Feeding ecology and its influence on social organization in Brown hyenas (*Hyaena brunnea*, Thunberg) of the Central Kalahari Desert

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Summary

(1) Observations are presented on the diet, feeding habits, hunting and foraging behaviour of Brown hyaenas of the Central Kalahari.

(2) The remains of kills left by other predators are the single most important food item in the Brown hyaena's diet. The diet also consists of small scavenged items, small prey such as rodents which the hyaena itself kills, and wild fruits.

(3) Brown hyaenas hunt and scavenge small items solitarily, but congregate for communal scavenging of the large kills left by other predators.

(4) Individual hyaenas are not territorial and there is great overlap in home ranges. They use common pathways and frequently meet to socialize while foraging.

(5) Resident adults form a group with a social hierarchy maintained through neck-biting, muzzle-wrestling, chasing, and other social interactions. Subadult hyaenas often leave the group when approximately 22 months old.

(6) Brown hyaenas have a complex system of communication including visual displays, social interactions, vocalizations, and extensive pasting. These are described.

(7) Since carrion is an important source of food, Brown hyaenas have developed distinct relationships with other predators and these are described.

(8) In conclusion, the Brown hyaena exhibits a highly flexible social system, foraging and hunting small items solitarily and congregating for the common utilization of a large carcass. The social organization is therefore influenced by the feeding ecology.

Introduction

A 5-year study of the social behaviour and feeding ecology of the Brown hyaena (*Hyaena brunnae*, Thunberg) and its relationship to two sympatric predators, lions (*Panthera leo*) and Black-backed jackals (*Canis mesomelas*) in the Central Kalahari Game Reserve of Botswana, began in May, 1974 and will continue until May, 1979. Observations presented here are from the first 3.5 years of the study.

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The Brown hyaena has been considered a nocturnal and solitary scavenger and predator (Smithers, 1971; Mills, 1973, 1976; Kruuk, 1976). It is sparsely distributed over the arid and semi-arid regions of Southern Africa in Botswana and Rhodesia (Smithers, 1971), South-West Africa and South Africa (Pienaar, 1969; von Richter, 1972), Angola (Mills, 1973) and Malawi (Sweeney, 1959). It has been widely persecuted as a stock killer and is listed as an endangered species in the IUCN Red Data Book.

The purpose of this paper is further to contribute to the discussion that feeding habits and the exploitation of niche affect the degree to which members of the family Hyaenidae socialize and the type of social organization maintained as discussed earlier by Kruuk (1972, 1976). The nine-member group under study exhibits a social hierarchy. Group sociality is elastic in that members may spend considerable periods foraging solitarily while meeting frequently to greet and otherwise reinforce social ties, or they may scavenge communally.

Study area

Deception Valley is one of the three fossil river systems which cross the Central Kalahari Game Reserve (Silberbauer, 1964). The dry, flat, narrow river bed is bordered on either side by elongate sand dunes and rolling bush savanna. The dunes slope gently over 3.2 km before joining the river bed.

The Central Kalahari typically experiences one wet and one dry season per year but prolonged droughts are not uncommon (B. Berghoffer, pers. comm.). The region is uninhabited and there is no past record of rainfall. We have recorded 449.9 mm, 417.9 mm, and 304.8 mm for the 1974–75, 1975–76, 1976–77 rainy seasons respectively. The onset of the rains, their duration and distribution are variable, but during this study, they have usually commenced in November and ended in late April or early May.

During the rains a significant cover of grasses (*Enneapogon desvauxii*, *Eragrostis* echinochloidea, Sporobolus ioclados) develop on the riber bed. These grade into mixed bush (*Acacia mellifera*, *Catophractes alexandri*, *Grewia spp.*, *Boscia albitrunca*) and grasses (*Stipagrostis hirtigluma*, *Digitaris spp.*) on the dune slopes, with quite dense woodland (*Terminalia prunoides*, *Combretum albopunctatum* and *Albizia anthelmintica*) established on the dune tops.

During the rains, large numbers of ungulates migrate into the area, the springbok (*Antidorcas marsupialis*) reaching densities of $362 \cdot 3$ animals per km² on the river bed. In addition, considerable numbers of Cape hartebeest (*Alcelaphus buselaphus*), gemsbok (*Oryx gazella*), giraffe (*Giraffa camelopardalis*), greater kudu (*Tragelaphus strepsiceros*) and steenbok (*Raphicerus campestris*) ultize the bush savanna and wood-lands.

Prides of lions also migrate into the research area during the rains and defend territories which include segments of the fossil river system. During the rains we have observed 92.0% of our recorded lion kills. Other predators, including leopards (*Panthera pardus*), cheetah (*Acinonyx jubatus*), Hunting dogs (*Lycaon pictus*) and rarely, Spotted hyaenas (*Crocuta crocuta*) were also observed much more frequently in this season. Thus, there is an abundance of carrion concentrated in a relatively small portion of the total range available to the resident Brown hyaena population during the rains.

For as much as 8 months of the year there is no rain or surface water available in the Central Kalahari Game Reserve. Ungulate herds disintegrate, the animals dispersing into small groups of from two to fifteen over thousands of square kilometres of sandveld. Almost no game remains in the valley, except for a few resident giraffe and steenbok. There is usually no more than one springbok per 18 km² during the dry months. Lions and other large predators leave the valley and are only rarely seen, and, therefore, the carrion resource utilized by the Brown hyaenas greatly diminishes.

Methods

Observations presented are from a resident group of nine Brown hyaenas which frequent an 11.3-km length of Deception fossil river system. Eight of these hyaenas were immobilized using phencyclidine hydrochloride (0.8 mg/kg) and tagged with Rho-tag coloured and numbered plastic ear tags for easy identification. Other hyaenas were easily recognized by scars, slits, or notches in the ears and other natural markings.

The hyaenas had had no previous interreactions with people and could be approached in a vehicle to within 20 m early in the study. Most observations were recorded using the unaided eye or 8×35 field binoculars while following the animal in a four-wheel drive vehicle. A spotlight assisted in locating hyaenas and observing scavenging behaviour, but it was turned off if the individual began hunting to prevent influencing the behaviour. On moonlight nights unassisted observations were made quite easily.

Individual hyaenas were quite easily followed over the fossil river bed where there is an absence of bush and grasses are short. This proved to be much more difficult in bush savanna and woodland areas and in these areas observations were made using radio telemetry equipment.

Feeding habits were studied through direct observation and by collecting and analysing fresh faecal samples as described by Kruuk (1972).

Results

Diet

Smithers (1971) reports Brown hyaenas to be lesser scavengers than Spotted hyaenas and has found fruits and species up to the size of adult lechwe (*Kobus lechwe*) in the stomach contents of Brown hyaenas. Shortridge (1934) records that they eat the carrion of dead porpoises, whales, fish and sea birds washed on shore in parts of South Africa and South-West Africa where their ranges include coastal regions. Vilgoen & Davis (1973) reported 64.8% mammalian and 34.6% plant material remains in the stomach contents of one individual from the Transvaal Province of South Africa.

Mills (1973, 1976) has described the diet of the Brown hyaena in the Southern Kalahari as consisting generally of scavenged bones from old and fresh kills made by other predators, small mammals and birds either hunted or scavenged, insects, reptiles, and miscellaneous scavenged material such as eggs, hides, horns, and fruits. Of the food items listed by Mills (1976) to have been eaten by the hyaenas during direct observation, only 0.8% were seen to have been killed by the hyaena itself. Six percent of all hunting attempts observed were successful, all directed toward prey smaller than a springbok lamb. It would appear from Mill's report that the Brown hyaena in the Southern Kalahari is primarily a scavenger supplementing its diet by occasional hunting and by eating fruits.

