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THE DIET OF THE BROWN HYAENA *HYAENA BRUNNEA* IN THE SOUTHERN KALAHARI

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Abstract – Four methods for studying the diet of the brown hyaena are discussed. A combination of direct observations (of individuals fitted with radio collars and beta lights) and faecal analysis yielded the best information. Analysis of food items found at dens was also useful, but tracking spoor had severe limitations. The brown hyaena in the southern Kalahari is predominantly a scavenger of all kinds of vertebrate remains, supplementing its diet with insects, wild fruits, birds' eggs and the occasional small animal which it kills. It is thus well adapted to the harsh conditions of this arid region where large ungulates are thinly distributed.

Introduction

The little that is known about the diet of the brown hyaena *Hyaena brunnea* indicates that it exploits a variety of foods: marine animals cast up on the sea shore, a wide range of terrestrial mammals, reptiles, birds and their eggs, insects and fruits (Sclater 1900; Shortridge 1934; Stevenson-Hamilton 1947; Roberts 1951; Pienaar 1969; Smithers 1971; Skinner 1976). Detailed quantitative data on the brown hyaena's diet are, however, lacking, mainly because of the nocturnal and shy habits of this endangered species.

This paper describes and evaluates four techniques which were used to study the brown hyaena's diet in the southern Kalahari, and analyses the results obtained. It forms part of a continuing study on the ecology and behaviour of this species designed to define the limiting factors operating on the population in this area (Mills 1973, 1976, 1977, 1978a, 1978b and *in prep.*).

The Study Area

The study was carried out in an area of 2 750 km² centered around Nossob Camp in the Kalahari Gemsbok National Park (KGNP), Republic of South Africa, and incorporating areas in both this Park and the neighbouring Gemsbok National Park in Botswana (Mills 1978b). This semi-desert region has an irregular rainfall (annual mean 220 mm) and experiences large temperature fluctuations both on a daily and seasonal basis (Leistner 1967). During the study the area received good rains in all years, particularly in 1974 (532,0 mm) and 1976 (602,4 mm).

The vegetation is described by Acocks (1975) as the western form of the Kalahari thornveld and is an extremely open shrub or tree savanna. For the purposes of this study two habitats are recognised; the dunes which make up the major portion of the area and which are covered with a layer of soft red windblown sand with shrubs and tall perennial grasses, and the river-bed and immediate environs where the sand is more compact. Details of these habitats can be found in Mills (1976, 1978b).

The southern Kalahari is rich in mammals, 35 species (except for small rodents, bats and insectivores) having been recorded (Mills 1977). Within the study area blue wildebeest *Connochaetes taurinus,* red hartebeest *Alcelaphus buselaphus* and springbok *Antidorcas marsupialis* are chiefly confined to the river-beds where their numbers fluctuate markedly from season to season and year to year. Gemsbok *Oryx gazella,* however, are more evenly distributed (Bothma 1972; Bothma & Mills, 1977). Large carnivores occur in low densities, also mainly in the vicinity of the river-beds, and small carnivores, in particular black-backed jackals *Canis mesomelas* and bat-eared foxes *Otocyon megalotis,* are common throughout the area. Ground nesting birds, reptiles and insects such as Coleoptera and Isoptera are common and widespread.

Material and Methods

Between April 1972 and July 1976 we spent 37 months in the field during which four techniques were used to collect data on the brown hyaena's diet: tracking spoor, direct observations, faecal analysis and the analysis of food items found at breeding dens.

Tracking spoor

From the initiation of the study until October 1973 much time was spent in following brown hyaena tracks in the Kalahari sand with the help of a Bushman tracker. Spoor was located by searching likely areas such as around windmills, dens or the rubbish dump at Nossob Camp. It was then followed for as long as possible, during which all food items indirectly observed to have been eaten were recorded. This method has been successfully used on lions *Panthera leo* by Eloff (1973 a, b and c).

Direct observations

Six individuals were caught in a baited drop-door trap and immobilised with a dart filled with Sernylan (phencyclidine hydrochloride) and the tranquiliser Combellem, fired from a Palmer Capchur pistol (Palmer Chemical and Equipment Co., Atlanta, U.S.A.). To each animal we fitted a radio collar (Dav-tron, Minneapolis, U.S.A.) which emitted a pulsed signal at a frequency of approximately 27 MHz. Onto each collar two beta lights (Sanders Roe Development Ltd., Hayes, England), which give off a green glow (Mills 1976, 1978b) were attached by means of an aluminium holder.

Between December 1974 and July 1976 (except for a break between October–December 1975) hyaenas equipped with transmitters were regularly located either by waiting at dens (particularly in the case of females with small cubs) or by driving around in a vehicle at night. We usually drove along the Nossob river-bed, but occasionally drove through the dunes, stopping every kilometre to switch on the receiver which was attached to a whip antenna mounted behind the cab of the vehicle. Once a signal was received from the whip antenna, it was replaced by the handheld directional loop antenna. The signal was then followed until visual contact was made with the hyaena, which was then followed for several hours ($\overline{X} = 7,4$ h). Of 89 nights that hyaenas were followed they were irrevocably lost on eight occasions (9,0%). The range of the radio signal using the whip antenna was 2,5 km–3,0 km depending on conditions such as the position of the animal relative to the antenna. With the loop antenna the range was less than 2 kilometres.

Visual contact with the brown hyaenas was maintained by the radio collars in the same way as Kruuk (1976) did with striped hyaenas *Hyaena hyaena*. In addition the two beta lights proved invaluable for keeping visual contact with the animals and meant that it was possible to follow them under all conditions of moon brightness. Head lights from the vehicle were not usually used, but when there was no moon the parking lights were kept on so that obstacles could be avoided. Whenever possible we kept as far away from the animals as we could without risking losing information (20 m–30 m), and this was usually much further than the distance at which they showed any reaction to the vehicle.

When the hyaena started eating, a handheld spotlight was switched on to identify the food item and to observe the animal's behaviour. By all appearances this did not affect the hyaena in any way. Even the use of a strong flash gun (Braun F 800) for taking photographs at distances as close as 10 m, had no apparent effect on the animal's behaviour. Notes were made into a tape recorder and transcribed at a later date.

In addition to these radio collared hyaenas we were able to follow three untagged cubs of approximately one year old between July and September 1973 when they foraged mainly during the day.

Faecal analysis

From April 1972 until September 1974 we frequently collected brown hyaena faeces throughout the study area. Each sample was kept separately in a polythene bag with a label giving the locality and date of collection. Only fresh faeces of not more than approximately two weeks old (subjectively determined) were collected.

During the study we observed that cubs regularly defaecated around the dens although adults were never observed to do so. We have assumed, therefore, that all faeces collected at dens belonged to cubs (i.e. animals under about 16 months of age) and that faeces collected away from dens (usually collected when following a known individual's spoor) belonged to adults. Although it is possible that some of the scats collected away from dens belonged to cubs, it is considered unlikely to have had a significant effect on the results.

Each scat, when it had dried out, was first broken up by hand. Then it was ground lightly in a mortar and all identifiable objects (Fig. 1) extracted with foreceps. What we considered to be an adequate sample of hair was extracted from scats containing a large amount of hair, and where a scat contained a small amount of hair all of it was extracted.

