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DIET AND FORAGING BEHAVIOUR OF THE BROWN HYAENA, HYAENA BRUNNEA THUNBERG, 1820 IN THE SOUTHERN KALAHARI

by

MICHAEL GEORGE LYNE MILLS

Submitted in partial fulfilment of the requirement for

the degree of

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in the

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DIET AND FORAGING BEHAVIOUR OF THE BROWN HYAENA, *HYAENA BRUNNEA* THUNBERG, 1820 IN THE SOUTHERN KALAHARI

by

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ABSTRACT

In the southern Kalahari direct observations of individual brown hyaenas (fitted with radio collars and beta lights) and faecal analysis, yielded the best information on diet. Analysis of food items found at dens was also useful, but tracking spoor had severe limitations. The brown hyaena is predominantly a scavenger of vertebrate remains, supplementing its diet with insects, wild fruits, birds' eggs and the occasional small animal which it kills. Observations on activity, searching behaviour, scavenging, food storing and hunting behaviour of the brown hyaena are presented. It

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is concluded that the brown hyaena is the best adapted of the large carnivores to this arid region. It would be worthwhile investigating the feeding habits of this species in other areas, to determine the extent to which it clashes with man's interests.

ACKNOWLEDGEMENTS

I would like to express my appreciation to Dr. R. Knobel, Chief Director of National Parks, South Africa, and to the National Parks Board of Trustees, for initially allowing me to live and work in the Kalahari Gemsbok National Park, and after my appointment as research officer, for allowing me to continue with the brown hyaena work and for then supporting most aspects of the project.

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I was away or sleeping during the day. Mr. W. Massyn and Mr. W. de Beer, official photographers, reproduced the photographs with the help of Mr. J. Makubyana. Mr. G. van Rooyen and Mr. T. Maritz, instrument makers in the Kruger National Park, made the beta light holders.

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CONTENTS

PAGE

CHAPTER 1 : INTRODUCTION 1

Recent distribution and status of the brown hyaena 1

The Hyaenidae 3

Aims of the study 4

The study area 5

Location 5

Climate 6

Geomorphology and physiography 7

Geology 9

Vegetation 10

Fauna 11

CHAPTER 2 : MATERIALS AND METHODS 14

Introduction 14

Tracking spoor 15

Direct observations and radio tracking 16

Construction and fitting of Dav-tron radio collars and method of mounting beta lights 20

Faecal analysis 22

Collection of food items around dens 24

Capture procedure 24

Capture from a moving vehicle during the day 24

Capture by means of a baited drop-door trap 25

Capture by means of darting free ranging animals at night 29

Immobilisation 30

Sernylan 30

Ketamine 32

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UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

PAGE

Advantages and disadvantages of the two drugs 32

CHAPTER 3 : DIET 34

Introduction 34

Results 35

Discussion on the four methods used to analyse the diet 36

Overall diet 39

Vertebrate food 40

Insects 42

Wild fruits 43

Tsama and gemsbok cucumber 43

Other fruits 46

Water relations 47

Consumption 49

CHAPTER 4 : FORAGING BEHAVIOUR 53

Activity patterns 53

Resting sites 55

Searching 57

Senses used when searching 58

Olfactory 58

Auditory 62

Visual 64

Scavenging 64

Scavenging from and interactions with other carnivorous animals 69

Lion 69

Leopard 70

Cheetah 71

Spotted hyaena 71

Black-backed jackal 72

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UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

PAGE

Caracal 75

Man 75

Birds of prey 76

Other sources 77

Foraging for fruits, fungi and birds' eggs 78

Tsamas and gemsbok cucumbers 78

Other fruits and fungi 79

Birds' eggs 80

Food storing 83

Hunting behaviour 87

Hunting mammals 87

Prey selection and hunting success rate 87

Hunting bat-eared foxes 90

Hunting springbok 92

Hunting springhares 94

Hunting black-backed jackals 95

Hunting striped polecats 96

Hunting other mammals 97

Hunting birds 98

Hunting frequencies in river and dune habitat 99

The brown hyaena's vertebrate hunting behaviour and comparison with other hyaenas 100

Hunting insects 102

CHAPTER 5 : DISCUSSION AND CONCLUSIONS 105

Methods of investigating the diet of the brown hyaena .. 105

A comparison of the diets of the four species of the Hyaenidae 106

Some adaptations of the brown hyaena to its environment 108

The conservation of the brown hyaena: some suggestions for future management and research 110

Digitised by the Department of Library Services in support of open access to information, University of Pretoria, 2021

UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

PAGE

SUMMARY 113

OPSOMMING 118

REFERENCES 123

APPENDIX A 131

APPENDIX B 134

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UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

LIST OF TABLES

TABLE		PAGE
1	Means of monthly and annual rainfall in mm at three stations in the Kalahari Gemsbok National Park, South Africa	7 b
2	Air temperature (^{o} C) at Twee Rivieren in the Kalahari Gemsbok National Park, South Africa (1961 - 1975)	7 b
3	Monthly relative humidity of the air in per cent at 08h00, 14h00 and 20h00 at Twee Rivieren in the Kalahari Gemsbok National Park, South Africa (1961 - 1975)	7 c
4	Wind direction and speed (m/sec) at Twee Rivieren in the Kalahari Gemsbok National Park, South Africa (1961 - 1975)	7 c
5	Number of times individual brown hyaenas (Hyaena brunnea) were caught in baited drop-door traps in the southern Kalahari; January 1973 - March 1976	28 a
6	Success rate in trapping brown hyaenas (Hyaena brunnea) in the same area of the southern Kalahari at different times; December 1974 - April 1975, May 1975 - September 1975, December 1975 - March 1976	28 b
7	Trapping success obtained with brown hyaenas (Hyaena brunnea) using old bait for a period and then fresh bait in the same traps in the southern Kalahari, 1975 ...	29 a
8	Dosage rates and reaction times for brown hyaenas (Hyaena brunnea) immobilised with Sernylan (Phencyclidine hydrochloride) in the southern Kalahari; April 1972 - July 1976	30 a
9	Dosage rates and reaction times for brown hyaenas (Hyaena brunnea) immobilised with Sernylan (Phencyclidine hydrochloride) (initial dart) and Ketamine hydrochloride (booster injections) in the southern Kalahari; April 1972 - July 1976	32 a
10	Dosage rates and reaction times for brown hyaenas (Hyaena brunnea) immobilised with Ketamine hydrochloride in the southern Kalahari; April 1972 - July 1976	32 b
11	Food eaten by brown hyaenas (Hyaena brunnea) as determined by following 1 205 km of spoor in the southern Kalahari; April 1972 - October 1973	35 a
12	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)	35 b

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UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

TABLE PAGE

13 Food items found in 383 brown hyaena (Hyaena brunnea) faeces from the southern Kalahari; April 1972 - September 1974 ..... 35 c

14 Food items found at eight brown hyaena (Hyaena brunnea) dens in the southern Kalahari; April 1972 - July 1976 ... 35 d

15 Insect remains found in brown hyaena (Hyaena brunnea) faeces from the southern Kalahari; April 1972 - September 1974 ..... 42 a

16 Analysis of some wild fruits which are eaten by brown hyaenas (Hyaena brunnea) in the southern Kalahari ..... 45 a

17 Biomass of food eaten by two lactating adult female brown hyaenas (Hyaena brunnea) in 13 nights in the southern Kalahari as determined from direct observations; January, April and August 1975, January and February 1976 ..... 51 a

18 Frequency and orientation of sniffs made by three, one year old brown hyaena (Hyaena brunnea) cubs, under different wind conditions, during daylight in the southern Kalahari; July - September 1973 ..... 60 a

19 Cause of death of fresh carcasses on which brown hyaenas (Hyaena brunnea) were observed feeding in the southern Kalahari; April 1972 - July 1976 ..... 66 a

20 Food items stored by brown hyaenas (Hyaena brunnea) in the southern Kalahari; April 1972 - July 1976 ..... 84 b

21 Analysis of aspects of hunting attempts made on mammals by brown hyaenas (Hyaena brunnea) in the southern Kalahari; April 1972 - July 1976 ..... 88 a

22 Analysis of aspects of hunting attempts made on birds by brown hyaenas (Hyaena brunnea) in the southern Kalahari; April 1972 - July 1976 ..... 98 a

23 Frequency of hunts by three individual brown hyaenas (Hyaena brunnea) followed in river and dune habitat in the southern Kalahari; December 1974 - July 1976 ..... 100 a

24 Percentage occurrence of various food categories in the faeces of spotted (Crocuta crocuta), brown (Hyaena brunnea) and striped (Hyaena hyaena) hyaenas and the aardwolf (Proteles cristatus) from different areas in Africa ..... 106 a

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UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

LIST OF FIGURES

FIGURE		PAGE
1	The Kalahari Gemsbok and Gemsbok National Parks and the Mabua Sehube Game Reserve, showing the main study area and other places mentioned in the text	5 a
2	Monthly rainfall for Nossob Camp, Kalahari Gemsbok National Park; January 1972 - July 1976	7 a
3	Habitats in the southern Kalahari: (a) Parallel dunes and the Nossob river valley south of Kwang Pan. (b) Auob river in flood, March 1973. (c) Pan and surrounding dune habitat, Seven Pans. (d) The Nossob river-bed near Bedinkt	9 a
4	Habitats in the southern Kalahari: (a) Stipagrostis obtusa plains, Rooikop. (b) Dune habitat. (c) Kwang Pan in the dry season, August 1972. (d) Kwang Pan and a herd of springbok (Antidorcas marsupialis) after good rains, February 1976	12 a
5	Periods when individual radio-collared brown hyaenas (Hyaena brunnea) were followed in the southern Kalahari; December 1974 - July 1976	17 a
6	Radio collar with beta lights attached as used in a study of the ecology and behaviour of the brown hyaena (Hyaena brunnea) in the southern Kalahari and showing: (a) The transmitter and battery pack encased in colrylic and (b) close up of attached beta lights, aluminium plate, beta light holders and glass fibre tape.....	21 a
7	Brown hyaena (Hyaena brunnea) scat (a) and food items from a scat (b) from the southern Kalahari.....	22 a
8	Food remains at a brown hyaena (Hyaena brunnea) den in the southern Kalahari; November 1972	22 a
9	Capture of brown hyaenas (Hyaena brunnea) by means of a baited drop-door trap in the southern Kalahari: (a) Set trap with meat hanging at the back. (b) Brown hyaena entering trap. (c) Shooting dart with Cap-Chur pistol. (d) Trap enclosed with grass to protect recovering hyaena from sun and to minimise disturbance	27 a
10	Time taken by brown hyaenas (Hyaena brunnea) to eat various food items in the southern Kalahari; December 1974 - July 1976	36 a
11	Percentage occurrence of food categories found in faeces versus percentage occurrence of food categories from direct observations of brown hyaenas (Hyaena brunnea) in the southern Kalahari; April 1972 - July 1976	39 a

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UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

FIGURE PAGE

12 Percentage occurrence of mammal species found in faeces of brown hyaena (Hyaena brunnea) cubs under 10 months old versus percentage occurrence of mammal species remains found at the same cubs' den in the southern Kalahari; April 1973 - October 1973 ..... 39 a

13 Brown hyaena (Hyaena brunnea) carrying a scavenged secretary bird (Sagittarius serpentarius) to its den in the southern Kalahari ..... 40 a

14 Stomach contents of an old female brown hyaena (Hyaena brunnea), Nossob Camp, southern Kalahari ..... 40 a

15 Large brown hyaena (Hyaena brunnea) cub eating its dead mother in the southern Kalahari ..... 40 a

16 Brown hyaena (Hyaena brunnea) drinking from a puddle of rain water in the southern Kalahari ..... 40 a

17 Monthly utilisation of gemsbok (Oryx gazella), hartebeest (Alcelaphus buselaphus), steenbok (Raphicerus campestris) and canids by brown hyaenas (Hyaena brunnea) in the southern Kalahari as determined from faecal analysis; April 1972 - September 1974 ..... 41 a

18 Monthly utilisation of Tenebrionidae by brown hyaenas (Hyaena brunnea) as determined from faecal analysis in the southern Kalahari; April 1972 - September 1974 ..... 43 a

19 Monthly utilisation of tsamas (Citrullus lanatus) and gemsbok cucumbers (Acanthosicyos naudianus) by brown hyaenas (Hyaena brunnea) in the southern Kalahari; April 1972 - September 1974 (faeces), April 1972 - July 1976 (tracking spoor and direct observations) ..... 44 a

20 Monthly utilisation of Grewia flava berries by brown hyaenas (Hyaena brunnea) as determined from faecal analysis in the southern Kalahari; April 1972 - September 1974 ..... 46 a

21 Mean percentage of each hour of the 24 h period that adult brown hyaenas (Hyaena brunnea) were active in the southern Kalahari; December 1974 - July 1976 ..... 54 a

22 Mean percentage of each hour of the 24 h period that one year old brown hyaena (Hyaena brunnea) cubs were active in the southern Kalahari; June - September 1973 ..... 54 b

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UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

FIGURE		PAGE
23	Time and duration of inactive periods between 20h00 and 06h00 of brown hyaenas (Hyaena brunnea) in the southern Kalahari; December 1974 - July 1976 ...	55 a
24	Relative time spent on various activities by brown hyaenas (Hyaena brunnea) in the southern Kalahari; December 1974 - July 1976	55 b
25	Location of resting sites used by a male and a female brown hyaena (Hyaena brunnea) in the southern Kalahari; December 1974 - July 1976	55 c
26	Percentage occurrence of different types of resting sites used by brown hyaenas (Hyaena brunnea) at different times of the year in the southern Kalahari; April 1972 - July 1976	56 a
27	Resting sites of brown hyaenas (Hyaena brunnea) in the southern Kalahari; April 1972 - July 1976	56 b
28	Frequency distribution of distances covered during one night's foraging by brown hyaenas (Hyaena brunnea) in the southern Kalahari; April 1972 - July 1976	57 a
29	Brown hyaena (Hyaena brunnea) foraging in the southern Kalahari	59 a
30	Brown hyaena (Hyaena brunnea) sniffing upwind in the southern Kalahari	59 a
31	Brown hyaena (Hyaena brunnea) in the southern Kalahari cocking its ears and listening to a sound originating close by	59 a
32	Brown hyaena (Hyaena brunnea) feeding on the remains of a springbok (Antidorcas marsupialis) in the southern Kalahari	66 b
33	Brown hyaena (Hyaena brunnea) eating a long bone of a red hartebeest (Alcelaphus buselaphus) in the southern Kalahari	66b
34	Two brown hyaenas (Hyaena brunnea) feeding together on a springbok (Antidorcas marsupialis) carcass in the southern Kalahari	68 a
35	Brown hyaena (Hyaena brunnea) in the southern Kalahari carrying off part of a springbok (Antidorcas marsupialis) carcass to its den	68 a
36	Brown hyaena (Hyaena brunnea) in the southern Kalahari standing on its hind legs in an attempt to reach a springbok (Antidorcas marsupialis) carcass in the tree	71 a

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UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

FIGURE PAGE

37 Brown hyaena (Hyaena brunnea) in the southern Kalahari feeding on the scraps of a springbok (Antidorcas marsupialis) carcass which a leopard (Panthera pardus) has dragged into a tree ..... 71 a

38 Brown hyaena (Hyaena brunnea) in the southern Kalahari at a springbok (Antidorcas marsupialis) carcass which it had just stolen from a female cheetah (Acinonyx jubatus) and her three small cubs ..... 71 a

39 Black-backed jackal (Canis mesomelas) in the southern Kalahari approaching a brown hyaena (Hyaena brunnea) feeding on the innards from a dead blue wildebeest (Connochaetes taurinus) ..... 73 a

40 Black-backed jackal (Canis mesomelas) in the southern Kalahari barking at a large brown hyaena (Hyaena brunnea) cub which is moving away with its hair raised ..... 73 a

41 Remains of a springbok (Antidorcas marsupialis). lamb killed by a martial eagle (Polemaëtus bellicosus) in the southern Kalahari and which might provide a meal for a brown hyaena (Hyaena brunnea) ..... 77 a

42 Bone chips left by a brown hyaena (Hyaena brunnea) after eating the remains of a red hartebeest (Alcelaphus buselaphus) calf in the southern Kalahari. These might be taken by white-backed vultures (Gyps africanus) to feed to their chicks ..... 77 a

43 Brown hyaena (Hyaena brunnea) eating a tsama (Citrullus lanatus) in the southern Kalahari ..... 79 a

44 Typical remains of a tsama (Citrullus lanatus) eaten by a brown hyaena (Hyaena brunnea) in the southern Kalahari ..... 79 a

45 Typical remains of a gemsbok cucumber (Acanthosicyos naduianus) eaten by a brown hyaena (Hyaena brunnea) in the southern Kalahari ..... 79 a

46 Number of tsamas (Citrullus lanatus) eaten per bout by brown hyaenas (Hyaena brunnea) in the southern Kalahari; April 1972 - July 1976 ..... 79 b

47 Number of gemsbok cucumbers (Acanthosicyos naudianus) eaten per bout by brown hyaenas (Hyaena brunnea) in the southern Kalahari; April 1972 - July 1976 ..... 79 b

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UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

FIGURE PAGE

48 Brown hyaena (Hyaena brunnea) raiding an ostrich (Struthio camelus) nest with 26 eggs in it, in the southern Kalahari: (a) Standing at the nest shortly after finding it. (b) Lapping up the contents of an egg. (c) The nest the next day after all the eggs had either been eaten or carried away for storage ..... 83 a

49 Diagrammatic representation of storing of ostrich (Struthio camelus) eggs by a brown hyaena (Hyaena brunnea) in the southern Kalahari; September 1975 ..... 83 b

50 Examples of food storing by brown hyaenas (Hyaena brunnea) in the southern Kalahari: (a) The hindquarters of a steenbok (Raphicerus campestris) under a bush from which the hyaena was flushed. (b) The leg of a gemsbok (Oryx gazella) stored in a clump of tall Stipagrostis amabilis grass ..... 84 a

51 Brown hyaena (Hyaena brunnea) in the southern Kalahari with a half eaten springhare (Pedetes capensis) that it had killed ..... 95 a

52 Large brown hyaena (Hyaena brunnea) cub in the southern Kalahari with a striped polecat (Ictonyx striatus) that it had killed: (a) Carrying it off approximately 10 m from the kill site before eating it. (b) Eating it. (c) Finishing off the tail ..... 96 a

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UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

CHAPTER 1 : INTRODUCTION

The brown hyaena (Hyaena brunnea Thunberg, 1820) is listed in the I.U.C.N. Red Data Book as an endangered species, where the reason for its decline is given as persecution by farmers and ranchers who regard it as a danger to their livestock.

