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Prey selection and prey preferences of spotted hyenas *Crocuta crocuta* in the Etosha National Park, Namibia

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Abstract The feeding ecology of the spotted hyena *Crocuta crocuta* was studied in the central and eastern part of the Etosha National Park, Namibia. Hyenas mainly hunted migratory ungulates such as springbok *Antidorcas marsupialis*, zebra *Equus burchelli*, and blue wildebeest *Connochaetes taurinus*, but also resident species such as the greater kudu *Tragelaphus strepsiceros* and gemsbok *Oryx gazella*. There were, however, major differences in the species most frequently killed by hyenas in central and eastern Etosha. The preferred prey species of spotted hyenas in central Etosha was springbok, whereas regarding the abundance of zebra and wildebeest, these two species were rather avoided. In contrast, the prey species preferred by hyenas in eastern Etosha was kudu. Zebra and gemsbok were taken in proportion to their abundance, whereas wildebeest and springbok seemed to be rather avoided. Differences in prey selection and preferences were also reflected in differences in hunting group sizes. In eastern Etosha, where spotted hyenas frequently hunted larger prey, hunting group sizes were significantly larger compared to those in the center of the park.

Keywords Spotted hyena · *Crocuta crocuta* · Prey selection · Hunting group size · Feeding ecology

Introduction

Spotted hyenas *Crocuta crocuta* are efficient hunters capable of killing herbivores several times their own size (Kruuk 1972; Mills 1994). The hyenas' main prey are medium to large-sized ungulates weighing between 40 and 350 kg (Kruuk 1972; Mills 1994; Henschel and

Tilson 1988), but sometimes they kill animals up to the size of adult buffalo *Syncerus caffer* and giraffe *Giraffa camelopardalis* (Pienaar 1969; Sillero-Zubiri and Gottelli 1992; di Silvestre et al. 2000). Unlike other large carnivores such as lion *Panthera leo*, leopard *Panthera pardus*, cheetah *Acinonyx jubatus* and African wild dog *Lycaon pictus*, which significantly prefer three to five prey species (Hayward and Kerley 2005; Hayward et al. 2006a, 2006b, 2006c), spotted hyenas do not exhibit a preference for any species of prey (Hayward 2006). The lack of prey preferences might be due to the hyenas' ability to hunt cooperatively in groups, to hunt alone, or to meet their food requirements through scavenging (Hayward 2006). As hyenas are very flexible in their diet, species mainly hunted were found to depend on the local abundance of prey (Cooper 1990). Furthermore, hyenas are able to quickly adapt to seasonal fluctuations of prey abundance in that they switch between herbivore species most frequently killed (Kruuk 1972; Cooper et al. 1999; Holekamp et al. 1997). Besides differences in prey abundance, variation in prey selection and prey preferences of spotted hyenas are caused by differences in hyena density (Cooper 1990). Higher predator density favors group hunts and thus larger prey species can be overcome (Kruuk 1972).

Within the Etosha National Park, Namibia, hyena densities vary largely, with clan sizes ranging from 11 to 30 animals (Trinkel 2003). In this study, I investigate the feeding ecology of spotted hyenas in two different areas and I predict that preferred prey species and hunting group sizes will be larger in areas with high hyena density.

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 (Smi-

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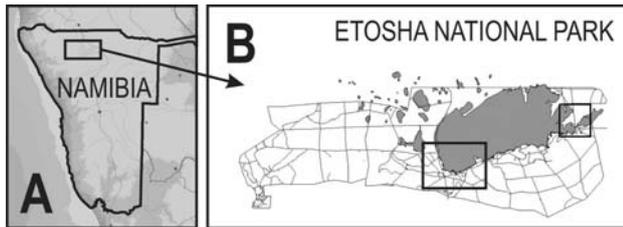


Fig. 1 Map of Namibia (a) with the Etosha National Park (b). The study areas were in the central and eastern parts of Etosha

thers 1983) in northern Namibia with its coordinates centered at 19°S, 16°E. Etosha occupies an area of 22,270 km², 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 less than 10% of Etosha's surface area. There is a wet season from January to April and a dry season from May to December. This study covered the central and eastern parts of the Etosha National Park (Fig. 1), an area of 1,490 km² (study area 1 in the center of Etosha) and 918 km² (study area 2 in eastern Etosha). The study areas contained grassy plains and adjacent woodland with *Colophospermum mopane*, *Acacia* and *Combretum* and *Terminalia* as the dominant tree species (Le Roux et al. 1988).

