Demography of Spotted Hyaenas in an arid savanna, Etosha National Park, South West Africa/Namibia

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ABSTRACT

Spotted hyaena *Crocuta crocuta* demography was studied in Etosha National Park, South West Africa / Namibia. In central and eastern Etosha, spotted hyaenas were most abundant in areas occupied by the migratory plains ungulates, e.g. zebras *Equus burchelli*, springbok *Antidorcas marsupialis*, wildebeest *Connochaetes taurinus*. Hyaena density (5 adults and subadults/100 km²) estimated in a portion of the migratory plains ungulate range was low compared with densities reported from most other conservation areas. The three study clans had at least 15 adults and subadults each and used large home ranges ($\bar{x}$ = 360 km²); large home ranges were likely adaptations to the patchy and temporally variable food distribution and widely scattered permanent waterholes. We observed no territorial behaviour by hyaenas while tracking them at night. Most dens were under calcrete slabs and small tunnels provided protection for cubs.

INTRODUCTION

The decline of Burchell's zebras *Equus burchelli* and blue wildebeest *Connochaetes taurinus*, beginning during the 1960's in Etosha National Park (Etosha), South West Africa/Namibia, raised concerns about the future of these two species and predators/scavengers that fed on them (Berry 1981a, 1982). Before the decline, Burchell's zebras (zebra) and wildebeest composed ≥80% of the ungulate biomass inhabiting Etosha's plains (Berry & Louw 1982a). An additional concern was that declining large mammal populations could adversely affect tourism.

The decline of zebras and wildebeest created a management problem that involved hyaenas in two ways. First, as predators (Kruuk 1972; Tilson *et al.* 1980; Mills 1984a; Henschel 1986), hyaenas may have contributed to the decline or continued low density of zebras and wildebeest (Sinclair 1985). Second, maintenance of Etosha's hyaena population is a conservation issue because hyaenas are uncommon in South West Africa/Namibia (SWA/Namibia) outside Etosha. If Etosha's hyaena population depends somewhat upon zebras and/or wildebeest for food as in the Serengeti, Ngorongoro, and Namib Desert (Kruuk 1972; Tilson *et al.* 1980), hyaenas may decline to low densities.

This paper provides baseline demographic data on hyaenas in the zebra and wildebeest range of central Etosha, and it describes relative hyaena densities throughout Etosha. Additionally, we describe adaptations of hyaenas to the patchy and temporally variable distribution of food and the widely scattered permanent waterholes.

STUDY AREA

Our extensive study area was Etosha with an intensive study area that included the large plains on the south and southwest edge of Etosha Pan and the adjacent Etosha Pan and woodlands (Figure 1). Vegetation is classed as arid savanna (Huntley 1982). Etosha's history, climate, vegetation, soils, geology, and management were reviewed by Berry (1980).

METHODS

Distribution and relative abundance of hyaenas throughout Etosha were based on counts at waterholes during dry seasons (May–October) and on incidental observations. The mean number of hyaenas seen at 56 waterholes during a total of 370 24-hour full moon counts from 1979 to 1986 was used as an index of local hyaena abundance (unpubl. data, Etosha Ecological Institute).

To investigate clan and home range size, 10 hyaenas in three clans were collared during April and May 1986. Eight hyaenas were radio-collared: two subadult males (Leubron clan); an adult female and adult male (Gemsbokvlakte clan); and a subadult male, adult male, and two adult females (Rietfontein clan). A subadult female and adult female were fitted with numbered neckbands (Rietfontein clan). We immobilized hyaenas with 630 mg Ketamine hydrochloride (Ketalar, Parke-Davis) and 300 mg xylazine hydrochloride (Rompun, Bayer) injected with 3 cc dart from a Cap-Chur rifle (Palmer Chemical and Equipment Co.). The antagonist, tolazoline hydrochloride (Weimer Pharmaceuticals, Rastatt, West Germany) was injected intramuscularly after 1–1,5 hours (4 mg/kg body weight; van Wyk and Berry 1986).