Recent distribution and status of the brown hyaena

The brown hyaena is essentially a species of the south-west arid and adjacent drier parts of the southern savanna biotic zones (Von Richter 1972), and the highest known population density occurs in the southern and central Kalahari (Smithers 1971, Mills 1973, Dawson pers. comm.).

Since 1970 several specimens have been recorded from various places in the Transvaal, especially in the west and south-west (Skinner 1976), although no definite records from the Kruger National Park are available since 1972 (Joubert In litt.). Sporadic records occur from the Orange Free State, especially the north-east (Lynch 1975), the north-western Cape (Von Richter 1972, Macdonald In litt.), the north-eastern Cape (Skinner 1976) and the Natal Drakensberg, where part of the skeleton of one was recently found (Rowe-Rowe In litt.). Along the coast of the southern Namib Desert brown

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J. Dawson. Department of Wildlife and National Parks, P.O. Box 131, Gaborone, Botswana. July 1974.

S.C.J. Joubert. Department of Nature Conservation, Private Bag X404, Skukuza, 1350. 30 June 1977.

I.A.W. Macdonald. Northern Cape Nature Conservation Station, Private Bag, Hartswater, 8570. 21 April 1977.

D.T. Rowe-Rowe. Natal Parks, Game and Fish Preservation Board, P.O. Box 662, Pietermaritzburg, 3200. 17 September 1975.

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hyaenas are common around Van Reenen Bay (Shaughnessy pers. comm.) and Bogenfels and, further inland, around the Klinghardts mountains (Mansell In litt.). Elsewhere in South West Africa this species is rare (Joubert and Mostert 1975), although individuals were seen on several occasions by Reid (In litt.) in 1972 and 1973 in the Etosha National Park. Huntley (1974) also recorded the brown hyaena in southern Angola. In Rhodesia brown hyaenas occur sporadically in the south-western regions (Smithers in prep.) and in Mocambique brown hyaenas possibly occur in the northern parts of the Gaza District and around Tete (Smithers and Lobão Tello 1976). Although there are no positive records, the possibility of the brown hyaena extending into Malawi cannot be discounted, and Sweeney (1959) and Hayes (1972) both believe that it occurs there.

Because of their secretive habits it is difficult to make an estimate of the numbers of brown hyaenas in these various areas, and any attempts to do so without the use of census techniques are of little value. Nevertheless, in countries where this species is known to occur or to have occurred in historical times, it is considered to be extinct in Swaziland, threatened with extinction in South Africa and possibly South West Africa, rare in Angola, Mocambique and Rhodesia, and safe in Botswana (Bothma 1975).

P.D. Shaughnessy. Department of Sea Fisheries, P.O. Box 251, Cape Town, 8000. October 1976.

M.W. Mansell. Department of Zoology and Entomology, Rhodes University, P.O. Box 94, Grahamstown, 6140. 2 December 1974.

R.C. Reid. c/o Medical School, University of the Witwatersrand, Johannesburg, 2000. 15 January 1974.

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The Hyaenidae

Species:

The four extant species of the Hyaenidae are the remnants of a much larger family that reached its peak in the early Pleistocene (Ewer 1967). Of these, the aardwolf (Proteles cristatus) is the most aberrant form where the cheek teeth have become rudimentary. The other three species, belonging to two genera, are the spotted hyaena (Crocuta crocuta), the striped hyaena (Hyaena hyaena) and the brown hyaena (sometimes referred to in this text as the hyaena), where the bone crushing premolars and the carnassial shear are well developed.

Distribution:

The spotted hyaena is distributed throughout Africa south of the Sahara, except for the Congo basin and the extreme south of the continent where it is now extinct. The striped hyaena is found in the northern half of the continent, excluding the Sahara and the west south of 10^{o} N, through the Middle East and southern Asia to the Gulf of Bengal. The brown hyaena occurs in the south of the continent mainly in the more arid regions, and the aardwolf in the arid and semi-arid regions of southern Africa, northwards on the east into Somalia, Ethiopia and the Sudan (Ewer 1973, Dorst and Dandelot 1970, Kruuk 1972 and 1976 a). Therefore, except for non-overlap between the brown and striped hyaena, the hyaena species all overlap with each other to a greater or lesser extent.

Other studies:

Of these species, most information is available on the spotted hyaena. Kruuk (1966 a and b, 1968, 1970 and 1972) has studied many aspects of its ecology and behaviour in the Serengeti and Ngorongoro Crater in East Africa, and Bearder (1975 and 1977) has studied its feeding ecology in the Timbavati

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Private Nature Reserve, Transvaal. In addition papers by Deane (1962) from Zululand, Eloff (1964 and 1975) and Mills (in press) from the Kalahari, Hirst (1969) from the Transvaal lowveld and Pienaar (1969) from the Kruger National Park have added useful information. The feeding and social behaviour of the striped hyaena have been superficially studied by Kruuk (1976 a) in the Serengeti and Israel, and by Macdonald (1977) in Israel. Information on the feeding habits of the aardwolf can be found in Bothma (1971 a) from the Transvaal and northern Natal, Smithers (1971) from Botswana and Kruuk and Sands (1972) from the Serengeti, where some information is also presented on social behaviour and organisation.

Little information is available on the ecology and behaviour of the brown hyaena, although recently Skinner (1976) has published observations from the Transvaal, and Roberts (1954), Stevenson-Hamilton (1947) and Pienaar (1969) have made contributions.

Aims of the study

The present study was initiated to collect information on various aspects of the ecology and behaviour of the brown hyaena, in an attempt to define the limiting factors operating on its population in the southern Kalahari, especially as an aid to its conservation. With this information a management policy designed to ensure the brown hyaena's survival in this area will be drawn up. The results from this study could also possibly assist in the design of further research projects on the brown hyaena in other areas, by pointing to some of the more important aspects which should be investigated.

From a more academic viewpoint it was hoped that a contribution towards the understanding of the relationship between ecology and social organisation could be made, as amongst carnivores this important field of study has

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received little attention to date. The Hyaenidae is an ideal family to work on as there are only four extant species, all of which have now been studied in some detail, the results showing a wide range of ecological adaptations and social organisations. As the diet and foraging behaviour of a carnivore form the foundation for its life style (Kruuk 1975 a, Wilson 1975), this report describes these for the brown hyaena, as the basis of a more extensive study designed to answer the questions outlined above (Mills in prep.).

The southern Kalahari was originally chosen as the study area because the brown hyaena population was considered large enough to ensure a reasonable volume of data, and because most of the area is covered in sand, making it possible to follow spoor. A third advantage, its openness, which makes it possible to follow animals in a vehicle at night, was discovered later.

The study area

Location

The study was done in the adjacent Kalahari Gemsbok (South Africa) and Gemsbok (Botswana) National Parks (Fig. 1). The Kalahari Gemsbok National Park, an area of 9 591 km^2, was proclaimed in 1931 and lies between 20°00' and 20°53' E and 24°45' and 26°30' S in the north-west Cape Province, Republic of South Africa. The western boundary has a game deterrent fence and forms the border between the Republic of South Africa and farming areas in South West Africa. The southern boundary, from Mata Mata to Twee Rivieren, also has a game deterrent fence which separates it from the Mier Settlement. The Nossob river forms the northern and eastern boundary, is unfenced, and the boundary with the Gemsbok National Park runs through it at midstream.

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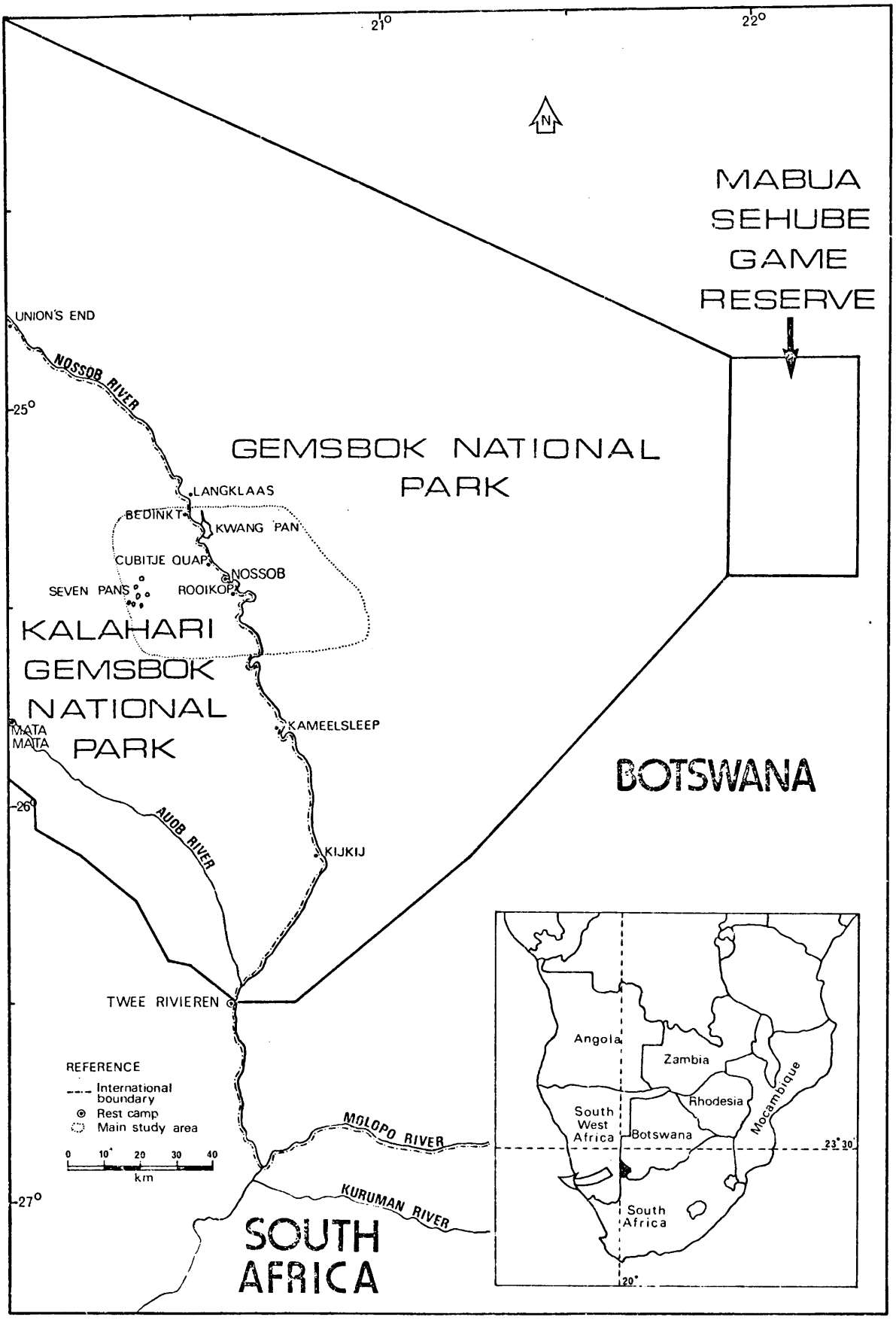


Figure 1. The Kalahari Gemsbok and Gemsbok National Parks and the Mabua Sehube Game Reserve, showing the main study area and other places mentioned in the text.

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The Gemsbok National Park, 24 800 km^2 in area (Child 1972) lies roughly between 20°00' and 21°51' E and 24°08' and 26°30' S in the extreme south-west of the Republic of Botswana. Most of it is surrounded by controlled hunting areas (Von Richter and Butynski 1973) except in the extreme east where it adjoins the Mabua Sehube Game Reserve, an area of 1 800 km^2 (Child 1972), the extreme south where it adjoins farming areas, and the west where it adjoins farming areas in South West Africa. The South West Africa boundary has a game deterrent fence and in 1976 a jackal proof stock fence was erected along the southern boundary for approximately 16 km east from Twee Rivieren. An area adjoining the Nossob river was proclaimed in the early 1940's as a Game Reserve of 6 035 km^2 and elevated to National Park status and increased to its present size in 1972 (Blair Rains and Yalala 1972, Child 1972).

Climate

The southern Kalahari is a semi-desert region having an irregular rainfall and experiencing large temperature fluctuations both on a daily and seasonal basis (Leistner 1967). Three basic seasons are recognised:-

(1) The hot, wet season; January to April, when the mean monthly temperature is approximately 20° C or higher and 70 per cent or more of the rain falls.

(2) The cold, dry season; May to September, when the mean monthly temperature is below 20° C and rainfall is rare.

(3) The hot, dry season; October to December, when the mean monthly temperature is above 20° C and usually not more than 20 per cent of the annual rain falls.

Rainfall:

Table 1 gives the rainfall data for three stations in the Kalahari Gemsbok National Park, and shows that most of the rain falls in late summer.

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Rainfall is, however, most erratic and can vary in one year over a relatively short distance. Furthermore, the minimum annual rainfall can be less than half the average and the maximum more than double (Blair Rains and Yalala 1972). During the study period the area received good rains in all years, particularly in 1974 and 1976 (Fig. 2).

Temperature:

Southern Kalahari summers are hot with November, December, January and February the hottest months (Table 2). When the air temperature is approximately 40° C the sand surface can heat up to 70° C (Leistner 1967). The winters are severe (Table 2) and ground frosts are common.

Humidity, evaporation and sunshine:

Table 3 gives the mean relative humidity of the air for Twee Rivieren at different times of the day, showing that it is generally low. Evaporation rates are high and the rainfall is unlikely to exceed evaporation for any month of the year (Blair Rains and Yalala 1972). The area receives 80 per cent of the possible sunshine with February being the cloudiest month when the percentage sunshine varies from approximately 70 to 80 (Leistner 1967).

Wind:

South and north winds dominate at Twee Rivieren (Table 4), although Leistner (1967) maintains that the north-westerly wind is dominant in the southern Kalahari.

Geomorphology and physiography

The Kalahari is a large sand-filled basin in the west of the south African sub-continent, covering nearly one third of the area and forming what is probably the largest sand-veld area in the world (King 1963). It stretches from the Orange river in the south to 1° N in Zaire, and from approximately

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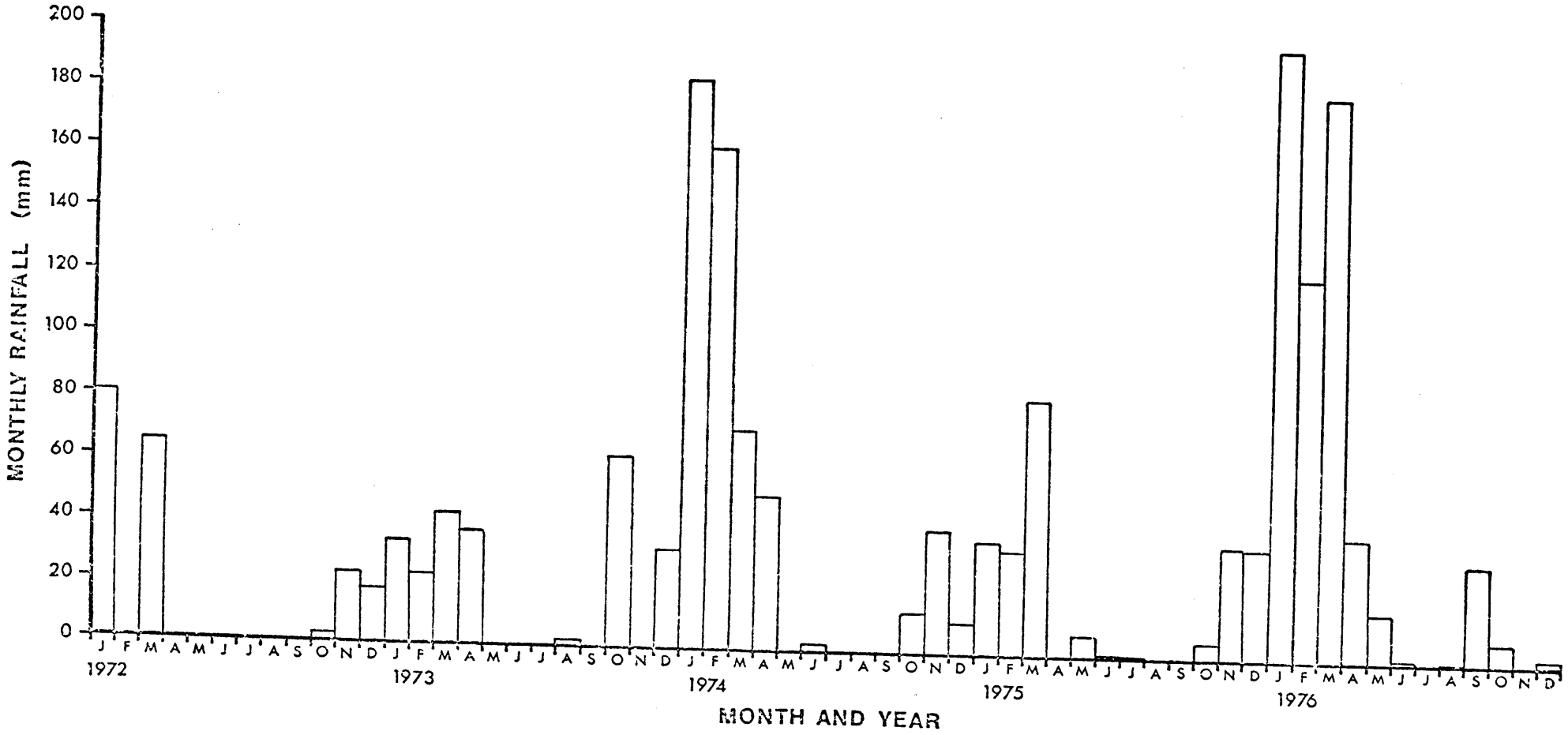


Figure 2. Monthly rainfall for Nossob Camp, Kalahari Gemsbok National Park; January 1972 - July 1976.

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Table 1. Means of monthly and annual rainfall in mm at three stations in the Kalahari Gemsbok National Park, South Africa.

MONTH	STATION		
	Twee Rivieren (1961 - 1975)	Mata Mata (1962 - 1975)	Nossob (1967 - 1975)
January	48,7	44,4	60,5
February	41,5	62,4	51,5
March	30,9	40,9	37,3
April	35,0	29,6	25,4
May	13,4	8,1	15,4
June	4,1	2,6	1,7
July	1,0	0,2	0,0
August	1,0	0,3	0,3
September	0,6	0,2	0,0
October	11,6	12,6	21,1
November	18,3	15,8	17,4
December	14,3	12,0	18,2
Year	220,3	229,5	248,9

Table 2. Air temperature ($^{\circ}$ C) at Twee Rivieren in the Kalahari Gemsbok National Park, South Africa (1961 - 1975).

