

SPATIAL ARRANGEMENT OF SPOTTED
HYAENA GROUPS IN A DESERT ENVIRONMENT, NAMIBIA

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SUMMARY

Spatial organisation of spotted hyaenas (Crocuta crocuta) in the central Namib Desert, SWA/Namibia was determined during a 21-month study (1977-1979). Clans of three, four and five adults occupied mutually exclusive home ranges that had no overlap at boundaries. Group home ranges averaged 570 km² (range = 383-816 km²). Core areas containing breeding dens, lairs, and water sources were scent-marked with faeces (= latrines), anal gland deposits (= pasting) and inter-digital gland deposits (scratch marks). Intergroup encounters and associated territorial behaviours described for East African hyaena populations were not observed in the Namib hyaena population. We suggest that small group size, large home range and temporal distribution pattern of spotted hyaenas in the central Namib are an adjustment to a dispersed, depauperate prey assemblage and limited availability of water and shelter that are characteristic of this desert environment.

INTRODUCTION

Next to lions, spotted hyaenas (Crocuta crocuta) are the second largest social carnivore in Africa. Where spotted hyaenas have been studied, they have been reported to feed on medium to large sized ungulates (Eloff, 1964; Kruuk, 1972; Bearder, 1977; Mills, 1985; Frank, 1985; Henschel, pers. comm.) For Namib Desert populations of spotted hyaenas, gemsbok (Oryx gazella) and mountain zebra (Equus zebra hartmanae) are the most important prey (Tilson, von Blottnitz & Henschel, 1980; Skinner & van Aarde, 1981). Further, as a result of the Namib's low rainfall of less than 15mm per year (Gamble, 1980) and corresponding sparse vegetation biomass (Seely, 1978a; 1978b; Seely & Louw, 1980), herds of these species are small and dispersed.

Spotted hyaena social and spatial organisation is based upon Kruuk's (1966; 1972) study in the Ngorongoro Crater and Serengeti Plains, Tanzania. Under conditions of high prey density and stability, hyaenas associated together in large territorial clans. Territories were marked at the periphery with huge accumulations of faeces (= latrines), anal scent markings (= pastings) and inter-digital gland deposits (= scratch marks). These territories were stable with only slight shifts in boundary positions. Where large fluctuations in prey numbers occurred, hyaenas associated in smaller temporary groups that formed wherever ungulates were concentrated; breaking up again when the prey left the area. Territories were less precisely defined. Rather than scent mark

boundaries, hyaenas marked routes which they travelled over long distances in search of game. These hyaenas tended to return to the same areas, indicating a degree of site fidelity. Where there were constant but low densities of both hyaenas and ungulates, hyaenas formed small, stable clans (Kruuk, 1972; Breader, 1977; Whateley and Brooks, 1978; Whateley, 1981). There are also nomadic hyaenas, which apparently follow herds as they migrate (Kruuk, 1972).

Here we describe the spatial organisation of spotted hyaenas in the desert environment of South West Africa/Namibia and compare their characteristics with those of the same species living at much greater population densities in savanna and woodland environments of East and South Africa respectively. We suggest that small group size, large home range and temporal distribution pattern of spotted hyaenas in the central Namib are: 1) an adjustment to the low population density of a depauperate prey assemblage and 2) a reflection of the dispersed and isolated location of shelter and water along a linear oasis. We also indicate how the characteristics of this desert environment may have influenced the hyaena's social and spatial organisation (see also Macdonald, 1983; Tilson & Hamilton, 1984).

STUDY AREA

The study area includes 3,080 square kilometers within the Namib-Naukluft Park, SWA/Namibia, where the Kuiseb River has incised a deep, narrow gorge through the Namib Desert (Fig. 1). South of the

canyon lies a vast tract of sand dunes lacking any free water. Resident mammalian species there relevant to this study include a dispersed population of gemsbok (32/100 km²) that feed upon perennial and annual grasses, tubers, and bulb (Hamilton, Buskirk and Buskirk, 1977) and small herds of springbok (Antidorcas marsupialis; 5/100 km²), which follow the sporadic rains and subsequent grass flushes into the fringes of the dunes. Rocky, sparse grasslands north of the canyon are the preferred habitat of mountain zebra (20/100 km²). Other ungulates living within the confines of the canyon are klipspringer (Oreotragus oreotragus; 4/100 km²) and steenbok (Raphicerus campestris; 2/100 km²). More detailed descriptions of the area are presented elsewhere (Hamilton et al., 1976; Tilson, 1980; Tilson et al., 1980)

Austral summer rains in the central highlands 400 km to the East produce a temporary and unpredictable summer surface water flow through the Kuiseb Canyon, where water is available throughout the year in small, isolated pools. Down river from the canyon there is a decreasing gradient of water, but an increasing gradient of food resources for herbivores, extending from marginal to abundant (Hamilton & Tilson, 1982). During summer droughts, growth of the perennial grasses away from the canyon slows and the food supply for these herbivores throughout the Namib Desert declines, forcing them to congregate near the river (Hamilton et al., 1977).

