

Prey selection by spotted hyaena (*Crocuta crocuta*) in the Namib Desert

by

Ronald Tilson

Desert Ecological Research Unit/Gobabeb
P. O. Box 1592,
Swakopmund, South West Africa

Frank von Blottnitz

Directorate of Nature Conservation,
Private Bag 13186,
Windhoek, South West Africa

and

Johannes Henschel

Desert Ecological Research Unit/Gobabeb,
P. O. Box 1592,
Swakopmund, South West Africa

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ABSTRACT

Species composition of prey eaten by three groups of spotted hyaena (*Crocuta crocuta*) in the central Namib Desert was evaluated. Age and sex categories of major prey are based on 55 carcasses and diets on 595 scats collected over 12 months. Gemsbok (*Oryx gazella*) was the most important food item in the overall diet of two groups, but in a third group gemsbok and mountain zebra (*Equus zebra hartmannae*) were almost equally represented. These differences were directly related to the availability of the prey within the hyaena foraging areas. Old animals of both prey species were the most common age class consumed by hyaenas. More male than female gemsbok were eaten, but female mountain zebra outnumbered males. Since hyaenas compete with no other large predator in the Namib, the composition of their diet reflects the sole impact of a predator/scavenger on a depauperate prey assemblage in a desert environment.

1 INTRODUCTION

The spotted hyaena (*Crocuta crocuta*) has dominated the early literature as a scavenger of carrion (see Kruuk, 1972), but recent studies have shown that part, and in some cases most, of the hyaena's food is acquired by hunting (Eloff, 1964; Kruuk, 1970, 1972; Bearder, 1977; Mills, 1978). Except in the Ngorongoro Crater of East Africa, where spotted hyaenas are the dominant predator, kills made by lions (*Panthera leo*) or other large predators may contribute much to the diet of hyaenas, but the percentage can be difficult to assess (Kruuk, 1972; Bearder, 1977). This restricts any meaningful assessment of the impact hyaena predation may have on local populations of prey. It also affects the evaluation of prey selection because opportunistic scavenging from kills of other predators often cannot be distinguished from the results of individual or group hunting by hyaenas.

Here we report on the diets of three groups of spotted hyaenas that rest in sheltered areas along the Kuiseb River but forage out into the sand-dunes and gravel plains of the central Namib Desert. Gemsbok (*Oryx gazella*) and mountain zebra (*Equus zebra hartmannae*) are the two most abundant ungulates in this desert, and the spotted hyaena is their only predator. The absence of other large felids and canids distinguishes this area from any other African locality in which spotted hyaenas have been studied (Eloff, 1964; Kruuk, 1972; Bearder, 1977; see also Deane 1960, 1962; Hirst, 1969; Pienaar, 1969; Mills, 1978). The absence of other predators enabled us to interpret the hyaenas' overall diet and to evaluate their impact on the age and sex categories of the prey populations.

2 STUDY AREA AND METHODS

The research area, situated along the Kuiseb River in the Namib Desert of South West Africa, is about 75 km from east to west and 40 km wide. It includes about 3 080 km² from the Namib Research Institute at Gobabeb (23°34'S, 15°03'E) to the confluence of the Kuiseb-Gaub Rivers and parts of the northern gravel plains and southern sand-dunes (Fig. 1). It is an extremely arid area, receiving an annual rainfall of about 17 mm (1962–1972: Seely and Stuart, 1976). Most precipitation occurs in the summer months from January to March, although some rain may be recorded in any month with considerable variation from year to year (1962–1978 range = 0–125 mm, Gobabeb meteorological records).

The study area can be separated into three distinct habitats. South of the Kuiseb River lies the dune field of the Namib. Approximately parallel linear sand-dunes up to 100 m high are oriented in a roughly north-south direction and separated by interdune valleys about one kilometre wide. Trees and shrubs are absent, but there are scattered hummocks of *Trianthema hereroensis* on the dune slope and patches of grass (*Asthenatherum glaucum* and *Stipagrostis* spp.) in the

sandy interdune areas. These plants are fed upon by several hundred widely dispersed gemsbok for all but the driest times of the year. Other ungulates generally do not penetrate this waterless habitat.

On the north bank of the Kuiseb a network of ruggedly eroded gulleys and washes drops from the gravel plains down into the river course. Small shrubs and grasses and occasional trees (*Acacia erioloba* and *A. reficiens*) are more common here but are not abundant anywhere. This is the preferred habitat of mountain zebra. Some gemsbok and springbok move into this area after seasonal rains, but during this study few were observed.