MONTH	TEMPERATURE				
	$\frac{\text{Max+Min}}{2}$	Mean maximum	Mean absolute maximum	Mean minimum	Mean absolute minimum
January	27,2	35,5	40,1	19,6	13,7
February	26,1	34,9	39,1	18,5	12,4
March	24,4	32,5	36,9	16,8	9,2
April	19,8	28,5	33,6	11,6	3,7
May	15,0	22,9	30,5	5,5	-1,9
June	11,8	21,5	26,9	2,2	-4,8
July	11,4	21,8	27,3	1,1	-5,9
August	13,3	23,8	31,2	2,7	-5,2
September	17,9	28,7	35,9	7,3	-0,8
October	21,3	30,9	38,2	11,8	2,3
November	24,2	33,5	39,4	15,9	9,2
December	26,2	33,1	40,6	17,9	11,3
Year	19,8	29,0	35,0	10,9	3,6

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Table 3. Monthly relative humidity of the air in per cent at 08h00, 14h00 and 20h00 at Twee Rivieren in the Kalahari Gemsbok National Park, South Africa (1961 - 1975).

MONTH	TIME		
	08h00	14h00	20h00
January	45	25	31
February	55	28	36
March	65	32	43
April	73	32	50
May	76	31	52
June	77	31	53
July	72	28	47
August	64	25	39
September	49	20	31
October	42	21	29
November	43	23	30
December	40	21	26
Mean	58	26	39

Table 4. Wind direction and speed (m/sec) at Twee Rivieren in the Kalahari Gemsbok National Park, South Africa (1961 - 1975).

WIND DIRECTION	MEAN ANNUAL PERCENTAGE OF WIND DIRECTION	AVERAGE SPEED
N	21,5	4,5
NE	12,1	3,6
E	4,2	3,3
SE	7,1	3,1
S	25,0	4,1
SW	12,7	3,6
W	4,9	3,6
NW	12,5	4,5
Total	100,0	-
Mean	-	3,9

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14° E in Angola to 28° E in Rhodesia (Leistner 1967). Most of the Kalahari Gemsbok and Gemsbok National Parks lie more than 900 m above sea level, except for an area around Twee Rivieren in the south which lies between 600 m and 900 m above sea level.

The Kalahari sand, which is usually pinkish to brownish-ochre in appearance (Leistner 1967) and of even grain size, is derived from rocks within the Kalahari basin itself, where since Gondwana detritus has been swept in from the surrounding areas (King 1963). In the southern Kalahari the sand deposits are arranged in a series of long, roughly parallel, longitudinal dunes which fuse and diverge at intervals and are fixed by vegetation (Figs. 3 a and 4 b). The valleys between the dunes are locally known as "strate" and vary in width, with the mean between dune crests being 228,5 m (Leistner 1967).

The southern Kalahari has a gentle southward tilt and the four rivers (the Nossob and the Auob, which run through one or both of the Parks, the Molopo and the Kuruman) all drain southwards. In the past these rivers cut broad flat floors several metres below the general level of the plain and ran into the Orange river (King 1963). For at least the last 1 000 years, however, the Molopo, into which the other three rivers used to flow, has been blocked by dunes near the Orange river (Leistner 1967) and today all the rivers in the Kalahari are usually dry (Figs. 3 a and d), only flowing for short periods during abnormally wet years. During the study the Auob river flowed in the Kalahari Gemsbok National Park in 1973 (Fig. 3 b) and 1974. The bed of the Nossob river between Kameelsleep and Union's End forms a wide, shallow, sandy trough up to 1 000 m wide. To the south it is a narrower channel 100 - 500 m wide with steep limestone banks in places, as is the Auob river-bed in most of the Kalahari Gemsbok National Park (Leistner and Werger 1973).

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A characteristic of the Kalahari is the large number of shallow flat depressions or pans (Fig. 3 c), which periodically hold water. Three types of pans are known in the southern Kalahari, with calc-pans, depressions in the sandy surface limestone, being the most common. The other pans are salt-pans, which have a high concentration of sodium chloride, and sand- or dune-pans, which are merely depressions lined with compact calcareous sand (Wellington 1955). Concentrations of pans occur in the extreme south-west of the Kalahari Gemsbok National Park and around Seven Pans (in the main study area), and particularly in Botswana, east of Union's End and in the Mabua Sehube Game Reserve. Details of the Kalahari pan ecosystem can be found in Parris (1976).

Geology

For the most part the geology of the Kalahari is hidden by the sand and it is only in places in the river-beds that the underlying strata are exposed. In recent years, however, the sinking of boreholes has yielded more information. Beneath the sand lies a vast sheet of calcareous or silicified sand or sandstone (Du Toit 1954) which also contains grits and minor conglomerates (Smit 1964). The calcareous sand or sandstone is exposed at places along the river courses and in a number of pans, and together with the upper sand layer and some underlying rocks, form the Kalahari system (Leistner 1967). Underlying the system lies blue shale of the Dwyka series with occasional intrusions of dolerite (Smit 1964).

No distinct soil horizons occur in the Kalahari sands and the basic division of soil types is between fine soils occurring in the river-beds and some pans, and sandy soils of the dunes (Leistner 1967). A more detailed description of the soils can be found in Louw (1964), Leistner (1967) and Leistner and Werger (1973).

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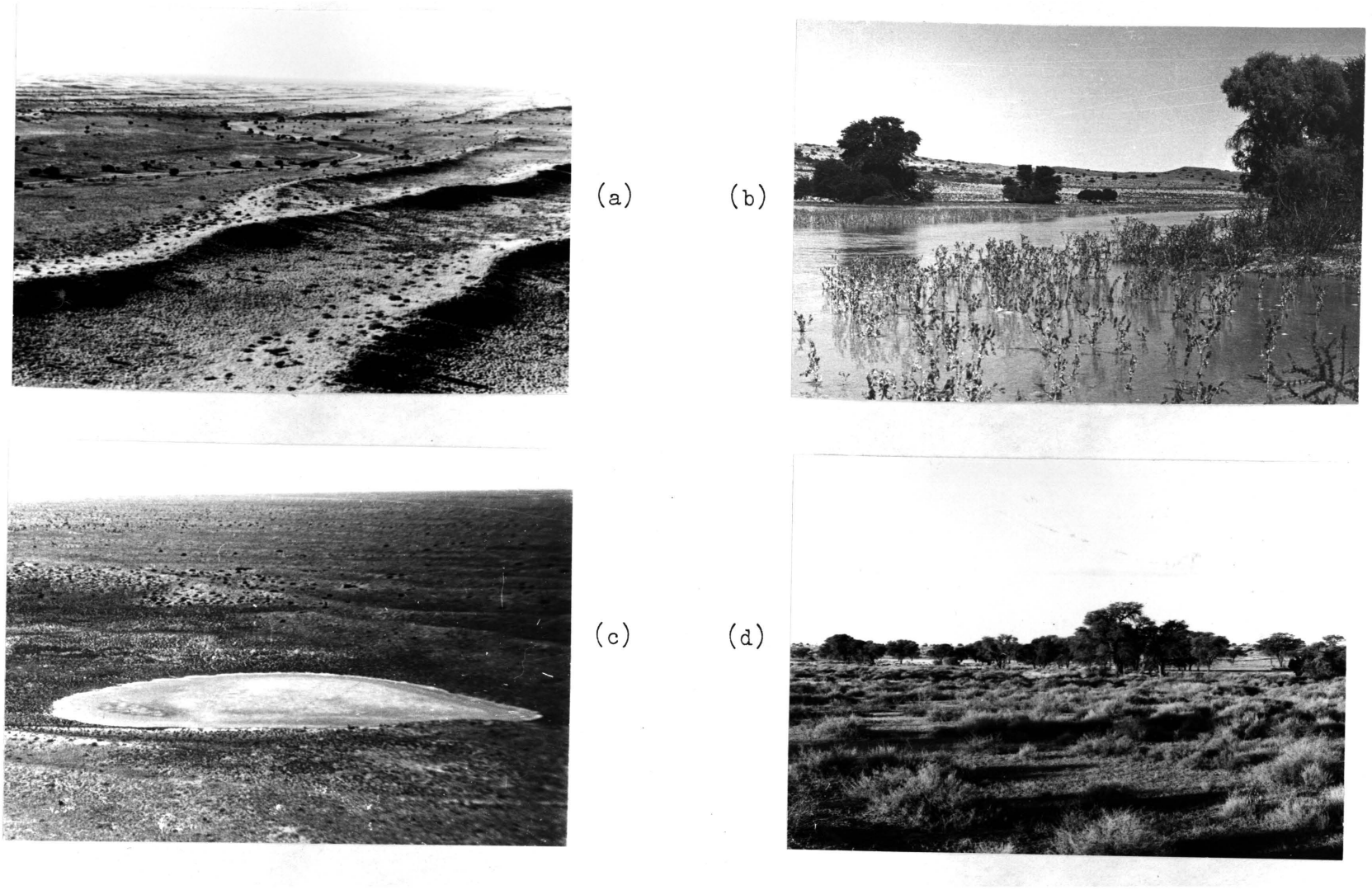


Figure 3. Habitats in the southern Kalahari: (a) Parallel dunes and the Nossob river valley south of Kwang Pan. (b) Auob river in flood, March 1973. (c) Pan and surrounding dune habitat, Seven Pans. (d) The Nossob river-bed near Bedinkt.

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Vegetation

Acocks (1975) defines the vegetation of this area as the western form of the Kalahari thornveld. More detailed descriptions of the vegetation in the southern Kalahari can be found in Leistner 1959 a and b and 1967), Blair Rains and Yalala (1972) and Leistner and Werger (1973) where it has been shown that there is a striking correlation between plant communities and soil types. A habitat map of the Kalahari Gemsbok National Park has been produced by Bothma and De Graaff (1973).

For the purposes of this study two main habitats are recognised and are referred to as river and dune. The river habitat (Fig. 3 d) includes the river-beds and banks as well as the areas close to the river where the sand is calcareous and compact. In the river-bed the dominant tree is Acacia erioloba although to the south of Kijkij and in the Auob A. haematoxylon is also common. The dominant grasses include the perennials Panicum coloratum and Eragrostis bicolor and the annuals Setaria verticillata, Chloris virgata and Schmidtia kalahariensis. In the main study area the most common shrub is Galenia africana. Where the banks of the rivers are not flanked by sand dunes they form exposed calcrete slopes or large sandy limestone flats (Fig. 4 a). These flats are common in the main study area and are dominated by the short perennial grass Stipagrostis obtusa with the shrub Rhigozum trichotomum also common in places, and are referred to as Stipagrostis plains in the text. The areas close to the river included as river habitat are characterised by Acacia erioloba, A. reficiens, A. mellifera subsp. detinens, Rhigozum trichotomum, and by the grasses Stipagrostis obtusa and Schmidtia kalahariensis.

At least 90 per cent of the surface of the southern Kalahari is covered by sand (Leistner 1967) and nearly all of this is what I refer to as dune

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habitat (Fig. 4 b). This is an extremely open savanna, the most common tree being Boscia albitrunca. Other woody plants include Acacia erioloba and A. haematoxylon, generally in a much more stunted form than in the rivers, A. mellifera subsp. detinens, Grewia flava and Rhigozum trichotomum. The grasses are tall and Eragrostis lehmanniana, Asthenatherum glaucum, Aristida meridionalis, Stipagrostis amabilis and S. ciliata are the dominant perennials, with Schmidtia kalahariensis the dominant annual. A large variety of annual herbs are also found in the sand-veld, Citrullus lanatus (tsama) being the most important for the brown hyaena as is the perennial herb Acanthosicyos naudianus (gemsbok cucumber). Pan vegetation resembles that of the river areas, particularly in that Stipagrostis obtusa and Rhigozum trichotomum are common on the edges.

Fauna

Invertebrates:

Several surveys of various arthropod classes and orders have been conducted in the area: Lepidoptera (Janse 1958, Van Son 1959); Coleoptera (Ferreira 1959); Isoptera (Coaton 1963); Diptera (Munro 1963); Arachnida (Lamoral 1973); Planipennia (Mansell in prep.). Smithers (1971) has shown the importance of these animals in providing food for small carnivores in the Kalahari and the brown hyaena regularly feeds on beetles (Coleoptera) and termites (Isoptera), both of which are well represented in the study area.

Reptiles:

Fitzsimons and Brain (1958) have surveyed the reptiles in the Kalahari Gemsbok National Park and Pianka (1971) the lizards in the southern Kalahari. At least 16 species of lizards and nine species of snakes, with eight other probables, occur. Reptiles are also utilised as food by many small carnivores (Smithers 1971) as well as by the brown hyaena.

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Birds:

An updated check list of the birds in the area can be found in Mills (1976 a) and a more intensive analysis of the avifauna in the southern part of the Kalahari Gemsbok National Park in Maclean (1970). The area is rich in terrestrial species such as the ostrich (Struthio camelus), kori bustard (Otis kori), black korhaan (Afrotis afra) and the red-crested korhaan (Eupodotis ruficrista), all of which are utilised as food by brown hyaenas.

Mammals:

Records of the distribution, status and habitat choice of the small mammals in the Kalahari Gemsbok National Park have been produced by Rautenbach (1971), Nel and Rautenbach (1975), Rautenbach and Nel (1975), and Smithers (1971) has surveyed the mammals in the Botswana region.

Several studies on the movements of the large herbivores have been made (Eloff 1959 a and b, 1961 and 1962, Bothma 1971 b and 1972, Bothma and Mills 1977), and recently an aerial monitoring program was commenced. Because of the vastness of the area and the migratory and nomadic nature of the herbivores, however, no accurate numbers are available, although generally the area has a low large ungulate density. The largest concentrations of large herbivores occur in and around the river-beds after the summer rains and the Nossob, in particular, experiences large fluctuations (Figs. 4 c and 4 d). During the dry season these animals move out into the dune areas, particularly in an easterly direction. In December 1972 when it was dry, for example, a count along the entire Nossob river (approximately 300 km), revealed 629 springbok (Antidorcas marsupialis), 39 gemsbok (Oryx gazella), 75 blue wildebeest (Connochaetes taurinus) and 21 red hartebeest (Alcelaphus buselaphus), whereas in February 1974, after exceptional rains, 7 350 springbok, 916 gemsbok, 367 wildebeest and 768 hartebeest were counted.

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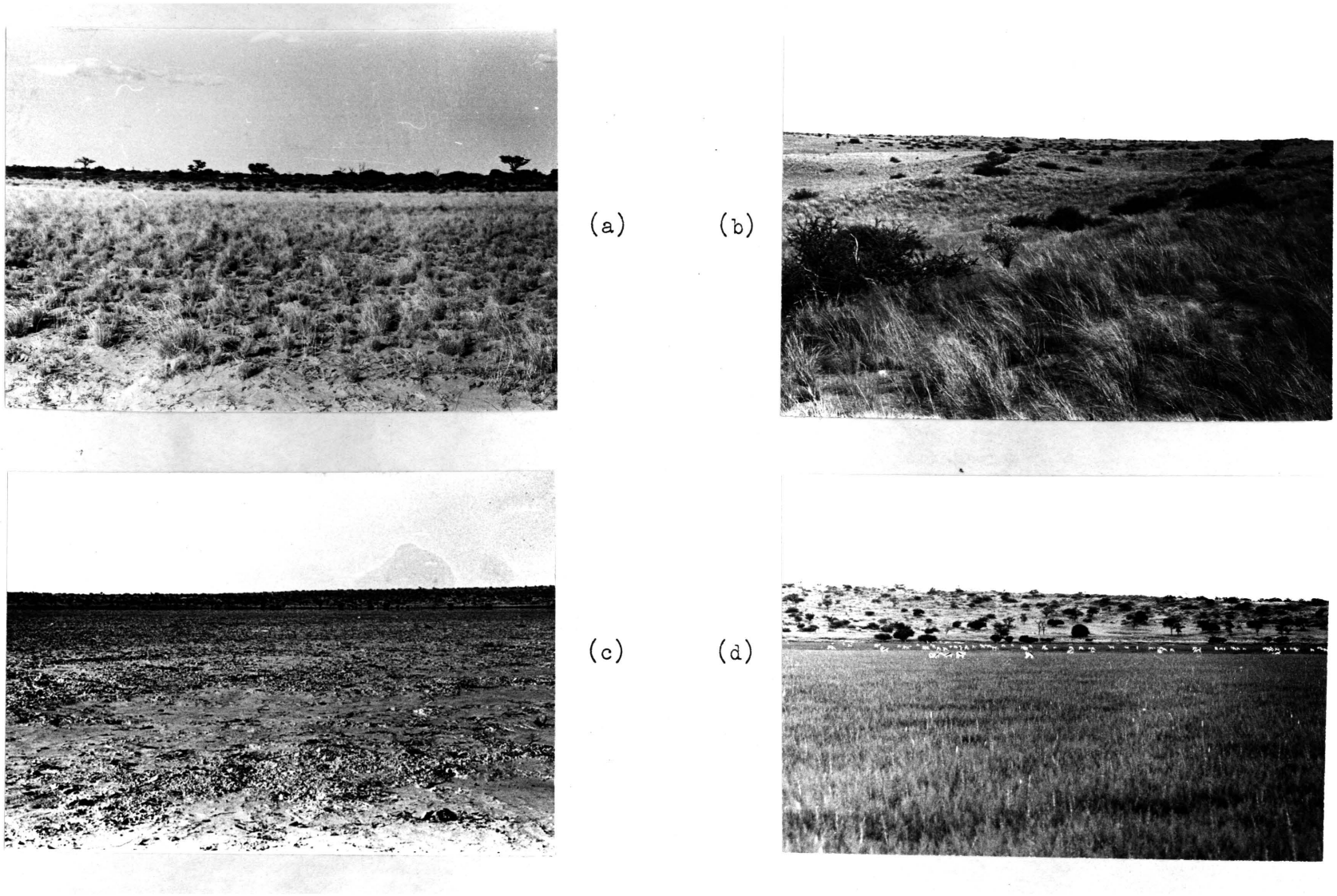


Figure 4. Habitats in the southern Kalahari: (a) Stipagrostis obtusa plains, Rooikop. (b) Dune Habitat. (c) Kwang Pan in the dry season, August 1972. (d) Kwang Pan and a herd of springbok (Antidorcas marsupialis) after good rains, February 1976.