Home ranges for April through August 1986 were delineated from direct observations during aerial and ground tracking of radio-collared hyaenas. Daytime aerial locations (n = 238, 25 – 37/hyaena) were made from a Super Cub aircraft at intervals ranging from twice daily to once per week from 16 April to 17 August 1986, except for two intervals of 10 and 14 days. We followed radio-collared hyaenas with a vehicle on 25 nights and used the hyaena's starting and most distant points during each night to delineate home range. Incidental sightings of radio-collared hyaenas collected from September through December 1986 were used to describe duration of home range use.

Home range area for radio-collared individuals and for radio-collared clan members combined was estimated by fitting a convex polygon to the outermost locations (Mohr 1947). Three locations of radio-collared hyaenas were excluded from the home range calculations but are reported; each location was >10 km outside the home range polygons reported here.

The minimum number of adults and subadults in study clans was the maximum number of hyaenas accounted for at one time. Furthermore, we estimated the number of adults and subadults in the Rietfontein clan using a Petersen index (Seber 1982); the ratio of marked (four radio-collared, two neck-banded, and one recognizable individual) to unmarked hyaenas was obtained while following radio-collared hyaenas during 10 nights from 10 through 21 June 1986.

The distribution of migrant prey (zebra, wildebeest, and springbok) in study clan home ranges during green and dry grass seasons was based on mid-monthly surveys along specified roads from September 1985 through August 1986 (T. Nott, M. Lindeque, P. Lindeque, unpubl. data), an aerial survey during March and another during April 1986, and incidental ground and aerial observations. Areas in central and eastern Etosha were assigned one of four relative density categories during green and dry grass periods.

To assist in comparing hyaena distribution to prey abundance throughout Etosha, dry season distribution and density of eight prey species were estimated from an aerial survey of Etosha during August and September 1984 (Berry 1984). Prey distribution during this survey was typical of the distribution during the 1986 dry season when no Etosha-wide survey was flown.

RESULTS

Hyaena demography

Relative hyaena density varied widely in Etosha (Figure 1). Hyaena densities were generally highest where prey were abundant and lowest where prey were scarce (Figure 1 – 3). Study clans were in the intermediate hyaena density area. Because few waterhole counts were available in the Leeubron clan home range, we classed its range as intermediate density based on frequent observations of hyaenas and on estimated density in relation to the other study clans (Table 1).