Between these two strikingly different areas the seasonally dry Kuiseb River has incised a deep narrow gorge that extends from above the Kuiseb-Gaub confluence to Nareb. Down-river the canyon is less marked as it gradually becomes wider and flatter. In the gorge there is little vegetation except for isolated wild fig trees (*Ficus sycamorus*) and irregular clumps of acacias. Down-river from Nareb the acacia dominated (*A. albida* and *A. erioloba*) riparian forest becomes progressively more dense (Fig. 1).

There are two important resources for ungulates in the Kuiseb River. Pods and leaves of the acacias are abundant in the lower parts of the study area, and this is where gemsbok congregate, especially during the dry summer months when food resources in the dunes decline (Hamilton *et al.*, 1977; Tilson, in prep.). Higher up the Kuiseb, particularly in the gorge, food resources are scarce, but water is freely available in irregularly spaced pools which are permanent. These pools are recharged from seasonal floods that originate in the central highlands and escarpment 250–400 km eastwards. Here gemsbok are replaced by mountain zebra that feed on the plains but descend the gorge at night to drink. Three other antelope species are found along the Kuiseb River course, but they constitute only a fraction of the ungulate biomass (Table 1). Klipspringers, *Oreotragus oreotragus*, are restricted to the canyon slopes; steenbok, *Raphicerus campestris*, are confined to the riparian forest; and springbok, *Antidorcas marsupialis*, occasionally visit the river between Gobabeb and Homeb (Tilson and Kok, in preparation).

TABLE 1: Estimated ungulate biomass in the study area (Fig. 1) calculated from an aerial census (Erasmus and Eyre, 1976) and from road censuses (Tilson and Kok, in preparation) during 1976/77.

Species	No.	%	Biomass/3,080 km ²	
			kg/km ²	%
Mountain zebra	980	50,5	87,5	66,9
Gemsbok	625	32,2	40,6	31,1
Springbok	160	8,2	1,8	1,4
Klipspringer	112	5,8	0,6	0,5
Steenbok	64	3,3	0,3	0,2
Total	1,941	—	130,7	—

Both Kruuk (1972) and Bearder (1977) have shown that the identification of prey hairs in spotted hyaena scats gives a relatively accurate assessment of the frequencies that different prey are consumed. Over a period of 12 months we collected a total of 595 fresh samples from three localities along 100 km of the Kuiseb River. The largest number was from the site called Nareb. They were air-dried, brushed to remove sand particles adherent to the surface, then pulverised and sifted in the laboratory at Gobabeb. The remaining hair and other items were transferred to numbered vials and later identified under a binocular microscope (magnifications 16–32 \times) by comparing them with a reference collection of hair types representing potential prey in the Namib (see Kruuk, 1972). Our samples were well represented with hundreds of hairs from only one species of prey in each scat. From the 595 samples 88.5 % (527) had one hair type, 2.7 % (16) had none, and only 8.4 % (52) had two or more hair types. This analysis was also facilitated by the relatively few prey species available to hyaenas in the study area, in contrast to other study sites.

Part of the substrate particles cemented inside each sample was kept with the associated hair. These particles were compared under a binocular microscope ($\times 32$) with a reference collection of substrate particles from the three habitats described above and in Table 2. Dune sand is the most distinctive substrate because of its orange colour and rounded granules. Substrate particles from the plains and river channel are less distinct but can be separated by a combination of characters (Table 2). With this method we could establish within reasonable limits where the prey was consumed.

Age and sex determinations of gemsbok and mountain zebra carcasses were based on skulls examined or retrieved from carcasses before the hyaenas carried them away. Mountain zebra show a clear sexual dimorphism in permanent canines, which are well developed in males but absent or rudimentary in females. Age classes closely follow a sequential eruption and subsequent wearing of deciduous and permanent teeth (Joubert, 1972a). Gemsbok were aged in a similar manner, but horn shape and size were used to determine sex (O. Kok, personal communication).

Analyses of the social organisation of hyaenas in the Namib and their feeding strategies will be presented elsewhere. For the present purpose, the study population of 17 individually identified hyaenas (13 adults and 4 offspring) can be divided into three separate groups. These groups may represent extended family units of a single clan or clans as described by Kruuk (1972). Each group maintained a relatively stable social and spatial organisation for most of this study. Some individuals, especially young males, showed great mobility and exchanged groups. However, group foraging areas were mutually exclusive, separated by distances of 10–20 km (Fig. 1). By plotting the outermost localities where hyaenas fed, we could calculate the approximate foraging area of each group. These should not be construed to represent individual or group home ranges, which are far larger. Thus, the presence of transients, which may feed in one foraging area, then move to another group and use its latrines, may influence our results but not sufficiently to obscure the general trends we establish here.

TABLE 2: Major characteristics of surface sand from the three habitats in the study area. Percentages of constituents are based on crude counts.