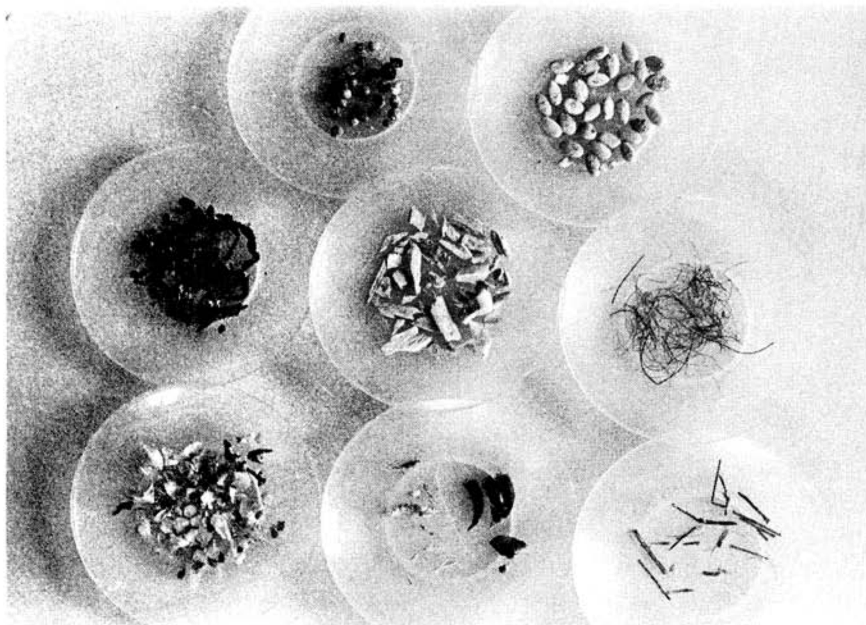

Fig. 1. Food items from a brown hyaena scat from the southern Kalahari. From left to right: Top row: *Grewia flava* pips, tsama pips. Middle row: Beetle remains, bone chips, hair. Bottom row: Reptile scales, pieces of quills from feathers and claws from a small carnivore, pieces of grass.

Prior to identification the hair was washed and then compared macroscopically, or under a low-powered dissecting microscope, with known hair samples. Then by using criteria such as length, thickness, shape and colour, the sample was identified to the species level if possible, or more often was placed into a broad category, such as small carnivore, antelope class A (hartebeest, springbok or steenbok *Raphicerus campestris*), large rodent or rodent like animal (springhare *Pedetes capensis* or hare *Lepus* sp.) etc. Next, in an attempt to identify these samples down to the species level, scale patterns and cross sections of some of the hairs were made in the manner described by Day (1966) and Brunner & Coman (1975) and these were compared with scale patterns and cross sections of known species. While this proved to be successful with herbivores, some of the carnivore samples were difficult to identify, especially when there were only a few hairs available. Where there was any doubt the sample was left as "unidentified small carnivore".

Other mammal remains such as teeth and claws were, where possible, identified to the species level by comparison with known samples. When such identified objects were found in a scat which contained no hair of that particular species, which happened in 11 cases (2,9%), the species was included as occurring in that scat. Where hair and other remains of the same species were found in the same scat the species' occurrence was only counted once.

Insect remains were also compared macroscopically or under a low-powered microscope with known samples and such criteria as shape of legs and mouthparts were particularly useful as aids to identification (M. Mansell *pers. comm.*). Reptile remains were identified as snake or unidentifiable (C. Sapsford *in litt.*). Bird remains which consisted of small pieces of quills or feathers could not be identified any further. Wild fruit pips were identified by macroscopic comparison with known specimens.

Collection of food items around dens

Whenever we visited a den during the day all food items present (Fig. 2) were recorded and the inedible parts, such as horns, skulls and hair, were collected for identification and to prevent double counting. In addition we recorded all items directly observed to be brought back to the den by the adult hyaenas and of which no remains were found later. A detailed analysis of the bones collected at five dens can be found in Mills & Mills (1977).

Fig. 2. Food remains at a brown hyaena den in the southern Kalahari.

Results and Discussion

Tracking spoor

Table 1 lists the food items which were indirectly observed to be eaten by brown hyaenas, showing the catholic nature of their diet, that much of their food is scavenged and that fruits are of importance.

Table 1

Food eaten by brown hyaenas (Hyaena brunnea) *as indirectly determined by following 1 205 km of spoor in the southern Kalahari; April 1972 – October 1973*

ITEM	NUMBER OF OBSERVATIONS	PER CENT
LARGE MAMMAL REMAINS	42	35,6
Gemsbok (adult)	9	7,6
Hartebeest	8	6,8
Gemsbok (calf)	2	1,7
Eland	1	0,8
Hide	13	11,0
Unidentified bone	8	6,8
Horn	1	0,8
MEDIUM-SIZED MAMMAL REMAINS	4	3,4
Springbok	2	1,7
Duiker	2	1,7
SMALL MAMMAL REMAINS	13	11,0
Steenbok	7	5,9
Aardwolf	1	0,8
Black-backed jackal	1	0,8
Suricate	1	0,8
Hare	1	0,8
Unidentified	2	1,7
BIRD REMAINS	2	1,7
Ostrich	2	1,7
BIRDS' EGGS	3	2,5
Ostrich	2	1,7
Korhaan	1	0,8
FRUITS	54	45,8
Tsama	42	35,6
Gemsbok cucumber	11	9,3
Grewia flava	1	0,8
TOTAL	118	100,0

The large distances travelled by brown hyaenas ($\overline{X} = 32,0$ km per night (Mills, 1978b)), their often erratic movements and the fact that spoor could not be followed in the river-bed because of the hard ground, made this technique difficult to carry out effectively.

Furthermore much of their food was consumed completely leaving no trace. Thus when the data collected from tracking spoor (which could only be collected in the dunes) are compared with those collected from direct observations in the dunes, significantly fewer feeding observations on identifiable food items were made with the former method, taking into account the relative distances from which these data were collected (Chi-squared = 37,5; df = 1; $p < 0,01$). Neither did the tracking spoor data reveal that brown hyaenas eat insects and reptiles.

Direct observations

The direct observations data (Table 2) show a wider range and larger number of food items than the tracking spoor data, as well as some observations on kills.

The main drawback of this method was that we were unable to identify many food items (Table 2). Eighty per cent of these unidentifieds were eaten in less than 1 min, whereas only 14,1% of identifiable vertebrate food items and 22,9% of fruits and eggs were (Mills 1977). Moreover, the fact that we could hear the bones being cracked when vertebrate remains were being consumed and could tell by the behaviour of the animal, the sound emitted or the leftovers in the case of eggs and fruits, we assume that they were eating some other type of food. As 42,0% of faeces from adults contained insect remains and 23,1% contained reptile remains, it is likely that these two items (with the exception of Hodotermitidae which we could easily identify) made up the bulk of these unidentified items, as so few positive identifications were made of insects and reptiles being eaten.

In addition, the presentation of the direct observations data gives all food items the same emphasis, for example a springbok carcass and a fruit such as a tsama (*Citrullus lanatus*), and this is obviously incorrect. It was impossible, however, to assess accurately the mass and caloric value of the diverse food items, and this must wait for more refined techniques.

Faecal analysis

The faecal analysis data (Table 3) show a similar composition to the direct observations data except for a higher incidence of reptiles, insects and small mammals (see below) and a lower incidence of medium sized mammals (see page 133).

