, 1978) and the Aberdare National Park (Sillero-Zubiri & Gottelli, 1992) most of the prey is resident resulting in stable, abundant and relatively uniformly distributed resources. In these areas, there is no need for spotted hyenas to alter their range sizes and consequently, they maintain permanent territories over years. The response to long-term changes in the resident prey populations on spotted hyenas was investigated in the Ngorongoro Crater. Höner *et al.* (2002) found that hyenas change their foraging behaviour with respect to their prey selection and their proportion of hunting versus scavenging rather than by changing their territory size and shape.

Territories larger than those described here have only been reported in spotted hyena populations in desert areas such as the Kalahari and the Namib (Mills, 1984; Tilson & Henschel, 1986), where prey densities are extremely low. In those areas, prey is widely dispersed, and the sparse herds are facultatively mobile when following the sporadic rainstorms (Mills, 1984; Tilson & Henschel, 1986). To meet their food requirements under such conditions, spotted hyena have vast territories over years, up to 1800 km^2 (Mills, 1984).

We conclude that in ecosystems characterized by strong fluctuations of migratory prey abundance, hyenas need to be more flexible with regard to their range sizes. Under strong fluctuations of the food sources, the spotted hyenas modulate their space-use strategy. This strategy was first postulated for Serengeti hyenas (Hofer & East, 1993*a*, 1995). The findings for the Nebrownii clan in the centre of Etosha illustrate this switch to larger territories when migratory prey density decreases. Such temporal variation in the territorial strategy may also have profound implications for the management of this species.

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