Region	Sand type	Colour	Shape	%
DUNES	Quartz stained with iron oxide and traces of feldspar, garnet, mica	orange	polished surface, sub-rounded to sub-angular	100
RIVER	Mica/mica-schist	shiny black	flat	20–30
	Granite, garnet and feldspar	opaque orange	rounded to well-rounded	20–30
	Quartz stained with iron oxide	orange	rounded to well-rounded	20–30
PLAINS	Quartz, unstained	white	well-rounded to angular	20–30
	Mica, fine	shiny black	flat	10–20
	Granite, garnet and feldspar	opaque orange	sub-rounded to sub-angular	10–20
	Quartz stained with iron oxide	orange	sub-rounded to angular	20–30
	Quartz, unstained	white	angular to very angular	40–60

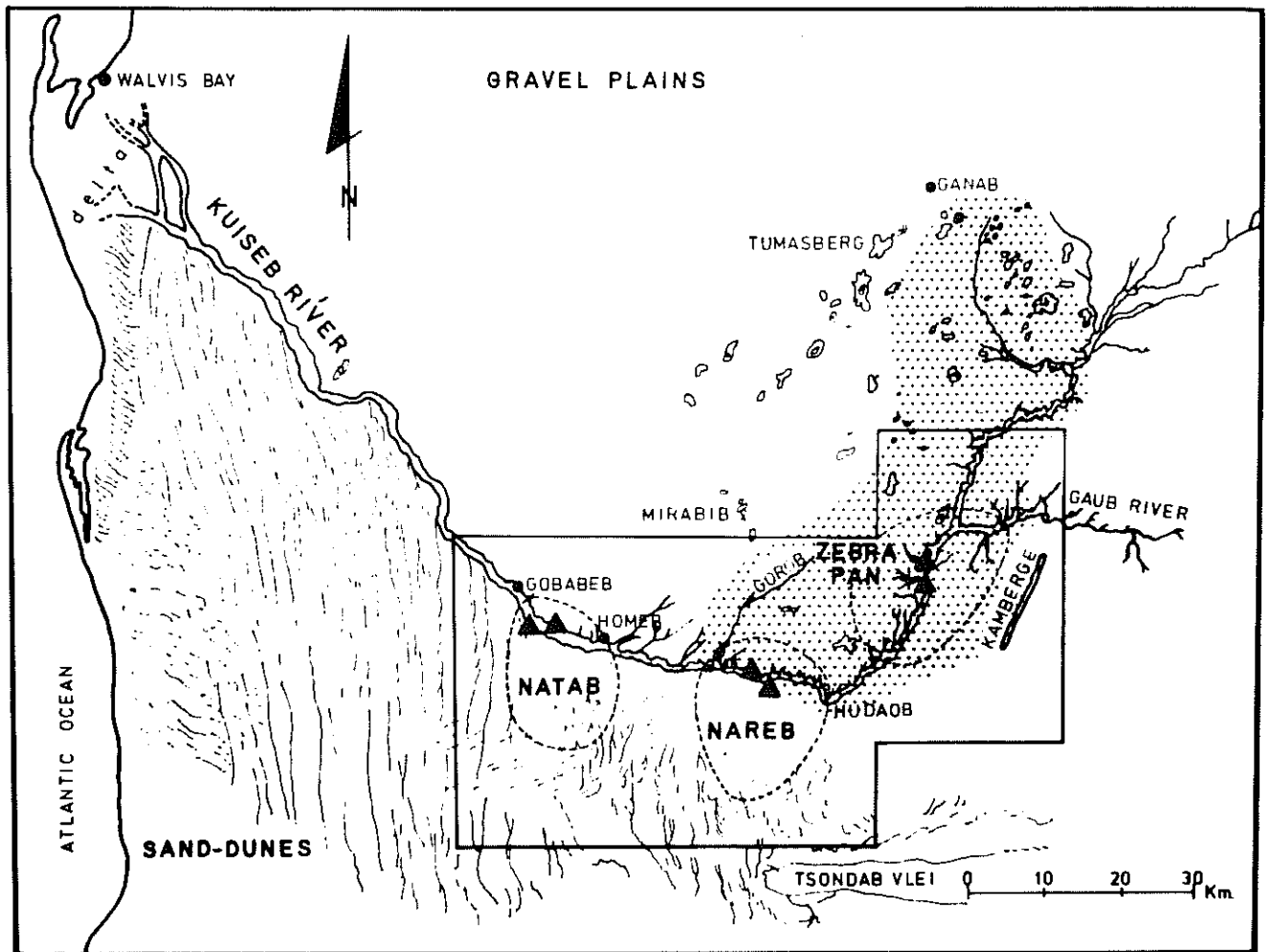


FIGURE 1: The study area within the Namib-Naukluft Park showing the spacing between the three hyaena groups located at Natab, Nareb and Zebra Pan. Dens and lairs as well as latrines are indicated by triangles. Foraging areas are outlined by dashed lines. Shaded areas represent the general distribution of mountain zebra. Gemsbok are more ubiquitous throughout the study area but tend to concentrate south of Homeb and Hudaob and around Ganab.