METHODS

Observations began in July 1977 and continued until March 1979. They include 692 observation hours of known individuals (see Tilson & Hamilton, 1984). Due to the steeply dissected and rugged terrain, foraging hyaenas could not be followed and observed. Some data on ranging patterns were obtained by following tracks, by searching the dune field with vehicles, by observing a series of water holes and by censusing the sandy river bed (see Tilson, 1980; Tilson & Kok, 1980; Tilson et al., 1980).

There are no other large predators in the central Namib. For this reason all ungulate deaths by predation were attributed to hyaenas. Other resident predators included black-backed jackals (Canis mesomeles), silver fox (Vulpes chacma), bat-eared fox (Otocyon megalotis) and caracal (Felis caracal), none of which prey on large ungulates. Even when hyaenas left carcasses unattended (e.g., daylight hours and during periodic absences at night), jackals and other predators seldom fed upon them (see also Stuart, 1976). Two species of large vultures (Torgos tracheliotus and Gyps coprotheris) occur in the study area, but seldom visited carcasses observed by us.

During 12 months, we routinely censused the dune field south of the Natab den area. Whenever we discovered a carcass, it was examined for hyaena damage, as hyaenas splinter long bones in a characteristic fashion (Henschel, Tilson & von Blottnitz, 1979). Active hyaena sites were then identified on a field map drawn from aerial photographs. We could thus locate a carcass to less than 0.5 km on our map (Fig. 1).

other carcasses not fed on by hyaenas were also mapped. This information, together with observations of foraging patterns, gave us an approximation of hyaena group home ranges.

RESULTS

Clan Size

In the Namib Desert, spotted hyaenas forage and feed in small, dispersed social units. We identified three hyaena clans along 75 km of the Kuiseb River Canyon, comprised of three, seven and eight individuals, respectively for an average of six individuals per clan. The Natab clan consisted of two adult females, two males, and an unsexed subadult who associated with them for varying intervals. One female gave birth to two cubs in November, 1977; the other female bore a single cub in April, 1978. The Nareb clan of three adults, which did not raise any cubs during the study, lived 35 km upriver from Natab. Another 45 km upriver from Natab lived the Zebra Pan clan of seven individuals; five adults and two cubs presumed to be siblings approximately 15 months old (see Fig. 1). The Nareb and Zebra Pan clans remained intact during the study; the Natab clan broke up and dispersed in September 1978 when its only source of water dried up.

Group Size: Foraging vs. Feeding

Spotted hyaenas in Timbavati, South Africa (Bearder, 1977), the Serengeti, East Africa (Kruuk, 1972), and the Namib usually foraged

solitarily but assembled at carcasses to feed. On only 9.7% of occasions when Namib hyaenas were seen moving about were more than three individuals together. By contrast, 68.4% of observations at carcasses were of more than three hyaenas (Table 1). Tracks at all freshly-killed carcasses indicated that two or more individuals were involved in the chase. In nights following the kill, hyaenas usually returned alone and met other clan members at the carcass. Young cubs always accompanied their mothers. Food was not the only attraction for hyaenas at carcass sites, because clan members remained in the vicinity to socialize for long periods of time (up to 12 hours) before departing together or singly (Tilson & Hamilton, 1984).

Home Range

Each spotted hyaena clan centered its activities at specific sites along the edge of Kuiseb River Canyon. These sites, which we term core areas, were characterized as having breeding dens, shady day-time lairs, and permanent access to waterholes, water seeps or running water. Our observations showed that hyaenas always ($N = 72$) returned to core areas at dawn, rather than remain in the vicinity of remote carcasses out in dune areas where there was little or no access to shade. Core areas of adjacent groups were separated by linear distances of from 20 km (Natab-Nareb) to 35 km (Nareb-Zebra Pan).

The location of clan home range boundaries was indicated by the outermost sites where hyaenas from a clan were observed feeding on carcasses or foraging for prey (Fig. 1). The space enclosed within

these boundaries was on the average 570 km²; 816 km² at Natab, 514 km² at Nareb and 383 km² at Zebra Pan. These home ranges were, on average, 20 times greater than spotted hyaena territories reported in Ngorongoro Crater (Kruuk, 1972) and twice the size of brown hyaena (Hyaena brunnea) territories (330 km²) in the Kalahari Gemsbok Park, South Africa (Mills, 1981; 1982; 1983). Boundaries between the home ranges of adjacent clans were separated by up to 15 km.