Faecal analysis

Faecal analysis results from this study are detailed in Table 1 which enumerates food items selected and reports the frequencies with which they were found in 258 samples collected during 1974 and 1975. A high frequency of large mammal remains is immediately apparent. 'Large mammal' is used here to include antelopes the size of steenbok weighing 13 kg and larger, and constitutes a category of animals generally considered by us to be scavenged rather than hunted by the Brown hyaena. Steenbok and Bush Duiker (*Sylvicapra grimmia*) could be occasional prey as they are certainly small enough to be killed by Brown hyaenas, but this has not been observed. Since we

	Frequency of	Number of
Food item	occurrence	samples
Large mammals		<u> </u>
Springbok (Antidorcas marsupialis	47.67	123
Gemsbok (Oryx gazella)	13-56	35
Hartebeest (Alcelaphus buselaphus)	6+58	
Steenbok (Raphicerus campestris)	5.03	17
Duiker (Sylvicapra grimmia)	3.10	13
Giraffe (Giraffa camelopardalis)	2.71	8
Springbok fawn	1 · 55	7
Gemsbok calf	Trace	4
Eland (Taurotragus oryx)	Trace	1
Kudu (Tragelaphus strepsiceros)	Trace	1
Unidentified ungulate	Trace	1
Small mammals		2
Springhare (Pedetes capensis)	28.68	74
Mouse (Mastomys natelensis)	7.36	19
Porcupine (Hystrix africaeaustralis)	6 · 58	17
Shrew (Crocidura sp.)	2.71	7
Desert rat (Zelotymus woosnami)	1 • 93	5
Hare (Lepus sexatilis)	Trace	2
Gerbil (Tatera sp.)	Trace	2
Tree rat (Thallomys paedulcus)	Trace	1
Ground Squirrel (Xerus inauris)	Trace	1
Slender mongoose (Herpestes sanguineus)	Trace	1
Unidentified rodent	1.16	3
Unidentified small mammal	2.32	6
Birds		
Crowned plover (Stephanibyx coronatus)	6.58	17
Guinea fowl (Numida meleagris)	6.20	16
Black korhaan (Afrotis afra afra)	2.71	7
Kori bustard (Ardeotis kori kori)	1.16	3
Cape dikkop (Burhinus capensis)	1.16	3
Ostrich (Struthio australis)	Trace	1
Unidentified bird	10.07	26
Reptiles		
Lizard	0.77	2
Lequon	0.77	2
Snake	Trace	1
Unidentified reptile	Trace	1

Table 1. Analysis of Central Kalahari Brown hyaena faeces 1975, 1976 (258 samples)

	Frequency of		Number of
Food item	occurence		samples
Arthropoda			
Beetles (Coleoptera)	6.20		16
Grasshopper (Arthroptera)	4.65		12
Millipede (Myriapoda)	2.3		6
Ants, termites (Hymenoptera & Isoptera)	Trace		2
Ticks (Arachnida)	Trace		2
Unidentified insects	6.97		18
Plant material			
Tsama melon (Citrullus vulgaris)	52.3		135
Hookeri melon (Cucumis hookeri)	32.9		85
Gemsbok melon (Citrullus naudinianus)	14.7		38
Seed pods (Acacia mellifera)	6.58		17
Rumen material	6.20		16
Unidentified plant seeds	5.03		13
Unidentified plant, misc.	2.71		7
Unidentified leaves	2.32		6
Unidentified seed pods	1.93		5
Acacia leaves	1.93		5
Boscia albitrunca leaves	1.16		3
Unidentified melon	Trace		2
Unidentified fruit	Trace		1
Albizia leaves	Trace		1
Percentage frequency of occurrence from total samples			
Large mammals	82·17%	Insects	19·37%
Small mammals	36.82%	Vegetation	68 · 99%
Birds	29 .06%	Bonemeal	100.00%

have observed that Brown hyaenas are solitary hunters of small prey, we may assume that the large mammals represented in the faeces are scavenged from other predators.

When the samples were divided into wet and dry season categories, it was found that a much greater percentage of large mammal remains was eaten in the wet season. In 1975, for example, only 17.0% of large mammal remains was found in the dry months June through December. The point to be made is that soon after the rains, springbok, gemsbok, and other large ungulate species diminish so that during the dry season few of these species and few large predators remain to provide carrion for the hyaenas. This is reflected in a lesser frequency of large mammal items in the dry season.

Table 1 demonstrates considerable diversity in the diet and many of the fiftyeight foods listed are quite small and could have been killed by the hyaena itself. As with the faecal analysis of any potential scavenger, however, it is difficult to conclude whether many of the species were hunted or scavenged. Many prey species such as springhare (*Pedetes capensis*) or Black korhaans (*Afrotis afra afra*) are both hunted by hyaenas and scavenged from jackals, Cape foxes (*Vulpes chama*), caracals (*Felis caracal*), and other predators.

In considering the frequency with which food items appeared in the samples, Mills (1976) found that 72.0% of the samples from the Southern Kalahari contained insects and 33.0% contained reptiles, as contrasted to the 19.37% and 2.71% respectively in the Central Kalahari samples.

118 M. J. Owens and D. D. Owens

Brown hyaenas consumed considerable amounts of vegetation (Table 1), particularly the fruits from the Tsama melon (*Citrullus vulgaris*), the Gemsbok melon (*Citrullus naudinianus*), and Hookeri melons (*Cucumis hookeri*), especially during the dry months when these plants become an important source of moisture for the hyaenas (Fig. 1). Occasional faecal samples collected during August or September were as much as 50% by volume composed of Tsama, Gemsbok, and Hookeri rind and seeds.



Fig. 1. Average percentage by volume of vegetation (---) contained in faecal samples per month (---), rainfall.

Sifted bone meal comprised over 50% by volume of most samples and was present in all of them.

Direct observation on food item selection

A summary of items which we have observed hyaenas eat is presented in Table 2. 35.9% were fresh remains of a large mammal (Steenbok size or larger) killed by another predator. 33.9% were miscellaneous scavenged items such as old bones, horns, eggs, and dung. 16% were items killed by the hyaena and 12.5% was vegetation, usually a melon. These observations involve some bias since it is much easier to observe a hyaena feeding on a large carcass than it is to see it pick up a small item as it forages.

In feeding on a large carcass, the hyaena first attacks those parts most easily ingested. The carcass may be nearly whole if it has been appropriated from a cheetah or leopard soon after the kill. Or, it may consist of little more than the skeleton with some skin attached, as is often the case with lion kills.