3 RESULTS

3.1 Prey items in the diet

Skulls, horns and large vertebrae were usually the only parts of a carcass to remain after hyaenas had fed, and even these were often carried away. Nevertheless, a number of carcasses was found by following tracks of hyaenas through the sand-dunes (see Eloff, 1964) and by random searching of the study area. The evidence indicated that hyaenas fed almost exclusively on gemsbok and mountain zebra, and that the relative frequency of these two prey species was significantly different between groups (see below). To supplement these observations 595 scats were analysed (Table 3). Viewed collectively, gemsbok were the single most important prey item for hyaenas in the area, accounting for 79,6 % of the total sample. Mountain zebra were a distant second at 12,6 %, but together these two

ungulates accounted for 92,2 % of the combined diets. The smaller antelopes (springbok, steenbok and klip-springer) constituted only 2,2 % of the total diet, with the remaining 5,6 % contributed by small miscellaneous mammals and ostriches. The relatively diverse spectrum of food items in the hyaenas' diet, relative to the species available (see Stuart 1975), indicates how opportunistic hyaenas can be in feeding on what are probably scavenged food items. But the predominance of gemsbok and mountain zebra suggests that the hyaenas are concentrating on larger sized prey, which agrees with other studies on hyaena feeding habits. In the open savannah of East Africa Kruuk (1972) documented wildebeest, *Connochaetes taurinus*, and zebra, *Equus burchelli*, as the major prey. In a woodland habitat of South Africa Bearder (1977) reported wildebeest, impala, *Aepyceros melampus*, and lion-killed giraffe, *Giraffe camelopardalis*, as the major food sources.

TABLE 3: Distribution of prey hairs from the three hyaena groups in the study area.

Prey	Natab		Nareb		Zebra Pan		Total	
	N	%	N	%	N	%	N	%
MAMMALIA								
Gemsbok (<i>Oryx gazella</i>)	67	93,1	389	82,2	38	50,0	494	79,6
Mountain zebra (<i>Equus zebra hartmannae</i>)	—		47	9,9	32	42,1	79	12,7
Springbok (<i>Antidorcas marsupialis</i>)	2	2,8	3	0,6	—		5	0,8
Klipspringer (<i>Oreotragus oreotragus</i>)	—		7	1,5	—		7	1,1
Steenbok (<i>Raphicerus campestris</i>)	—		2	0,4	—		2	0,3
Domestic goat (<i>Capra sp.</i>) ¹	2	2,8	1	0,2	—		3	0,5
Spotted hyaena (<i>Crocuta crocuta</i>)	—		3	0,6	—		3	0,5
Genet (<i>Genetta genetta</i>)	—		1	0,2	—		1	0,2
Hare (<i>Lepus capensis</i>)	—		1	0,2	—		1	0,2
Hyrax (<i>Procavia capensis</i>)	—		1	0,2	—		1	0,2
Rodentia	—		9	1,9	1	1,3	10	1,6
Unknown ²	—		—		2	2,6	2	0,3
AVES								
Ostrich (<i>Struthio camelus</i>)	1	1,4	9	1,9	3	3,9	13	2,1
Total	72		473		76		621	
Samples	71		460		64		595	

¹ These specimens presumably came from a Topnaar settlement near Homeb.

² Hair specimens tentatively identified as *Poecilogale albimucha* by the Mammal Research Institute, Pretoria (J. Skinner, pers. comm.).

Hyaenas are known to have catholic tastes and will consume a variety of animal, vegetative and inorganic objects (Van Lawick—Goodall and Van Lawick, 1970; Kruuk, 1972; Bearder, 1977). Pieces of rubber, plastic and cloth were occasionally found in regurgitations, but hyaenas in the Kuiseb River are relatively isolated and have little exposure to such material. Stuart (1976) reported that spotted hyaenas in the Namib occasionally eat the spiny fruit of the narra (*Acanthosicyos horrida*), a cucurbit that grows in the sand-dunes. Although we did find narra seeds in two regurgitations, this practice is not considered to be widespread or frequent. The seeds of acacias and fragments of leaves, grass stems and twigs were present in half of the scats (50,5 %), but we believe these items were derived from eating the rumen of the prey rather than purposely eaten to aid regurgitation (Bearder, 1977).