Maximal linear distance from the Natab core area to outer carcasses was approximately 30 km. Gemsbok carcasses at greater distances from the core area were not fed on by hyaenas (Fig. 1). Thus, for the Namib population of hyaenas, a round trip distance of 60 km was within their range; 80 km was beyond it. By comparison, spotted hyaenas in the Kalahari Gemsbok Park, South Africa, reportedly travelled up to 40 km from their dens to obtain food and returned to them during the same night (Eloff, 1964). Other long distance excursions are reported for spotted hyaenas in the Hluhluwe Game Reserve, South Africa (Whateley & Brooks, 1978), and in the Serengeti Plains (Kruuk, 1972).

Scent marking of the home range by Namib spotted hyaenas (i.e., placement of latrines, pastings, and scratch marks) was concentrated in core areas and on trails that fan out from them. At Natab most scats (97 of 118; 91%) were within 200 m of the den area. A similar situation was found at Nareb (202 of 281; 72% were within 200 m of the den). Home range boundaries were marked less extensively. This is similar to the situation reported for spotted hyaenas in the Serengeti (Kruuk 1972) and comparable to the way brown hyaenas mark their

territories in the Kalahari (Mills, Gorman & Mills, 1980). Namib spotted hyaenas often pasted, defecated or urinated in the vicinity of carcasses. The smell of these scents elicited other group members to mark on the same site. On average six (range = 2-18) scats were found at 16 carcasses located in the Natab home range. The combination of these marking behaviours, scats at abandoned carcasses and associated scent marks, probably represent signposts of a hyaena clan's home range.

Intergroup Contacts

During 67 observation nights at carcasses, no interclan interactions were noted. Three carcasses provisioned by us in between home ranges were left uneaten for periods of three to seven days, after which we moved them closer to core areas (see Fig. 1), demonstrating that these areas were not regularly visited.

Clans were considered to be largely exclusive, but movement between clans occurred occasionally. On one occasion we found a recently dead unidentified subadult male with a deep hyaena inflicted bite on the neck. His stomach contained a freshly consumed adult female klipspringer minus the skull and cervical vertebrae found nearby. From tracks we deduced the hyaena arrived in the Nareb clan's core area, caught and ate the klipspringer, and immediately afterwards was killed by the Nareb hyaenas. Two nights later, two members of this clan returned and devoured him. On other occasions, a subadult of unknown origin successfully joined the Natab clan, and an adult male of the Natab group associated with the Nareb clan for five

nights, fed alongside them, and later returned to Natab. In both instances, the interlopers were tolerated, but subjected to periodic harassment by one or more resident clan members.

Late in the study, the Natab clan was forced to disperse when the only waterhole near their den became dry. One adult female abandoned her three month old cub and together with a subadult male joined the Nareb clan. The other adult female and her two ten-month old cubs moved to an open waterhole near the eastern boundary of their home range. The other two males were never seen again.

Discussion

Spotted hyaenas living along the linear oasis of the Kuiseb River showed a high degree of site fidelity, but seasonal fluctuations of limited resources precluded the development of stable territorial hyaena clans. Although Namib spotted hyaena home ranges were large, distinct and essentially exclusive, some interchange of individuals, especially males, occurred between clans. However, intruders were sometimes confronted and attacked. The presence of temporarily nomadic solitary males on the northern gravel plains suggests that some hyaenas, especially males, survive in marginal habitat, where conditions are not suitable for the existence of clans.

The population density of Namib spotted hyaenas appears regulated by a combination of factors, including resource availability affecting recruitment rate (success in rearing young), intensity of competition, especially when new individuals attempt to join another clan, and local dispersion or aggregation of clan members. Elsewhere we (Tilson

et al., 1980; Tilson, 1983; Tilson and Hamilton, 1984) and others (Skinner & van Aarde, 1981) suggest that clan cohesion and hunting cooperatively permit spotted hyaenas to exist in the Namib. Here we suggest that these clans must be flexible to accommodate capricious fluctuations in the availability of food and water. Whereas the abundance and distribution of food influenced hyaena clan size and home range size, available water was a key resource that dictated where the clan's core area was located. Regardless of prey availability, once water became unattainable, the clan was forced to relocate their core area, at the expense of abandoning the den-dependent cubs in the process.

Our observations lend support to Macdonald's (1983, p. 379) suggestion that "there are ecological circumstances in which the benefits of 'spatial groups', (and equally perhaps the evolutionary origins of contemporary highly social groups) may have little or nothing to do with advantages directly dependent upon sociality. Rather, resource (particularly food) dispersion is fundamental to the spacing and structure of carnivore society in that it may set the limits to the group and territory sizes, within which other combinations of selective pressures operate". Thus, the spatial organisation of social carnivores may vary geographically according to the availability and spatial arrangement of key resources, such as food and water, as suggested here for spotted hyaenas in the Namib.

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Fig. 1.