Table 2

Food eaten by brown hyaenas (Hyaena brunnea) *as determined from direct observations in the southern Kalahari; July – September 1973 (cubs), December 1974 – September 1975 and January – July 1976 (adults).*

AGE CLASS	LARGE CUBS		ADULTS					
HABITAT	DUNES		RIVER		DUNES		TOTAL	
DISTANCE FOLLOWED (KM)	151		1 083		1 316		2 399	
ITEM	Number of observations	Per cent	Number of observations	Per cent	Number of observations	Per cent	Number of observations	Per cent
TOTAL OF ALL MAMMAL REMAINS	29	34,1	116	63,4	92	26,5	208	39,2
LARGE MAMMAL REMAINS	13	15,3	25	13,7	28	8,1	53	10,0
Gemsbok (adult)	1	3,4	4	3,4	8	8,7	12	5,8
Hartebeest (adult)	2	6,9	6	5,2	3	3,3	9	4,3
Wildebeest	0	0,0	5	4,3	0	0,0	5	2,4
Eland	0	0,0	0	0,0	1	1,1	1	0,5
Gemsbok (calf)	0	0,0	0	0,0	1	1,1	1	0,5
Hartebeest (calf)	0	0,0	1	0,9	0	0,0	1	0,5
Lion	0	0,0	1	0,9	0	0,0	1	0,5
Unidentified bone	5	17,2	6	5,2	7	7,6	13	6,3
Hide	2	6,9	1	0,9	7	7,6	8	3,8
Horn	3	10,3	1	0,9	1	1,1	2	1,0
MEDIUM-SIZED MAMMAL REMAINS	6	7,1	53	29,0	9	2,6	62	11,7
Springbok (adult)	0	0,0	39	33,6	5	5,4	44	21,2
Springbok (lamb)	0	0,0	5	4,3	0	0,0	5	2,4
Brown hyaena	2	6,9	0	0,0	0	0,0	0	0,0
Duiker	1	3,4	0	0,0	0	0,0	0	0,0
Unidentified bone	3	10,3	8	6,9	4	4,3	12	5,8
Horn	0	0,0	1	0,9	0	0,0	1	0,5
SMALL MAMMAL REMAINS	5	5,9	4	2,2	10	2,9	14	2,6
Steenbok	5	17,2	0	0,0	4	4,3	4	1,9
Black-backed jackal	0	0,0	1	0,9	2	2,2	3	1,4
Springhare	0	0,0	1	0,9	1	1,1	2	1,0
Bat-eared fox	0	0,0	1	0,9	0	0,0	1	0,5
Cape fox	0	0,0	0	0,0	1	1,1	1	0,5
African wild cat	0	0,0	0	0,0	1	1,1	1	0,5
Suricate	0	0,0	1	0,9	0	0,0	1	0,5
Pangolin	0	0,0	0	0,0	1	1,1	1	0,5
VERY SMALL MAMMAL REMAINS	0	0,0	1	0,5	2	0,6	3	0,6
Unidentified rodent	0	0,0	1	0,9	2	2,2	3	1,4
UNIDENTIFIED MAMMAL REMAINS (mainly pieces of bone)	5	5,9	33	18,0	43	12,4	76	14,3
BIRD REMAINS	0	0,0	5	2,7	7	2,0	12	2,3
Ostrich	0	0,0	1	20,0	6	85,7	7	58,3
Korhaan (black or red-crested)	0	0,0	0	0,0	1	14,3	1	8,3
Dove	0	0,0	1	20,0	0	0,0	1	8,3
Spotted eagle owl	0	0,0	1	20,0	0	0,0	1	8,3
Secretary bird	0	0,0	1	20,0	0	0,0	1	8,3
Unidentified small bird	0	0,0	1	20,0	0	0,0	1	8,3
REPTILE REMAINS	0	0,0	0	0,0	1	0,3	1	0,2
Mole snake	0	0,0	0	0,0	1	100,0	1	100,0
KILLS MADE BY BROWN HYAENAS	1	1,2	4	2,2	6	1,7	10	1,9
Korhaan (black or red-crested)	0	0,0	0	0,0	3	50,0	3	30,0
Springhare	0	0,0	1	25,0	1	16,7	2	20,0
Springbok (lamb)	0	0,0	1	25,0	0	0,0	1	10,0
Bat-eared fox	0	0,0	1	25,0	0	0,0	1	10,0
Striped polecat	1	100,0	0	0,0	0	0,0	0	0,0
Black korhaan chicks	0	0,0	0	0,0	1	16,7	1	10,0
Unidentified rodent	0	0,0	1	25,0	0	0,0	1	10,0
Unidentified small bird	0	0,0	0	0,0	1	16,7	1	10,0
BIRDS' EGGS	0	0,0	0	0,0	8	2,3	8	1,5
Ostrich	0	0,0	0	0,0	7	87,5	7	87,5
Black korhaan	0	0,0	0	0,0	1	12,5	1	12,5
INSECTS	10	11,8	0	0,0	1	0,3	1	0,2
Isoptera	10	100,0	0	0,0	0	0,0	0	0,0
Orthoptera	0	0,0	0	0,0	1	100,0	1	100,0
FRUITS	9	10,6	14	7,7	154	44,4	168	31,7
Tsama	9	100,0	14	100,0	50	32,5	64	38,1
Gemsbok cucumber	0	0,0	0	0,0	72	46,8	72	42,9
Terfezia pfeilii (fungus)	0	0,0	0	0,0	21	13,6	21	12,5
Grewia flava	0	0,0	0	0,0	8	5,2	8	4,8
Merremia tridentata	0	0,0	0	0,0	3	1,9	3	1,8
OTHERS	9	10,6	4	2,2	6	1,7	10	1,9
Carnivore faeces	9	100,0	4	100,0	4	66,7	8	80,0
Honey comb	0	0,0	0	0,0	1	16,7	1	10,0
Rummaging in rubbish dump	0	0,0	0	0,0	1	16,7	1	10,0
UNIDENTIFIED	27	31,8	40	21,9	72	20,7	112	21,1
TOTAL	85		183		347		530	

Notes. 1. The number of observations for each item refer to the number of feeding bouts observed irrespective of the number of items eaten. For example, a brown hyaena may eat five tsamas at one place, this will be recorded as one observation.

2. Per cent of categories (capital letters) have been calculated from the total number of items in each column, per cent of mammal items from the total number of mammal remains category and for other items from the total in the relevant category. For example, 6,9 per cent of all mammal remains eaten by cubs were hartebeest and 85,7 per cent of bird remains eaten by adults were ostriches.

Table 3

Food items found in 383 brown hyaena (Hyaena brunnea) *faeces from the southern Kalahari; April 1972 – September 1974.*