One example of cannibalism was observed, and the presence of numerous hyaena hairs in three samples (0,5 %) from the area where it occurred were later noted (Table 3). In another 7,5 % of the samples a few hyaena hairs were found, but these probably originated from hyaenas licking one another and themselves (Kruuk, 1972). In other areas cannibalism has also been reported (Pienaar, 1969; Van Lawick—Goodall and Van Lawick, 1970; Kruuk, 1972) but it is relatively rare.

3.2 Prey variation between groups

Kruuk (1972) reported that spotted hyaenas in East Africa live in large communities called clans comprised of 40 to 80 individuals. These clans aggressively defend territories that are marked along the boundaries with scats (= latrines) and with anal scent marking (= pasting). In the Ngorongoro Crater, where prey are numerous and year-round residents, clans and territories are relatively stable, but in the Serengeti, where there are large temporary fluctuations in food supply when the ungulate migrations occur, the clan system is disrupted and territories less precisely defined. Rather than marking boundaries, hyaenas in the Serengeti mark along certain routes which they travel over long distances in search of game. Hyaenas in the Namib are similar to those in the Serengeti. Near dens and lairs, and the trails leading from them, latrines are conspicuous, but peripheral boundaries are not well marked. We found three general areas containing latrines close to dens of three different hyaena groups (called the Natab, Nareb and Zebra Pan groups (Fig. 1)).

We were able to distinguish roughly the foraging areas of these three hyaena groups. As some individuals occasionally transferred between groups, we use foraging areas to define the space in which a particular

group, rather than an individual, confined its foraging activities. Boundaries of foraging areas represent the outermost sites where the group was observed feeding on a carcass (Fig. 1). Group boundaries were separated by up to 15 km, so foraging areas were considered to be mutually exclusive. Each foraging area contained at least one den or lair near open water along the Kuiseb River. Because of the distances between locations (20–35 km) and the relative stability of hyaena groups living there, we believe it is reasonable to presume that prey hairs from separate latrines reflect what hyaenas are feeding on in that foraging area.

The frequency of prey items in the diet samples of the Natab (6 hyaenas), Nareb (4 hyaenas) and Zebra Pan (7 hyaenas) groups is presented in Table 3. Considering only the main prey, gemsbok and mountain zebra, there is a significant dietary difference among the three groups ($t^2 = 2,25$, $p < .01$). Hyaenas at Natab had a diet comprised almost exclusively of gemsbok (93,1 %) but mountain zebra were conspicuously absent. At Nareb gemsbok (82,2 %) were still the most important prey, but some mountain zebra (9,9 %) were represented in this group's diet. In contrast, Zebra Pan hyaenas had about equal numbers of gemsbok (50,0 %) and mountain zebra (42,1 %) in their diet. These differences can be explained by the differential distribution of the two prey species within the respective hyaena foraging areas.

Gemsbok occur throughout the study area but reach their largest numbers in the north-eastern areas of the Namib near Ganab (Fig. 1). They also are the only large ungulate that range far into the dunes. Towards the end of the dry season part of the dune population moves into the Kuiseb River, mostly between Natab and Hudaob. In contrast, mountain zebra do not range down river from the Gorob canyon confluence. Most are found in the vicinity of Zebra Pan and parts north along the river's course. Both gemsbok and mountain zebra show some seasonal movements, but nowhere in their range are they ever completely absent. The Nareb area represents the zone of overlap for these two ungulates as well as for klipspringer and steenbok (Tilson, in preparation).

3.3 Seasonal variation in prey

After the rains fall in the Namib gemsbok and mountain zebra leave the confines of the Kuiseb River to disperse into the dunes and plains, and hyaenas must travel further afield to find them. This seasonal adjustment is not reflected in an analysis of hair types. The only evidence of seasonal change in diet was the presence of gemsbok calves (distinguished by their distinctive post-natal coloration) during the months of November through January (Fig. 2). Gemsbok do not have a short, sharp birth season like wildebeest (Estes, 1976), but they do show a peak in November (Hamilton *et al.*, 1977). After about four months calves closely resemble adults in coloration and could not be distinguished

