

THE COMPARATIVE BEHAVIOURAL ECOLOGY OF THE BROWN HYAENA *Hyaena brunnea* AND THE SPOTTED HYAENA *Crocuta crocuta* IN THE SOUTHERN KALAHARI

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Abstract – The diet, foraging behaviour, social organisation and social behaviour of the brown hyaena *Hyaena brunnea* and the spotted hyaena *Crocuta crocuta*, and the interactions between these two species in the southern Kalahari are discussed. The brown hyaena is a scavenger of a wide variety of vertebrate remains, supplementing its diet with wild fruits and insects and is well adapted to this arid region. The spotted hyaena is a hunter-scavenger of large and medium-sized mammals and is not found in such numbers in the southern Kalahari as is the brown hyaena. These differences in diet have led to the evolution of large differences in foraging behaviour, social organisation, denning behaviour and communication patterns in the two species; spotted hyaenas having a more highly developed social system and living in far larger territories than brown hyaenas. Spotted hyaenas are dominant to brown hyaenas, but because of their low density in the southern Kalahari, have little effect on the brown hyaena population there.

Introduction

In this paper I review certain aspects of the diet, foraging behaviour, social organisation and social behaviour of the brown hyaena *Hyaena brunnea* and the spotted hyaena *Crocuta crocuta* in the southern Kalahari. The manner in which these two closely related species are able to co-inhabit the region, by exploiting largely different food sources, and the influence that this has on the social organisation and social behaviour patterns of each species are examined. Furthermore, the relationships between the two species and the influence they have on each other's populations are discussed. These questions are of importance for the management of these carnivores and in understanding the evolution of their social systems (Kruuk 1972, 1975; Mills 1981).

The information on the brown hyaena has been taken from a series of publications arising from an intensive study on this species between 1972 and 1980 (Mills 1978a, 1978b, 1981, 1982a, 1982b, 1982c, 1983a, 1983b; Mills, Gorman & Mills 1980; Mills

& Mills 1978, 1982). Most of the information on the spotted hyaena has not yet been published (Mills *in prep.*), except for some preliminary findings (Mills 1978b), and is the result of an ongoing study initiated in 1979. Some observations on the spotted hyaena in the southern Kalahari have also been published by Eloff (1964, 1975).

Results and discussion

Density and comparative size

Of the two species the brown hyaena is by far the more common in the southern Kalahari. The brown hyaena is, in fact, the most common of the larger carnivores in the region. Because of its shy nature and nocturnal habits, however, it is difficult to obtain an accurate figure of the number of brown hyaenas in the area. Recently (Mills 1981) a figure of 172 brown hyaenas in the Kalahari Gemsbok National Park (KGNP), at a density of 1,8 hyaenas/100 km², has been calculated.

It is easier to obtain an estimate of the number of spotted hyaenas in the area as they are more conspicuous and easier to contact. At present it is believed that there are approximately 85 spotted hyaenas in the KGNP, at a density of 0,9 hyaenas/100 km².

Spotted hyaenas are considerably larger than brown hyaenas. The average mass of seven adult female spotted hyaenas from the study area was 70,9 kg ± S.E. 1,3 and that of 12 adult males was 57,2 kg ± S.E. 1,3. Brown hyaena males and females do not differ significantly in mass. The average mass of 20 adult brown hyaenas was 39,1 kg ± S.E. 0,7.

Feeding habits

Figure 1 shows the diets of the two species as determined from direct observations made when following individuals in a vehicle at night. The total number of hyaenas of both species which were observed feeding on different food items have been recorded and expressed as the percentage of the total for each species. The data for mammals have been analysed on a mass rather than a species basis. Thus, for example, gemsbok *Oryx gazella* and blue wildebeest *Connochaetes taurinus* calves under one year of age have been recorded as medium-sized mammals, whereas those over one year of age have been recorded as large mammals.

From Fig. 1 it can be seen that there are large differences in the diets of the two species. Brown hyaenas feed on many small food items such as small mammals, bones, wild fruits and insects, whereas spotted hyaenas are mainly consumers of large and medium-sized mammals. Furthermore, brown hyaenas are predominantly scavengers; only 5,8% of the biomass of food observed to be eaten by brown hyaenas was killed by them, whereas spotted hyaenas kill much of their food themselves; 49,2% of the large mammals they were observed feeding on and 77,5% of the medium-sized mammals.