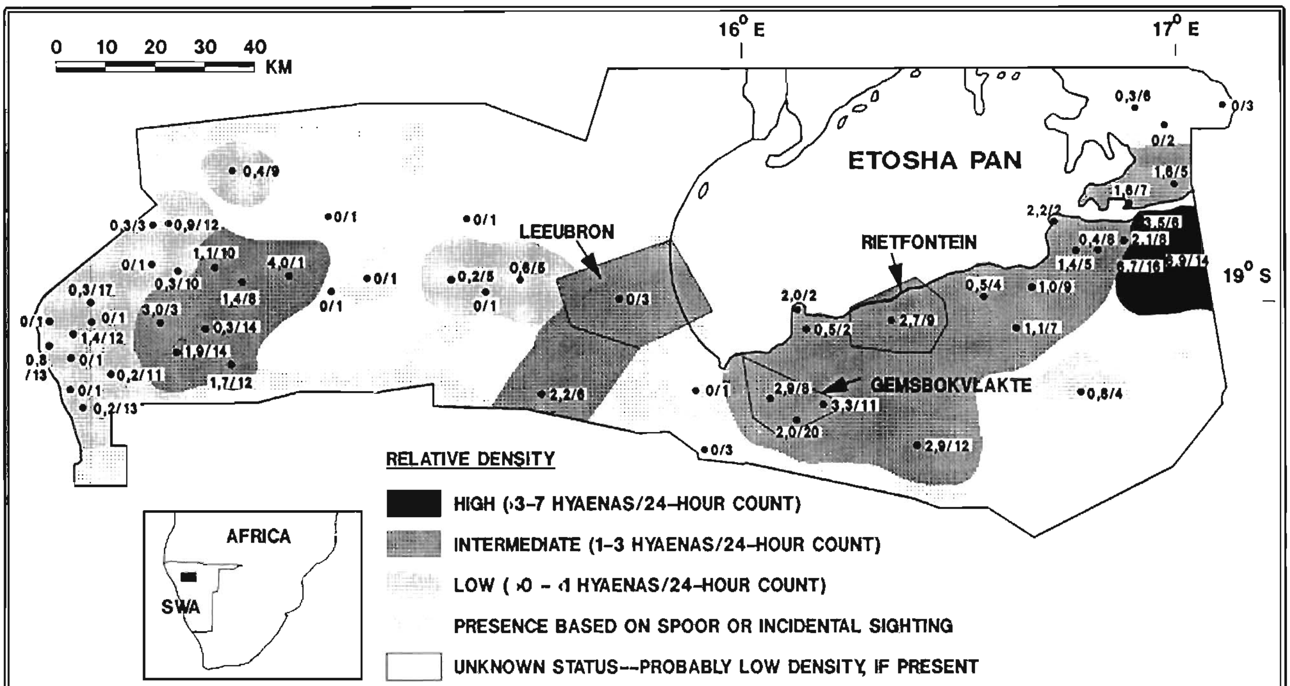

FIGURE 1. Distribution and relative density of spotted hyaenas in Etosha National Park based on the mean number of hyaenas seen at 56 waterholes (●) during 24-hour counts over 370 full moon periods (May 1979 – Sep. 1986) on an incidental observation (Jan. 1983 – Sep. 1986). Values next to waterholes are the mean number of hyaenas observed per 24-hour count and the number of counts, i.e., mean/n. Observed home ranges of the Leeubron, Gemsbokvlakte, and Rietfontein study clans are indicated by solid lines.

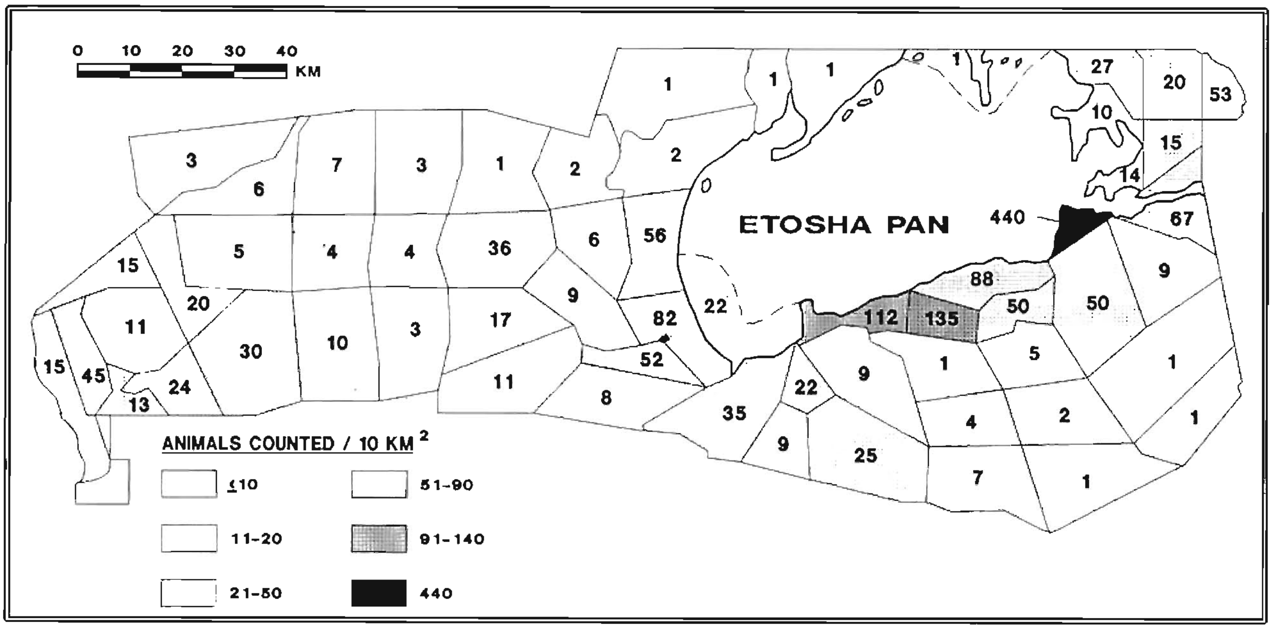

FIGURE 2. Dry season density (animals/10 km²) of Burchell's zebra, Hartmann's zebra *E. z. hartmannae*, springbok, gemsbok, wildebeest, hartebeest, kudu, and ostrich observed during an aerial survey, August–September 1984, in Etosha National Park (from Berry 1984).