If the carcass is quite fresh, the hyaena usually begins feeding on the viscera, especially nibbling fat from the mesentery along the intestine with the incisors. However, most time and effort is spent in separating a leg, usually a hind leg, for caching. The carnassial shear is used in cutting away the skin, exposing the muscle which is then eaten away from the joint. The carnassial shear is then used as a wedge

% Probably frequency Probably scavenged × obs. of killed from other od item eaten total by hyaena predator Percentage	
frequency Probably scavenged × obs. of killed from other od item eaten total by hyaena predator Percentage rge mammals	
x obs. of killed from other od item eaten total by hyaena predator Percentage rge mammals	
od item eaten total by hyaena predator Percentage	×
rge mammals	Food item
Springhok 16 0.1% 16 Percent frequence	Large mammals
10 - 10 - 10	1. Springbok
2. Gemsbok 38 21.8% 38 Brown hyaena scavenge	2. Gemsbok
3. Hartebeest 2 $1 \cdot 1\%$ 2 large kills from othe	3. Hartebeest
4. Springbok fawn 3 1.7% 3 predator 35.9%	4. Springbok fawn
5. Giraffe $3 1.7\%$ 3	5. Giraffe
5. Steenbok 1 0.6% 1	6. Steenbok
all mammals	Small mammals
1. Porcupine 1 0.5% 1	1. Porcupine
2. Springhare $2 1 \cdot 1\%$ 2	2. Springhare
3. Unidentified rodent 4 $2 \cdot 2\%$ 4	3. Unidentified rodent
4. Hare $1 0.5\% 1$	4. Hare
rds	Birds
1. Korhaan 2 1.1% 2 Percent frequence	1. Korhaan
2. Unidentified Brown hyaena observe	2. Unidentified
bird 2 1.1% 2 eating object killed to itself 16.0%	bird
sects	Insects
1. Moths, Grasshoppers 4 $2 \cdot 2^{\circ}$, 4	1. Moths, Grasshopper
2. Termites $2 1 \cdot 1\%$ 2	2. Termites
3. Ants 3 1.7% 3	3. Ants
4. Unidentified 8 4.5% 8	4. Unidentified
getation	Vegetation
1. Tsama melon 10 5.7% Percent frequence	1. Tsama melon
2. Gemsbok melon 6 3.4% observed eating	2. Gemsbok melon
3. Hookeri melon 6 $3 \cdot 4\%$ vegetation 12.5%	3. Hookeri melon
iscellaneous scavenged	Miscellaneous scavenged
1. Gemsbok dung 5 $2 \cdot 8^{\circ}_{0}$ Percent frequence	1. Gemsbok dung
2. Springbok dung 1 0.5% observed selectin	2. Springbok dung
3. Lion dung 3 1.7% small scavenge 33.9%	3. Lion dung
4. Leopard dung $2 1 \cdot 1\%$	4. Leopard dung
5. Old bone $12 - 6 \cdot 8\%$	5. Old bone
6. Horn (old) $4 2.2\%$	6. Horn (old)
7 Ostrich egg 1 0.5%	7 Ostrich egg
8. Unknown 32 18·3%	8. Unknown

Table 2. Food items eaten by Brown hyaenas during direct observation

to separate the ball of the femur from its socket. Once this separation is complete, the leg may be ripped free. The hyaena holding it in its jaws, often has the tail and hackles raised as it plants its feet forward and firmly on the ground then lunges backwards repeatedly. If the hind legs have been removed, a foreleg is separated in a similar manner. When the legs are gone, the meat along the spine and that along the ends of the ribs is eaten.

If only the skeleton is left when the hyaena arrives, it usually chews the ends from the ribs and from the spines of the vertebrae. If leg bones are present, it soon begins separating one for caching. The rate at which Brown hyaenas feed on carcasses appears to be much more leisurely than that reported in Spotted hyaenas (Kruuk, 1972). Brown hyaenas also apparently eat considerably less. Kruuk (1972) fed two gazelle fawns weighing a total of 14.5 kg to one Spotted hyaena which ate them both in 45 min. A Brown hyaena may feed for 200 min. or more at a carcass yet ingest no more than 4.5-5.0 kg of fresh meat if available, or 1.5-3.0 kg of skin and bones. Usually, the hyaena feeds, stands, looks off into the distance, feeds, chases a jackal, or interacts with another Brown hyaena, and then feeds again.

Large carcasses represent important meeting points for frequent and often prolonged socialization as discussed below (Sociality).

Hunting

When Brown hyaenas have been observed hunting they have always been alone. The hunting technique is rather unsophisticated or primitive as described by Kruuk (1976) in Striped hyaenas, involving a short dash when in pursuit of a mouse or bird, or a long zig-zag chase covering distances of up to 1 km when hunting springhare. When seizing a springhare or prey of similar size, it is given a quick shake before being eaten. During the chase the head is held in a 3/4 down position with ears erect, tail hanging nearly straight down or 3/4 down. The hyaena makes no attempt to move noiselessly and can often be heard walking through dry grass at a distance of over 100 m. However, Brown hyaenas do stalk on occasion, and we have observed this when watching them hunt korhaans. Kruuk (1972, 1976) has observed stalking in Spotted and in Striped hyaenas. On one occasion, an adult female Brown hyaena, its mane raised, chased two ratels (Mellivora capensis) for approximately 170 m in what appeared to be a hunting attempt. The chase was aborted, however, when both ratels turned and stood facing the hyaena emitting the alarm cry. Kruuk (1976) considers the raising of the mane while hunting to be maladaptive in Striped hyaenas as it may slow the animal's pursuit of prey. We have observed mane-raising while hunting in Brown hyaenas only on this single occasion and it may reflect a higher state of arousal experienced in hunting a more formidable prey species such as the ratel.

Brown hyaenas have also been observed digging at springhare burrows in an attempt to dig out this prey species.

Prey selection has been summarized in Table 3. Most of the hunting occurs in bush savanna and open woodland where bush and tall grass may almost completely conceal the hyaena and where prey species are more numerous. Hyaenas appear to hunt more often when there is less carrion available, as in the dry season, and this contention is supported in Table 3. Of the hunts observed, 13.7% were successful.

Drinking

Each year there is no available water for up to 8 months and Brown hyaenas almost certainly can exist for extended periods without water to drink, since the Kalahari experiences periodic droughts lasting for several years (B. Berghoffer, pers. comm.). During the rains when water is available, however, they visit a waterhole to drink at least once nightly, and often the forage period will include two or three stops at waterholes.

	Times		Season	Hab	itat type
Species hunted	observed	Wet	Dry	Valley	Bush
Mammals					
Springhare	7	1	6		7
(Pedetes capensis)					
Small rodent	6	2	4		6
(unidentified)					
Hare	1		1	1	
(Lepus saxatilis)					
Bat-eared fox	4	2	2	3	1
(Octocyon megalotis)					
Jackal	2		2	1	1
(Canis mesomelus)					
Springbok	1	1		1	
(Antidorcus marsupialis)				
Ratel	1	1			1
(Mellivora capensis)					
Birds					
Kori bustard	1		1		1
(Ardeotis kori kori)					
Korhaan	3		3	2	1
(Afrotis afra afra)					
Crowned plover	1		1	1	
(Stephanibyx coronatus)				
Unidentified bird	2		2		2
Insects					
Moths grasshoppers	4	4		2	2
(unidentified)	•			-	-
Ants, termites	5	2	3	1	4
(unidentified)	-	_	-	-	•
Unidentified insects	10	5	5	5	5
Totals	48	18	30	18	30
Percent of total	10	37.5%	62.5%	37.5%	62.5%

Table 3. Hunting observations in Brown hyaenas

Of total 13.7% were successful (excluding insects).

Diet summary

The Brown hyaena eats most frequently the scavenged remains of fresh kills left by other predators and miscellaneous items such as horns, eggs, and old bones. The diet is supplemented year round by hunting small mammals, birds, insects and reptiles, while vegetation becomes an important source of moisture during the dry months of the year. The hyaena is very opportunistic, taking advantage of any food resource when it becomes available, this determining, for the most part, its dietary components.

Activity period

Brown hyaenas are reported to be nocturnal (Smithers, 1968, 1971; Mills, 1973, 1976) and this does not differ from what we have observed in the Central Kalahari. We have, however, observed hyaenas foraging on cool, cloudy days during the rains as late as 11.00 hours, sometimes beginning the activity period as early as 17.00 hours under similar conditions. Brown hyaenas appear to be quite heat sensitive and almost always leave a carcass by sun-rise, even if it is fresh and they have hardly fed.