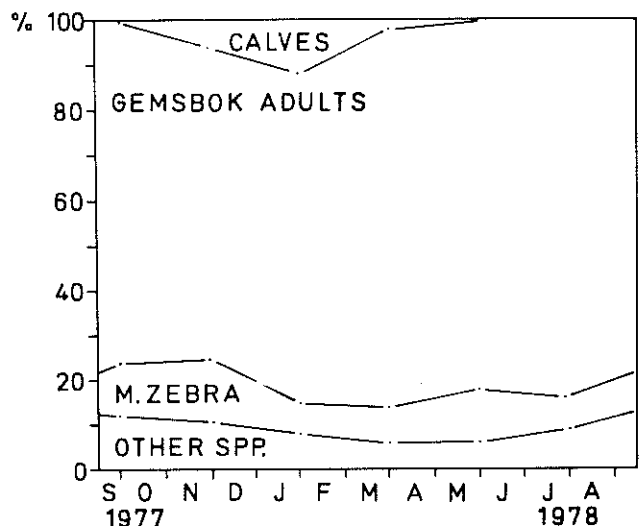


FIGURE 2: Hyaena diet from the Nareb group at different times of the year. The category "other" refers to species listed in Table 3.

by hair type from adults. For similar reasons mountain zebra foals were not separated from adults in the analysis. Thus, our values most likely under-represent the percentage of immature animals in the overall diet.

In other areas the consumption of calves is a more striking seasonal phenomenon (wildebeest in East Africa, Kruuk, 1972; impala in South Africa, Bearder, 1977). In Ngorongoro Crater wildebeest calves accounted for over 60 % of the hyaenas' diet during the short birth season (Kruuk, 1972). Predation on calves has promoted breeding synchrony and the formation of large aggregations of wildebeest, partly to satiate the predators and partly to create confusion to prevent one-day-old calves from being detected (Estes, 1976). Aside from the restrictions of methodology cited, the less pronounced emphasis on calves in the Namib hyaena diet may be attributed to the low density and wide dispersion of the prey populations. A greater emphasis on calf predation would be expected when gemsbok congregate at resource rich areas during severe droughts, such as observed by Hamilton *et al.* (1977).

3.4 Age and sex of prey

In our study we never observed hyaenas killing their prey, but we did find 29 gemsbok and 26 mountain zebra carcasses. About half of these were killed by hyaenas, and at least four were natural deaths (Tilson, in prep.).

The age and sex categories of gemsbok and mountain zebra consumed by hyaenas are presented in Table 4. The sex ratio of adult gemsbok (over one year of age) was 1.9 males for every 1,0 female. But in a sample of 2 884 gemsbok counted in the Namib gravel plains no significant deviation from a 1:1 sex ratio was found (O. Kok, personal communication). Even though male gemsbok outnumbered females in the carcass counts,

the difference was not significant ($X^2 = 2,79, p < .10$). In contrast, significantly more female mountain zebra were eaten (0,4 males vs. 1,0 females, $X^2 = 3,85, p < .05$) even though these animals have nearly equal sex ratios in the wild (Joubert, 1972b).

The age class separation of both gemsbok and mountain zebra shows that old animals (over eight years old) were more often eaten than young ones (70,1 % vs. 29,1 %, Table 4). These figures are significant for gemsbok ($X^2 = 9,97, p < .001$) but not for mountain zebra ($X^2 = 1,38, p < .30$). If only adults are considered then even the mountain zebra figures are significant ($X^2 = 5,75, p < .02$). This sample may be biased towards older individuals, because the probability that young skulls will remain intact is much less than that for adult skulls. However, within the adult categories (over one year of age) older animals still form the greatest percentage. Animals from 1–8 years constituted 23,8 % of the mountain zebra and 12,5 % of the gemsbok contrasted to 76,2 % and 87,5 %, respectively, for individuals 8–16 years old. We found only a single mountain zebra in the 1–4 year old category. The evidence presented here suggests that hyaenas are selecting older individuals over younger, but the contribution of immature calves and foals is probably underestimated.

TABLE 4: Age and sex categories of gemsbok (O. Kok, personal communication) and mountain zebra (from Joubert, 1972a) consumed by hyaenas. The two oldest gemsbok categories were combined. Numbers in parentheses refer to percentage of that species.

Age (years)	Gemsbok		Mountain zebra	
	Male	Female	Male	Female
Immatures				
1	2 (6,9)	1 (3,5)	1 (3,9)	4(15,4)
Adults				
1–4	0	0	0	1 (3,9)
4–8	2 (6,9)	1 (3,5)	2 (7,7)	2 (7,7)
8–12			3(11,5)	8(30,8)
12–16	15(51,7)	8(27,6)	2 (7,7)	3(11,5)
Total	19(65,5)	10(34,5)	8(30,8)	18(69,2)

3.5 Site of prey consumption

Different prey species showed associations with different substrate types, even though a considerable amount of overlap was evident (Fig. 3). The Natab hyaenas, which fed almost exclusively on gemsbok (93,1 %, Table 3), consumed over half of their prey on a sandy substrate, presumably in the dune fields south of the Kuiseb. Another third of the gemsbok were eaten in the vicinity of the river, and only a few on the gravel plains (Fig. 3A). At Nareb, where gemsbok again were the predominant food item