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Large carnivores are well represented in the area although none reach a high density. The brown hyaena is the most common carnivore over the entire area, followed by the lion (Panthera leo). A recent census in the Kalahari Gemsbok National Park revealed approximately 140 lions in the area (Mills in prep.).

Appendix A lists the mammals of the area, except for the Insectivora, Chiroptera and small rodents, with a subjective evaluation of the habitat preferences and abundance of each (Smithers 1971 and personal observations).

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CHAPTER 2 : MATERIALS AND METHODS

Introduction

Because of the size of the study area it was impossible to cover all of it in detail and therefore I worked almost exclusively in an area of approximately 2 750 km^2 centered around Nossob Camp in the Kalahari Gemsbok National Park, incorporating portions of both this and the Gemsbok National Park (Fig. 1). The study area contained representative samples of the three basic habitat types of the southern Kalahari: dunes, pans and a dry river-bed (Nossob river) (Leistner 1967).

The project was initiated in April 1972 and continued until the end of July 1976. During this period 38 months were spent in the field (April 1972 - December 1973, December 1974 - August 1975, December 1975 - July 1976), the gaps in field work largely being due to breakdowns in the radio tracking system.

Brown hyaenas, like many wilderness carnivores, are difficult to study and it is only with the development of techniques such as live-trapping and radio telemetry that it has become possible to learn about many aspects of their life histories (Mech 1974). Thus during this study several methods, some entailing the use of specialised equipment, were used.

Statistical treatment of the data was done by using information from Siegal (1956), Bailey (1959) and Du Toit (pers. comm.).

S.C.H. du Toit. Department of Statistics, University of Pretoria, Pretoria, 0002. December 1976.

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Tracking spoor

Description:

From the initiation of the study until December 1973, much time was spent in following brown hyaena tracks in the Kalahari sand. For this purpose a Bushman tracker was employed who would follow the spoor while I followed in a four-wheel drive Land Rover. If another driver was available I would accompany the tracker. Whenever possible the behaviour of the animal was reconstructed from tracks. In this way approximately 1 200 km of spoor were tracked.

Discussion:

This technique has been used extensively in the Kalahari by Eloff (1973 a, b and c) on lions and to lesser extents by Labuschagne (pers. comm.) on cheetahs (Acinonyx jubatus) and Le Riche (pers. comm.) on leopards (Panthera pardus) with a large measure of success. In my study, however, it was not as successful for the following reasons:-

(1) The hyaenas' movements tend to be much more erratic than those of the cats and the tracks are much smaller than a lion's. Thus any disturbance of the spoor, such as caused by strong winds or much rodent activity, made it difficult to follow the spoor. For example, due to disturbance by rodent activity, on 6 June 1973,7 h were spent following a hyaena spoor for only 6,8 km.

(2) When foraging, brown hyaenas usually travel much longer distances than the cats do. The mean distance travelled per night by a brown

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W.J. Labuschagne. Johannesburg Zoological Gardens, Jan Smuts Avenue, Parkview, Johannesburg, 2193. June 1972

E.A.N. le Riche. Kalahari Gemsbok National Park, Private Bag X5890, P.O. Gemsbok Park, 8815. May 1972.

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hyaena was 32,0 km, whereas lions travel an average of 16,0 km per night (Eloff 1973 a), cheetahs 11,5 km (Labuschagne 1970) and leopards 6 - 10 km (Bothma pers. comm.)

(3) Brown hyaenas frequently devour a food item completely, leaving no trace, therefore many food items were missed when tracking spoor.

(4) If a hyaena came into the Nossob river-bed its spoor was usually lost unless it crossed straight to the other side, because the river-bed ground was too hard for a footprint to be made. Thus I had no idea to what extent they were utilising this important habitat.

(5) It was impossible to make accurate observations from spoor on the foraging behaviour of the hyaenas.

Direct observations and radio tracking

Introduction:

For the reasons outlined above I decided to try and collect data by directly observing the animals from a vehicle as was done by Kruuk (1972 and 1976 a) with spotted hyaenas and striped hyaenas respectively, and Schaller (1972) with lions. To get reliable and regular data by this method, therefore, I turned to the use of radio telemetry. The first set used was made by the Electronic Instrumentation Division of the C.S.I.R., Pretoria, South Africa, described by Anderson (1971), but was not successful for a number of reasons:-

(1) Transmitters were unreliable, often breaking down a few hours after being put on an animal. Of eight transmitters that were used only two produced satisfactory results for more than four weeks.

J.duP. Bothma. Eugène Marais Chair of Wildlife Management, University of Pretoria, Pretoria, 0002. August 1977.

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(2) The antenna system, a double yagi, was cumbersome and unsuitable for following a moving animal at night.

(3) The high frequency of the transmitters, approximately 150 MH_z was unsatisfactory for an area like the Kalahari where the undulating dunes do not give the "line of sight" conditions required for such a frequency (Seidensticker, Hornocker, Knight and Judd 1970).

The second radio tracking system obtained was manufactured by the Dav-tron division of Zipperman Company, Minneapolis, Minnesota, U.S.A. These transmitters operated on approximately 27 MH_z and the antenna system utilised a whip and a loop. Eleven transmitters were fitted to various animals between December 1974 and May 1976. Three of these stopped working within a month, two came off the animal within a month of being fitted and a third after four months, two transmitted for six months, one for at least nine months, one was still transmitting after three months at the termination of the study, and the fate of the last was unknown, although it transmitted for at least three months.

The receiver for this latter apparatus ceased functioning in May 1975, and considerable difficulty was experienced in getting it repaired, so that at the termination of the field work it had not been returned. However, in December 1975, a second receiver was obtained. The experience gained from these frustrations proves the necessity of having a reliable radio tracking system backed up by enough spare transmitters, and an additional receiver. In spite of the problems encountered, however, the telemetry equipment proved successful and between December 1974 and July 1976 it was possible to follow individual animals for approximately 2 400 km (750 h) while they were foraging (Fig. 5).

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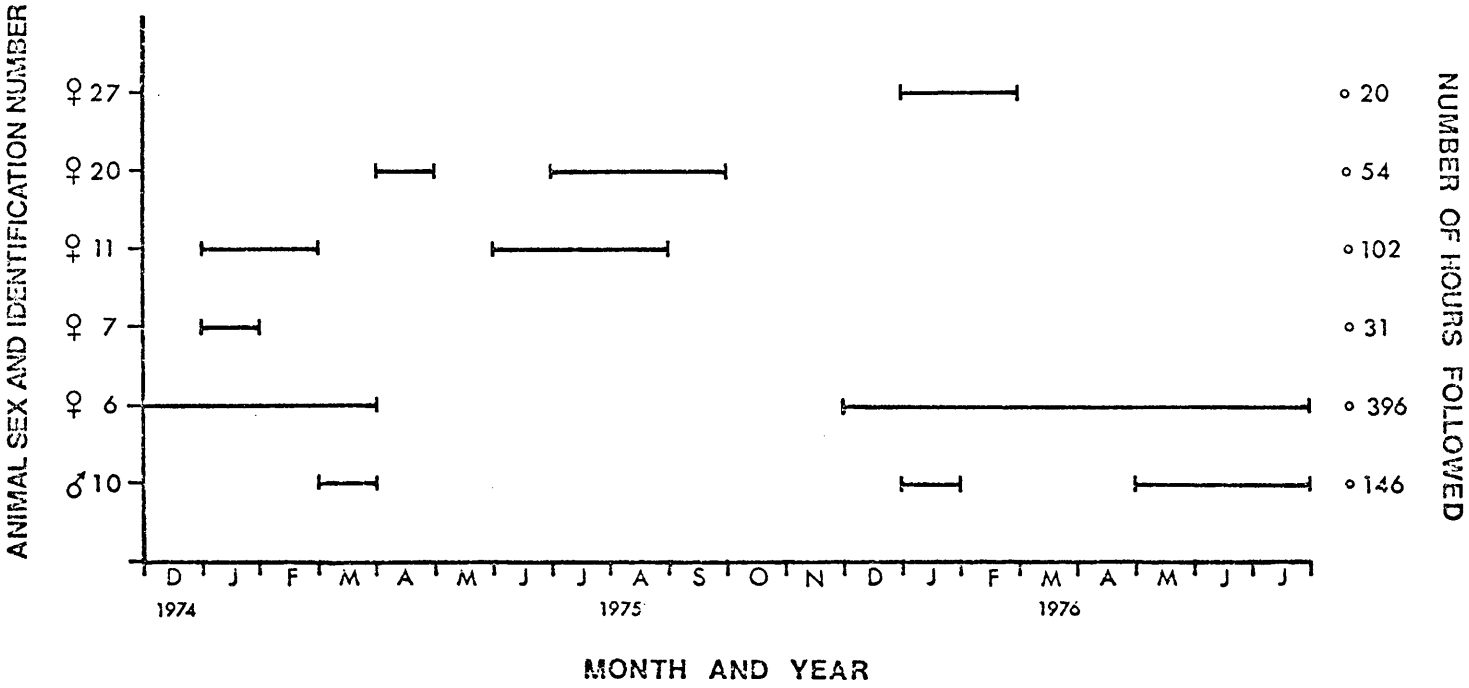


Figure 5. Periods when individual radio-collared brown hyaenas (Hyaena brunnea) were followed in the southern Kalahari; December 1974 - July 1976.

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Description:

Hyaenas equipped with transmitters were located by driving around in a vehicle at night, usually along the Nossob river-bed, but occasionally also through the dunes, and 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 ($\bar{X}$ = 7,4 h). Of 89 nights that hyaenas were followed they were irrevocably lost on eight occasions (9,0 per cent). The range of the radio signal using the whip antenna was 2,5 - 3 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 km.

Females in particular were also located by visiting dens and waiting for them to arrive. This was especially successful if the female had small cubs. Occasionally, if difficulty was being experienced in finding an animal, I would drive to the top of a high dune in what was thought to be a likely area, there to wait for a while with the radio switched on. This was hardly ever successful and the best chance of finding an animal was to keep on driving around.

Visual contact with a hyaena was maintained by the radio collars in the same way as Kruuk (1976 a) did with striped hyaenas. In addition two beta lights (Saunders Roe Development Limited, Hayes, Middlesex, England) were mounted on each collar (Figs. 6 a and 6 b). Beta lights are sealed glass capsules coated internally with a phosphor and filled with tritium gas. The tritium, an isotope of hydrogen, emits low energy beta particles (electrons) which strike the phosphor causing it to emit light of a colour characteristic of the phosphor used, in this study green. The

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half-life of a beta light is between 10 and 20 years. These 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. Similar success with beta lights on European badgers (Meles meles) and red foxes (Vulpes vulpes) has been reported by Kruuk (In litt.). 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. When the hyaena started eating, a handheld spotlight was switched on to identify the food item and to observed 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 behaviour of radio collared animals.

Additional equipment used included a pair of 7 x 50 binoculars, a tape recorder for recording field notes, and a 35 mm SLR camera with standard, 200 mm and 90 - 230 mm zoom lens.

Discussion:

It is difficult to gauge the effect that the vehicle had on the hyaenas that were being followed, and on any other animals that they might interact with. The mere fact that a vehicle was following a hyaena, sometimes with a fair amount of noise, as when accelerating to climb a dune or bumping over a particular piece of rough terrain, must have affected its behaviour, particularly as regards hearing low intensity sounds. Whenever possible I kept as far away from the animals as I could without risking losing information (20 - 30 m), and this was usually much further than the distance at which they showed any reaction to the

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H. Kruuk. Institute of Terrestrial Ecology, Banchory, Kincardineshire, AB3 4BY, Scotland. 12 March 1974.

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vehicle. As far as potential prey was concerned, the general impression gained was that these animals were less disturbed by a vehicle at night without lights on, than they were by one with the lights on, or even than they were by a vehicle during the day, a conclusion also reached by Kruuk (1972) and Schaller (1972). Social encounters between hyaenas and encounters with hyaenas and other predators also did not appear to be affected by my presence.

It must be pointed out that the direct observations data were mainly collected from females, although no significant differences in the foraging behaviour between the male and females were noticed.

Construction and fitting of Dav-tron radio collars and method of mounting beta lights.

The transmitter and battery pack were encased in colrylic (Fig. 6 a). The transmitter formed a loop made of wire braid and was enclosed in nylon webbing which was stitched on either side of the antenna. At both ends of the antenna were two copper plates, each with three pairs of holes 15 mm apart, through which two bolts were inserted when fastening the collar around the animal's neck. The batteries were activated by joining two wires by means of a plug (Fig. 6 a) and these were then encased in Pratley white epoxy putty for protection. Because adjusting the circumference of the loop antenna too much detuned the transmitter, it was necessary to get large-sized collars and then to pad the inside of the loop with thin layers of conveyor belting until the desired fit was obtained for each individual. This also served to strengthen the collar.

A thin aluminium plate 240 x 45 mm, with two holes 32 mm in diameter and 110 mm apart, was fastened to the collar by means of eight bifurcated

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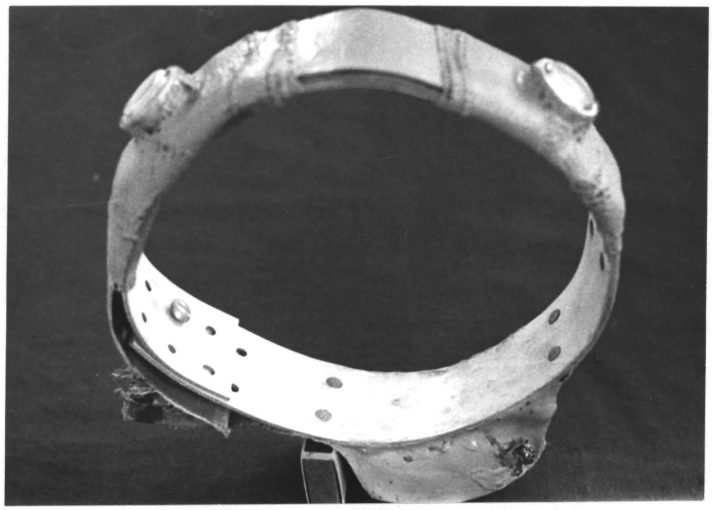
rivets and Pratley white epoxy putty, or 50 mm wide glass fibre tape coated with epoxy resin, and bent to fit the shape of the animal's neck. Through each hole a button-shaped axial pip beta light of 900 microlamberts brightness and 25 mm inside diameter was fitted in an aluminium holder, so that it stood out approximately 14 mm from the surface of the collar and was protected around the sides by the holder (Fig. 6 b). To give the beta light more protection, a thin layer of Pratley clear epoxy glue was applied to the surface of each after it was discovered that two had broken on animals. This did not affect the performance of the light perceptively. To comply with the demands of the Atomic Energy Board whose permission has to be obtained before beta lights can be used, the following words were punched onto the aluminium plate: "Danger Radioactive Return to Department Zoology, University of Pretoria. Gevaar Radioaktief Besorg aan Departement Dierkunde, Universiteit van Pretoria".

Those areas of the collar that were not covered by the aluminium plate were also coated with Pratley clear epoxy glue for durability after the first collar was damaged there and eventually came off. The region where the copper plates were joined was also enclosed with Pratley white epoxy putty. The mean mass of the collars was 1,2 kg (approximately 3,0 per cent of a hyaena's mass).

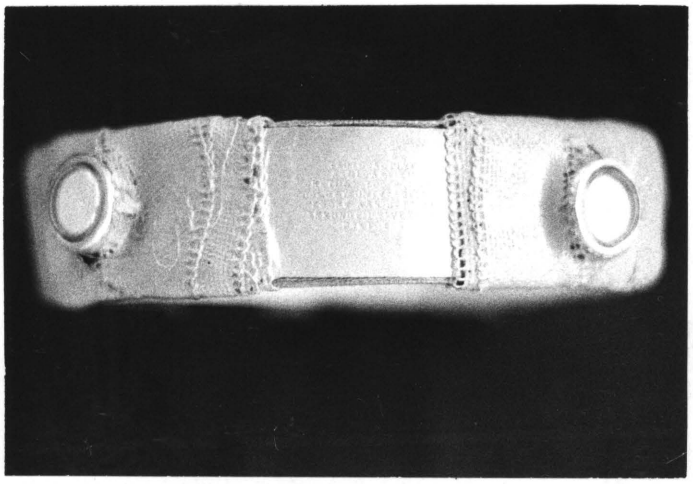
The animals readily took to wearing the collars. On eight occasions I followed an animal for one or two nights immediately on release, after fitting a radio collar, thus giving a good opportunity to gauge the effect that the collar had on the animal. On only one of these occasions did the animal make a determined effort to get rid of its collar, when at 01h00 (7 h after being released) it vigorously shook its head for 5 min.

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(a)



(b)

Figure 6. Radio collar with beta lights attached as used in a study of the ecology and behaviour of the brown hyaena (Hyaena brunnea) in the southern Kalahari and showing: (a) the transmitter and battery pack encased in colrylic and (b) close up of attached beta lights, aluminium plate, beta light holders and glass fibre tape.

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Faecal analysis

From April 1972 until September 1974 I frequently collected brown hyaena faeces (Fig. 7 a) 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. As it is impossible to tell the difference between a spotted and brown hyaena scat with any confidence I only collected those scats that were definitely dropped by a brown hyaena such as around dens, whilst following spoor, and at latrines that were known to be used by brown hyaenas only. Altogether 383 scats were collected.

During the study I observed that cubs regularly defaecated around the dens although adults were never observed to do so. I have assumed, therefore, that all faeces collected at dens belonged to cubs (i.e. animals under 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 at latrines belonged to cubs, it is considered unlikely to have had a significant effect on the results.