Nevertheless there is a measure of overlap in the diets of these two hyaenas, particularly as regards scavenging from large and medium-sized mammal carcasses. This is important as these are usually rich food sources. It would be a serious loss

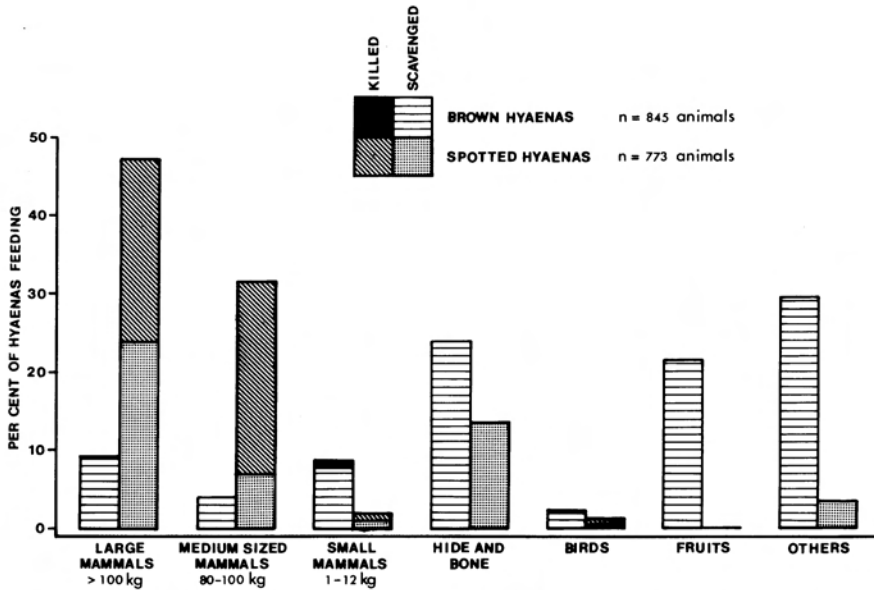


Fig. 1. The diets of the brown hyaena and the spotted hyaena in the southern Kalahari as determined from direct observations. The number of hyaenas observed feeding on each food item is expressed as the percentage of the total number of hyaenas of each species observed feeding. The proportions killed : scavenged are the percentages of the number of each species observed feeding on each food item. The heading "Others" includes reptiles, insects, birds' eggs, carnivore faeces and small unidentifiable pieces of food.

to a hyaena should it lose this type of food to the other species, either directly through being chased off a carcass, or indirectly through members of the other species finding and consuming the carcass first.

Foraging behaviour

Both brown and spotted hyaenas are predominantly nocturnal in the southern Kalahari. On average brown hyaenas were active for 42,6% of the 24 h period, 80,2% of the period between 18h00 and 06h00, whereas spotted hyaenas were active for 31,0% of the 24 h period, 55,3% of the period between 18h00 and 06h00. The difference in time active between 18h00 and 06h00 for the two species is significant (Mann-Whitney test: $U = 15,5$; $P < 0,0001$; one-tailed). The mean distance observed to be covered per night by brown hyaenas was $31,1 \text{ km} \pm \text{S.E. } 2,1$ (range 1,2-54,5 km), and that by spotted hyaenas was $26,5 \text{ km} \pm \text{S.E. } 1,7$ (range 0,5-69,1 km), a non-significant difference ($d = 1,705$; $P > 0,05$). The average distance moved between finding a relatively large meal (for brown hyaenas, a vertebrate food item or 10 wild fruits; for spotted hyaenas, a kill or practically intact carcass), however, varied greatly between the two species; the average distance

moved by brown hyaenas being 9,2 km and that by spotted hyaenas 32,7 km.

Brown hyaenas are almost exclusively solitary foragers. On the rare occasions that more than one brown hyaena are seen moving together they seem to be more interested in each other than in looking for food. Spotted hyaena foraging group sizes, however, vary. The mean size of 405 foraging groups followed for more than 1 km was $3,0 \pm \text{S.D. } 2,2$, with 32,6% comprising one animal, 19,3% two animals, 40,2% three to six animals and 8,9% more than seven animals. The largest foraging group observed was 12.