122 M. J. Owens and D. D. Owens

As in Striped and Spotted hyaenas (Kruuk, 1972, 1976) and in other carnivores (Kruuk, 1964) there appears to be two peaks in Brown hyaena activity period, similar to the 'bigeminus pattern' of Aschoff (1966). They are most active early in the night from approximately 19.30 hours to 24.00 hours, after which there is a resting period. From 02.30 to 06.00 hours, there is another period of activity. The timing of the beginning and end of the night's activity seems very definitely correlated with the season and, more specifically, with temperature. When there is no cloud cover during August, September and October, temperatures may reach 40°C and often higher on the river bed. Foraging periods at these times may be shortened by as much as 3–4 h, apparently to avoid these severe temperatures.

Foraging behaviour

In their movements over the range, Brown hyaenas make extensive use of a network of common pathways used by all members of the group and maintained through scent marking (pasting). In places these pathways are coincidental with game trails or our vehicle spoor. However, many segments are utilized only by the hyaenas themselves. A trail near a waterhole or other point of interest may be used by five or more hyaenas. It is not uncommon to see tufts of grass, with their stalks having been marked thirteen times or more collectively, individual stalks often bearing five pastes of varying ages, spaced at intervals of from 0.1 km to 1 km along the path in these areas. The entire network connects current and long-standing points of interest including fresh carcasses, water points and carcasses up to 3 months old. Specific pathways within the network are used with greater or lesser frequency depending on the habitat in which they are found and according to the season. But, generally, all lie in areas where food items are most likely to be encountered at one time or another.

Since hyaenas utilize common pathways along which they frequently deposit scent as they forage, they often meet, greet, separate or sometimes move together for a short way while socializing (see under range below).

In foraging, hyaenas walk at $3\cdot 2-6\cdot 4$ km per h, head threequarters raised and ears erect. They seldom move in a straight line of travel, but, generally, use a zig-zag mode of progression apparently maximizing the possibility for encountering food items. When a scent is located, the zig-zag becomes more exaggerated in amplitude until the source is very near to the hyaena.

Smell is the major sense used in foraging, and in many places the hyaena cannot see more than a few feet ahead in the tall grasses and thick bush. While foraging, hyaenas often turn abruptly into the wind, standing with head held fully raised, the muzzle inclined upward and moving side to side in locating scents.

One adult female we were following suddenly changed course 120 degrees upwind raising her muzzle high. After standing for 20 s, she ran 0.6 km through thick *Acacia mellifera* bush to where an oryx was giving birth. The hyaena attempted to approach the oryx but after being charged three times it moved off.

Brown hyaenas do move downwind in locating food sources and hearing becomes much more important over a short range in these instances. One night a hyaena turned and loped downwind 400 m to where two jackals had just killed a Kori bustard. The jackals had not begun eating and the hyaena could have been attracted only by the sounds of the kill. Within 15 min after appropriating the kori from the jackals, the hyaena was joined by two others. Brown hyaenas may cover considerable distances in a night's foraging. One female travelled 30.3 km during 12 h of continuous dry season observation. This is not at all uncommon and ranges generally vary from 20 to 30 km or more per night during the dry months.

Wet season forage distances are considerably shorter as there are often two or more fresh kills near the river bed and it is not necessary for individuals to cover such large distances in obtaining adequate sustenance. One hyaena stayed in an ardvark hole near a waterhole and giraffe catcass for 3 days, not moving more than 2 km a night during that time. Wet season forage distances typically cover 10–20 km.

One female with small cubs generally visited her den twice during a night and this limited the scope of her range considerably.

During rains hyaenas forage more frequently on the open grassland of the river bed, spending greater portions of the forage period where large concentrations of plainsgame congregate, and where predation frequency by large predators is greatest.

In the dry season, hyaenas are most frequently found in open to closed *Acacia* spp. scrub and in open woodlands which support a greater concentration of resident kudu, giraffe, oryx and small prey such as springhare and porcupine during this time of year.

A typical dry season forage period was exhibited by female 'A', a radio-tagged hyaena who left her lair in thick Acacia mellifera bush at 19.00 hours. The next 2 h were spent foraging in Acacia scrub, moving at about 2 km per h in the zig-zag fashion described. At 21.00 hours, she entered the open river bed where she began moving at 4.8 km per h, stopping periodically, turning into the wind and raising her muzzle high. On two of these occasions, she walked upwind for 12-15 m and put her nose to the ground while walking in tight circles, apparently investigating a scent. 'A' walked 4 km south along the river bed until she turned sharply east into the wind and after 75 m entered a thick stand of Cymbopogon plunoides, a very tall grass. There she fed for 10 min on a gemsbok leg which had been cached by her 3 nights before. After pasting next to the spot, she walked another 1.7 km south along the river bed. She turned west, passing through bush bordering the river channel, moving into an open Terminalia woodland. There she spent 40 min. feeding on a giraffe which had died 2 months before from an infection in the joints of the legs. 'A' pasted three times at the carcass then moved along a game trail for a short distance before she laid down to sleep for 2 h. After resting, she moved north 3 km pasting about once every 0.1 km along the game trail which passed through several dry waterholes in the woodland. When in an open bush savanna, she stopped, raised her head high but canted her ears forward with muzzle inclined down and looked at three female ostriches some distance ahead. She then began loping toward the ostriches which scattered from the spot. For 4 min 'A' crossed and re-crossed the area where the ostriches had been roosting, apparently trying to locate the nest. After pasting twice, she left the area without success, crossing the river bed to the open dune woodland on the eastern side. There she met female 'B' who did not submit readily and there ensued a muzzle wrestling contest with 'A' biting and vigorously shaking 'B' by the scruff for 8 s before 'B' broke and ran with 'A' in pursuit. The chase lasted 1.5 min, the hyaenas running in circles ahead of the vehicle until 'B' ran off. 'A' then moved into thicker bush where she dug into springhare burrows, removing and eating a springhare on the third attempt. From there 'A' walked through bush savanna 1.3 km to where she had spent the previous day's resting period. Pasting frequencies are underrepresented in this sample since the

hyaena spent considerable periods in tall grass and dense bush where continuous direct observation was impossible.

Food storage

Kruuk (1972) has reported the storage of food to be rare in Spotted hyaenas, but quite common in the Striped hyaenas (1976). On 70% of the occasions when a Brown hyaena was observed leaving a carcass where it had been scavenging it carried away some part, usually a leg, to be cached. These items may be stored in clumps of dense bush bordering the river bed 100-600 m from the kill site where the hyaena returns to feed the beginning of the next night. Portions may be carried for 2 or more km to den sites or lying-up places in the bush savanna. Caching is an effective way of spreading a carcass resource over time and a cache may be visited and fed upon for many nights after the main carcass is expended. Caching is also an effective form of competition and the hyaena which locates a large carcass first may be able to dismember, carry off and cache as many as three legs before other hyaenas arrive. It would seem that the utilization of common pathways would eliminate the advantage gained through caching as although a hyaena pastes 15-20 m away from the cache site, other hyaenas do occasionally discover caches which are not their own. However, this is almost certainly compensated for since the hyaena who loses a cache is quite likely to find one left by another.

It is interesting to note that while competition between hyaenas and Black-backed jackals is very keen, jackals do not usually follow hyaenas to cache sites and we have only once seen a cache exploited by a jackal.