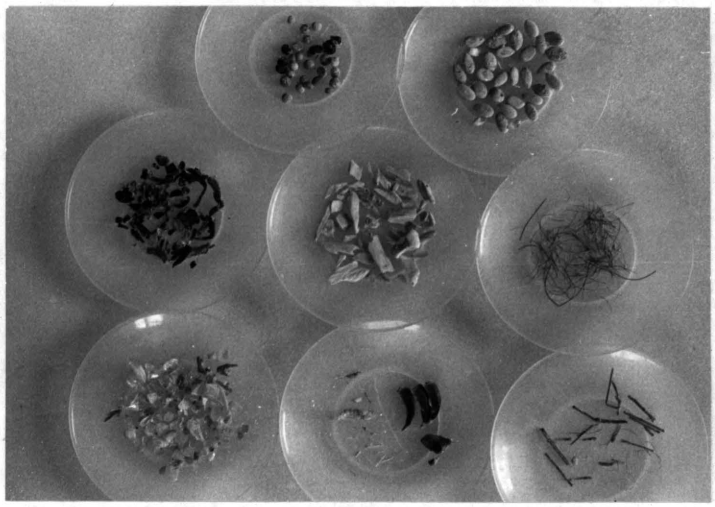
Each scat, when it had dried out, was first broken up by hand. Then it was ground lightly in a mortar and all identifiable objects (Fig. 7 b) extracted with foreceps. What I considered to be an adequate sample of hair was extracted from scats containing a large amount of hair, and where a scat contained a small amount of hair all of it was extracted. 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,

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(a)



(b)

Figure 7. Brown hyaena (Hyaena brunnea) scat (a) and food items from a scat (b) from the southern Kalahari. From left to right: Top row: Grewia pips, tsama pips. Middle row: Beetle remains, bone chips, hair. Bottom row: Reptile scales, pieces of quill from feathers, claws from a small carnivore (these last two in the same dish), pieces of grass.



Figure 8. Food remains at a brown hyaena (Hyaena brunnea) den in the southern Kalahari, November 1972.

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shape and colour, the sample was identified to the species level if possible, or more often was placed into a broad category, for example, small carnivore, antelope class A (hartebeest, springbok or steenbok (Raphicerus campestris), large rodent or rodent like animal (springhare (Pedetes capensis) or hare (Lepus species)). 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 and 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" (Mills pers. comm.).

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, the species was included as occurring in that scat, but 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 (Mansell pers. comm.). Reptile remains were identified as snake or unidentifiable

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M.E.J. Mills. Kalahari Gemsbok National Park, Private Bag X5890, P.O. Gemsbok Park, 8815. November 1976.

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(Sapsford In litt.), bird remains which consisted of small pieces of quills or feathers could not be identified any further and wild fruit pips were identified by macroscopic comparison with known specimens.

A discussion of the results obtained by this method is given in Chapter 3.

Collection of food items around dens

Whenever I visited a den during the day all food items present (Fig. 8) were recorded and the inedible parts, such as horns, skulls and hair, were collected for identification and to prevent double counting. In addition I recorded all items observed to be brought back to the den by the adult hyaenas and of which no remains were found later.

The items collected at five of the dens, as well as all bones present when the hyaenas abandoned these dens, were sent to the South African Museum, Cape Town and have subsequently been sent to the Transvaal Museum, Pretoria. These collections are of interest to palaeontologists and taphonomists (Klein 1975, Mills and Mills 1977).

Capture procedure

Capture from a moving vehicle during the day

Description:

Initially brown hyaenas were caught by tracking a spoor to a day-time

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C.W. Sapsford. Department of Biological Sciences, University of Natal, Durban, 4001. 2 December 1975.

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resting site and then by chasing the animal with a vehicle when it ran off. These chases were over distances varying from 1 - 4 km at speeds of up to 40 km/h. When I got near enough to the animal I fired a dart from a carbon-dioxide powered Cap-Chur pistol (Palmer Chemical and Equipment Co., Atlanta, U.S.A.). After the animal had been hit I would stop for a few minutes to give the drug time to take effect, when we would track the spoor again until the animal was found immobilised.

Results and discussion:

Eight animals, including three that were caught twice, were captured by this method. It is an undesirable and traumatic technique, both for the hyaena and everyone else concerned, and will cause the animal to become shy of the vehicle for several months afterwards, making it difficult to get near it again. Furthermore it contributed to the death of one and possibly two of the animals. Animal 4, an adult male, suddenly turned in front of the vehicle and was run over just as I shot him with the dart. He immediately got up and ran off and when I found him later could detect no visible damage. He never, however, recovered properly and two days later was found drowned in one of the reservoirs of a windmill. Subsequent autopsy of the carcass revealed no evidence of bruising, although it is possible that some sort of brain damage had resulted. The conditions surrounding the death of animal 2 are reported on later. Here the chase with the vehicle is believed to be an indirect cause of death.

Capture by means of a baited drop-door trap

Description:

As an alternative to capture by vehicle, brown hyaenas were captured by using the baited drop-door trap technique (Figs. 9 a and 9 b) of Kruuk (pers. comm.) for striped hyaenas. This method has also been used

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successfully on other large carnivores (Bothma 1973, Bailey pers. comm.).

After gauging the potential of this technique with a modified steel cage, four traps were made. These measured 1 800 x 850 x 775 mm and were made from scrap steel bars 30 mm thick and 90 mm apart. After being used for a short while one modification was made in that the cross bars on the door and the back were taken off (Fig. 9 c). This was done after it was observed that some hyaenas would bite these, especially the bars on the door because it would move up and down easily, sometimes damaging their teeth. The sides, roof and floor of the trap were bolted together and so the whole trap could be taken apart for transportation.

The traps were placed at points throughout the study area where it was thought that hyaenas were likely to pass, such as near a windmill, a latrine or a den. Each trap was positioned next to a large tree so that the back of the trap was against the trunk, preventing the hyaenas from getting at the meat from the back, as they would sometimes try to do, pulling at it with their forefeet and causing the door to fall. When the trunk was too narrow branches were packed around the back of the trap as well (Fig. 9 a). A rope of approximately 20 m long was attached to the trap-door and passed through a pulley tied to a branch in the tree. This was done so that the hyaenas could be released on foot from a reasonable distance without undue disturbance, and the few lions and leopards that were caught, from the safety of a vehicle. Hyaenas were dealt with on foot, as it was thought desirable to keep the vehicle away so that the experience of being caught and darted was not associated with the vehicle, from which most observations during the study were made.

T.N. Bailey. P.O. Box 1809, Soldotna, Alaska, 99669, U.S.A. 7 June 1974.

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To set the trap a large piece of meat was tied to the release mechanism by means of a thin rope and left hanging in the back of the cage. The floor of the cage was covered with sand (Fig. 9 a). Traps were inspected every morning and if an unmarked animal was caught I would walk up to the cage and shoot it with a dart fired from the Cap-Chur pistol (Fig. 9 c). After working with the animal it was placed back in the cage and left to recover. I would then return later to release it in the method described above. When the animal was recovering from the drug the cage was covered with grass and twigs to shelter the animal from the sun and to minimise disturbance (Fig. 9 d). Whenever the traps were not being checked any spare meat was left hanging in them with the door removed, to serve as a trap conditioning process.

Results and discussion:

The traps were set for a total of 497 trap-nights and 80 brown hyaenas (involving 20 individual hyaenas), four lions and two leopards were caught. In addition one brown hyaena was caught in one of the traps when attempts were being made to use them to catch black-backed jackals (Canis mesomelas) (Ferguson pers. comm.). Thus 21 individual hyaenas were caught by trapping of which 12 were males and nine were females.

The overall success rate achieved in 497 trap-nights, therefore, was one brown hyaena per 6,2 trap-nights (16,1 per 100 trap-nights) and one unmarked hyaena per 24,9 trap-nights (4,0 per 100 trap-nights). This was a higher success rate than reported by Hornocker and Bailey (1973) using a similar method for wolverines (Gulo gulo) in Montana, where the capture rate was

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J.W.H. Ferguson. S.A. Lombard Nature Reserve, P.O. Box 174, Bloemhof, 2660. 18 November 1975.

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(a)



(b)



(c)



(d)

Figure 9. Capture of brown hyaenas (Hyaena brunnea) by means of a baited drop-door trap in the southern Kalahari: (a) Set trap with meat hanging at the back. Note the branches packed around the back to prevent hyaenas from getting at the bait. (b) Brown hyaena entering trap. (c) Shooting dart with Cap-Chur pistol. (d) Trap enclosed with grass to protect recovering hyaena from sun and to minimise disturbance.

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one per 49 trap-days, and by Bailey (in prep.) for leopards in the Kruger National Park, where it was one per 22 trap-nights. It was not, however, as high as that reported by Piekielek and Burton (1975) for black bears (Ursus americanus) in California, where one bear was caught per 3,7 trap-nights and one unmarked bear per 5,0 trap-nights.

Table 5 shows the number of times that each individual hyaena was caught and illustrates the large amount of variation in the propensity for different individuals to go into the traps as, except for the cases of some subadult males which may be nomadic (personal observations), all the animals probably encountered the traps with more or less the same frequency. This is an important consideration when evaluating the trapability of individuals (King 1975). Animal 8, for example, was caught in September 1973 and was seen regularly in the area for the rest of the study, yet he was never caught again, and there were other mature animals in the study area that were never caught. Animal 11, an adult female, on the other hand, was extremely trapable and the distribution of the traps even influenced her movements; on several occasions she was observed walking directly from her day-time resting site to a trap. Thus, a drawback for the study was the fact that certain individuals whose radio collars I wished to replace were not easily recaught, and it often took several weeks before they were recaptured.

Table 6 shows the variation in trapping success at different times during the intensive trapping campaigns of the study. Initially, as would be expected, several unmarked animals were caught fairly quickly, but as the study progressed, fewer and fewer were caught. During the winter of 1975 the overall trapping success was at its highest, mainly due to the fact that certain individuals were caught repeatedly, but in early 1976 it dropped off. This was because for some of the time I was trying to

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Table 5. Number of times individual brown hyaenas (Hyaena brunnea) were caught in baited drop-door traps in the southern Kalahari; January 1973 - March 1976.

IDENTIFICATION NUMBER	SEX	AGE AT FIRST CAPTURE	DATE OF FIRST CAPTURE	NUMBER OF TIMES TRAPPED
27	Female	Subadult	2 June 1975	12
11	Female	Adult	14 January 1975	10
22	Male	Large cub	14 August 1975	9
7	Female	Old adult	17 September 1973	8
15	Male	Adult	1 June 1975	6
6	Female	Young adult	6 February 1973	5
20	Female	Adult	25 April 1975	5
21	Male	Large cub	13 August 1975	5
14	Male	Adult	29 May 1975	4
10	Male	Adult	23 March 1975	2
13	Male	Subadult	5 February 1975	2
16	Female	Adult	28 August 1975	2
23	Female	Large cub	15 August 1975	2
24	Female	Adult	19 August 1975	2
8	Male	Adult	3 September 1973	1
9	Male	Subadult	19 December 1974	1
17	Male	Subadult	18 November 1974	1
18	Male	Subadult	26 May 1975	1
19	Male	Adult	3 May 1975	1
25	Female	Subadult	27 December 1975	1
26	Male	Subadult	27 March 1976	1

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Table 6. Success rate in trapping brown hyaenas (Hyaena brunnea) in the same area of the southern Kalahari at different times; December 1974 - April 1975, May 1975 - September 1975, December 1975 - March 1976.

TRAPPING PERIOD	NUMBER OF TRAP-NIGHTS	NUMBER OF UNMARKED HYAENAS CAUGHT	NUMBER OF MARKED HYAENAS CAUGHT	TOTAL NUMBER OF HYAENAS CAUGHT	NUMBER OF HYAENAS CAUGHT PER 100 TRAP-NIGHTS	NUMBER OF UNMARKED HYAENAS CAUGHT PER 100 TRAP-NIGHTS
December 74 - April 75	72	5	5	10	13,9	6,9
May 75 - September 75	171	10	40	50	29,2	5,8
December 75 - March 76	165	2	18	20	12,1	1,2
Total	408	17	63	80	-	-
Mean	-	-	-	-	18,4	4,6

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recapture some individuals difficult to catch, and I had concentrated the traps in a smaller area where, except for animal 22, the other highly trapable individuals were unlikely to go.

The type of bait used is an important consideration when trapping animals. With brown hyaenas, which will eat any type of meat, the only important factor was the age of the bait. As dried out meat does not give off as much scent as fresh or moist, decaying meat does, the former would not be expected to attract hyaenas from so great a distance as the latter, a conclusion also reached by Bothma (1971 c) when trapping black-backed jackals. Table 7 shows the success obtained when using old bait for a period compared with that obtained when fresh bait was used immediately afterwards in the same traps, showing that more hyaenas were caught with fresh bait (Sign test; $p = 0,035$).

Capture by means of darting free ranging animals at night

To circumvent the problem of recapturing trap-shy individuals two animals, 6 and 10, were darted from the vehicle at night when I wished to replace their collars. I attempted this on these two because they were tame and would allow a vehicle to approach to within 6 m, a reasonable distance for a shot with the gas pistol. Animal 6 was a female with small cubs and I waited at the den until she arrived, darting her soon after she had moved off. Animal 10 was a male and more difficult to find. A springbok carcass was put out on a large open pan (Kwang) after having been dragged for a few kilometres either side of the pan. This area was known to be well frequented by this individual, but only on the fifth night did he come to the carcass where he was easily darted. For both these animals the drug used was Ketamine because of its quick-acting properties, which minimise the chance of a darted animal running off and being lost. For

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Table 7. Trapping success obtained with brown hyaenas (Hyaena brunnea) using old bait for a period and then fresh bait in the same traps in the southern Kalahari, 1975.

OLD BAIT				FRESH BAIT			
Trapping period	Number of trap-nights	Number of hyaenas caught	Number of hyaenas caught per 100 trap-nights	Trapping period	Number of trap-nights	Number of hyaenas caught	Number of hyaenas caught per 100 trap-nights
5- 6 Jan.	9	0	0,0	7- 8 Jan.	10	2	20,0
14-19 Feb.	15	0	0,0	20 Feb.	4	1	25,0
2-14 May	14	1	7,1	15-25 May	17	1	5,9
26-28 May	8	0	0,0	29 May-1 Jun.	18	9	50,0
15-16 Jun.	8	2	25,0	17-20 Jun.	15	4	26,7
31 Jun.-1 Jul.	10	4	40,0	2 Jul.	5	2	40,0
22-23 Aug.	9	3	33,3	24-28 Aug.	16	7	43,8
5-11 Sep.	26	5	19,2	12 Sep.	4	1	25,0
14-21 Dec.	28	1	3,6	22-29 Dec.	29	9	31,0
Total	127	16	-		118	36	-
Mean	-	-	14,2		-	-	29,7

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a short while after capture these two individuals were relatively wary of the vehicle, but they soon settled down again.

Immobilisation

During the study, brown hyaenas were immobilised 47 times (27 individuals), using Sernylan (phencyclidine hydrochloride) on 21 occasions, Ketamine hydrochloride on 18 occasions, and a combination of both on eight occasions. Sernylan was used when I was fitting a radio collar on an animal because of the longer effect of the drug, or when no Ketamine was available. Ketamine was used when I was merely clipping the animal's ears for identification purposes (Mills in prep.). A suitable tranquiliser was used in all but two of the cases; Combellem 41 times and acetyl promazine four times. On all occasions the drug was first administered by means of a dart fired from a Palmer Cap-Chur pistol, shot usually into the haunch or occasionally into the neck or shoulder, and booster doses were administered with a syringe and needle.

Sernylan

The first four animals which were caught received an excessive dosage of Sernylan through inexperience (Table 8). The effect of these heavy dosages gave rise to serious convulsive seizures, choking and salivation, and even 24 h after being darted the animals were still most unsteady. Three of them recovered completely from the experience even though, in addition to the high dosages, they were caught by the unsatisfactory method of being chased by the vehicle as outlined earlier. The fourth (animal 2), an adult female which received 1,6 mg/kg, was first attacked by a leopard and then by six spotted hyaenas when she was still under the influence of the drug, 28 h after being darted. She died as a result.

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Table 8. Dosage rates and reaction times for brown hyaenas (Hyaena brunnea) immobilised with Sernylan (Phencyclidine hydrochloride) in the southern Kalahari: April 1972 - July 1976.

ANIMAL'S NUMBER	SEX	AGE	MASS (KG)	DOSAGE OF SERNYLAN (MG)	TRANQUILISER USED	DOSAGE OF TRANQUILISER (MG)	ADDITIONAL DOSAGE OF SERNYLAN (MG)	TIME (H) OF ADDITIONAL DOSAGE OF SERNYLAN AFTER FIRST DART	TOTAL SERNYLAN (MG)	DOSAGE RATE OF SERNYLAN (MG/KG)	TIME (MIN) OF ATAXIA AFTER FIRST DART	TIME (MIN) RECUMBANT AFTER FIRST DART	TIME (MIN) TRACTABLE AFTER FIRST DART	TIME (H) OF FIRST SIGNS OF RECOVERY AFTER FIRST DART	TIME (H) AMBULENT AFTER FIRST DART	TIME (H) FULLY RECOVERED AFTER FIRST DART
1	♂	Large cub	24,4	80	Combellem	0,20	0	-	80	3,3	6	6	7	7,50	26,00	>26,00
2	♀	Adult	38,2	80	Combellem	0,20	0	-	80	2,1	?	?	?	7,00	19,00	>27,00
3	♂	Large cub	29,3	40	Combellem	0,20	0	-	40	1,4	?	5	5	6,50	18,00	>28,00
4	♂	Adult	42,2	40	Combellem	0,20	15 15 20	3,33 4,33 10,00	90	2,1	?	10	15	3,00	3,25	?
2	♀	Adult	38,2	40	Combellem	0,15	20	1,00	60	1,6	?	41	50	9.00	11,00	*
4	♂	Adult	42,2	25	Combellem	0,15	0	-	25	0,6	10	12	15	6,00	8,00	**
5	♀	Adult	36,8	25	Combellem	0,15	0	-	25	0,7	?	?	45	3,00	?	<30,00
6	♀	Young adult	40,0	30	Combellem	0,15	0	-	30	0,8	15	20	25	4,00	4,50	>12,00
7	♀	Old adult	?	30	Combellem	0,20	0	-	30	?	15	39	50	?	3,50	?
8	♂	Adult	40,0	35	Combellem	0,20	0	-	35	0,9	5	6	6	?	?	>21,00
1	♂	Sub=adult	38,2	35	Combellem	0,20	0	-	35	0,9	?	?	33	?	?	?
9	♂	Sub=adult	35,0	25	Combellem	0,50	0	-	25	0,7	3	7	10	3,00	?	>24,00
7	♀	Old adult	28,0	30	Combellem	0,50	0	-	30	0,9	5	17	21	5,00	?	50,00
10	♂	Adult	37,3	35	Combellem	0,45	0	-	35	0,9	15	25	30	?	?	50,00
11	♀	Adult	35,5	25	Combellem	0,50	0	-	25	0,7	20	22	26	?	?	<30,00
12	♂	Adult	36,5	25	Combellem	0.50	0	-	25	0,7	10	30	45	?	?	?
13	♂	Sub=adult	34,1	20	Combellem	0,50	0	-	20	0,6	8	11	30	?	?	<24,00
14	♂	Adult	39,5	20	Combellem	0,50	0	-	20	0,5	8	15	38	?	?	<24,00
11	♀	Adult	37,9	10	Combellem	0,30	20	1,25	30	0,8	?	?	?	?	?	<26,00
15	♂	Adult	42,9	20	Combellem	0,50	10	1,00	30	0,7	10	65	67	2,66	?	<20,00
10	♂	Adult	37,3	20	Combellem	1,00	0	-	20	0,5	22	27	34	?	?	>36,00

Notes. Overlap in animal's number occurs if same individual immobilised more than once. * Animal killed by spotted hyaena. ** Animal died.