When foraging, brown hyaenas move erratically at a walk of approximately 4 km/h. The olfactory sense is most important for locating food and they repeatedly make upwind sniffs, locating much of their food from downwind. Hunting behaviour is unspecialised and opportunistic and is directed at small mammals such as springbok *Antidorcas marsupialis* lambs, springhares *Pedetes capensis* and bat-eared foxes *Otocyon megalotis*, and ground nesting birds such as korhaans, in chases of usually not more than 100 m. Of 104 hunting attempts observed only 10 (9,6%) were successful. Whenever a large amount of food is found the excess is stored close by in a clump of tall grass, under a bush, or, rarely, down a hole. Alternatively it will be carried back to the den for the cubs.

Spotted hyaenas often move more quickly and less erratically than brown hyaenas do; approximately half the distance covered is done so at a lope of approximately 10 km/h. Hunting is directed mainly at large and medium-sized mammals and prey are run down at speeds of up to 50 km/h, usually over distances of from 500 m to 2,5 km. Prey is killed by disembowelling, although small animals may be killed by a bite directed at the head region. Olfactory and auditory cues are used for locating prey and sight is important in prey selection. Carrion is located through the olfactory sense and auditory cues often lead other spotted hyaenas to a carcass on which conspecifics are already feeding.

Gemsbok of under one year of age made up 31,7% of the 104 spotted hyaena kills observed, followed by blue wildebeest subadults and adults (13,5%), wildebeest under one year of age (11,5%) and gemsbok adults and subadults (10,6%). Carcasses are consumed rapidly by several hyaenas feeding simultaneously and food storing is rare.

Social organisation

Although solitary foragers, most brown hyaenas live in small social groups of varying sizes. The members of a social group share and defend a common territory, feed together on large food items and carry food back to the den for the cubs. The number of brown hyaenas inhabiting a territory depends on the quality of food in the territory; the mean number of adults and subadults in six brown hyaena groups was $3,7 \pm \text{S.E. } 0,8$ (range 1–9). No dominance hierarchy is apparent in these social groups.

Some male and female brown hyaenas leave their natal groups at subadulthood, but others stay for varying periods; at least some females doing so for life. The majority of the members of a group are related to each other, although two males were known to join groups that they were not born into, one staying with the new group for a minimum of three years, the other for at least one year.

Approximately 8% of the brown hyaena population in the southern Kalahari (33% of the adult male segment of the population) are nomadic adult males. These animals range widely and do not belong to any group. They do, however, perform an important function as they are the males responsible for mating with the group-living females. Group-living brown hyaena males were never observed to mate with their own or any other females.

The mean number of adults and subadults in six spotted hyaena social groups, known as clans (Kruuk 1972), was $8,0 \pm \text{S.E. } 1,6$ (range 3–12). The members of a clan do not always forage together, and so there is a difference between mean foraging group and mean clan sizes. While the quality of the food resources in the southern Kalahari is thought to be responsible for the small clan size, in comparison with, for example, the Serengeti and Ngorongoro (Kruuk 1972), the reasons for the differences in clan sizes within the southern Kalahari have not yet been established. In the clans the larger females dominate the smaller males.

All males (nine) born into an intensively studied spotted hyaena clan over a four year period, disappeared from the clan at the attainment of adulthood. One of these males was known to join another clan and at the time of writing has spent at least one year with the clan. Five others were known to range widely for at least one year after departure. A young male whose origin was unknown was observed to join a clan that was not his natal clan and to spend a minimum of two and a half years with the clan. An old male was seen four times over a period of one year within the ranges of three different clans. One clan was known to have three separate males at different times over a two year period.

Two females born into the intensively studied clan mentioned above remained with their clan at the attainment of adulthood and bred, but a third disappeared at the attainment of adulthood. Four females from another clan moved to an area some 60 km away, although it is unknown whether they established a new territory or joined an existing clan. One of these females either joined or formed a neighbouring clan, with two other females of unknown origin, about three years later.

It seems, therefore, that male spotted hyaenas may be nomadic or group-living for varying periods. The indications are that the group-living males do the mating. Female spotted hyaenas show more fidelity towards their groups, but this is not rigid.

The mean size of six brown hyaena group territories was $330 \text{ km}^2 \pm \text{S.E. } 41$ (range 235–481 km^2). Territory size was related to the dispersion pattern of food in the territory and was not correlated with group size.