Interactions with other predators

Lions. While lions are at a kill site Brown hyaenas avoid the immediate area and we have never observed them approach closer than 200 m while the lions are in attendance. Even after lions have left, Brown hyaenas are very cautious in their approach to the carcass. On one occasion, a hyaena observed a lion pride leaving a gemsbok carcass, yet took 36 min of slow, circuitous movements to approach. This behaviour is probably well adapted as we have seen two adult male lions attack a Brown hyaena and similar observations have been reported elsewhere (Eloff, 1973). Browns generally shun contact with lions, though they frequently visit the general area of a lion kill, apparently to see if the predators are still present.

Cheetah. Brown hyaenas easily appropriate kills from cheetahs and we have, on four occasions, observed a single individual taking adult springbok or springbok lambs from them. When a hyaena sees a cheetah it often runs in its loping gait toward the cat to investigate, apparently to see if it has made a kill.

Leopard. One night a male leopard killed an adult springbok 150 m from our camp. Before it could feed, a female Brown hyaena, apparently having seen or heard the kill, loped up, chased the leopard from the carcass and began feeding. After some time, the leopard returned and charged the hyaena from 20 m. Raising its hackles, the hyasna returned the charge chasing the leopard 150 m into camp and up a tree. The hyaena returned to feed and the leopard did not reappear. On two other occasions we have observed a leopard being treed by a hyaena when there was no kill in contention.

Wild dogs. Brown hyaenas are apparently not tolerated by Wild dogs at a kill. Once, after a hyaena had appropriated a springbok from a cheetah, the hyaena moved off and stood 1 m away upon the arrival of four Wild dogs. Five minutes later the hyaena began cautiously feeding on the head of the carcass while the dogs were feeding at the rear. After 2 min, one dog darted after the hyaena biting it in the hindquarters as it fled, limping and uttering a loud 'howl-bark' vocalization. Five minutes after the dogs had finished with the carcass the hyaena returned to feed.

However, Wild dogs are rarely seen in the research area. In 3.5 years, they have been observed only thirteen times with an average pack size of 8.6 individuals.

Spotted hyaenas. In 3.5 years we have encountered Spotted hyaenas on only nine occasions. They were twice seen as a pair while the other sightings were of a single individual each. On one occasion, one was observed feeding on an oryx carcass left by lions. The Spotted hyaena walked some distance away, but remained in the area. A Brown hyaena approached to within 300 m of the carcass but moved off at a fast walk without feeding while looking in the direction of the Spotted hyaena.

Black-backed jackals. Black-backed jackals are the most common predator/ scavenger in the research area and there is considerable competition between jackals and Brown hyaenas at a carcass and for food items obtained elsewhere on the range. There is great overlap in the diets and the mode of existence both of which involve shifts toward scavenging during the wet season and hunting small animals the year round. Thus, Brown hyaenas directly interact more frequently with jackals than with any other carnivore in the Central Kalahari.

As many as eight jackals will feed on a carcass with a Brown hyaena, the latter chasing the jackals off to a distance of 10-12 m as often as 0.9 times per min. The jackals immediately reapproach the carcass after being chased and often a 'tug-of-war' occurs with numerous jackals pulling at one end of a diminishing carcass while a hyaena pulls at the other. When jackal competition is very keen, a hyaena may separate a portion of the carcass and carry it away to feed. On two occasions, jackals have been seen to nip a hyaena under the tail and while the hyaena whirled to attack, the jackal dashed in, grabbed the piece of carrion and ran off with it. This once led to a chase which lasted for 5 min.

Conversely, hyaenas frequently chase jackals from miscellaneous scavenged material such as old bones, pieces of skin, and Tsama melons. On three occasions, hyaenas have been observed appropriating springbok fawns from jackals. On two occasions, a hyaena has been seen chasing a jackal on the river bed in what appeared to be a hunting attempt, both of which were unsuccessful. Mills (1973, 1976) reported a Brown hyaena eating a jackal.

Jackals often follow hyaenas over the range and we have seen as many as five jackals queued up behind a Brown hyaena as it moved along. When the hyaena laid down to rest the jackals all laid down within 10 m of it.

In summary, if we rank the largest Central Kalahari predators in terms of their competitive success and influence one over the other in the Central Kalahari community of large carnivores, we may develop a hierarchy on this basis with the following order of development: lion – Spotted hyaena – Wild dog – Brown hyaena – leopard – cheetah. This hierarchy, however, does not present a representative picture of the community because Spotted hyaenas and Wild dogs are so infrequently active competitors in any portion of the range at any given time. Since these two predators are so rarely encountered and occur in such small groups it means that whatever a Brown hyaena finds to scavenge it is virtually assured of no competition from Spotted hyaenas or Wild dogs. In addition, during the dry months lions are nearly as

infrequently encounted as are Spotted hyaenas and Wild dogs. In this season, Brown hyaenas are usually the largest and most dominant carnivore in the area.

Social organization

Home range. Individual Brown hyaenas do not defend a given portion of their home range and therefore are not territorial. Each individual has a home range to which it generally adheres in its movements, but there is great overlap between members of the group (Fig. 2). Dry season home range sizes (maximum during year)



Fig. 2. Home ranges of four Brown hyaenas of Deception Valley determined through direct observation and radio telemetry. ———, L (female with cubs); ——, Sh (female with cub); ……, St (female); – – –, O.Y. (male).

are an average of 40 km². Hyaenas within the group extensively use common pathways over the range and often meet, socialize, and separate to continue foraging. Individuals may even pass through caching or denning areas of others. One female with a cub only a few weeks old had a den only 200 m from a path well used by the other hyaenas in the group.

As discussed below, as many as six hyaenas may congregate at a common food source, and different individuals use the same waterhole. It may be that members of the Deception Valley group defend their portion of the range against members of another group. We have observed some indications of this but more observations are needed for confirmation.

Communication

Scent marking. Pasting or scent marking appears to be the most important means of communication, at least over distances greater than 300-400 m. Both male and female Brown hyaenas paste similar to that described in Striped hyaenas by Kruuk (1976). The tail is raised, and as the hindquarters are lowered over a grass stem, the rectum with its anal glands is everted. The glands are drawn along the grass, depositing a white, viscous substance having a very strong musty odour, about 14 cm from the top end of the stalk. Two cm above this mark is another rust-coloured secretion with a different odour. Analysis is being conducted to determine the chemical components of these glandular secretions. The grass species most frequently marked by the hyaenas are Sporobolus ioclados, Cymbopogon plunnoides and Stipagrostis hirtigluma.

Pasting usually occurs very frequently as the hyaena moves over its range. For example, it has been observed every $2\cdot3$ min for 43 min, every $3\cdot9$ min for 47 min, and every $1\cdot3$ min for 13 min. Of ten different individuals which were observed moving over the river bed, each marked an average of once every $5\cdot91$ min. Hyaenas may mark the same grass stalk twice within 1 min at points of great interest, i.e. kill sites, food storage points. Conversely, individuals may only paste once or twice during an entire observation period.

Sites most commonly marked are places where the hyaenas leave the river bed to enter the bush, carcass sites where they have fed, the site of a small scavenge, a waterhole, after an interaction with another hyaena, at a cache site, and often as they move over the common hyaena pathways. Grass stalks are often smelled carefully before marking. On these occasions, the hyaena is examining an old mark left by itself or another hyaena.