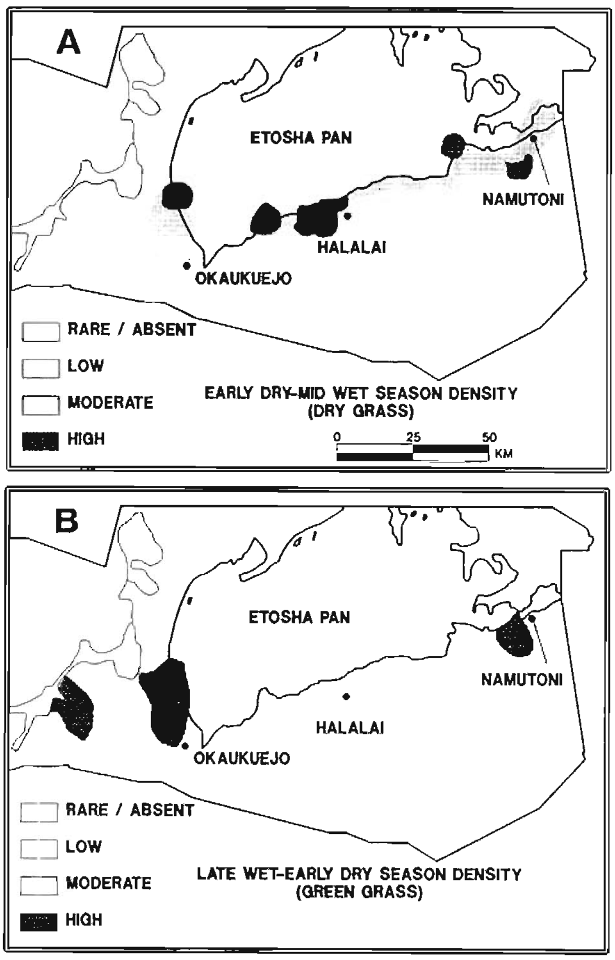

FIGURE 3. Seasonal distribution and relative density of Burchell's zebra, wildebeest, and springbok in Etosha National Park (Apr. 1985–Aug. 1986) during (a) early dry through mid wet seasons when primarily dry grasses are available (May–Jan.) and (b) late wet to early dry season when primarily green grasses are available (Feb.–Apr.). Small within-season fluctuations in distribution and density also occurred but are not reflected in these figures.

Observed home ranges for study clans averaged 360 km² (Table 1, Figure 4). Gemsbokvlakte and Rietfontein clan home ranges may have been underestimated because daytime locations tended to clump in the central portion of home ranges and clan home ranges were estimated from a small proportion of the clan members. Estimated clan home range increased with the number of hyaenas radio-collared (Figure 4, Henschel & Skinner 1987). The large Leeubron home range was the result of a subadult male that may have been making predispersal movements (Henschel & Skinner 1987).

The minimum number of adult and subadult hyaenas in study clans was 15 or 16 (Table 1). The mark-recapture estimate for the Rietfontein clan was 23.

Mean estimated hyaena density was 5/100 km² in study clan home ranges (Table 1). This density may approximate hyaena density in the intermediate density area near Etosha Pan (Figure 1).

Land tenure system

We observed no territorial behaviour by hyaenas in study clans. No pasting, latrines, or interclan strife were observed during the night-tracking of hyaenas, nor were latrines located during daytime. Confirming the scarcity of latrines, P. Stander located only three latrines while extensively walking and driving in our study clan ranges and other portions of Etosha from 1982 through 1987.

Our study clans lived in discrete home ranges (Figure 4) most of the year, and they may have been year-round residents. After the intensive tracking period (April–August 1986), incidental observations of collared hyaenas suggest the Leeubron, Gemsbokvlakte, and Rietfontein clans occupied their ranges through

TABLE 1: Estimated number and density of adult and subadult spotted hyaenas in home ranges of three clans in Etosha National Park, March – August 1986.