The way in which the dens of spotted hyaena clans are distributed and the movement patterns of hyaenas from the various clans are indicative of a territorial land-tenure system (Davies 1978), although considerable overlap in the territories occurs. Spotted hyaena territory sizes have not as yet been established accurately, but appear to be in the region of 1 000–2 000 km^2 or more. There does not appear to be a correlation between group size and territory size in spotted hyaenas from the southern Kalahari and, as with brown hyaenas and many other carnivores (Macdonald 1983), territory size appears to be dependent on the dispersion pattern of food in the territory.

Denning behaviour

Both species of hyaena keep their cubs in holes in the ground. Although the entrances to these dens may be large, they quickly narrow down into tunnels about 40 cm wide; only large enough for the cubs to go into. The dens, therefore, provide ideal refuges for the cubs during the long periods of absence from the den of the adults. Both brown and spotted hyaena cubs spend a year or more attached to a den.

At most brown hyaena dens in the southern Kalahari only one litter of cubs is found, although occasionally (three out of 12 dens observed) two females may raise their cubs at the same den. The modal size of 15 brown hyaena litters from the southern Kalahari is 3 (range 1-4). Spotted hyaena dens, on the other hand, are usually communal; used by several females with cubs of varying ages, although no female was ever observed to have more than two cubs. Brown hyaena females occasionally suckle each other's cubs, whereas spotted hyaena females never do so.

Brown hyaenas regularly carry food back to the den for the cubs to eat whereas spotted hyaenas do not do so. Spotted hyaena females may on occasion carry back to the den the remains (skin and bones) of any animal they have killed and the cubs may chew on these. However, they obtain little food in this manner. The food carried back to the den by brown hyaenas often consists mainly of meat and is usually presented to the cubs.

The milk diet of brown hyaena cubs, therefore, is substituted from about 12 weeks of age with meat, whereas spotted hyaena cubs only obtain a substantial amount of meat when they are nine to 12 months old and able to accompany the adults when foraging. Both species are weaned at 12-15 months of age.

Communication

The brown hyaena has a small vocal repertoire, eight vocalisations have been identified; a yell, a hoot, two whines and four growls. All are short distance vocalisations aimed at conspecifics or competitors in sight of the vocalising animal, and, except for the yell, can only be heard over a few hundred metres.

The spotted hyaena has a larger vocal repertoire comprising 12 vocalisations; two whoops, a groan, a low, a giggle, a yell, two growls, two grunt laughs and two whines (Kruuk 1972). Some of the vocalisations, particularly the whoop, often function as long distance calls and the whoop is often directed at conspecifics not in sight of the vocalising animal. In addition to their larger vocal repertoire, spotted hyaenas are far noisier than brown hyaenas; they vocalise far more frequently and, even where the two species have equivalent calls, the spotted hyaena's tend to be louder.

Visual communication patterns are also better developed in the spotted hyaena than in the brown hyaena. The dark tail of the spotted hyaena contrasts markedly with its light coloured body, thus enhancing the signalling function of the tail, which is raised or curled over the back whenever the hyaenas are excited. The brown hyaena's dark tail does not contrast with the rest of its body colour and so the signalling function of the tail is less striking. Furthermore, the spotted hyaena uses a greater variety of head movements in communication than the brown

hyaena does. The large, prominent ears of both species and the position in which the body is held also convey the mood of the animals to their conspecifics.

The spotted hyaena has evolved an elaborate greeting ceremony, coupled with the modification of the female's sexual organs so that they mimic those of a male. Two animals greeting stand head to tail, lift the leg nearest to the other and mutually sniff and lick at each other's erected sexual organs. This occurs irrespective of the sexes or ages of the animals concerned, and there is no sexual connotation to this behaviour. Brown hyaenas greet in a far less elaborate manner. One animal presents its anal region to the other, protruding its anal pouch, which is then sniffed at by the presentee. Then the two animals often switch roles as presentee becomes presenter. There is no modification of the sexual organs in the brown hyaena. Spotted hyaenas also indulge in communal social activities such as social sniffing and communal scent marking (Kruuk 1972), which are not found in the brown hyaena.

The most striking visual display of the brown hyaena is pilo-erection of the long hair over the back and neck, which occurs in any situation where there is a tendency to either attack or flee. Spotted hyaenas have much shorter hair, and although they erect the hairs on their necks during aggression it is not nearly so striking a display as in the brown hyaena.