It appears that hyaenas mostly mark areas of interest within the range, with no evidence to suggest that the mark warns off other hyaenas. The glandular sceretions apparently contain information on group member temporal and spatial location needed for meetings on the range as well as that necessary for a hyaena to relocate points of interest such as a cache or an old kill site. Marks apparently contain information on social status and perhaps even communicate an individual's identity. We have observed fifteen occasions where hyaenas have pasted over the marks left by other individuals of the group. One adult female was observed pasting over a mark left by an adult male only 4 min before. The female then moved off in the same direction. The two hyaenas so far as we know, were unrelated and not a mated pair, nor did mating occur later. On another occasion, we were following female 'B' which had drunk and pasted at a watering point 1.5 km and 25 min before. Suddenly we were passed by female 'A' moving at a fast walk from the area where 'B' had pasted and proceeding to 'B' where she began muzzle-wrestling, neck-biting and chasing 'B'. The interaction covered 1.5 km and lasted 12 min.

Subordinate hyaenas smelling the mark of one more dominant often turn their ears and partially flatten them, raise their hackles and increase their pace. One hyaena even responded similarly to scent picked up by the vehicle in passing over the scent mark of another.

Latrines. Brown hyaenas do have areas used for defaecation, though these are not used to the extent reported for Spotted hyaenas (Kruuk, 1972). Kruuk (1976) reported the Brown hyaenas of the Southern Kalahari to be intermediate between Striped hyaenas which use no dung heaps and Spotted hyaenas which use them extensively. This is consistent with what we have observed. The hyaenas of the Central Kalahari quite often use latrines which may contain as many as 12–15 defaecations. These latrines may serve a communicative function as they do in Spotted hyaenas (Kruuk, 1972), especially considering that Brown hyaenas in passing latrines often paste if they do not defaecate at the site. The latrines are usually positioned along the common pathways of the group, and are, therefore, passed by other hyaenas. We have not observed more than one hyaena utilize the same latrine, however, we often see other hyaenas visit these areas and smell around them extensively before pasting.

Latrines are usually located under a thick bush of Acacia tortillus, Terminalia prunnoides, Ziziphus mucronata, or Boscia albitrunca.

Urination. Urine does not appear to serve any special communicative function and it may be released at any location, even while lying down. The lack of a communicative function in the urine has also been reported by Kruuk for Spotted hyaenas (1972) and Striped hyaenas (1976).

Vocalizations. The vocalizations of Brown hyaenas have been summarized in Table 4. Browns do not laugh as do spotted hyaenas, and vocalizations for the most

Vocalization	Description of sound	Posture when used	Situation
1. 'Squeal' or whine	Shrill, sharp cry	Body low, head low, cocked one side, ears flat, tail over back, or stretched out	Used when subordinate hyaena approaches a dominant feeding, greeting, used by young
2. 'Growl' or grunt	Breathless, deep throaty sound, low pitch	Ears up or flat, body high, heads high, throwing muzzles around, teeth exposed, mouth open, hackles raised, tail up	Muzzle-wrestling
3. 'Yell'	Loud cry, high pitch	Hackles raised, mouth open, teeth exposed, tail low	Making a stand against lions before fleeing, any tendency to flee
4. 'Scream'	Loud shriek, high pitched, 'ack-ack-ack' sound	Body low, ears flat to side, grin, head cocked, hackles raised or not, tail over back or down	Subordinate in neck-biting
5. 'Squeak'	Rasping squeak, hoarse rattle, like sound of a rusty gate opening	Body low in carpal crawl position	Subordinate during crawl

Table 4. Vocalizations by Brown hyaenas

part are limited to short range communication and would not be heard unless one was within 100-300 m of the hyaena. The Brown hyaena is a quieter animal than the Spotted hyaena and in this way more similar to the Striped hyaena (Kruuk, 1976). The Brown hyaena repertoire of vocalizations is however, more elaborate than reported by Kruuk (1976) and has important communicative value in social situations.

Social interactions. Social interactions include neck-biting or scruff holding as described in Canids by Kleiman (1967) and Fox (1969), a type of 'carpal crawl' as described in Spotted hyaenas by Darwin (1872) and Kruuk (1972), prolonged chasing

and muzzle-wrestling similar to that described by Fox (1969) in Canids, greeting, food acquisition, and social grooming. All of these interactions and the contexts in which they occur are described in more detail in Table 5. Table 6 describes visual displays such as positions of ears, lips, tail, and body postures used in communication. Interactions are not sexually delineated and occur between related and unrelated adults.

All overt fighting is directed toward the neck or side of the face of the subordinate hyaena. Neck-biting is often very vigorous, the subordinate at times being thrown off its feet and blood colouring its neck hairs. It can become quite protracted and we have observed it between two unrelated females for 2 h, 15 min, the neck actually being bitten for continuous periods of 18 min, 12 min, 11 min, 4 min and 1 min. Neck-biting with intermittent chasing and breaks for rest has been observed between two unrelated adult males for over 3 h. Hyaenas darted for ear-tagging were found to have very thickened skin covering the neck and shoulders, so much so, that the removal of a barbed dart from this area was nearly impossible without incision. In addition, hyaenas of lower social rank exhibited much more heavily scarred necks than did those of higher status.

Sociality

Little has been reported about the sociality of Brown hyaenas. Smithers (1971) described them as solitary or only in pairs. And after more than 1 year of study in the Southern Kalahari, Mills (1973) had not seen two adult hyaenas together. Kruuk (1976) maintains that the feeding ecology of the species in its Southern Kalahari range limits members to a solitary existence, as in Striped hyaenas. The Brown hyaenas under study in Deception Valley remain solitary foragers and hunters but are social scavengers at carcasses left by other predators and demonstrate other signs of socialability as described below.

Large carcasses, such as gemsbok and giraffe, often attract more than one hyaena to the immediate area to scavenge. Thus hyaenas congregate for communal scavenging of a carcass killed by another predator. We have observed hyaenas feeding on eighty-seven carcasses of springbok size or larger. On 41.3% of these occasions only one hyaena came, however, on 58.6% two or more hyaenas were attracted to the carcass at the same time. Regardless of how many hyaenas arrive at a carcass site, they do not all feed at the same time, in fact, some never feed. Although there may be six hyaenas in the immediate area, the most we have observed feeding together was three. On twentythree occasions, we have observed two unrelated adults feeding at the same time. None of these groups involved mated pairs.

There is a great frequency of social interactions between hyaenas not actually feeding but in the immediate carcass area, involving considerable time and effort. At times the carrion is left unattended (except for jackals) for considerable periods while the hyaenas engage in social interactions, lying around in close proximity, and on occasion, socially grooming. Table 7 provides information on the amount of time various hyaenas actually fed on three carcasses as contrasted to the time spent in socialization and that time spent lying around the area.

Group members are listed in order of dominance within a social hierarchy, highest ranking individuals are listed first. From the Table it can be seen that dominant hyaenas spent greater portions of their time at a carcass actually feeding. Lower ranking hyaenas spent less time feeding and a greater portion lying some distance