The study area within the Namib-Naukluft Park showing approximate home ranges of spotted hyaena clans at Natab, Nareb and Zebra Pan. Site names are indicated with a closed triangle. Dens and lairs are indicated by a closed square (= core area). Closed circles are permanent waterholes in the Kuiseb River. The symbols G (= gemsbok), Z (= mountain zebra) and K (= klipspringer) within circles represent carcasses fed on by hyaenas; carcasses not fed on are enclosed in squares. The letter X indicate sites where carcasses were provisioned by the authors but not fed on by hyaenas.

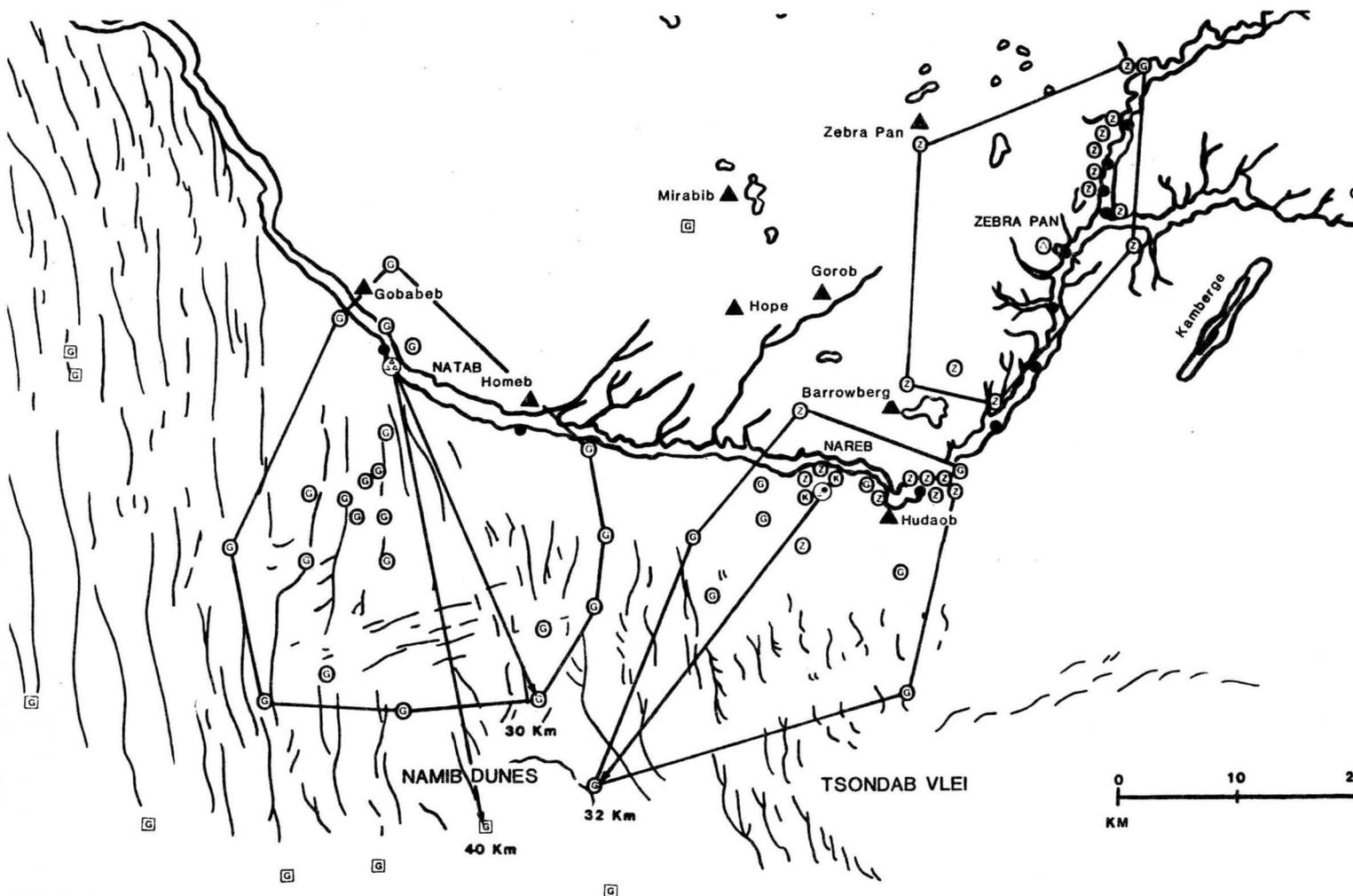


Table 1. Group size of Namib spotted hyaenas assembled and feeding at large carcasses (N=54) and observed foraging elsewhere (N=93).

Group Size	Feeding		Foraging	
	N	%	N	%
1	5	9.3	54	58.1
2	7	13.0	18	19.4
3	5	9.3	12	12.9
4	15	27.8	2	2.2
5	12	22.2	7	7.5
6	4	7.4	0	
7	6	11.1	0	