ITEM	ADULTS n = 143			CUBS n = 240			CHI./SQUARED (number of scats) FOR ADULTS v CUBS
	Number of scats	Percentage of scats	Percentage occurrence	Number of scats	Percentage of scats	Percentage occurrence	
TOTAL FOR ALL MAMMALS	143	100,0	51,9	240	100,0	46,3	
LARGE MAMMALS	135	94,4	24,7	95	39,6	11,3	109,96; $p < 0,01$
Gemsbok	74	51,7	26,1	49	20,4	12,6	
Hartebeest	39	27,3	13,7	33	13,8	8,5	
Wildebeest	22	15,4	7,7	13	5,4	3,3	
MEDIUM-SIZED MAMMALS	18	12,6	3,3	38	15,8	4,5	1,04; $p > 0,05$
Springbok	13	9,1	4,6	23	9,6	5,9	
Duiker	2	1,4	0,7	11	4,6	2,8	
Porcupine	3	2,1	1,1	2	0,8	0,5	
Caracal	0	0,0	0,0	2	0,8	0,5	
SMALL MAMMALS	90	62,9	16,5	192	80,0	22,8	14,33; $p < 0,01$
Steenbok	12	8,4	4,2	70	29,2	17,9	
Unidentified small carnivore*	22	15,4	7,7	59	24,6	15,1	
Bat-eared fox	10	7,0	3,5	25	10,4	6,4	
Springhare	17	11,9	6,0	11	4,6	2,8	
Black-backed jackal	8	5,6	2,8	13	5,4	3,3	
Hare	15	10,5	5,3	4	1,7	1,0	
Honey badger	0	0,0	0,0	7	2,9	1,8	
African wild cat	4	2,8	1,4	0	0,0	0,0	
Cape fox	0	0,0	0,0	1	0,4	0,3	
Aardwolf	0	0,0	0,0	1	0,4	0,3	
Yellow mongoose	0	0,0	0,0	1	0,4	0,3	
Suricate	1	0,7	0,4	0	0,0	0,0	
Striped polecat	1	0,7	0,4	0	0,0	0,0	
VERY SMALL MAMMALS	8	5,6	1,5	13	5,4	1,5	0,03; $p > 0,05$
Other rodents	6	4,2	2,1	13	5,4	3,3	
Rodent mole	2	1,4	0,7	0	0,0	0,0	
UNIDENTIFIED MAMMALS	33	23,1	6,0	52	21,7	6,2	0,04; $p > 0,05$
BIRDS	22	15,4	4,0	34	14,2	4,0	0,03; $p > 0,05$
REPTILES	33	23,1	6,0	43	17,9	5,1	1,19; $p > 0,05$
Snake	22	15,4	66,7	21	8,8	48,8	
Tortoise	1	0,7	3,0	4	1,7	9,3	
Unidentified	10	7,0	30,3	18	7,5	41,9	
BIRDS' EGGS	1	0,7	0,2	3	1,3	0,4	1,07; $p > 0,05$
INSECTS	60	42,0	16,8	170	70,8	32,5	32,36; p 0,01
Coleoptera	50	35,0	54,3	151	62,9	55,1	
Isoptera	12	8,4	13,0	62	25,8	22,6	
Hymenoptera	12	8,4	13,0	23	9,6	8,4	
Diptera	1	0,7	1,1	9	3,8	3,3	
Lepidoptera	7	4,9	7,6	2	0,8	0,7	
Arachnidae	2	1,4	2,2	7	2,9	2,6	
Orthoptera	1	0,7	1,1	1	0,4	0,4	
Dictyoptera	1	0,7	1,1	0	0,0	0,0	
Unidentified	6	4,2	6,5	19	7,9	6,9	
FRUITS	87	60,8	21,0	79	32,9	11,6	27,32; $p < 0,01$
Tsama	68	47,6	59,1	55	22,9	56,1	
Gemsbok cucumber	26	18,2	22,6	10	4,2	10,2	
Grewia flava	21	14,7	18,3	26	10,8	26,5	
Wild cucumber	0	0,0	0,0	7	2,9	7,1	
TOTAL ITEMS			547			842	

Notes. 1. *Black-backed jackal, bat-eared fox, Cape fox, African wild cat or aardwolf.

2. The per cent figures for categories (capitals) indicate the percentage scats with the occurrence of that particular category and is not necessarily the same as the sum of the percentages of the individual food items in the category. For example, a scat might contain springhare and steenbok remains and these would contribute only one to the small mammals category.

3. The percentage occurrence figures for categories indicate the percentage occurrence of all the items in that category with respect to all the food items found in the scats. For example, 24,7 per cent of the 547 remains found in adult scats were large mammals. The percentage occurrence figures for the items in each category indicate the percentage occurrence of each item in that category except for mammals where the total of all mammals category has been used. For example, 12,6 per cent of the mammal remains found in cub scats were gemsbok and 55,1 per cent of the insects were Coleoptera.

The problems encountered when quantitatively assessing data from faecal analysis in the Hyaenidae have been discussed by Kruuk (1972) and Bearder (1977) for the spotted hyaena *Crocuta crocuta* and by Kruuk (1976) for the striped hyaena, where it has been argued that the only practical way to score the results is on a presence or absence basis, as we have done (Table 3). This is because the amount of hair ingested per kilogram of food eaten varies depending on what species and what part of a mammal that the hyaena was feeding on. It does not necessarily follow that a large amount of hair in a faeces means that the hyaena ate a large amount of that species.

Bearder (1977) argues that the excess hair from smaller mammals, which are generally more hirsute than larger mammals, is regurgitated by spotted hyaenas. Brown hyaenas do not regurgitate often and therefore this excess hair is likely to be found in their faeces, thus biasing the results towards smaller mammals. Furthermore, many of the vertebrate food items eaten by the brown hyaenas were bones devoid of hair and these were completely digested, so that only a few bone chips and dry bone powder, which were impossible to identify, were left in the faeces. Only mammalian food items containing hair (except for the few cases of claws and teeth mentioned earlier), therefore, were identified in the faecal analysis of our study and this again favours the smaller mammals, as large mammal remains are more likely to consist only of bone.

On the other hand some hair is easier to identify than others. The large herbivores, for example, have easily identifiable hair whereas the hair of small carnivores is more difficult to identify. Therefore we were more likely to leave these as unidentifiable or at best as unidentified small carnivore. Also, when small amounts of a species' hair are present in a scat containing a large quantity of another species' hair, this small amount is more likely to be overlooked if it is similar to the dominant one than if it is markedly different. Thus, for example, a scat may contain mainly steenbok hair with some springbok hair, resulting in the springbok hair being overlooked.

The fact that the various items were scored on a presence or absence basis again means that all categories receive equal prominance and it cannot be taken that insects, for example, which were present in 42,0% of the faeces from adults, are more important than medium-sized mammals, which were present in 12,6 per cent. It must also be remembered that certain food items such as soft-bodied insects and the fungus *Terfezia pfeilii,* will be completely digested by a hyaena, thus leaving no remains in the faeces.

It is difficult to say how these biases affect the results of the faecal analysis. When the divisions into categories (with insects and reptiles lumped) on a percentage occurrence basis for faeces from adults are compared with those from direct observations for adults, and when the unidentifiable food items from direct observations are placed in the reptile/insect category (as we suggested earlier that most of the unidentified items were reptiles and insects), there is a significant correlation (r = 0,646; df = 8; $p < 0,05$) (Fig. 3). This suggests that the various biases (except for the one of equal prominance for all categories) in the faecal analysis tend to cancel each other out.

Collection of food items around dens

The food items found at dens are tabulated in Table 4 where the collections from dens 3 and 7 are the most complete.

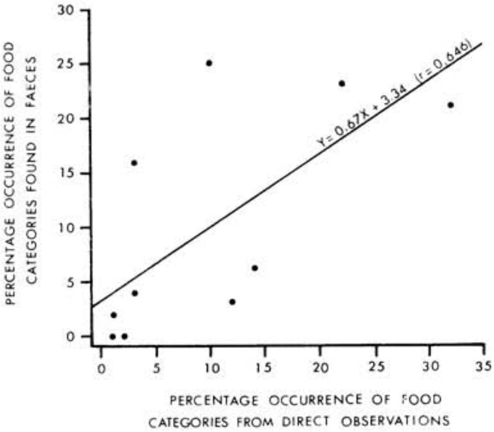

Fig. 3. Percentage occurrence of food categories found in faeces versus percentage occurrence of food categories from direct observations of brown hyaenas in the southern Kalahari.

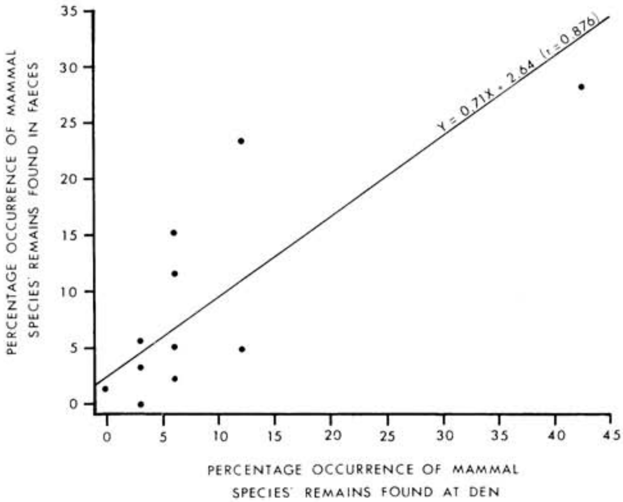

Fig. 4. Percentage occurrence of mammal species found in faeces of brown hyaena cubs under 10 months old versus percentage occurrence of mammal species remains found at the same cubs' den in the southern Kalahari.