Clan	Observed home range (km^2)	Number of hyaenas: Known minimum (Mar–Aug 1986)[a]	Known minimum (Dec 1982–Aug 1986)[b]	Estimated number	Density in home range (hyaenas/100 km^2)[c]
Rietfontein	320	16	16	23 (15 – 35, 80% CI)	7
Gemsbokvlakte	200	9	15		8
Leeubron	550	8	15		3
Mean	360	11	15		5

[a] Maximum number observed or accounted for at one time.

[b] Maximum number observed or accounted for at one time; observation was June 1986 for Rietfontein, December 1982 for Gemsbokvlakte, and March 1985 for Leeubron.

[c] Calculated by dividing estimated number of subadults and adults by home range area and multiplying by 100. We assumed 15 hyaenas in the Gemsbokvlakte and Leeubron clans.

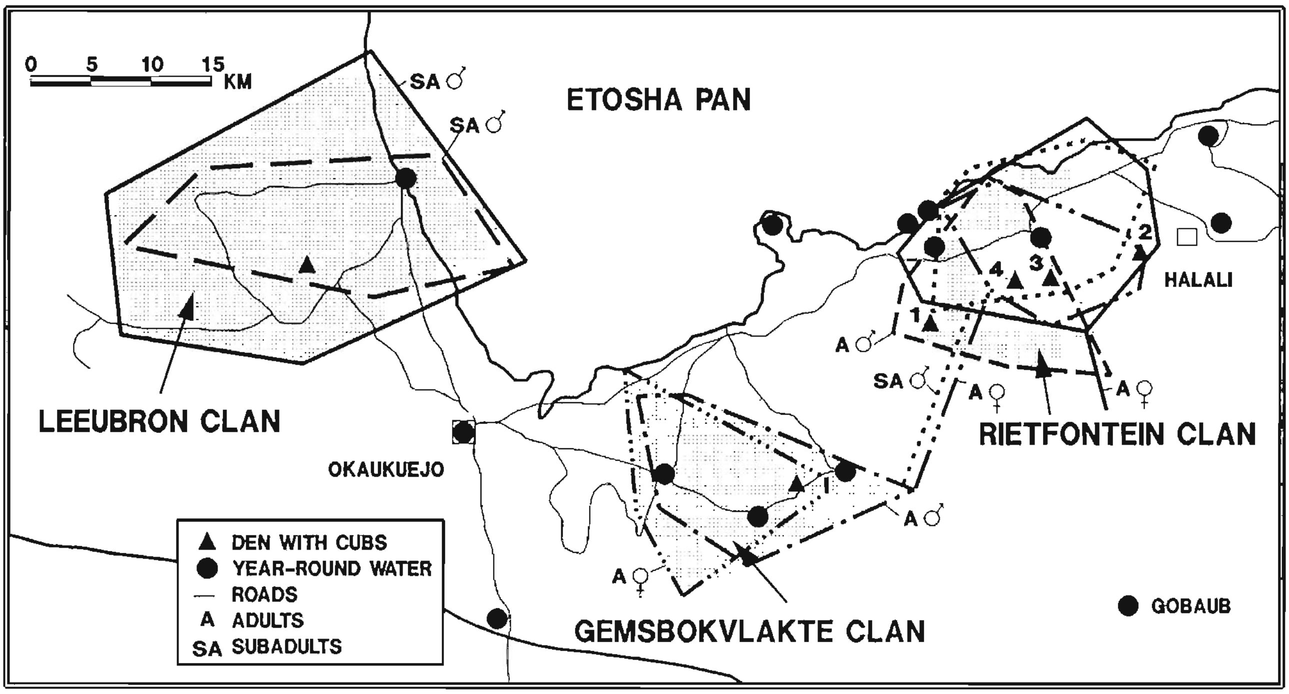

FIGURE 4. Estimated observed home ranges for individual radio-collared spotted hyaenas (coded lines) and for study clans (shaded areas) in Etosha National Park, April–August 1986.