(82,2 %) for hyaenas, a similar relationship prevailed (Fig. 3B). The small number of mountain zebra (9,9 %) eaten at Nareb showed nearly equal values for all three habitats. In contrast to these two groups, hyaenas at Zebra Pan consumed the greater part of their prey on the gravel plains or in the river-bed. Only a fraction of the gemsbok were associated with a dune sand substrate (Fig. 3C). These patterns of prey type and substrate associations support the observations on each group's foraging area depicted in Fig. 1. Hyaenas at Natab and Nareb concentrate their foraging activities in the river and sand-dunes to the south where gemsbok congregate. At Zebra Pan the gravel plains and areas adjacent to the river are more commonly used by hyaenas.

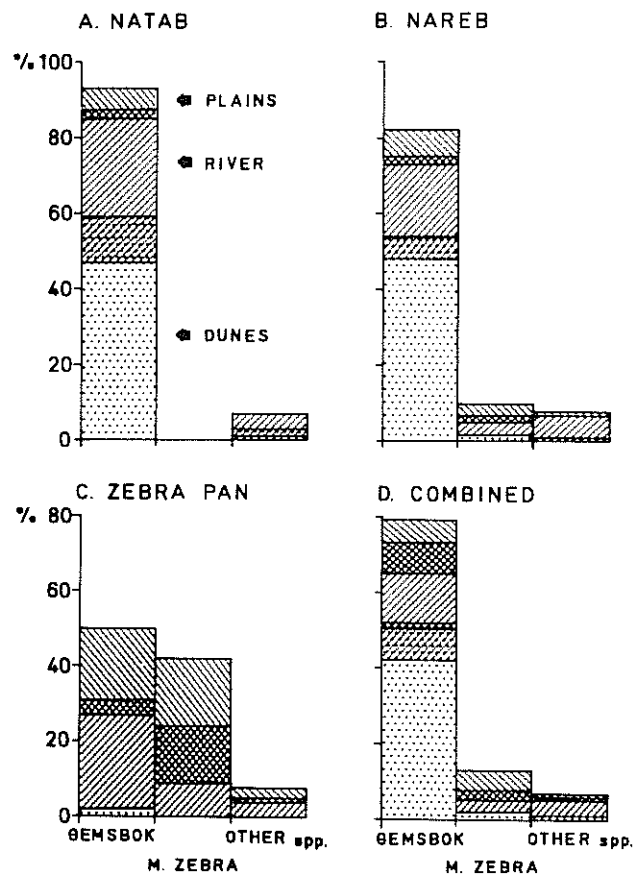


FIGURE 3: The distribution of substrate types (dunes, river and plains) associated with the different prey species consumed by hyaenas at (a) Natab, (b) Nareb, and (c) Zebra Pan, and (d) all three sites combined. The category "other" refers to species listed in Table 3.

The distribution of substrate associations for the combined diets of the hyaena population is presented in Fig. 3D. Aside from some minor differences, the combined values reflect the general trends shown for the Nareb group, which was the most intensively sampled area (77,5 % of the total 595 samples). Excluding mixed samples (where two habitats are represented) the following trends were established. Of the 477 gemsbok, a significant number ($X^2 = 20,46, p < .01$) were consumed in the dunes (50,5 %)

compared with the riverine habitat (35,6 %) or gravel plains (13,8 %). A significant number of the 59 mountain zebra samples ($X^2 = 21,13$, $p < .01$) came from the gravel plains (50,9 %) rather than the riverbed (35,6 %) or dune field (13,5 %), a converse relationship to the gemsbok trend.

4 DISCUSSION

The Kuiseb River and its surroundings in the central Namib Desert do not support an abundant or diverse mammalian community (Coetzee, 1969; Stuart, 1975). This is especially true of large ungulates and their predators. Outside of the narrow riparian forest of the Kuiseb River food resources are sparse and patchy in distribution due to the unpredictable and low rainfall regime that characterises the Namib (Seely and Stuart, 1976). The most abundant large ungulates in the central Namib, gemsbok and mountain zebra, are more common in the eastern and northern parts of the Namib-Naukluft Park, but nowhere do they reach the enormous numbers of the savannah or woodland habitats described elsewhere. In East Africa the estimated biomass of the ungulate population is approximately 55 (Serengeti Plains) to 120 (Ngorongoro Crater) times greater (Kruuk, 1972) than in the Namib (Table 1): in a woodland habitat of South Africa (Timbavati) it is about 35 times as great (Bearder, 1977). Thus, the low species diversity and impoverished numbers of potential prey in the Namib, coupled with the lack of competition from large predators, distinguishes this desert from other localities where spotted hyaenas have been studied. Despite these dissimilarities, hyaenas in the Namib have a diet that is not much different from that of hyaenas in East Africa. There, medium sized ungulates (wildebeest and zebra) are more frequently taken than larger (buffalo) or smaller ones (gazelles). Also, hyaenas in East Africa show no clear preference for either wildebeest or zebra, and the presence of these species in the annual diet corresponds closely with their relative abundance (Kruuk, 1972). An analogous relationship between gemsbok and mountain zebra occurs in the Namib. In southern Africa (Timbavati) impala and lion-killed giraffe were the two most important food items for hyaenas (Bearder, 1977). Thus, where hyaenas are the sole or dominant predator in the system their diet may reflect the relative abundance of medium sized ungulates in the area, but where they are sympatric with other large carnivores, especially lions, this relationship is obscured or totally absent.