Table 4

Food items found at eight brown hyaena (Hyaena brunnea) *dens in the southern Kalahari; April 1972–July 1976.*

ITEM	DEN 1	2	3	4	5	6	7	8	TOTAL	PER CENT
LARGE MAMMALS	5	6	8	7	5	1	1	5	38	15,4
Gemsbok (adult)	1	1	2	2	3	1	0	1	11	4,5
Wildebeest	1	2	1	2	0	0	1	1	8	3,3
Hartebeest (adult)	1	1	1	0	0	0	0	3	6	2,4
Gemsbok (calf)	1	0	2	1	0	0	0	0	4	1,6
Eland	0	0	0	0	2	0	0	0	2	0,8
Domestic cow (calf)	1	1	0	0	0	0	0	0	2	0,8
Hartebeest (calf)	0	0	1	0	0	0	0	0	1	0,4
Camel	0	1	0	0	0	0	0	0	1	0,4
Unidentified herbivore	0	0	1	1	0	0	0	0	2	0,8
Unidentified felid	0	0	0	1	0	0	0	0	1	0,4
MEDIUM-SIZED MAMMALS	6	7	6	5	1	5	20	21	71	28,9
Springbok (adult)	3	2	3	3	0	4	15	14	44	17,9
Springbok (lamb)	0	0	0	0	0	0	2	5	7	2,8
Caracal	0	1	1	0	1	0	3	0	6	2,4
Duiker	0	0	1	2	0	0	0	2	5	2,0
Sheep/goat	1	4	0	0	0	0	0	0	5	2,0
Porcupine	2	0	0	0	0	0	0	0	2	0,8
Aardvark	0	0	0	0	0	1	0	0	1	0,4
Unidentified herbivore	0	0	1	0	0	0	0	0	1	0,4
SMALL MAMMALS	5	7	22	22	3	5	22	19	105	42,7
Bat-eared fox	2	2	4	7	0	1	6	7	29	11,8
Black-backed jackal	1	1	7	4	2	0	8	5	28	11,4
Steenbok	0	3	5	8	0	2	2	4	24	9,8
Aardwolf	0	0	2	1	0	2	3	0	8	3,3
Honey badger	1	0	2	0	0	0	1	0	4	1,6
Springhare	1	1	0	0	0	0	0	2	4	1,6
Cape fox	0	0	2	0	0	0	1	0	3	1,2
African wild cat	0	0	0	0	0	0	0	1	1	0,4
Yellow mongoose	0	0	0	0	0	0	1	0	1	0,4
Hare	0	0	0	0	1	0	0	0	1	0,4
Unidentified carnivore	0	0	0	2	0	0	0	0	2	0,8
BIRDS	1	1	3	5	2	1	2	6	21	8,5
Ostrich	1	1	0	1	1	1	0	2	7	2,8
Kori bustard	0	0	1	1	0	0	2	1	5	2,0
Secretary bird	0	0	1	0	0	0	0	1	2	0,8
Korhaan	0	0	1	0	0	0	0	1	2	0,8
Spotted eagle owl	0	0	0	0	0	0	0	1	1	0,4
Unidentified large bird	0	0	0	3	1	0	0	0	4	1,6
OSTRICH EGG	0	1	3	1	2	0	1	1	9	3,7
TORTOISE	0	0	1	1	0	0	0	0	2	0,8
TOTAL	17	22	43	41	13	12	46	52	246	100,0

In the analysis of these food items care must be taken to avoid double counting and small animals can be missed as they might be completely consumed. There is, however, a significant correlation between the percentage occurrence of food species found at den 3 when the cubs were under 10 months old (and thus getting nearly all their food from the adults), and the percentage occurrence of the various species found in the faeces of these cubs ($r = 0,876$; $df = 9$; $p < 0,01$) (Fig. 4). This suggests that an accurate presentation of the food items brought to the den by the adults, is found in food remains scattered around the den.

Overall diet

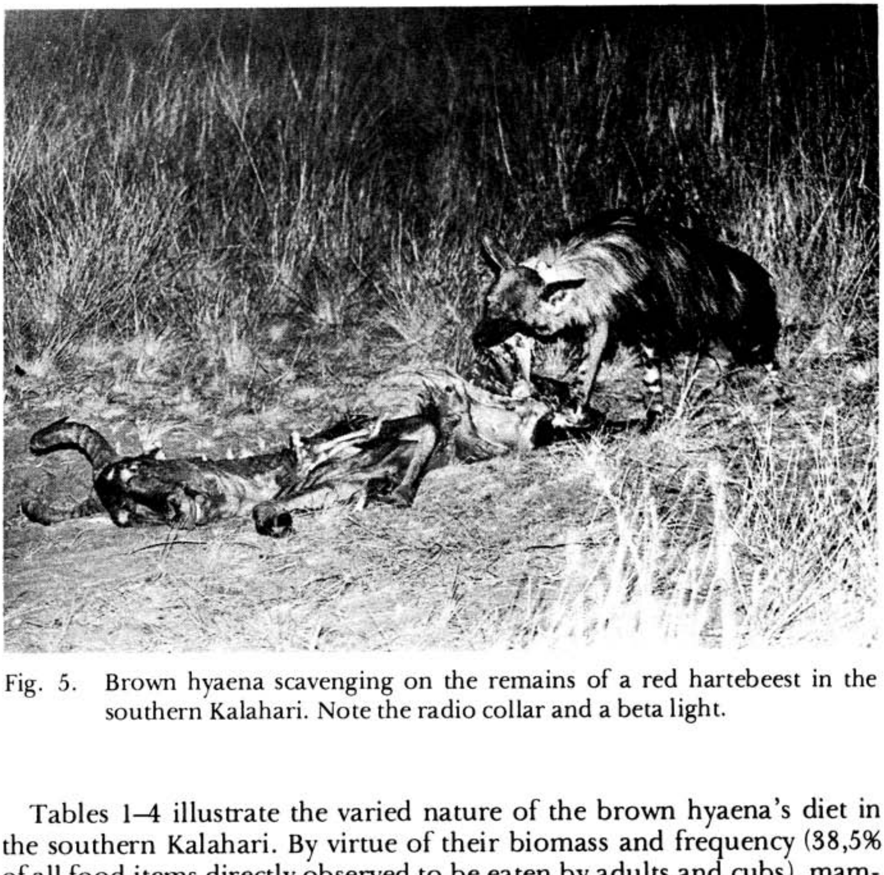

Fig. 5. Brown hyaena scavenging on the remains of a red hartebeest in the southern Kalahari. Note the radio collar and a beta light.

Tables 1–4 illustrate the varied nature of the brown hyaena's diet in the southern Kalahari. By virtue of their biomass and frequency (38,5% of all food items directly observed to be eaten by adults and cubs), mammal remains are the brown hyaena's most important food (Fig. 5). They have been recorded feeding on 25 of the 35 (71,4%) larger mammals listed as occurring in the area (Mills 1977), as well as at least three species of domestic mammal. In addition wild fruits and insects are also important and other vertebrates (Fig. 6), birds' eggs, as well as most other edible foods, except herbage, are eaten. The manner in which this food was obtained is discussed in Mills (1978b), but here it should be

Fig. 6. Brown hyaena carrying a scavenged secretary bird to her den in the southern Kalahari.

noted that 95,8% of all vertebrate food items consumed by hyaenas during direct observations were scavenged.