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The heavy dosage of Sernylan, the exhaustive chase before being caught and the fact that she was heavily pregnant all could have contributed to her reaction to the drug. Furthermore, during the day she had lain in the hot October sun for 2 h before I was aware of the fact and her temperature had risen to 41,6° C. The other animal to receive an excessive dosage was animal 4 which received 90 mg (2,1 mg/kg) over a 10 h period, but he recovered completely.

Four individuals received dosages of 0,9 mg/kg. Two of these (animals 7 and 10) had not recovered completely when they were released 30 h later. They were followed and were unsteady on their feet, occasionally stumbling into bushes, standing for long periods looking in one direction and giving the impression of being disorientated. It was not until approximately 50 h after being darted that they had completely recovered. A third individual (animal 8) was released 21 h after being darted (i.e. the next morning) and he ran off unsteadily. The fourth (animal 1) escaped from the cage sometime during the night.

All the other animals received dosages of 0,8 mg/kg or less and had recovered fully on being released, with the exception of animal 4 (the second time he was caught), which was the other fatality referred to earlier. This was usually about 30 h after the first dart except in the case of animal 10, who had not fully recovered after 36 h, but had after 46 h when he was released. Pienaar, Le Riche and Le Roux (1969) record recovery times of 10 h for hyaenas (brown and spotted) immobilised with 0,7 - 1,0 mg/kg which is much shorter than was observed in this study (Table 8). This may be because of differences in interpretation of recovery. An animal may be able to walk off some distance and be regarded as having recovered, but longer observation will show that it is still under the influence of the drug and is not in full command of its senses.

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Success was experienced in this study with combining Sernylan and Ketamine (Table 9). The animals were initially immobilised with a low dosage of Sernylan (approximately 0,6 mg/kg) and then, if they became inconvenient to work with, were injected with small booster dosages of Ketamine.

Ketamine

Animals immobilised with Ketamine received dosages varying between 9,7 and 26,8 mg/kg, depending on how long it was necessary to keep them immobilised (Table 10). Although complete data are not available, the indications are that the time to full recovery for Ketamine was considerably less than for Sernylan. The mean time for brown hyaenas to show the first signs of recovery after the first dosage for Ketamine was 0,96 $\pm$ 0,1 h, compared with 4,7 $\pm$ 0,2 h for Sernylan ($d = 5,39$; $df = 10$; $p < 0,01$). Smuts (1973) and Smuts, Bryden, De Vos and Young (1973) report much more rapid recovery for lions, leopards, cheetahs and spotted hyaenas immobilised with Ketamine than those immobilised with Sernylan.

Advantages and disadvantages of the two drugs

Smuts (1973), Bertram (1976) and Bertram and King (1976) have all pointed out the disadvantage of the prolonged anaesthesia reaction of Sernylan. If, however, the animals are allowed to recover in a suitably protected enclosure as suggested by Pienaar et al. (1969) and as done in this study, this problem is alleviated. The advantage of Sernylan is that it is far cheaper to use, especially if prolonged anaesthesia is desired. Ketamine is an ideal drug for short duration immobilisation and also has the advantage of being quicker to act than Sernylan. The mean induction period until animals became recumbant for Ketamine was 4,5 $\pm$ 0,05 min

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Table 9. Dosage rates and reaction times for brown hyaenas (Hyaena brunnea) immobilised with Sernylan (Phencyclidine hydrochloride) (initial dart) and Ketamine hydrochloride (booster injections) in the southern Kalahari; April 1972 - July 1976.

ANIMAL'S NUMBER	SEX	AGE	MASS (KG)	DOSAGE OF SERNYLAN (MG)	TRANQUILISER USED	DOSAGE OF TRANQUILISER (MG)	ADDITIONAL DOSAGE OF SERNYLAN (MG)	TIME (H) OF ADDITIONAL DOSAGE OF SERNYLAN AFTER FIRST DART	BOOSTER DOSAGE OF KETAMINE (MG)	TIME (H) BOOSTER DOSAGE OF KETAMINE ADMINISTERED AFTER FIRST DART	TOTAL SERNYLAN (MG)	DOSAGE RATE OF SERNYLAN (MG/KG)	TOTAL KETAMINE (MG)	DOSAGE RATE OF KETAMINE (MG/KG)	TIME (MIN) OF ATAXIA AFTER FIRST DART	TIME (MIN) RECUMBANT AFTER FIRST DART	TIME (H) TRACTABLE AFTER FIRST DART	TIME (H) OF FIRST SIGNS OF RECOVERY AFTER FIRST DART	TIME (H) AMBULENT AFTER FIRST DART	TIME (H) FULLY RECOVERED AFTER FIRST DART
20	♀	Adult	37,0	20	C	0,5	10	3,47	50	2,80	30	0,8	50	1,7	8	?	0,55	3,47	?	30
6	♀	Adult	37,1	25	C	0,5	-	- -	200 150 150	2,12 2,53 5,76	25	0,7	500	13,5	7	12	0,28	2,12	?	30
11	♀	Adult	35,5	20	C	0,5	-	-	200 100	0,88 2,25	20	0,6	300	8,5	8	18	0,92	?	?	30
27	♀	Sub-adult	37,0	20	C	0,5	5	0,62	300	1,13	25	0,7	300	8,1	14	54	1,18	1,90	?	30
27	♀	Sub-adult	37,0	20	C	1,0	-	-	200	1,00	20	0,5	200	5,4	?	?	1,03	2,75	4,25	30
6	♀	Adult	37,1	20	C	1,0	-	-	60 100 100	0,75 1,00 1,33	20	0,5	260	7,0	24	39	0,83	1,33	?	30
27	♀	Sub-adult	37,0	25	C	1,0	-	-	200 200	1,27 2,05	25	0,7	400	10,8	48	78	1,33	2,05	5,00	30
6	♀	Adult	37,1	30	C	0,5	-	-	500	1,65	30	0,8	500	13,5	?	?	?	?	?	30

Notes. Overlap in animal's number occurs if same individual immobilised more than once. C = Combellem.

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Table 10. Dosage rates and reaction times for brown hyaenas (Hyaena brunnea) immobilised with Ketamine hydrochloride in the southern Kalahari; April 1972 - July 1976.

ANIMAL'S NUMBER	SEX	AGE	MASS (KG)	DOSAGE OF KETAMINE (MG)	TRANQUILISER USED	DOSAGE OF TRANQUILISER (MG)	ADDITIONAL DOSAGE OF KETAMINE (MG)	TIME (H) OF ADDITIONAL DOSAGE OF KETAMINE AFTER FIRST DART	TOTAL KETAMINE (MG)	DOSAGE RATE OF KETAMINE (MG/KG)	TIME (MIN) OF ATAXIA AFTER FIRST DART	TIME (MIN) RECUMBANT AFTER FIRST DART	TIME (MIN) TRACTABLE AFTER FIRST DART	TIME (H) OF FIRST SIGNS OF RECOVERY AFTER FIRST DART	TIME (H) AMBULENT AFTER FIRST DART	TIME (H) FULLY RECOVERED AFTER FIRST DART
16	♀	Large cub	-	300	Combellem	0,20	-	-	300	-	?	3	3	0,73	1,05	1,10
10	♂	Adult	37,3	500	Combellem	0,50	-	-	500	13,4	3	4	5	1,88	2,08	?
17	♂	Sub-adult	37,3	200	Combellem	0,40	150 75 200	0,15 0,67 1,07	625	16,8	5	?	15	0,65	?	<9,00
18	♂	Sub-adult	31,0	300	Combellem	0,50	-	-	300	9,7	2	2	3	0,82	?	<7,00
19	♂	Adult	39,0	270	Combellem	0,50	270	0,23	540	13,8	5	9	19	0,98	1,05	?
20	♀	Adult	37,0	500	Combellem	0,50	120	0,32	620	16,8	4	4	21	1,50	?	?
21	♂	Large cub	31,5	250	-	-	100	0,32	350	11,1	3	5	6	?	2,25	?
22	♂	Large cub	28,0	300	-	-	150	0,30	450	16,1	5	8	26	1,12	1,20	?
23	♀	Large cub	31,0	250	Acetylp.	0,40	50	0,25	300	9,7	3	5	7	0,67	1,20	?
24	♀	Adult	37,0	550	Acetylp.	0,80	300	0,63	850	23,0	?	?	8	0,63	?	?
16	♀	Sub-adult	38,0	500	Acetylp.	0,50	150 200	0,32 0,40	850	22,4	2	?	?	1,15	?	?
7	♀	Old adult	31,1	330	Acetylp.	0,50	-	-	330	10,6	2	4	5	0,67	1,37	?
16	♀	Adult	38,0	400	Combellem	1,00	-	-	400	10,5	3	5	7	0,62	0,65	?
25	♀	Sub-adult	-	450	Combellem	0,50	200 150	0,38 0,62	800	-	8	27	32	?	?	?
26	♂	Sub-adult	33,5	600	Combellem	0,50	-	-	600	17,9	2	3	4	0,92	?	?
10	♂	Adult	37,3	600	Combellem	1,00	-	-	600	16,1	?	?	4	?	?	<9,00
10	♂	Adult	37,3	600	Combellem	1,00	400	1,25	1000	26,8	1	2	4	1,13	?	?
6	♀	Adult	37,1	550	Combellem	1,50	-	-	550	14,8	?	?	2	?	?	?

Notes. Overlap in animal's number occurs if same individual immobilised more than once. Acetylp. = Acetylpromazine.

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as opposed to 19,1 $\pm$ 0,51 min for Sernylan ($d = 9,650$; $df = 21$; $p < 0,01$). This is an advantage when free ranging animals are darted, especially at night, as they are not then nearly so easily lost if they run away.

The new drug Cl - 744 (Parke Davis) appears to be a satisfactory compromise between Sernylan and Ketamine (Bertram and King 1976, Smuts pers. comm.), but has yet to be tested on brown hyaenas.

G.L. Smuts. Department of Nature Conservation, Private Bag X404, Skukuza, 1350. August 1976.

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CHAPTER 3 : DIET

Introduction

The little that is known about the diet of the brown hyaena indicates that it exploits a wide variety of food sources. Along the west coast of southern Africa it is reported to subsist mainly on the remains of marine animals such as crabs, fish, birds, whales, porpoises and seals which have been cast up on the sea-shore (Sclater 1900, Shortridge 1934, Roberts 1954, Mansell pers. comm.). Inland in South West Africa it feeds on offal of all descriptions, the injured and new-born of small and medium-sized animals, reptiles, the young and eggs of ostriches and other ground-nesting birds, locusts, and probably fruits and berries (Shortridge 1934). Roberts (1954) cites observations of a brown hyaena eating a Cape fox (Vulpes chama) in Etosha Pan and a black-backed jackal in the central Kalahari. In north-western Botswana, Smithers (1971) found the remains of a lechwe (Kobus leche) and the pulp and pips of a melon in one stomach, and in another from the south-west, the remains of a spotted hyaena which had been used as bait. Stevenson-Hamilton (1947) found the remains of impala (Aepyceros melampus), baboons (Papio ursinus), cheetah, guinea fowl (Numida meleagris) and a boomslang (Dispholidus typus) at a brown hyaena den in the Kruger National Park, as well as bushbuck (Tragelaphus scriptus) and water tortoises (Stevenson-Hamilton 1942, In: Pienaar 1969). From the same area Pienaar (1969) lists a number of mammals that brown hyaenas have been reported eating, the most common being kudu (Tragelaphus strepsiceros), impala and waterbuck (Kobus ellipsiprymnus), but including most of the ungulates found in this area as well as aardvark (Orycteropus afer).

A more detailed study of the brown hyaena's diet was done by Skinner

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(1976) in various areas of the Transvaal, where cattle (known to be carrion), impala, steenbok and rodents were the most common remains found in faeces and around dens. Skinner's list also includes several other herbivores as well as baboon, aardwolf, mongoose, caracal (Felis caracal), black-backed jackal, domestic cat (Felis catus) and dog (Canis familiaris) and the seeds of several wild fruits. He mentions watermelons and ostrich eggs as being eaten by them as well.

Results

In this section, after presenting the food data collected during the study, an evaluation of the four techniques used to obtain these data is given. The rest of the chapter is devoted to a more detailed analysis of the food data and to a discussion on the diet of the brown hyaena in the southern Kalahari.

Tracking spoor:

Table 11 lists the food items eaten by brown hyaenas which I found by tracking spoor. It shows the catholic nature of the hyaenas' diet, that much of their food is scavenged and that fruits are important.

Direct observations:

Table 12 lists the food items that brown hyaenas were directly observed to be eating. This table shows a wider range of food items than is shown in Table 11, as well as observations on brown hyaena kills, but Table 12 has a large "Unidentified" category.

Faecal analysis:

These data are presented in Table 13, which shows a similar composition to Table 12 except for a higher incidence of reptiles, insects and small

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Table 11. Food eaten by brown hyaenas (*Hyaena brunnea*) as 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

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Table 12. 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.

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Table 13. 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)
	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.

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Table 14. Food items found at eight brown hyaena (Hyaena brunnea) dens in the southern Kalahari; April 1972 - July 1976.

ITEM	DEN								TOTAL	PER CENT
	1	2	3	4	5	6	7	8		
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
Antbear	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

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mammals and a lower incidence of medium-sized mammals. Table 13 also reflects differences in the diets between adults and cubs.

Remains found at dens:

These data are tabulated in Table 14, where the collections from dens 3 and 7 are the most complete. Dens 2, 3 and 4 were the dens where I collected faeces and it was the cubs from den 3 on which the direct observations were made.

Discussion on the four methods used to analyse the diet

Of the 35 large mammal species inhabiting the study area (Appendix A), the spoor data revealed 10 (28,6 per cent) to be eaten by brown hyaenas, the direct observations data 16 (45,7 per cent) and the faecal analysis and observations at dens data 19 (54,3 per cent) each.

When the food data collected from tracking spoor 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.

The main drawback of the direct observations method was that I was unable to identify many food items (Table 12). Eighty per cent of these were eaten in less than 1 min, whereas only 14,1 per cent of identifiable vertebrate food items and 22,9 per cent of fruits and eggs were (Fig. 10). Moreover, the fact that I 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 (Figs. 44, 45 and 48 c)

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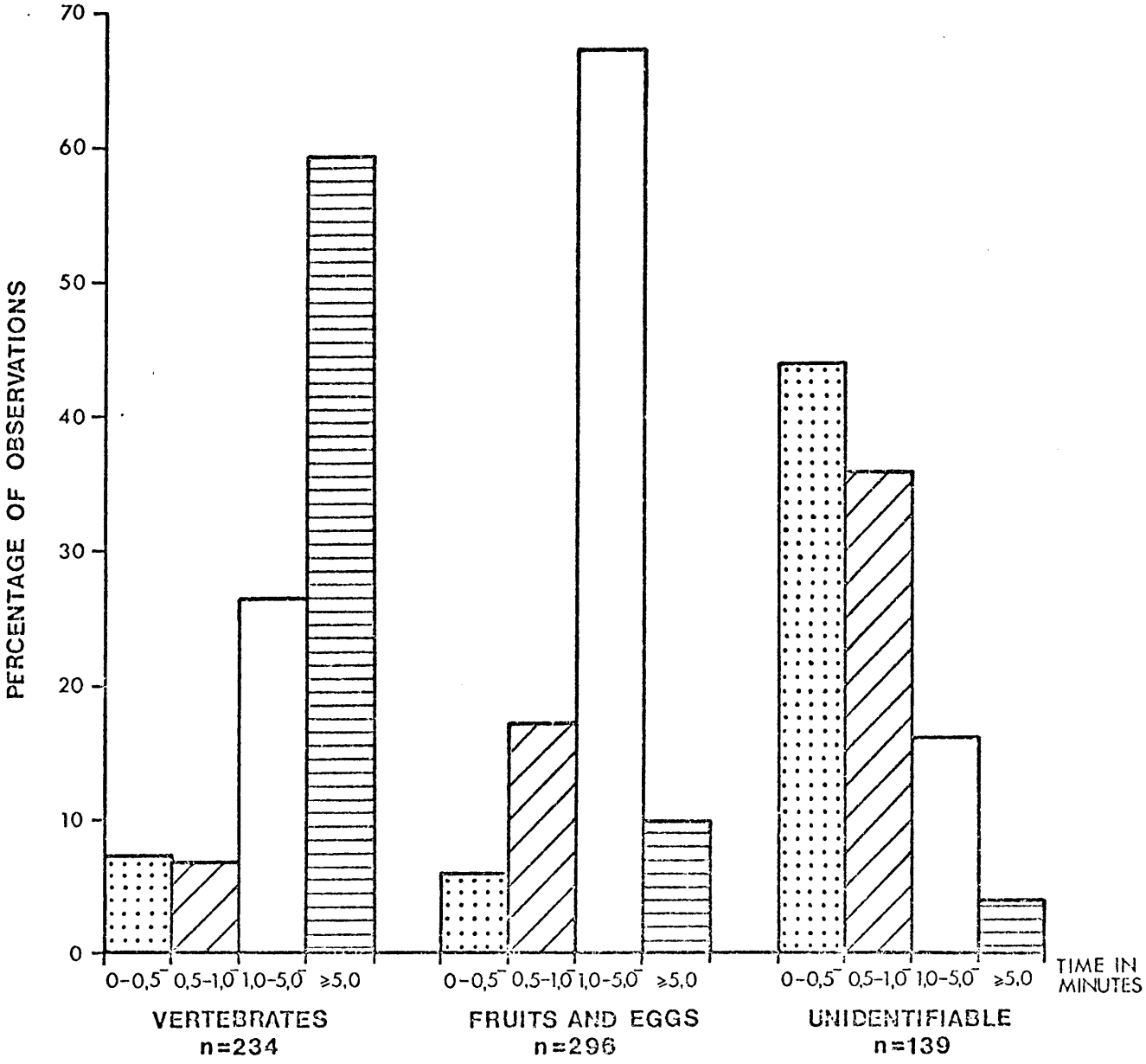


Figure 10. Time taken by brown hyaenas (Hyaena brunnea) to eat various food items in the southern Kalahari; December 1974 - July 1976.