The manner in which most Namib prey was obtained is not well documented. There was no evidence of large scale mortality of gemsbok or mountain zebra through drought or starvation during the period of this study; so hyaenas were either finding a large number of animals which had died through natural causes, or they were responsible for killing a number of animals themselves. Several lines of evidence suggest the latter.

In 1976 over 125 mm of rain fell in most parts of the research area (Gobabeb meteorological records). This was a sevenfold increase over the annual average, and as a result range conditions improved dramatically. The general physical condition of gemsbok also improved. For comparison, we used a system described by Hamilton *et al.* (1977) to quantify the apparent relative physical condition of individual gemsbok censused in the Kuiseb. On a scale of 1 (= good) to 5 (= poor) a significant decline in the condition of the herd (male/female values decreased from 1.2/1.8 to 2.7/3.7; $p < .01$) occurred in late summer 1972/73, and considerable mortality resulted from a decrease in food and water resources (Hamilton *et al.*, 1977). In the same area during late summer 1976/77 the general condition of the herd was maintained at higher values (male/female values = 1.2/1.5), and very little natural mortality was observed. No comparable figures are available for mountain zebra or springbok, but general observations suggest their condition paralleled that of gemsbok. It is unlikely that any stable population of hyaenas could subsist entirely on random and unpredictable instances of natural death occurring in such widely dispersed and relatively healthy populations of prey.

If gemsbok and mountain zebra have nearly equal sex ratios how can the differential selection of one sex be reconciled? A similar pattern was noted in East Africa by Kruuk (1972). Adult male wildebeest were killed twice as often as females in the Serengeti, but male/female ratios were almost equal in Ngorongoro. The cause of the difference in mortality between males and females could not be explained. We believe the difference in mortality between male and female gemsbok may result from intrasexual aggression that is more prevalent among males than females. In 1976/77 monthly censuses of the Kuiseb River, 479 gemsbok were counted. Of 230 adult males 15 (6,5 %) were hobbling on injured legs. Horn punctures in the ribs, flanks or buttocks were noted on about half of them. Also, 35 (15,2 %) males were missing part or all of one horn, and another 8 (3,5 %) were missing both horns. Among the 249 females 3 (1,2 %) were missing part of a horn, and only one was observed limping. The loss of horns and other injuries to males presumably were inflicted during intermale combat in order to gain access to females or to certain key resources (see Hamilton *et al.*, 1977). In the absence of other evidence, it is suggested that such injuries could influence an animal's ability to flee or to deter hyaenas during encounters, and may explain why male gemsbok outnumber females in the carcass counts.

The selection of female mountain zebra over males requires a different explanation. In East Africa Kruuk (1972) noted that hyaenas killed more female zebra in both the Serengeti and the Ngorongoro, which he attributed to the zebra's antipredator behaviour. Zebra stallions aggressively defend their family units from attacks by hyaenas, while mares do not. The greater aggressiveness of stallions can be an effective deterrent

to hyaenas, and only by separating a mare from the family unit can hyaenas be successful (Kruuk, 1972). Mountain zebras are similar in social organisation and behaviour and have nearly equal sex ratios in the Namib (Joubert, 1972b). This alone may explain the differential selection of females over males.

The greater number of old individuals in the carcass counts, regardless of sex, suggests that hyaenas scavenge as well as hunt in the Namib. During severe droughts, as observed in the summer of 1972/73 (Hamilton *et al.*, 1977), natural mortality of the prey population may enable hyaenas to rely solely on scavenging. But during periods of better range and herd condition, hunting would be necessary to maintain a resident population of hyaenas. As Kruuk (1972) points out, predation by hyaenas is not merely supplementary to other sources of mortality but interacts closely with them. If alternate causes of mortality are numerically important, then predation merges with them, and hyaenas take what has died already. If other causes of mortality are absent, then hyaenas act as independent mortality agents.

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