Hyena observations

Spotted hyenas are medium-sized carnivores (50–75 kg) that live in social groups, or clans, comprising several usually related matrilineal females. Females are philopatric (i.e., remain in their natal groups), while most males disperse (Kruuk 1972; Frank 1986; Henschel and Skinner 1991; Mills 1994; East and Hofer 2001). Each clan shares a communal den. It is estimated that there are 339 ± 176 spotted hyenas in the Etosha National Park (Trinkel 2009). The study focused on five clans of spotted hyenas: three groups in central Etosha (study area 1) and two clans in eastern Etosha (study area 2). Hyena clan sizes in these two areas differed: central Etosha clan sizes ranged from 11 to 15 adults and sub adults, whereas eastern Etosha clan sizes were two to three times larger comprising 25–30 animals (Trinkel 2003; Trinkel et al. 2004). In 2000, 2004, and 2005, hyenas were observed during the dry season between 6 weeks to 6 months per year for a total of 1,265 h. Data on feeding ecology were obtained when incidentally encountering hyenas feeding or while following the hyenas in a vehicle throughout the night, usually between 18:00 in the evening and 8:00 in the morning. A kill was defined as a prey killed by one or more hyenas. When hyenas were observed incidentally, the carcass and nearby tracks were investigated to determine whether hyenas were responsible for a kill (Kruuk 1972; Mills 1994). When hyenas and other predators, e.g., lions, were observed together at a kill, fresh blood covering heads and full stomachs were indicative

of which species had killed (Trinkel and Kastberger 2005). While following hyenas, they were viewed with binoculars aided by a red-filtered spotlight, or with an infrared sensitive camera. The study areas were subjected to high tourist pressure, and therefore hyenas and prey animals were habituated to the presence of vehicles.

To determine hyena hunting group sizes, hunting attempts and successful hunts were considered. A hunting attempt is a chase by one or more hyenas of a selected prey animal that covers at least 50 m, and a successful hunt is one in which the prey is killed by the pursuing hyenas (Kruuk 1972). The number of hyenas participating at the beginning and the end of a chase often differs (Kruuk 1972), and hunting group size was defined as the number of hyenas participating at the end of a chase.

Determination of prey density and prey preferences

Aerial surveys were conducted by the Ministry of Environment and Tourism during the dry season in 2000, 2004, and 2005 and covered the whole Etosha National Park, an area of 18,551 km², excluding the Etosha pan (Kilian and Kolberg 2004, 2005). Species included into the count were migratory ungulates such as springbok *Antidorcas marsupialis*, zebra *Equus burchelli* and blue wildebeest *Connochaetes taurinus*, as well as resident herbivores (red hartebeest *Alcephalus bussephalus*, greater kudu *Tragelaphus strepsiceros*, gemsbok *Oryx gazella*, giraffe *Giraffa camelopardalis* and eland *Tragelaphus oryx*). Both study areas were sampled at intensities of 40% (Kilian and Kolberg 2004, 2005), and prey numbers and distribution were statistically evaluated according to Jolly's (1969) method for unequal-sized sampling. In the study area in central Etosha, there were 139 ± 48 springbok/100 km², 157 ± 37 zebra/100 km², and 69 ± 28 blue wildebeest/100 km² (Fig. 2a). Resident prey species occurred at low densities of about 64 ± 24 animals/100 km² (Fig. 2b). In eastern Etosha, there were 132 ± 57 springbok/100 km², 168 ± 58 zebra/100 km², and 123 ± 71 blue wildebeest/100 km² (Fig. 2a). Resident prey species occurred at densities of about 120 ± 45 animals/100 km² (Fig. 2b).

To determine the prey preferences of spotted hyenas in both study areas, Jacobs' index was used because it minimizes the problems associated with electivity indices (Jacobs 1974; Hayward and Kerley 2005; Hayward 2006). Jacobs' index

$$D = (r - p) / (r + p - 2rp)$$

standardizes the relationship between the relative proportion that each species makes up of spotted hyena kills r and prey relative abundance p (i.e., the proportion that each species makes up of the total abundance of all censused prey species in the study area). The standardized values range from +1 to -1, where +1

indicates maximum preference and -1 indicates maximum avoidance.