Cubs utilise most of the same food items as adults do, but in somewhat different proportions (Table 3), as is the case in some other carnivores such as the coyote *Canis latrans* (Hawthorne 1972). This is further discussed below.

A. *Vertebrate food*

Figure 7 shows how the more common mammalian food was utilised by brown hyaenas on a monthly basis as determined from faecal analysis. In compiling this graph the unidentifiable small carnivores have been included as canids, as Table 4 suggests that most of these were black-backed jackals or bat-eared foxes. From Fig. 7 it can be seen that for the most part there is little seasonal variation, the most seasonality occurring in the red hartebeest with most being eaten in March and April. Of the more heavily utilised species the hartebeest is the most migratory, reaching a peak in and around the Nossob river-bed in late summer, and moving out of the main study area as conditions become drier (Bothma & Mills 1977). The low in the utilisation of steenbok in March may be related to the fact that these hyaenas were feeding relatively heavily on hartebeest at this time, and in December because of the high number of canids eaten.

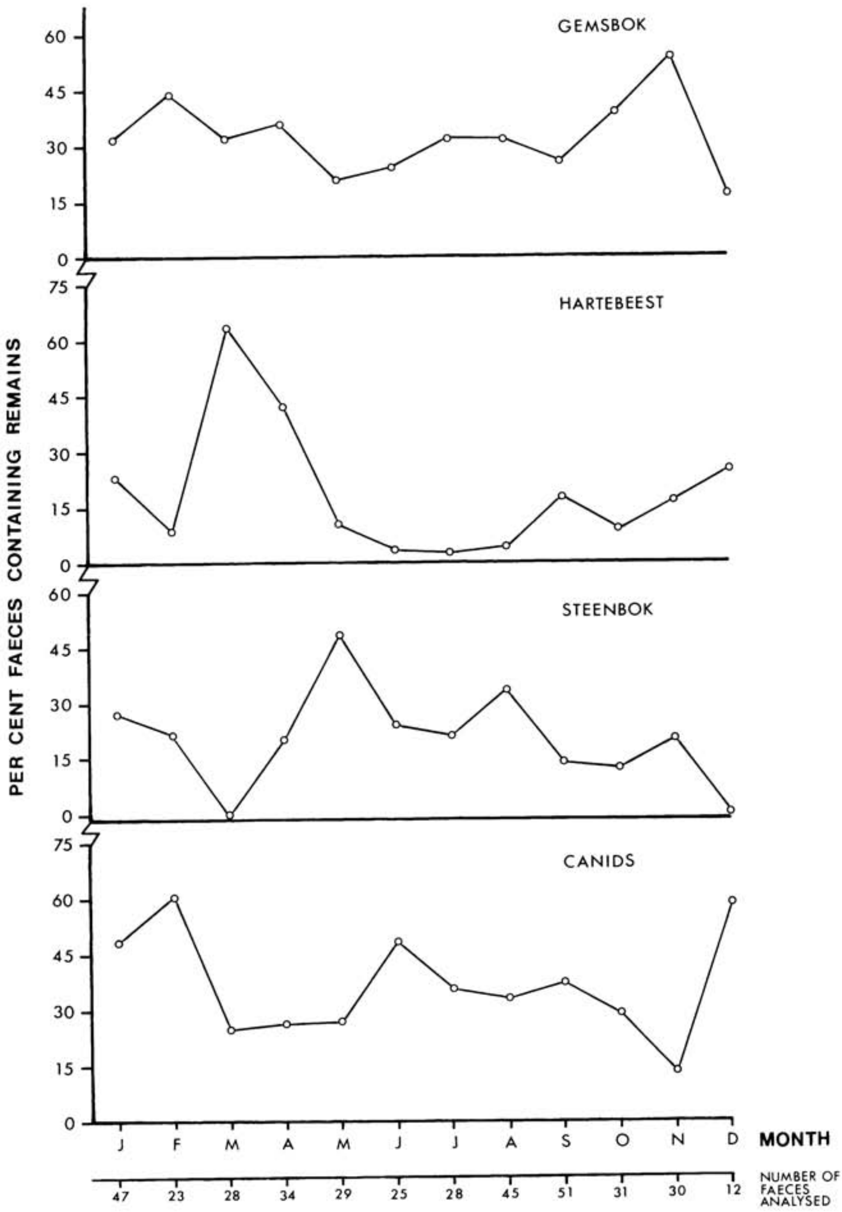

Fig. 7. Monthly utilisation of gemsbok, red hartebeest, steenbok and canids by brown hyaenas in the southern Kalahari as determined from faecal analysis; April 1972 – September 1974.

The high incidence of carnivores in the diet, particularly canids, is worth noting. Leopards *Panthera pardus* also readily eat canids (Estes 1967; Kruuk & Turner 1967; Schaller 1972; and personal observations) and striped hyaenas appear to eat bat-eared foxes readily (Kruuk 1976), but spotted hyaenas do not appear to find jackals palatable (Kruuk 1972; Bearder 1975) and only rarely eat bat-eared foxes (Kruuk 1972). The fact that most canids are eaten in December, January and February (Fig. 7) may be related to the fact that there are many young ones around at this time. Bat-eared foxes are one of the most commonly hunted animals by brown hyaenas (Mills 1978b) and in most prey species young animals are particularly vulnerable to predation.

It is difficult to quantify the availability of most of the food to a scavenger, as the selection is almost entirely secondary depending on what has been killed and left by other agents. Abundance in terms of living prey animals clearly plays a role as in the case of red hartebeest related above. With springbok, as well, 45 out of 50 (90,0%) that were observed to be eaten by hyaenas were eaten in river habitat, which is where the concentrations of springbok occur. Furthermore dens 7 and 8, which were close to large springbok concentrations, had the highest incidence of springbok remains (Table 4). This also explains the discrepancy between the number of springbok remains present in the faeces as compared with the number eaten based on direct observations, as the former data were collected at a time and in an area where springbok were relatively less abundant than they were when the direct observations were made.

One of the biggest discrepancies in diet between adult and cub brown hyaenas is that cubs eat more small mammals and fewer large mammals than adults do (Table 3). This is because adults are more likely to bring back a small mammal carcass than a large one to the den (Table 4), presumably because the cubs' teeth and jaws are not yet sufficiently developed to deal with large bones.

B. *Insects*

Table 5 shows the detailed analysis of the insect remains that we found in the hyaena faeces. Coleoptera, especially Tenebrionidae (common ground-living beetles) were the most common, followed by Hodotermitidae (harvester termites). The relatively high incidence of Formicidae is worth noting and although some of these were no doubt eaten incidently, others were apparently deliberately eaten. The Trogidae, Histeridae and Staphylinidae (Coleoptera) were almost certainly ingested incidentally (M. Mansell *pers. comm.*).