Chemical communication by means of defaecating at latrines, pasting, and scratching the ground with the forefeet, is found in both species. Pasting, however, is performed by brown hyaenas at a far higher frequency (2,6 pastings/km) than by spotted hyaenas (0,1 pastings/km). Furthermore brown hyaenas secrete two distinct types of paste at each pasting, whereas spotted hyaenas only secrete one type of paste. Brown hyaenas deposit scent marks throughout their territory, whereas spotted hyaenas scent marks almost exclusively at latrines which, although not exclusively so, tend to be located in areas away from the more heavily utilised areas of their territory, where hyaenas from other territories are likely to encounter them.

Scent-marking and particularly pasting in brown hyaenas, probably have both inter- and intragroup functions; demarcating territories and passing information on to fellow group members. Scent-marking in spotted hyaenas appears to have mainly an intergroup function only.

Relationships between brown hyaenas and spotted hyaenas

Brown hyaenas and spotted hyaenas compete for food mainly when they are scavenging from large and medium-sized mammal carcasses (Fig. 1). Should the two clash, spotted hyaenas will easily displace brown hyaenas from these carcasses. On the other hand brown hyaenas sometimes benefit from spotted hyaenas by feeding on the remains of their kills.

Whenever the two species meet, even if no food is present, the spotted hyaenas are clearly dominant. This dominance may sometimes resort to outright aggression with a spotted hyaena grabbing a brown hyaena by the side of the neck and shaking it. Once a group of four spotted hyaenas were even known to kill a large brown hyaena cub. In spite of this there is often a measure of attraction shown by one species towards the other, and when sensing each other they often approach closer.

This attraction is also sometimes exhibited when one of the two species encounters the other's scent marks; they sometimes use the same latrines and may even paste on the same grass stalk.

It has been found that brown hyaenas tend to avoid areas well frequented by spotted hyaenas. In two similar areas along the Nossob riverbed, one with a higher density of spotted hyaenas than the other, brown hyaenas were observed significantly less often in the former area than the latter. Spotted hyaenas deprived brown hyaenas of a substantial amount of food in the former areas, through both interference and exploitation competition. Furthermore, the aggressive manner in which spotted hyaenas often deal with brown hyaenas, even when there is no food present, may have been an important factor.

Discussion

To a large degree brown hyaenas and spotted hyaenas exploit different food sources in the southern Kalahari (Fig. 1). The spotted hyaena is far more of a specialist than the brown hyaena is, living mainly off large and medium-sized mammals, whereas the brown hyaena is an opportunist scavenger, supplementing its diet to a large extent with wild fruits, insects and other small items. Competition for food between them is mainly limited to scavenging from large and medium-sized mammal carcasses. This is more important for brown hyaenas than for spotted hyaenas, as this type of food is potentially one of the richest that brown hyaenas can exploit. However, because of the comparatively low density of spotted hyaenas in the southern Kalahari, it is only in a few local areas that this competition for food becomes limiting to brown hyaena numbers.

These differences in feeding habits between these two species have led to the evolution of large differences in foraging behaviour, social organisation and social behaviour. These are summarised in Table 1.

Foraging group sizes vary between the two species. Brown hyaenas forage alone as very often each food item found only provides enough food for one hyaena and group foraging would not greatly improve their efficiency in finding food. Spotted hyaenas on the other hand, often forage in small groups as they usually feed on food items which are able to feed several hyaenas at once and group foraging probably enhances their killing efficiency.

Because spotted hyaenas frequently feed on large food items which satiate them, once they have found their food they can afford to rest for some time. Brown hyaenas on the other hand typically have to move from one small food item to the next and, therefore, they spend more time foraging than spotted hyaenas do. However, the actual distances covered during foraging by the two species is similar, as spotted hyaenas move far more quickly, looking for large and medium-sized ungulates, whereas brown hyaenas spend time investigating a wider range of smaller potential feeding opportunities.

Although solitary foragers, brown hyaenas do live in small stable social groups, the main factor regulating the size of these groups being the quality of the food resources in the territory. Spotted hyaena social group sizes are usually larger than those of brown hyaenas, because of the generally richer food sources that they tap and the advantage of co-operation in obtaining some of their food.