Type	No. of times	Sex and relation hyaenas involved	Description and duration	Situation
1. Neck-biting	45	Unrelated, 2 \Rightarrow or 2 \Rightarrow or 3 \pm or 2 d out siblings	Dominant hyaena rushes in, grabs subordinate by neck, shakes neck vigorously, subordinate lies down, screams in submissive posture, often develops into chase, blood often drawn, observed up to 18 min	$37 \cdot 7\%$ observations at carcass site. elsewhere on range. $62 \cdot 2\%$
2. Muzzle- wrestling	18		Hyperas stand opposite each other, usually at approximately 135 degree angle, stand tall, throw heads wildly, biting at and pushing each other's muzzle, hackles may be raised, ears erect or flat, mouth held open, teeth exposed, emiting growl or breathless emitting for the standard of t	When two hyaenas meet on range or when travelling together
3. 'Carpal' crawl	12		Suburdinate hyaena lowers itself to carpal joints, actually crawls Suond dominant, both hold tails up, smell under each other's tail as both turn in a circle, subordinate emits 'cackling' sound, ears flat prin	Either near a carcass or when two hyaenas meet on range
 'Leap-frogging' extension of crawl 	3	Unrelated 2 \downarrow Unmated $3 + \uparrow$	After crawl, dominant hyaena moves on, subordinate gets up, moves quickly in front of dominant, lies down, initiates another crawl. Up to five times in succession. 5 min	Once after crawl on range, once near carcass
5. Social grooming or licking	S,	Unrelated 2 5 2 3 3 + 2 siblings	One hyaena (dominant) lying down, other hyaena approaches, either lies down beside or stands, licks (dominant) hyaena's face or back (does not include genital licking of a mated pair)	80% near carcass site $20%$ hyaenas moving together
6. Social chase	20	Unrelated 2 <i>δ</i> Unmated ♀+ <i>δ</i>	Usually after muzzle-wrestling or neck-biting, subordinate hyaena runs, dominant chases, both hackles up, tails flicking, not fast run, medium gallop, often interrupted by more neck-biting or muzzle-wrestling, subordinate makes no real attempt to escape, often walks back to dominant. Usually observed 2-10 min once aver 3 h with many interruptions	80% around carcass site 20% hyaenas meet on range
7. Food acquisition	۲	Unrelated 2 ♀ Unmated ♂+♀	subordinate hyacan runs up to dominant hyacna which is carrying bone, subordinate flattens cars to side, lowers body, 'squeals', subordinate grabs meats, usually dominant lets go of food, returns to carcass to get more. Only once did dominant tug for possession of meat. 30 s-2 min	Near carcass site
8. Greeting	<i>LL</i>	2 2 2-2 3 3 + 2 Unrelated Unmated	Mutual neck and anal sniffing as hyaenas stand head to rear, subordinate lowers body and head, sometimes lies down, sometimes develops into 'crawl' $5 \text{ s-}5$ min usually 2-5 min	Anywhere on range and at carcass site

Table 5. Some social interactions between Brown hyaenas

M. J. Owens and D. D. Owens

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Type	Description	Situation
 Position of ears a. Ears to side b. Ears erect c. Ears flat back 	a. Ears held out flat from head at different degreesb. Ears at highest positionc. Ears flattened back along skull	 a. Appeasement, used when subordinate hyaena approaches dominant on a kill, usually accompanied by 'squeal' b. Normal position in hunting, foraging. Used by dominant in chasing, neck-biting and most interactions
2. 'Grin'	Lips raised and corners of mouth pulled back,	c. Extreme submission during neck-biting Used by subordinate hyaena during neck-biting
3. 'Hackles' or mane and back hairs raised	motars exposed Hairs on scruff and back stand erect	Used by dominant hyaena during neck-biting, chasing; used by subordinate feeding on a carcass when dominant approaches; used when hyaena chases a jackal or approaches a lion kill, seen once in
4. Tail positions	a. Up over body b. Straight out from body c. Hanging down	a. Observed in dominant and subordinate in neck-biting. Used by dominant when subordinate approaches a carcass, used when subordinate walked away from dominant, used by dominant and submissive during crawl b. Similar to a., hyaenas often give a greeting with tail in this position often used this way after nesting
5. Body positions	a. Standing tallb. Slightly crouchedc. Extreme crouchd. Lying down	position, orten walk this way after pasting c. Usual position; used by dominant in some interactions a. Used by dominant hyaena in greeting, approaching a carcass, feeding, etc. b. Used by slightly less dominant hyaena when approaching dominant hyaena feeding, greeting, etc.
	1	 C. Used by subordinate in greeting, neck-biting, approaching a dominant and feeding, etc. d. Subordinate during neck-biting, crawling, feeding next to a dominant
 6. Head positions a. Head high b. 3/4 position c. Head low d. Head cocked 	a. Neck extended, head highb. Normal position, straight from bodyc. Head lowered toward groundd. Head cocked to one side	 a. Dominant hyaena in greeting, hyaena in neck-biting when subordinate retaliates, both hyaenas in muzzle-wrestling b. Dominant hyaena in greeting, approaching another hyaena, foraging c. Used as subordinate approaches a dominant, dominant hyaena d. Constitue approaches a jackal or hunting d. Subordinate approach a dominant, dominant hyaena
 Muzzle positions a. 45 degree down usually used with lowered head posture b. Straight from body c. Muzzle raised 	 a. Muzzle inclined 45 degrees downward c. Muzzle inclined 45 degrees up from level—used with head high posture 	 a. Subordinate insubmission to dominant hyaena a. Subordinate in submission to dominant hyaena b. Aggression directed at another hyaena or stalking a prey c. Usually observed when hyaena is taking scent

Table 6. Visual displays by Brown hyaenas

Hyaena identity and sex	Time feeding (%)	Time social interaction (%)	Time lying down or milling around (%)	Total time at kill site (min)
Kill no. 1				
1. Ivey (්)	57·0	4 · 4	38.5	135
2. Star (♀)	20.4	3.3	76.2	240
3. Hawkins (්)	15.1	4.9	79.9	204
4. Spooky (්)	11.2	4.8	84.0	250
Kill no. 2				
1. Star (9)	41 · 9	8.0	50·0	62
2. Spooky (්)	25.9	7.4	66.6	108
3. Hy 4	26.3	1.3	72.2	72
4. Hy 3 (f2) ♀	22 · 2	24 · 4	53 · 3	45
Kill no. 3				
1. Star (♀)	19.2	19.7	60.9	228
2. Hawkins (3)	19 ·7	$2 \cdot 1$	78·0	228
3. Pogo (♀)	24 · 2	26.3	49 • 4	190
Average	25.73	9.69	64 · 45	

 Table 7. Examples of feeding time, socializing time and lying around time of Brown hyaenas at a large carcass

away, standing while watching another feed or interacting with arriving or departing hyaenas.

During the course of this study, most observations have been made on fourteen Brown hyaenas. At any one time the number of resident adults in the area (101.7 sq. km) has remained relatively constant at eight or nine, although there has been a high turnover from immigration and emigration. Young adults of both sexes have been excluded from the group through conflicts with established adults of the same sex, though in total, more males have emigrated than females. When 22 months old, one female and one male subadult of one of the resident and tagged females were the object of frequent and very vigorous and prolonged neck-biting and chasing from two established adults. These encounters continued for 7 months between the males and 3 months between the females after which the two subadults apparently left the area as they have not been seen for 15 months.

A total of four males and two females have emigrated while two males and one female have joined the group. This turnover suggests that the group is not a closed family unit. Mills (1976) reported that in the Southern Kalahari, female young remained resident while young males left the area.

The tendency of Brown hyaenas to socialize is summarized in Table 8. Since 37.81% of 333 hyaena observations have involved the association of two or more individuals (not for breeding purposes) it is readily apparent that Brown hyaenas are quite social animals. Some elements of Brown hyaena socialization within the resident group are as follows.

(1) Individual hyaenas of the group recognize each other as is evident from dominant and submissive behavioural postures elicited at distances of 300 m or more when hyaenas meet.