October, December, and December 1986, respectively. Also, observations and spoor of hyaenas in these home ranges during other months suggest the clans may be resident.

Observed home ranges provided requirements for year-round occupancy by hyaenas. Home ranges contained year-round water (Figure 4) and resident woodland prey (gemsbok *Oryx gazella*, kudu *Tragelaphus strepsiceros*, hartebeest *Alcelaphus buselaphus*, giraffe *Giraffa camelopardalis*, steenbok *Raphicerus campestris*, and ostrich *Struthio camelus*) that provided a low density (about 7 animals counted/10 km^2 during an aerial survey) food base when plains migrants were scarce or absent in the Gemsbokvlakte and Rietfontein clan ranges (Berry 1984).

Dens and denning behaviour

Most dens in the home ranges of the study were dug under a fractured surface layer of calcrete and were in mopane shrub or woodland (Table 2). Only one den was dug primarily in soil.

The Rietfontein, Leeubron, and Gemsbokvlakte clans were observed with cubs at four, one, and one den(s), respectively, during April through August 1986 (Table 3, Figure 4). However, clans may have had more dens than we located. The probability of us locating a den increased with the number of radio-collared hyaenas in a clan because radio-collared hyaenas were not observed at all known dens; examples are given for the Rietfontein clan (Table 3). The Rietfontein clan simultaneously used at least two dens 17 km apart. Den

TABLE 2: Description of 10 dens in and one den near the home ranges of Leeubron, Gemsbokvlakte and Rietfontein spotted hyaena clans in Etosha National Park, 1986.

Construction	Number of dens observed	Number of entrances				Number in habitat type		
		x̄	SD	Range	n	Plains-pan edge junction	Acacia thickets	Mopane shrub or woodland
Dug under calcrete	10	2,3	2,0	1 – 7	8[a]	1	3	6
Dug in soil	1		–[a]			0	0	1

[a]Number of entrances could not be accurately counted on two dens seen only from aircraft.

TABLE 3: Use of dens by Rietfontein clan cubs from 10 June through 17 August 1986 in Etosha National Park. Den locations are shown on Figure 4.

Den number	Minimum period of use	Minimum number of cubs	Cub size (proportion of adult size)	Age, sex, and identifier of radio-collared hyaenas located at den[a]	Comments
1	10 Jun – 20 Jun	2	0.50	SAM-H3, AM-H9	
2	10 Jun – 22 Jun	2	0.25	AF-H10	Not lactating[b]
3	3 Jul – 17 Aug	2 2	0.25 0.25	SAM-H3, AF-H6 AM-H9, AF-H10	Females not lactating[b]
4	24 Jul – 17 Aug	1	neonate	AF-H6	Parturition den for H6

[a] Adult = A, subadult = SA, female = F, male = M; individual hyaena identifier is H followed by a number, e.g., H3.

[b] Females are not the mothers of cubs seen at den.

number 3 was the only confirmed communal den, i.e. contained more than one litter.

DISCUSSION

Adaptations to a patchy and temporally variable environment

Three factors caused the patchy and variable distribution of food and water in Etosha. First, migratory ungulates comprised most of the prey biomass and their movements were sensitive to specific habitat types and to the grass distribution resulting from erratic rain distribution (Berry 1980, 1981a, 1984; T. Nott & P. Stander, unpubl. data). Second, anthrax and rabies among herbivores contributed seasonally, annually, and spatially variable quantities of carrion to hyaenas (Ebedes 1976; Berry 1981b; P. Lindeque, M. Lindeque & H. Berry, unpubl. data). Finally, permanent dry season water sources were scarce and clumped in distribution (Berry & Louw 1982b; Figures 1 & 4).

The study clans coped with the patchy and variable resources by using large home ranges. This land use pattern conforms with the conclusions of Macdonald (1983), Mills (1984a), Henschel (1986) and Tilson & Henschel (1986) that home range size is dependent upon the dispersion of resources. Home range sizes of Etosha's clans were exceeded only by those in the Kalahari and Namib Deserts where food and water were scarce and widely dispersed (Mills 1984a; Tilson & Henschel 1986; Table 4). Where resources were stable, abundant and relatively uniformly distributed, home ranges or territories were small (Ngorongoro, Mara, Umfolozi, Kruger, Hluhluwe) compared with those in Etosha (Table 4).