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in the case of eggs and fruits, I assume that they were eating some other type of food. As 60,1 per cent of faeces from adults contained insect remains and 19,8 per cent contained reptile remains, it is likely that these two items (with the exception of Hodotermitidae which I 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 tsama, 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.

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 and by Kruuk (1976 a) 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 I have done (Table 13). 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 in the present study 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.

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Only vertebrate food items containing hair, therefore, were identified in the faecal analysis of my 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 I was 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 that 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 40,2 per cent 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 I suggested earlier that most of the unidentified items were reptiles and insects), there is a significant

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correlation ($r = 0,646$; $df = 8$; $p < 0,05$) (Fig. 11). 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.

In the analysis of food items at dens 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. 12). 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.

Thus it is concluded that a combination of direct observations and faecal analysis portrays an accurate picture of the overall diet of the brown hyaena, although the exact importance of various items is not well established. Faecal analysis has an added advantage in that it can be used for various comparative purposes. The analysis of food items found at dens gives an accurate assessment of the food cubs are brought, although no clues as to their origin are gained. Tracking brown hyaena spoor is a laborious technique, misses many of the smaller food items, yields little information on the amount eaten and cannot be used in the river-beds.

Overall diet

Tables 11 to 14 illustrate the varied nature of the brown hyaena's diet in the southern Kalahari. By virtue of their biomass and frequency (38,5 per cent of all food items observed to be eaten by adults and cubs),

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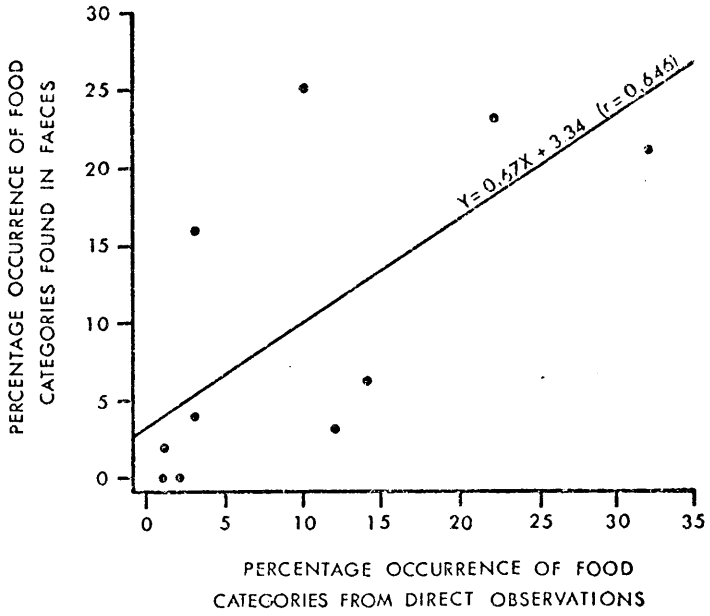


Figure 11. Percentage occurrence of food categories found in faeces versus percentage occurrence of food categories from direct observations of brown hyaenas (Hyaena brunnea) in the southern Kalahari; April 1972 - July 1976.

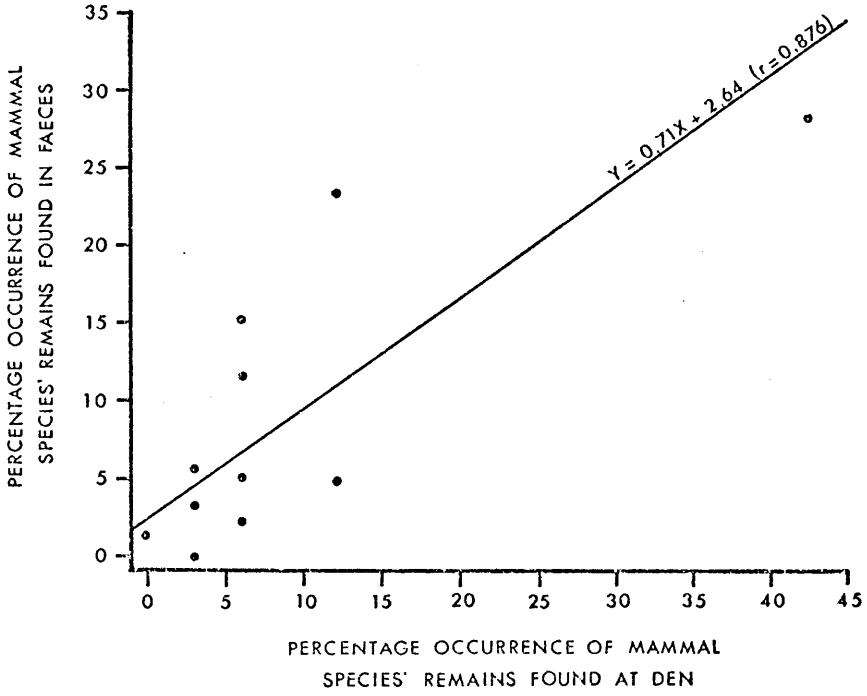


Figure 12. Percentage occurrence of mammal species found in faeces of brown hyaena (Hyaena brunnea) cubs under 10 months old versus percentage occurrence of mammal species remains found at the same cubs' den in the southern Kalahari; April 1973 - October 1973.

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mammal remains are the brown hyaena's most important food and they have been recorded feeding on 25 of the 35 (71,4 per cent) mammals listed in Appendix A, as well as at least three species of domestic mammal. In addition wild fruits and insects are also important and other vertebrates (Fig. 13), birds' eggs, as well as most other edible foods, except herbage, are eaten. An extreme example of the catholic nature of their diet was provided by an old female brown hyaena that was killed in the Kalahari Gemsbok National Park and which had a few pieces of bone, a large buckle (35 x 45 mm) and several pieces of an old leather belt in her stomach (Fig. 14). Brown hyaenas will also eat conspecifics as is illustrated in Fig. 15, where a cub is shown to be eating his dead mother. The manner in which this food was obtained will be discussed later, but for the moment it should be noted that 95,8 per cent 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 13), as is the case in some other carnivores such as the coyote (Canis latrans) (Hawthorne 1972). This is further discussed below.

Vertebrate food

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. For example, in the case of springbok, where 45 out of 50 (90,0 per cent) that were observed to be eaten by hyaenas were eaten in river habitat, which is where the concentrations of springbok occur, and where dens 7 and 8, which were close to a large springbok concentration, had the highest incidence of

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Figure 13. Brown hyaena (Hyaena brunnea) carrying a scavenged secretary bird (Sagittarius serpentarius) to its den in the southern Kalahari.

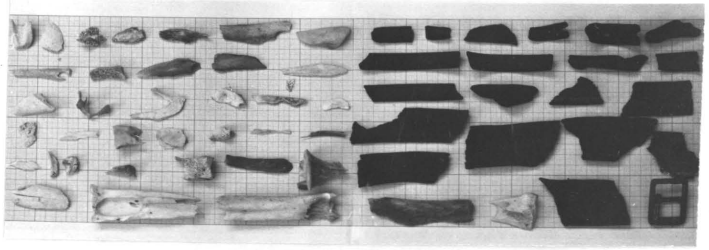


Figure 14. Stomach contents of an old female brown hyaena (Hyaena brunnea), Nossob Camp, southern Kalahari. Note: Bone chips, pieces of an old leather belt and a buckle.



Figure 15. Large brown hyaena (Hyaena brunnea) cub eating its dead mother in the southern Kalahari.



Figure 16. Brown hyaena (Hyaena brunnea) drinking from a puddle of rain water in the southern Kalahari.

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springbok remains (Table 14). 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 that they were when the direction observations were made.

Figure 17 shows how the more common mammal 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 14 suggests that most of these were black-backed jackals or bat-eared foxes (Otocyon megalotis). From Fig. 17 it can be seen that for the most part there is little seasonal variation, the most seasonality occurring in the hartebeest with a peak abundance in March. This is the only one of the more heavily utilised species that tends to be migratory, reaching a peak in and around the Nossob river in late summer, and moving out of the main study area as conditions become drier (Bothma and 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.

Ewer (1973) mentions the importance of palatability when looking at food availability, but points out the paucity in our knowledge of this phenomenon, and several observations in this study support this palatability hypothesis. Once, for example, a brown hyaena stole half an African wild cat (Felis libyca) from a caracal and carried it off for 3,7 km before putting it down. Close by she found a black-backed jackal carcass which had possibly been stored by her, ate it and then moved away leaving the wild cat carcass. On another occasion I found the carcass of a caracal at a den, but it took three weeks for it to disappear, an unusually long time. On a third occasion a hyaena found a fairly old and

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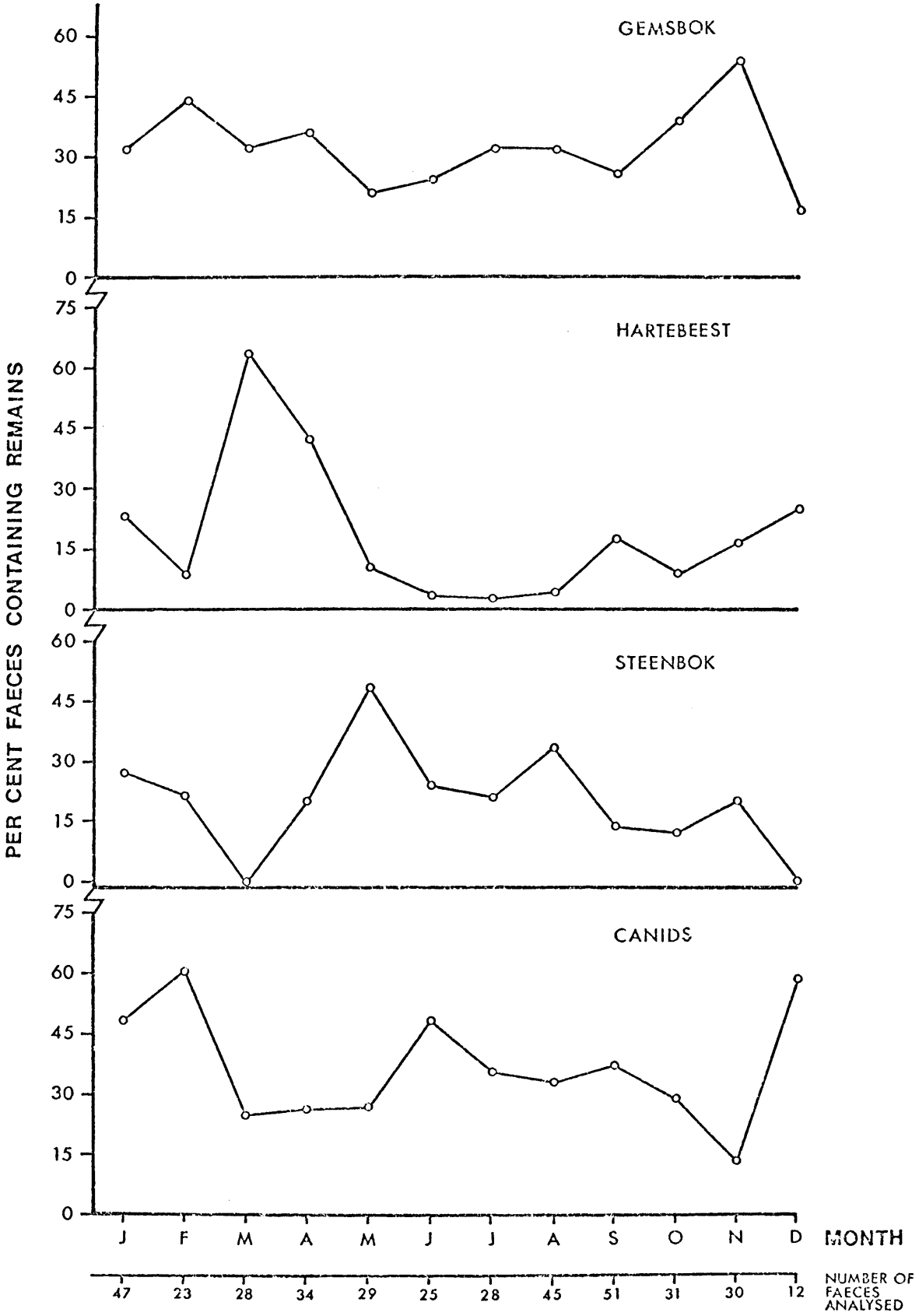


Figure 17. Monthly utilisation of gemsbok (Oryx gazella), hartebeest (Alcelaphus buselaphus), steenbok (Raphicerus campestris) and canids by brown hyaenas (Hyaena brunnea) in the southern Kalahari as determined from faecal analysis; April 1972 - September 1974.

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dry ostrich carcass and sniffed at it for a few minutes before moving on. Later that night she found a fresh hartebeest carcass, which she possibly knew about as she did not appear to locate it by olfactory sense, and ate on it for an hour and a half. Three nights later I was following this same individual when she returned to the same ostrich carcass and this time fed on it for 38 min. Striped polecats (Ictonyx striatus) also might not be regarded as palatable by brown hyaenas as will be discussed later.

The high incidence of carnivores in the diet, particularly canids, is worth noting. Leopards also readily eat canids (Estes 1967, Kruuk and Turner 1967, Schaller 1972, and personal observations) and striped hyaenas appear to eat bat-eared foxes readily (Kruuk 1976 a), but spotted hyaenas do not appear to find jackals palatable (Kruuk 1972, Bearder 1975) and only rarely eat bat-eared foxes (Kruuk 1972).

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 13). This is because adults are more likely to bring back a small mammal carcass than a large one to the den (Table 14), presumably because the cubs' teeth and jaws are not yet sufficiently developed to deal with large bones.

Insects

Table 15 shows the detailed analysis of the insect remains that were found in the hyaena faeces. Coleoptera, especially Tenebrionidae (common ground-living beetles) and Scarabaeidae (dung 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, it seems that others were deliberately

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Table 15. 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

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eaten (see later). The Trogidae, Histeridae and Staphylinidae (Coleoptera) were almost certainly ingested incidentally (Mansell pers. comm.).

Table 13 shows a significant difference between the number of insect remains in faeces from adults compared with faeces from cubs. The two most important groups contributing to this difference are the Tenebrionidae and the Hodotermitidae. Figure 18 shows the distribution of Tenebrionid remains in faeces throughout the year where it can be seen that the peak is reached in March but that they are utilised throughout the year, especially by cubs. The zero figure for December for adults and cubs means little because of the inadequate sample (four scats from adults and eight from cubs). Unfortunately the species of Tenebrionid are unknown; there are some species 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 (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.

Wild fruits

Tsama and gemsbok cucumber

The tsama and the gemsbok cucumber are the two most important fruits eaten by brown hyaenas in the southern Kalahari, Fig. 19 showing how these fruits were utilised throughout the year. Three sources of

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S. Endrödy-Younga. Transvaal Museum, P.O. Box 413, Pretoria, 0001.
December 1976.

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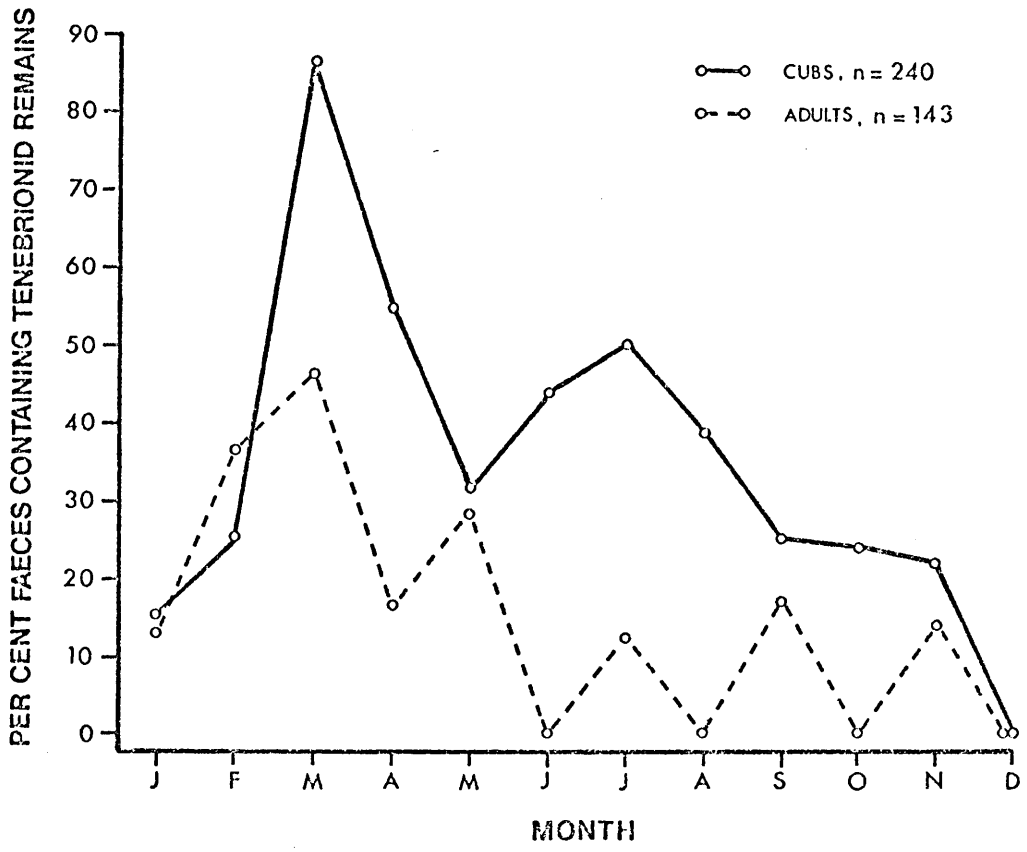


Figure 18. Monthly utilisation of Tenebrionidae by brown hyaenas (Hyaena brunnea) as determined from faecal analysis in the southern Kalahari; April 1972 - September 1974.

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information have been used in compiling this graph: the percentage of faeces with pips in them collected each month from hyaenas over six months old, the number of tsamas and gemsbok cucumbers observed to be eaten for every 100 km hyaenas were followed and the number observed to be eaten for every 100 km hyaenas were tracked. These last two sources of information are compatible and have therefore been combined in Fig. 19. The zero figures for December from faecal analysis and November from tracking spoor and direct observations may be due to the small size of the samples.