Table 1

A summary of certain aspects of the behavioural ecology of brown and spotted hyaenas in the southern Kalahari

	BROWN HYAENA	SPOTTED HYAENA
Diet	All kinds of vertebrate remains, wild fruits, insects, birds' eggs	Large and medium-sized ungulates
Manner in which food acquired	Scavenged	Killed or scavenged
Mean foraging group size	1,0	3,0
Percent of 24 h period active	42,6	31,0
Mean distance moved per meal	9,2 km	32,7 km
Mean social group size	3,7	8,0
Mean territory size	330 km ²	±1 250 km ²
Method of feeding cubs	Suckling and carrying food to den	Suckling
Chief means of communication	Chemical	Vocal and visual
Density	1,8/100 km ²	0,9/100 km ²

Spotted hyaenas forage over a much larger territory than do brown hyaenas. This is because spotted hyaenas are the more specialised feeders and have to travel longer distances in order to find their food. Nevertheless ratios between territory size and mean distance moved per relatively large meal are similar for both species: 1 : 36 in the case of the brown hyaena and 1 : 38 in the case of the spotted hyaena, suggesting that the dispersion pattern of food is the chief determinant of territory size in both species.

The most marked difference in the denning behaviour of the two species is that brown hyaenas carry food to their cubs whereas spotted hyaenas do not. Because brown hyaenas so often feed alone, an individual which finds a suitable food item for cubs can usually eat some of it and then carry the rest back to the den, as there are unlikely to be any other hyaenas competing with it for the food. At the den there are normally few cubs and competition for the food is likely to be spread amongst cubs of equal age. The social feeding behaviour of spotted hyaenas makes it important for each individual to eat as much as it can as quickly as possible. Mostly therefore, there is little meat left over to take back to the cubs. The large size and dominance of the females gives them priority at carcasses so that they can meet the increased demands of lactation and quickly satiate themselves before returning to suckle their cubs. It is possible that the smaller litter size (1-2) of spotted hyaenas in comparison with brown hyaenas (1-4) has evolved as a result of the heavy dependence of the spotted hyaena cubs on milk. By providing additional nourishment for the cubs brown hyaenas can raise larger litters.

The differences in emphasis on the use made of the various communication mechanisms by the two species are further manifestations of the differences in their ecology and sociality.

The more complex social system of the spotted hyaena is evident in the context of visual communication; the involved greeting ceremony and greater emphasis on head and tail movements are examples of this. The fact that pilo-erection is so well developed in the brown hyaena may seem inconsistent with the above argument. It is perhaps significant that this posture, which at least under some conditions makes the animal performing it appear to be larger, has evolved in this smaller and less aggressive member of the family. Amongst other things it is used in defence against larger and more aggressive competitors.

It is often important for spotted hyaenas to know where the other members of their clan are at any one time so that they can rapidly come together to form a hunting group, or to interact with their major competitors, lions *Panthera leo*. They have, therefore, evolved a long range call (the whoop), one of the functions of which is to help accomplish this. They have also evolved a number of other vocalisations such as the fast whoop, the low and the giggle which are important in communal antagonistic situations at food, in territory defence and against competitors. Brown hyaenas do not need to quickly join up with fellow group members, nor do they need a complex repertoire of group orientated vocalisations, as most of their feeding and foraging occurs solitarily.

It may, however, be important for brown hyaenas to know where other members of their group have foraged in the recent past, so as not to waste time and energy foraging in areas which are likely to be unproductive. It may also be important for group members to reinforce their presence in the territory, even though they do not often meet up with their fellow group members. To this end they employ pasting at a high frequency within their territories. Both species need to demarcate their territories, and thus reduce the possibility of competing with conspecifics for limited resources. They use scent marking to help accomplish this. Pasting, therefore, is of more importance to brown hyaenas than spotted hyaenas. This is reflected both in the higher frequency at which they paste and in the more complex secretions they deposit.

Of the two species the brown hyaena is the most successful one in the arid southern Kalahari where the larger ungulates are erratically distributed. It is in fact the most common and widespread, and therefore the best adapted, of the large carnivores to the area. Its ability to survive on small, sparsely distributed food items of many kinds and its suitably adapted social system are better adaptations to the southern Kalahari ecosystem than the dependence on large and medium-sized prey animals and associated higher degree of sociality of the spotted hyaena. Management practices in the area which lead to an increase in the number of resident ungulates would also probably lead to an increase in spotted hyaena numbers. This would almost certainly lead to a decrease in the brown hyaena population through both interference and exploitation competition.

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