Table 3 shows a significant difference between the number of insect remains in faeces from adults compared with faeces from cubs. The most important group contributing to this difference is the Tenebrionidae. From Table 5 it can be seen that Tenebrionidae remains were found in faeces throughout the year especially in cubs' faeces. Unfortunately the species of Tenebrionid are unknown; there are some species

Table 5

Insect remains found in brown hyaena (Hyaena brunnea) *faeces from the southern Kalahari; April 1972 – September 1974*

ITEM	PER CENT OF FAECES CONTAINING REMAINS							
	ADULTS				CUBS			
	Jan.–Apr. n=51	May–Aug. n=38	Sep.–Dec. n=54	Total n=143	Jan.–Apr. n=81	May–Aug. n=89	Sep.–Dec. n=70	Total n=240
COLEOPTERA	58,8	10,5	29,6	35,0	65,4	70,8	50,0	62,9
Tenebrionidae	27,5	7,9	13,0	16,8	40,7	40,4	21,4	49,4
Scarabaeidae	11,8	0,0	9,3	7,7	6,2	11,2	21,4	12,5
Cicindelidae	15,7	0,0	0,0	5,6	0,0	0,0	1,4	0,4
Chrysomelidae	0,0	0,0	1,9	0,7	2,5	7,9	0,0	3,8
Histeridae	0,0	0,0	1,9	0,7	2,5	1,1	1,4	1,7
Curculonidae	0,0	0,0	0,0	0,0	0,0	2,2	0,0	0,8
Trogidae	0,0	0,0	0,0	0,0	1,2	1,1	0,0	0,8
Staphylinidae	0,0	0,0	0,0	0,0	0,0	1,1	1,4	0,8
Carabidae	0,0	0,0	0,0	0,0	0,0	0,0	1,4	0,4
Buprestidae	0,0	0,0	1,9	0,7	0,0	0,0	0,0	0,0
Unidentified	3,9	2,6	1,9	2,8	12,3	5,6	1,4	6,7
ARACHNIDAE	0,0	0,0	3,7	1,4	2,5	4,5	1,4	2,9
Aranidae	0,0	0,0	0,0	0,0	1,2	1,1	0,0	0,8
Scorpionidae	0,0	0,0	3,7	1,4	1,2	3,4	1,4	2,1
HODOTERMITIDAE	13,7	2,6	7,4	8,4	21,0	30,3	25,7	25,8
FORMICIDAE	11,8	0,0	11,1	8,4	7,4	10,1	11,4	9,6
LEPIDOPTERA LARVA	7,8	10,5	0,0	4,9	1,2	0,0	1,4	0,8
DICTYOPTERA	2,0	0,0	0,0	0,7	0,0	0,0	0,0	0,0
ORTHOPTERA	2,0	0,0	0,0	0,7	0,0	1,1	0,0	0,4
DIPTERA	0,0	0,0	1,9	0,7	5,0	5,6	0,0	3,8
Diptera larva	0,0	0,0	0,0	0,0	2,5	2,2	0,0	1,7
Diptera pupa	0,0	0,0	1,9	0,7	2,5	3,4	0,0	2,1
UNIDENTIFIED	7,8	0,0	3,7	4,2	6,2	11,2	5,7	7,9
PER CENT FAECES WITH INSECTS	72,5	31,5	31,5	42,0	74,1	75,3	61,4	70,1

which have a high longevity in the adult stage, surviving the winter in a passive phase and showing a strong tendency for sheltering in burrows of mammals (S. Endrödy-Younga *pers. comm.*). This might explain the high incidence of tenebrionids in faeces from cubs in the winter months, as cubs spend far more time in burrows than adults do.

Hodotermitidae were also more commonly eaten by cubs than by adults particularly in winter (Table 5). Limited observations suggest that cubs are more diurnal in winter than adults are (Mills 1978b). As Hodotermitidae are strongly diurnal in winter (personal observations), one of the reasons for this greater utilisation of Hodotermitidae by cubs may be that cubs simply encounter them more often than adults do.

C. *Wild fruits*

Fig. 8. Brown hyaena eating a tsama in the southern Kalahari.

Tsama and gemsbok cucumber: The tsama (*Citrullus lanatus*) (Fig. 8) and the gemsbok cucumber (*Acanthosicyos naudiniana*) are the two most important fruits eaten by brown hyaenas in the southern Kalahari. Figure 9 shows how these fruits were utilised throughout the year as determined from faecal analysis of hyaenas over six months of age.

From Fig. 9 it can be seen that tsamas were utilised over a longer period than the cucumbers were, with most cucumbers being consumed between April and June, after which few were eaten. The reason is that

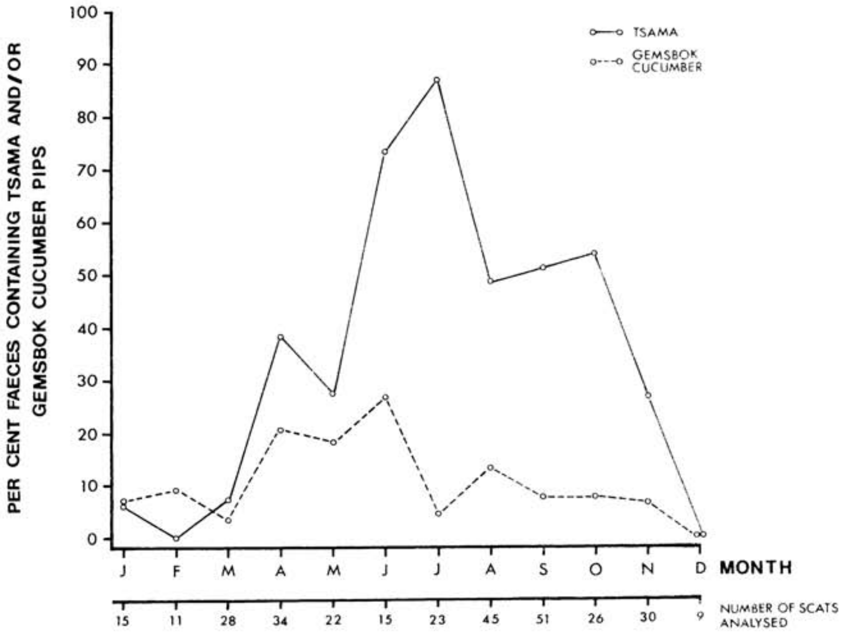

Fig. 9. Monthly utilisation of tsamas and gemsbok cucumbers by brown hyaenas in the southern Kalahari as determined from faecal analysis; April 1972 – September 1974.

the gemsbok cucumber crop does not last as long as the tsama crop does. By July most of the cucumber crop has disappeared, because they are more susceptable to frost than tsamas are. The fact that gemsbok cucumbers tend to be utilised at a higher rate than tsamas in January and February, is because the former develop slightly earlier than tsamas do. A 20 km drive through the dunes in early February 1977 revealed no tsama fruits or even vines, whereas 22 gemsbok cucumber vines, some of them bearing a few ripe fruits, were observed.

Towards the end of the year the number of tsamas eaten also decreases. Twenty randomly selected strips in the study area of 1 km × 10 m, sampled in July 1976, showed that 30% of 3 600 tsamas counted had been eaten by various animals (e.g. rodents, ungulates, brown hyaenas), and in late November in the same area 89% of 1 155 counted in 10 similar strips had. Thus this decrease in utilisation of tsamas by brown hyaenas in the middle of summer is apparently due to the fact that there are not as many available. For optimum development both these fruits require effective rains at short intervals from about December to April (Leistner 1967) and when these conditions occur, as had happened during this study (Mills 1977), the bulk of the crop becomes available from about March onwards.

Both tsama and cucumber fruits have a low caloric value. The mean caloric value of three tsamas was 53,2 kJ per 100 g and that of one gemsbok cucumber 98,1 kJ per 100 g (Table 6). Both these fruits do, however, have a high moisture content, the mean of the three tsamas being 95,1% and the gemsbok cucumber containing 91,5% water (Table 6). They are, therefore, an important source of moisture for brown hyaenas which get less moisture from meat and blood than the other large carnivores do, as so much of their vertebrate food is dry by the time they find it. There are, however, indications that hyaenas eat these fruits for other nutritional reasons as well, as individuals were observed on occasions to drink and to eat fruits on the same night. On average they ate $2,3 \pm 1,1$ tsamas or cucumbers on a night that they drank ($n = 9$; range 0 – 10) and $3,5 \pm 1,0$ on a night that they did not drink ($n = 20$; range 0 – 14), a non-significant difference (Mann-Whitney test; $z = 0,70$; $p = 0,2236$). The trace elements and vitamins, especially vitamin C, could be important, coupled with the fact that brown hyaenas obtain some energy value from these fruits as well.