Results

In Etosha, springbok was the most frequently killed prey species (40.0%), followed by zebra (32.0%), wildebeest (12.0%), kudu (12.0%), and gemsbok (4.0%). However, there were major differences in species most frequently killed by hyenas in central and eastern Etosha (Table 1). In central Etosha, most kills were springbok (61.5%; $n = 16$), followed by juvenile zebra (23.1%; $n = 6$), adult zebra (7.7%; $n = 2$) and adult wildebeest (7.7%; $n = 2$). Jacobs index shows that springbok is the pre-

ferred prey species in central Etosha, whereas regarding the abundance of zebra and wildebeest, these two species are rather avoided. In contrast, eastern Etosha hyenas most frequently killed zebra (25.0%; $n = 6$) and kudu (25.0%; $n = 6$), followed by blue wildebeest (16.7%; $n = 4$), springbok (8.3%; $n = 4$), zebra foals (8.3%; $n = 2$), and gemsbok (8.3%; $n = 2$). The prey species preferred by hyenas in eastern Etosha is kudu, whereas zebra and gemsbok seem to be taken in proportion to their abundance. Wildebeest and springbok seem to be rather avoided (Table 1).

Differences in prey selection and preferences were also reflected by differences in hunting groups sizes (Fig. 3). In eastern Etosha, where hyenas frequently hunted larger prey such as zebra and kudu, hunting group sizes (7.4 ± 4.4 hyenas; $n = 24$) were significantly larger compared to those in the center of the park (3.2 ± 1.7 hyenas; $n = 18$), where hyenas mostly preyed on springbok (Student's t -test, $P < 0.05$). Figure 4 shows that the mean hunting group sizes strongly correlated with the prey body weight (linear correlation, $r = 0.97$; $P = 7.0 \times 10^{-4}$).

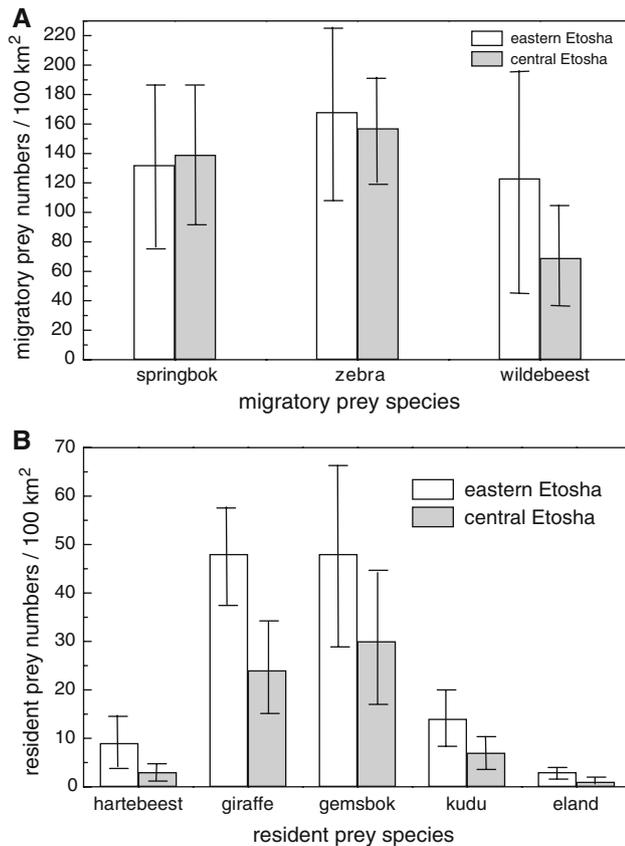


Fig. 2 Migratory and resident prey density (animals/100 km²) in central and eastern Etosha

Discussion

The main prey of Etosha hyenas are migratory herbivores such as springbok, zebra, and wildebeest. There are, however, major differences in prey preferences and prey selection of spotted hyenas within the national park. While hyenas in central Etosha mainly fed on small-sized herbivores weighing less than 50 kg, eastern Etosha hyenas hunted medium and large-sized ungulates. Similarly, Gasaway et al. (1991) found that springbok were most frequently hunted by spotted hyenas in central Etosha. In other areas in east and southern Africa, hyenas were also found to prey on medium to large-sized herbivores such as warthog and zebra foals (Cooper 1990), oryx (Mills 1994; Henschel and Tilson 1988), zebra (Kruuk 1972; Henschel and Tilson 1988) and wildebeest (Kruuk 1972). Differences in prey selection and prey preferences were mostly due to differences between the compositions of herbivore populations (Cooper et al. 1999). However, hyenas also respond to altered prey compositions in that they switch between preferred herbivore species. For example, in the Masai Mara National Reserve, Kenya, prey availability

Table 1 Spotted hyena kills in central and eastern Etosha

Species	Central Etosha		Eastern Etosha	
	No. of kills	Jacobs index	No. of kills	Jacobs index
Springbok	16	0.47 ± 0.13	4	-0.60 ± 0.16
Zebra	2 (6) ^a	-0.28 ± 0.06	6 (2) ^a	-0.04 ± 0.04
Blue Wildebeest	2	-0.49 ± 0.08	4	-0.23 ± 0.11
Kudu	0	–	6	0.74 ± 0.12
Gemsbok	0	–	2	-0.12 ± 0.13