(2) There exists a definite, well-defined rank order among adult hyaenas within the

Solitary 62.15% total observations	51.35%	(Total observations) solitary hyaena moving over range, hunting, foraging, sleeping, etc.
	10·8%	(Total observations) solitary hyaena feeding at a carcass left by another predator
Hyaenas in groups 37.81% total observations	7.5%	 (Total observations) 2 hyaenas moving together, over range Observations in 2♀, 2♂, ♀+♂. Mated, ♀+♂ unmated siblings
	1 · 20%	3 hyaenas moving together over range
		Observations $\Im w/2$ adult siblings, $2\Im + 1\Im$ unrelated adults
	12.31%	2 hyaenas, each moving separately, meet, greet,
	12 31/0	separate, or go on together
		d + q mated pair,
		$^{\circ}+_{\circ}$ not mated
		2 ♀
	1.50%	3 hyaenas meet while foraging, greet, separate
	6·9%	2 hyaenas at a common carcass killed by another predator
		2 3, 29, 3+9 unmated and mated
	4·8%	3 hydenas at a common carcass $2^{\varphi}, 2^{\varphi}, d + \varphi$
	1.8%	4 hyachas scavenging at a common carcass 2 $2, 23, 3+9$
	1 · 5%	5 hyaenas scavenging at a common carcass $\frac{3}{2}$
	0·30%	6 hyaenas scavenging at a common carcass ♂♂+♀♀

Table 8. Social grouping of Brown hyaenas (percentage of 333 observations)

group. This hierarchy is not sexually delineated. Some members of each sex dominate members of the other. The hierarchy is maintained through neck-biting and other social interactions.

(3) Brown hyaenas have a well-developed communication system including extensive scent marking, vocalizations, visual displays, and elaborate social interactions.

(6) There is extensive overlap of home range and Brown hyaenas constantly use the same network of pathways maintained through scent marking.

(5) Individuals usually make no attempt to avoid each other when moving over the range at night and often greet. The greeting ceremony usually involves initial sniffing of the neck, flank and anus for up to 1 min. Greeting may involve 'crawling' which lasts for as long as 5 min.

(6) Brown hyaenas often engage in communal scavenging of carcasses left by other predators. These carcasses become focal points for socialization for several nights.

Discussion

It has been suggested that complex expressive movements involving sophisticated visual signals may be used as an index to the degree of sociability among species of Canids (Kleiman, 1967, Fox, 1970) and in general (Wilson, 1975). If a similar index

is applied to Hyaenidae it would appear that the Brown hyaena, exhibiting the repertoire of socio-behavioural elements as enumerated and described above, may be considered to be a far more social species than has been previously recorded. In addition, observations during the present study have shown that Brown hyaenas socialize (37.8% of 333 observations) for purposes other than breeding.

Kruuk (1972, 1975, 1976) has shown that the diet and exploitation of ecological niche by members of the family Hyaenidae have directly influenced their social organization and spatial distribution. There exists a relationship between the degree of 'gregariousness' and the mode of foraging. The Striped hyaena forages over considerable distances, feeding and preying on small food items and maintains a solitary existence. Spotted hyaenas hunt large prey cooperatively but remain solitary when foraging or hunting for small items (Kruuk, 1976).

The Central Kalahari environment presents two types of resources for exploitation by Brown hyaenas; sparsely distributed small food items, all that is generally available as food in the dry season, and large carcasses left by lions and other predators most frequently during the rains. Brown hyaenas exhibit a flexible social system, remaining solitary when foraging for items sparsely distributed but equipped with the necessary social mechanisms which permit the communal exploitation of a concentrated food resource and socialization in other contexts.

In the dry season, hyaenas may range 30 km or more in a forage period, scavenging and occasionally hunting single food items, each of which constitutes but a small portion of the subsistence requirement. Through a sophisticated long range olefactory communication system operating over the network of common pathways, hyaenas are able to meet, reinforcing and maintaining social ties and group cohesion.

With the rains a relatively concentrated carrion resource becomes available to the hyaenas in Deception Valley. Brown hyaenas are not territorial, members of the group utilizing coincidental ranges, as many as six hyaenas meeting at a carcass. Such behavioural mechanisms as neck-biting, muzzle wrestling, and chasing permit the resolution of conflict over social status at carcasses and elsewhere on the range so that hyaenas may scavenge communally for the more efficient utilization of the carrion resource.

Kruuk (1971) has observed that Spotted hyaenas compete at a carcass by feeding rapidly rather than by fighting or caching. Brown hyaenas, however, eat very leisurely for considerable periods of time, consuming relatively small portions of a carcass composed mostly of bone, which could not be consumed rapidly in any case. There is seldom aggression between two feeding Brown hyaenas and thus, hyaenas compete at a carcass indirectly by competing for social status and directly by caching.

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References

ASCHOFF, J. (1966) Circadian activity pattern with two peaks. Ecology, 47, 657-702.

DARWIN, C. (1872), The Expression of the Emotions in Man and Animals. John Murray, London.

ELOFF, F.C. (1973) Ecology and behaviour of the Kalahari lion. In: The World's Cats. Vol. 1 (Ed. by

R. L. Eaton). Ecology and conservation. World Wildlife Safari, Winston, Oregon.

- EWER, R.F. (1968) Ethology of Mammals. Logos Press, London.
- Fox, M.W. (1969) The anatomy of aggression and its ritualization in Canidae: A developmental and comparative study. *Behaviour*, **35**, 242–258.
- Fox, M.W. (1970) A comparative study of the development of facial expressions in Canids; wolf, coyote and foxes. *Behaviour*, 36, 49-73.
- JOHNSON, R. P. (1973) Scent marking in mammals. Anim. Behav. 21, 521-535.
- KLEIMAN, D.C. (1967) Some aspects of social behavior in the Canidae. Amer. Zool. 7, 365-372.
- KRUUK, H. (1964) Predators and anti-predator behaviour of the black-headed gull (*Larus ridibundus* L.). Behaviour, suppl. 11, 1–130.
- KRUUK, H. (1972) The Spotted Hyena. University of Chicago Press, Chicago.
- KRUUK, H. (1975) Functional aspects of social hunting by carnivores In: Essays on Animal Behaviour (Ed. by C. P. Baerends and A. Mannings). Oxford University Press, Oxford.
- KRUUK, H. (1976) Feeding and social behaviour of the striped hyena (*Hyaena vulgaris*, Desmarest). E. Afr. Wildl. J. 14, 91-111.
- MILLS, M.G.L. (1973) The brown hyena. Afr. Wildl. 27, (4) 150-153.
- MILLS, M.G.L. (1976) Ecology and behaviour of the brown hyena in the Kalahari with some suggestions for management. In: Proceedings of a symposium of endangered wildlife in Southern Africa. University of Pretoria, Pretoria.
- PIENAAR, U. de V. (1969) Predator-prey relationships amongst the larger mammals of the Kruger National Park. Koedoe, 12, 108-176.
- VON RICHTER, W. (1972) Remarks on present distribution and abundance of some South African carnivores. J. S. Afr. Wildl. Mgmt Assoc. 2, 9–16.
- SHORTRIDGE, G.C. (1934) The Mammals of South West Africa. Vol. 1. Heienmann, London.
- SILBERBAUER, C.B. (1965) Bushman Survey Report. Bechuanaland Press, Mafeking, South Africa.
- SMITHERS, R.H.N. (1968) A check list on the mammals of Botswana. Trustees of National Museums of Rhodesia, Salisbury.
- SMITHERS, R.H.W. (1971) *Mammals of Botswana*. Museum Memoir No. 4, Trustees of the National Museums of Rhodesia, Salisbury.
- SWEENEY, R.C.N. (1959) A preliminary annotated check list of the mammals of Nyasaland. The Nyasaland Society.
- VILJOEN, S. & DAVIS, P.H.S. (1973) Notes on stomach contents analysis of various carnivores in Southern Africa. Ann. Transvaal Mus. 28, 353-363.
- WILSON, E.O. (1975) Sociobiology The New Synthesis. Belknap Press, Cambridge, Massachusetts.