Schaller (1972) estimated that the energy value of 1 kg of meat eaten by wild lions was 6 300 kJ. The mean mass of the edible portions of 20 tsamas was calculated as 540 g per tsama (Mills 1977). If the mean energy value of a tsama is 542 kJ per kg, therefore, a brown hyaena would have to eat 22 tsamas to gain the equivalent amount of energy gained from eating 1 kg of fresh meat. They rarely come near to this number in a night's foraging, the most we observed being 18 (discerned from spoor).

Other fruits: The next most important fruits utilised by brown hyaenas are the small berries of the rosyntjiebos (*Grewia flava*). These bushes are well distributed throughout the southern Kalahari and flower in early summer, sometimes before the first rains (Leistner 1967). Figure 10 shows that, except when the bushes are in flower, the fruits are eaten throughout the year by brown hyaenas over six months old. The reason for the sharp increase in June may be due to a sampling bias in that several scats were collected over three days when following the spoor of an individual which fed several times on these fruits.

During 1975 and 1976, when most of the direct observations were made, fire had destroyed a large number of the bushes in the study area when they were flowering, and there were few berries available. This explains the low number of direct observations of brown hyaenas eating them (Table 2).

The wild cucumber (*Cucumis africanus*) has a similar life cycle to the gemsbok cucumber, although the crop lasts for an even shorter period, and they were uncommon in the study area. This probably explains why so few were eaten. The fungus *Terfezia pfeilii* was observed to be eaten 21 times by one individual in two nights in April 1975. The fruits of *Merremia tridentata*, a summer annual, are available from the middle of summer and we observed a hyaena eating these on three occasions in February 1976.

Brown hyaena cubs eat far fewer fruits than adults do (Table 3), and

Table 6

Analysis of some wild fruits which are eaten by brown hyaenas (Hyaena brunnea) *in the southern Kalahari, A. S. Wehmeyer* (pers. comm.).

FRUIT	UNIT OF MEASURE AND COMPONENT																		
	g/100 g						kJ/100 g	mg/100 g								mg/100 g			
	Moisture	Ash	Protein	Fat	Fibre	Carbohydrate	Energy value	Calcium	Magnesium	Iron	Sodium	Potassium	Copper	Zinc	Phosphorus	Thiamin	Riboflavin	Nicotinic acid	Vitamin C
Tsama	96,2	0,7	0,3	0,01	0,7	2,2	42,0	12,3	6,3	3,2	0,6	—	0,50	0,07	6,2	0,03	0,004	0,051	4,0
Tsama	97,9	0,5	0,1	0,02	0,6	0,9	29,4	18,3	9,1	0,2	0,7	68,6	0,06	—	—	0,02	0,003	0,127	3,8
Tsama	91,3	—	0,4	0,09	1,7	4,7	88,2	—	30,6	0,2	3,7	135,0	0,14	0,10	3,8	—	0,027	0,983	7,5
Gemsbok cucumber	91,5	0,6	1,2	0,10	2,2	4,4	98,0	16,1	13,9	0,4	0,2	295,0	0,08	0,19	7,2	0,11	0,019	0,602	25,7
Wild cucumber	88,2	1,2	2,8	1,60	2,9	3,3	159,6	13,1	29,2	1,1	1,1	439,0	0,20	0,40	20,2	0,20	0,030	3,700	12,8
Grewia flava	11,6	2,8	5,4	1,10	22,1	57,0	1 090,0	13,9	217,0	4,8	25,9	1 093,0	1,49	1,87	71,0	0,06	0,040	2,353	0,0

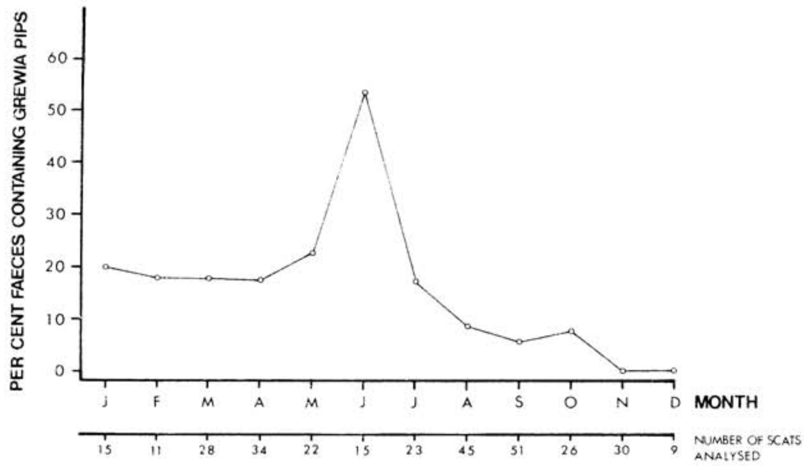

Fig. 10. Monthly utilisation of *Grewia flava* berries by brown hyaenas in the southern Kalahari as determined from faecal analysis; April 1972 – September 1974.

for the first six months of their lives their intake of fruits is negligible. Only 5 of 74 (6,8%) scats analysed from this age class contained pips. As cubs grow older they begin to forage for themselves a little and also receive less milk from their mother. At this stage the cubs begin to eat fruits.

Conclusions

A number of methods, both direct and indirect, can be used to investigate the diet of a carnivore. The most effective one depends on several factors, such as the habits and size of the animal, the nature of the study area and the money at the disposal of the researcher. A study area such as the Kalahari makes it feasible to track animals' spoor, but because of the foraging habits of the brown hyaena this technique is laborious and does not yield satisfactory results as many of the smaller food items are missed. Furthermore it cannot be used in the river-bed and it yields little information on the amount eaten.

Neither can much information on diet be gleaned by driving around, even at night, and looking for animals feeding or for remains from brown hyaena kills, as the density of brown hyaenas is low and they do not usually spend long feeding on each item (Mills 1976).

However, the brown hyaena's trapability and tolerance to immobilising drugs (Mills 1977), and its large size, making it possible to fit a large and powerful radio collar, together with the openness of the southern Kalahari, make it feasible to follow certain individuals for long periods at night. This method yields much worthwhile data and is considerably enhanced by the use of beta lights.

As a back up, faecal analysis is invaluable as a means of identifying certain food items which were not identifiable from direct observations, and as a means by which various comparisons can be made (Kruuk 1972, 1976; Mills, 1978a, *this study*).

The fairly simple method of keeping a record of food items found at brown hyaena dens gives a food picture of the type of food the cubs are fed by the adults, but does not reveal how the hyaenas acquired this food.

The brown hyaena has a catholic diet and can be described as a highly opportunistic scavenger where, in the southern Kalahari at any rate, hunting plays a small part in its acquisition of food. The fact that it is not solely dependant on large numbers of herbivores for its food makes it the best adapted of the larger carnivores in southern Africa to live in an arid region like the Kalahari where for the most part herbivores are thinly distributed. It is important for the well being of this species, therefore, to maintain the ecological conditions in this area as the Kalahari Gemsbok National Park contains the largest and only viable, conserved brown hyaena population in South Africa.

The study was carried out during a period of abnormally high rainfall when it was assumed that food for brown hyaenas was abundant. By way of comparison, and to gain a better understanding of the food ecology of this species, it would be valuable to repeat such a study during drought years. Furthermore, little is still known about the availability of brown hyaena food and how this influences their density, movements and diet. It would also be useful to determine how important the tsama and gemsbok cucumber are to brown hyaenas, exactly how they derive benefit from them and how they cope when these fruits are in short supply.

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