^aAdult (juvenile)

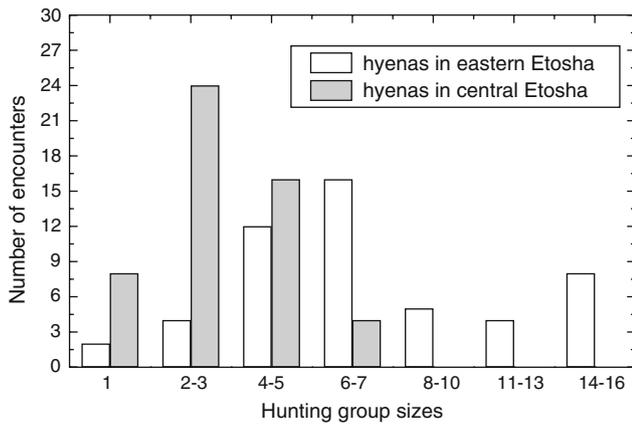


Fig. 3 Encounters with groups of spotted hyenas actively hunting

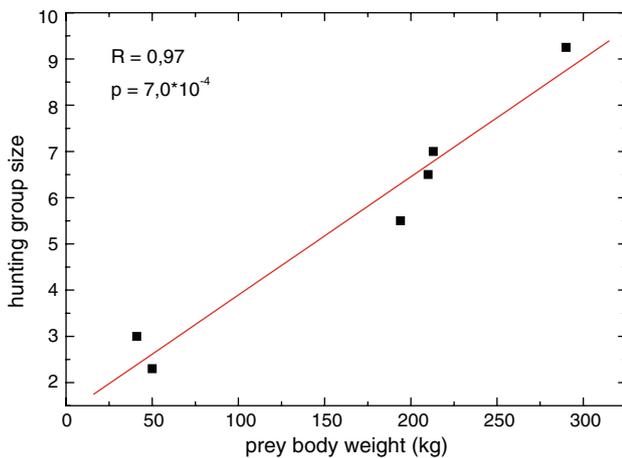


Fig. 4 Hyena hunting group size and prey body weight. The regression graph $y = 1.34x + 0.03$; $R = 0.97$ reflects a linear correlation between the hyenas' hunting group size and the body weight of their prey (kg)

varied seasonally, and hyenas tended to hunt whichever prey species were most abundant during each month of the year (Holekamp et al. 1997; Cooper et al. 1999). Similar observations were made by Kruuk (1972) and Cooper (1990) who found that seasonal fluctuation in prey abundance influenced spotted hyenas' prey preferences. Höner et al. (2002) reported a functional response of spotted hyenas in the Ngorongoro Crater, Tanzania, in that hyenas responded to long-term changes in prey populations: changes in prey abundance between the 1960s and 1990s led to increased predations of buffalo calves and adult wildebeest (Höner et al. 2002). Because of the hyenas' dietary flexibility, Hayward (2006) did not find any preferences when he analyzed preferred prey species of spotted hyenas from 15 study sites. Hayward (2006) argued that the hyenas' behavioural opportunism was the reason for the lack of prey preferences in this comparative study.

In Etosha, prey densities in both study areas were similar, and therefore differences in prey abundance cannot be the reason for the hyenas' differences in prey

selection. Rather than differences in prey abundance, hyena densities between central and eastern Etosha varied significantly (Trinkel 2009). The adaptation to hunt larger ungulates in eastern Etosha seems to be caused by differences in hyena clan sizes: while hyenas in eastern Etosha live in clans of 25–30 animals, clan sizes of hyenas in central Etosha are only a third to half the size compared to their conspecifics in the eastern part of the park. Therefore, hyenas in eastern Etosha are able to hunt in larger groups and to overcome large prey such as zebra. Similarly, Kruuk (1972), Cooper (1990), and Holekamp et al. (1997) reported that hyenas generally formed larger groups to hunt zebra and wildebeest than to hunt smaller ungulates. Kruuk's (1972) mean size for groups hunting zebra was 12, and Cooper (1990) reports that at least five hyenas were needed to kill zebra in Chobe, Botswana. Thus, the hyenas' ability to hunt alone or to hunt cooperatively in groups to satisfy their dietary requirements makes them very flexible, and therefore, for every region, the effect of hyenas as predators of a particular species will depend on hyena population density and the number of prey species available to the hyenas.

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