Hyaena densities range widely in Africa (Table 4) and are related to availability of resources. Compared with most other areas, Etosha has both low prey biomass (Berry 1981b) and low hyaena density in study clan ranges. Moreover, the overall density for Etosha was probably less than in study clan ranges because of the large areas of low hyaena density (Figure 1).

Territorial behaviour

Territorial behaviour ranges from rare to intense among hyaena populations. For example, we observed no territorial behaviour in our study animals, and it was rare in the Mara during a nine year study (Frank 1986, pers. comm.). In contrast, intermediate levels of territorial marking occurred in the Kalahari (Mills 1984a; Mills & Gorman 1987) and the Namib (Tilson & Henschel 1986) while intense competition for space occurred in Ngorongoro (Kruuk 1972) and Kruger (Henschel 1986). Infrequent territorial behaviour in the Mara occurred because adjacent clans rarely met (Frank 1986, pers. comm.); each clan usually remained in a core area containing high prey densities which was surrounded by an area with few prey. The intense competition for space in Kruger and Ngorongoro may result from frequent contact between clans using small home ranges where food resources are more evenly distributed than in Etosha, Mara, Kalahari, and Namib.

Dens and denning behaviour

Dens used by the study clans offered protection from predators. Den entrances and/or tunnels were too

TABLE 4: Clan size, home range or territory area, and density of adult and subadults reported for spotted hyaenas in Africa.

Area	No. of clans	Mean no. of adult and subadult hyaenas/clan	Mean home range or territory (km^2)	Mean density (hyaenas/ 100 km^2)	Reference
Ngorongoro, Tanz.	8	54	30	170	Kruuk 1972
Serengeti, Tanz.		– [a]		12	Kruuk 1972
Mara, Kenya	1	52	60	86	Frank 1986
Savuti, Bots.	2	28			Cooper, unpubl. data
Etosha, SWA	3	>15	360	5	This study
Umfolozi, RSA	1	14	39	36	Whateley 1981
Timbavati, RSA	1	11	>25	<44	Bearder 1977
Kruger, RSA	4	10	130	9[b]	Henschel 1986
Kruger, RSA				7–20[c]	Mills 1985b
Hluhluwe, RSA	3	9	13	46	Whateley and Brooks 1978
Kalahari Desert, Bots.	6	8	1 250	0,6	Mills 1984a
Namib Desert, SWA	3	4[d]	570	0,7	Tilson and Henschel 1986

[a] Hyaenas did not form clearly defined clans.

[b] Density was artificially lowered by culling during the 1970's; density was 2–3 times greater before culling (Henschel 1986).

[c] May be artificially lowered as a result of hyaena culling in a portion of Kruger; also, see Henschel (1986). Densities reported were minimum and maximum estimates.

[d] Including "young cubs" that accompanied adults. In other areas, young cubs did not travel with adults, hence, group size was only based on subadults and adults.

small for adult or subadult lions and adult hyaenas to enter or penetrate deeply, and protective tunnels continued beyond our view.

Residential hyaena clans typically use a communal den that houses all litters of a clan, except for short-term parturition dens (Kruuk 1972; Mills 1978, 1984a; Frank 1986; Tilson & Henschel 1986; Mills & Gorman 1987). The Rietfontein clan deviated from this generalization by simultaneously using at least two widely spaced nonparturition dens (Table 3; Figure 4).

CONCLUSION

1. In central and eastern Etosha, hyaenas were most abundant in the major areas used by migratory plains ungulates (zebras, wildebeest, and springbok).

2. Study clans contained ≥15 adults and subadults each and were intermediate in size compared with clans elsewhere in Africa.

3. Hyaena density was low and clan home ranges large in Etosha compared with most other areas. In concurrence with Macdonald (1983), we suggest that hyaenas maintained large home ranges as an adaptation to the patchy and temporally variable distribution of food and the widely scattered permanent waterholes.

4. Study clans appeared to invest little effort in territorial behaviour.

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