From Fig. 19 it can be seen that tsamas were utilised over a longer period than the cucumbers were, with most cucumbers being consumed between April and July, after which few were eaten. The reason is that 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 early in 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 x 10 m, sampled in July 1976, showed that 30 per cent 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 per cent 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

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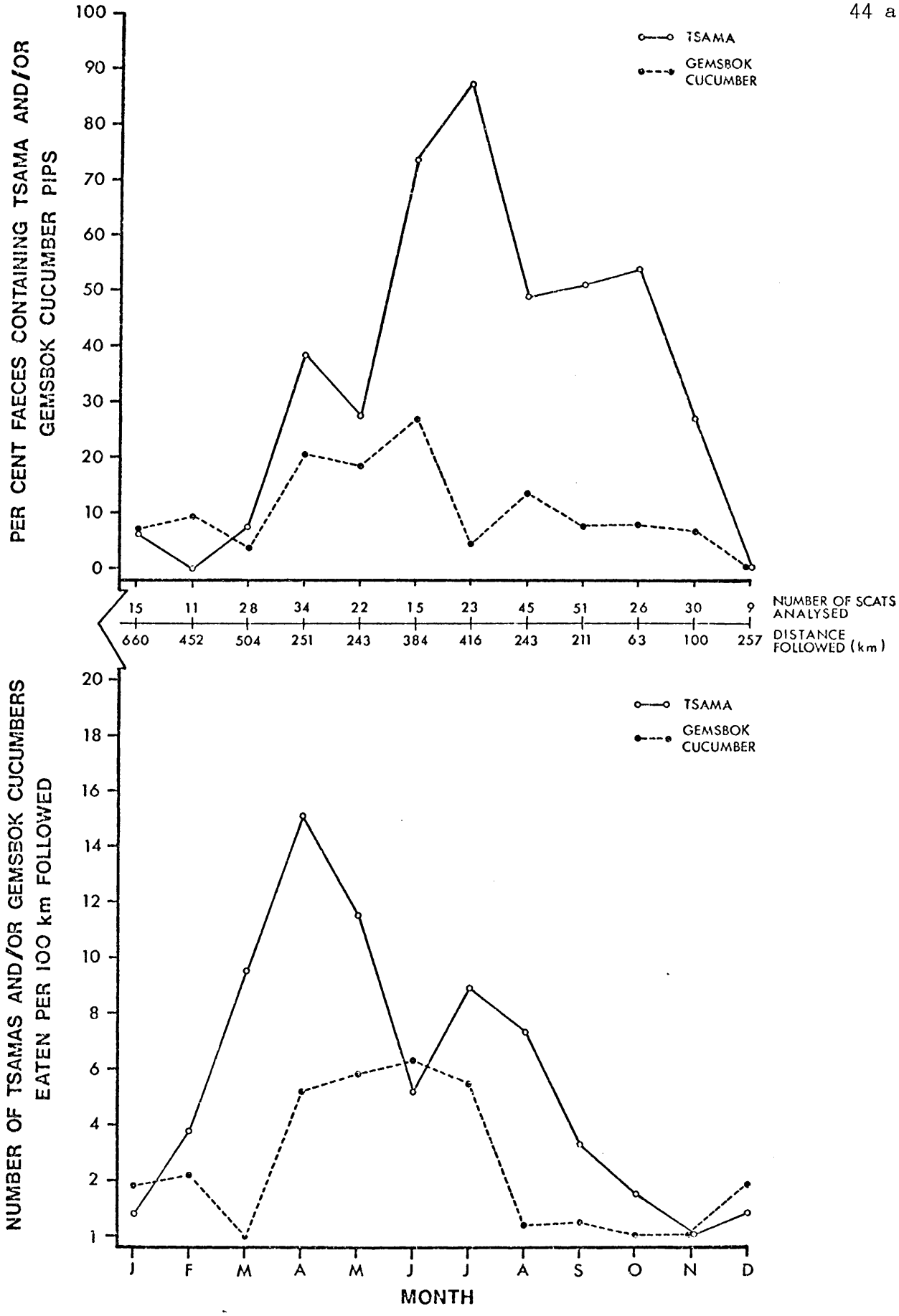


Figure 19. Monthly utilisation of tsamas (Citrullus lanatus) and gemsbok cucumbers (Acanthosicyos naudianus) by brown hyaenas (Hyaena brunnea) in the southern Kalahari; April 1972 - September 1974 (faeces), April 1972 - July 1976 (tracking spoor and direct observations).

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require effective rains at short intervals from about December to April (Leistner 1967) and when these conditions occur, as had happened during this study (Fig. 2), the bulk of the crop becomes available from about March onwards.

Both fruits were abundant during the study, although their relative abundance varied from area to area and the hyaenas living in an area where one dominated ate more of the dominant kind. For example, in the area north of Nossob Camp and east of the Nossob river, tsama patches were 10 times as numerous as cucumber patches were in July 1976, and the hyaenas observed in this area in 1976 ate 10 tsamas for every two cucumbers. In an area to the west of the river, however, gemsbok cucumber patches were far more common than tsama patches were in 1975, although I have no figures from this year to substantiate this, and in 1975 the hyaenas in this area ate one tsama for every six cucumbers.

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 16). Both these fruits do, however, have a high moisture content, the mean of the three tsamas being 95,1 per cent and the gemsbok cucumber containing 91,5 per cent water (Table 16). 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 water 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-

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Table 16. Analysis of some wild fruits which are eaten by brown hyaenas (Hyaena brunnea) in the southern kalahari, Wehmeyer* (pers. comm.).

FRUIT	UNIT OF MEASURE AND COMPONENT																		
	g/100g						kJ/100g	mg/100g								mg/100g			
	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	1090,0	13,9	217,0	4,8	25,9	1093,0	1,49	1,87	71,0	0,06	0,040	2,353	0,0

* A.S. Wehmeyer. National Food Research Institute, C.S.I.R., P.O. Box 395, Pretoria, 0001. December 1976.

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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 (see later). If the mean energy value of a tsama is 532 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 I observed being 18 (discerned from spoor).

Other fruits

The next most important fruits utilised by brown hyaenas are the small berries of Grewia flava (rosyntjiebos). These bushes are well distributed throughout the southern Kalahari and flower in early summer, sometimes before the first rains (Leistner 1967). Figure 20 shows that, except when the bushes are in flower, the fruits are eaten throughout the year by brown hyaenas over six months old, with the peak in June. 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 12).

The wild cucumber (Cucumis africanus) has a similar life cycle to the gemsbok cucumber, although the crop lasts for even a shorter period, but was uncommon in the study area. This 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 (see later). The fruits of Merremia tridentata, a summer annual, are available from the middle of summer and I observed a

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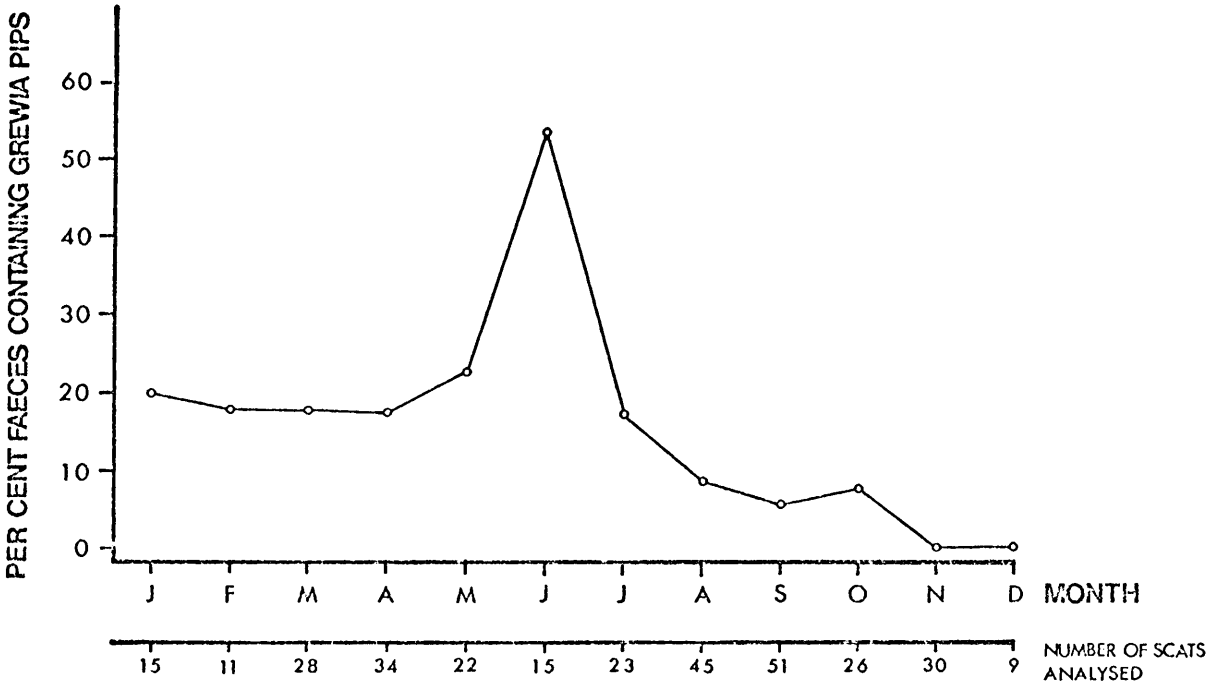


Figure 20. Monthly utilisation of Grewia flava berries by brown hyaenas (Hyaena brunnea) as determined from faecal analysis in the southern Kalahari; April 1972 - September 1974.

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hyaena eating these on three occasions in February 1976.

Brown hyaena cubs eat far fewer fruits than adults do (Table 13), and for the first six months of their lives their intake of fruits is negligible. Only 5 of 74 (6,8 per cent) 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.

Water relations

Brown hyaenas, like all the animals living in the Kalahari, are faced with long periods when there is no water available to them. In the Kalahari Gemsbok National Park, particularly along the dry river-beds, artificial water has been provided, but this is available to a small percentage of the brown hyaena population only. In any case, brown hyaenas survived in the area before any water was provided. Some of these articicial waterholes have highly mineralised water and others have reasonably potable water (Child, Parris and Le Riche 1971, Le Riche pers. comm.). On 13 occasions a brown hyaena was observed to pass within 500 m of a potable waterhole (Nossob, Cubitje Quap or Kwang), actually stopping to drink nine times. One nine occasions one passed a mineralised waterhole (Rooikop, Bedinkt or Seven Pans) but never drank. Thus there was a significant difference in the use of potable and mineralised boreholes by brown hyaenas (Fisher exact probability test; $p = 0,01$), and it seems that these mineralised waterholes are of little or no value to them.

During the rainy season brown hyaenas drink regularly from rain puddles which form on pans and in the river-beds (Fig. 16) and once I got the

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impression that an animal had purposefully gone to a pan in order to drink. In January, February and March 1976 I followed hyaenas for all or part of the night on 30 occasions in the vicinity of the Nossob river when there were many pools of water, and they drank on 17 (56,6 per cent) of these occasions (14 times from a natural pool and three times from an artificial waterhole) for a mean of 2,4 $\pm$ 0,4 min (range 1 - 6,5 min). In May, June and July 1976, when there were no rain pools, I followed the same animals on 25 occasions and they drank six times (24 per cent) at artificial waterholes for a mean of 1,8 $\pm$ 0,4 min (range 1 - 4,5 min) (Binomial; $p = 0,01$). Thus they were drinking significantly more in the wet, hot season than in the cool, dry season, probably because there was more water available to them. Unfortunately I have no comparative data for the hot, dry season.

As has been illustrated earlier, the tsama and gemsbok cucumber provide moisture for brown hyaenas. However, in dry years and even towards the end of wet years these fruits are in short supply when it would be expected that they are needed the most. These times are probably critical for brown hyaenas in the southern Kalahari and it might be that their large home range (Mills 1976 b) ensures, amongst other things, that the optimum number of these moisture holding fruits, which are unevenly distributed, are available to them.

Another way in which moisture is obtained by brown hyaenas is by licking dew off the grass; I observed this on three occasions, but here again this source of moisture is unavailable at the driest time of the year. A similar way of getting moisture was observed in the Kalahari lion by Eloff (1973 c) when during light rain, one lion licked the moisture from the pelage of another.

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The brown hyaena has also evolved several behaviour patterns for keeping cool, thus conserving water. Their nocturnal activity rhythm, habit of choosing the coölest place to rest during the day at the hottest time of the year (see later) and habit of kicking cool sand under their belly (Fig. 27 b), are probably all designed to this end. Furthermore, their long hair, which is thin in summer and thick in winter, probably serves as a protection from solar radiation and helps to slow down the conduction of heat from the environment to the animal. If the hair is well ventilated, moreover, it allows the evaporation of sweat to occur at the base of the hairs so that heat may be drawn from the animal itself (Cloudsley-Thompson and Chadwick 1964). Nevertheless, no data are available on the physiological adaptations of the brown hyaena or any other of the desert-living carnivores to conserving water, and such a study would undoubtedly yield much interesting information.

Consumption

Method:

Two adult females (animals 6 and 20), both suckling cubs, were followed on six occasions for a total of 13 nights, consisting of one period of three nights and five periods of two nights. On four of these occasions the animals were followed after being released from a trap, so that it was known that they had not eaten the previous night and had eaten well, at least 3 kg of meat, skin and bones (the bait) the night before. On the other two occasions the animals had been followed for part of the previous night and there was no indication that they had fed exceptionally well. The mean distance travelled by the hyaenas during these 13 nights was 27,8 km (range 17,4 - 47,7 km) which is close to the mean distance of 32,0 km travelled per night by all hyaenas during the study (see later), suggesting that these were normal nights of foraging for a brown hyaena.

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All food items eaten were recorded and a subjective assessment of the mass of each was made. For carcasses, I took the mean mass of the particular species being consumed from Smithers (1971), or in the case of juveniles an assessment using Smithers' figures, and then gauged how much the hyaena had actually eaten. Bones of various sizes were weighed and the results used as a guideline in assessing the mass of those that the hyaenas were observed eating, after recording each bone's approximate size. To calculate the mean percentage of the edible portion of a tsama, I weighed 10, removed the edible portion of each, and reweighed them. This edible portion was found to be 46,6 per cent. I then took the mean mass of 115 tsamas (1 158 g) and subtracted 46,6 per cent of this mass (540 g) which was then used as the mass eaten for each tsama. Unfortunately no gemsbok cucumbers were available for working out the average percentage of the edible parts and so I have assumed it to be the same as for the tsama. The mean mass of 35 cucumbers was 268 g and the mean mass of the edible portion (46,6 per cent) was calculated as 130 g. Terfezia pfeilii specimens were given an arbitary mass of 20 g as none were available for weighing. The mean mass of the remains of eight eaten ostrich eggs was 265 g (Kemp pers. comm.) and an uneaten one has a mass of approximately 1 000 g (Siegfried and Frost 1974), therefore the mass of the edible portions was taken as 735 g for the calculations. Unidentified small items such as insects and small reptiles were given an arbitary mass of 5 g each, after determining the mass of several different beetles and lizards.

The calculations are based on estimations and there is undoubtedly a

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A.C. Kemp. Transvaal Museum, P.O. Box 413, Pretoria, 0001. December 1976.

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measure of error, although I do not know in which direction or how much. As all the food items are small, however, each error does not significantly change the total biomass of food eaten and I believe that the figure obtained gives a reasonable estimate of the true biomass of food consumed by these brown hyaenas.

Results and discussion:

One hundred and thirty eight items were eaten by the hyaenas during 13 nights (Appendix B), giving a total biomass of 36,48 kg (range 0,23 - 5,89 kg) or 2,8 ± 0,78 kg per hyaena per night (Table 17). This figure is higher than would be expected for a hyaena whose mass is 37 kg (the average of these two individuals) if one considers that spotted hyaenas, which have an average mass (12 males and eight females) of 52 kg in the Serengeti, consume 3 kg of food per day including wastage (Kruuk 1972). The main reason for this is that much of the food eaten by brown hyaenas, such as tsamas and pieces of bone, is of low energy value when compared with the food of the Serengeti spotted hyaenas, which were eating large amounts of fresh meat. In addition, my figure may be higher than the population mean because none of the observations were made during those times when tsamas and gemsbok cucumbers are scarce, and when it would be expected that the daily food consumption rate would be reduced. Also these hyaenas were suckling cubs at the time of observation and this would probably mean that they would need more food. Pregnant and lactating coyotes require approximately 1,5 times the amount of food per day needed by them at other times and by males (Gier 1975).

Many carnivores live under a feast or famine regime (Schaller 1972) and are capable of not only consuming large quantities of meat at a time, but also of going without any food for an extended period. A spotted hyaena in the Serengeti, for example, was observed to eat approximately one

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Table 17. Biomass of food eaten by two lactating adult female brown hyaenas (Hyaena brunnea) in 13 nights in the southern Kalahari as determined from direct observations; January, April and August 1975, January and February 1976.

TYPE OF FOOD	NUMBER EATEN	BIOMASS (KG) EATEN	PER CENT OF TOTAL BIOMASS EATEN
ANIMAL	71	18,68	51,2
Meat, skin and bones	38	16,32	44,7
Ostrich eggs	3	2,21	6,1
Unidentified small items	30	0,15	0,4
VEGETABLE	67	17,80	48,8
Tsama	28	15,12	41,4
Gemsbok cucumber	17	2,21	6,1
Terfezia pfeilii	21	0,42	1,1
Merremia tridentata fruits	1	0,05	0,1
TOTAL	138	36,48	99,9
MEAN	-	2,81	-

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third of its mass in 45 min and another in the Ngorongoro Crater of going without anything to eat for at least five days (Kruuk 1972). In the Soviet Union it has been recorded that a wolf (Canis lupus) went without anything to eat for 17 days (Makridin 1972, In: Mech 1970), and in the southern Kalahari three subadult male lions existed on three porcupines (Hystrix africaeaustralis) and one bat-eared fox, a total of approximately 58 kg, over a period of 10 days (Eloff 1973 b).

Brown hyaenas are also capable of eating large quantities of food quickly, but are rarely given the opportunity to do so. Once I put out the remains of a springbok carcass the mass of which was 23 kg, which two brown hyaenas fed on during the night, leaving only the head of 3 kg. Some of the food, however, had been carried off and stored and I calculated that these two animals had consumed roughly 15 kg between them in 3 h. As far as going without food is concerned, however, when brown hyaenas were followed all night, they always found something to eat, as their feeding habits are such that they usually find some food scraps to feed on. Thus, there is less fluctuation in the mass and volume of the diet of a brown hyaena than there is in most of the other large carnivores.

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CHAPTER 4 : FORAGING BEHAVIOUR

Activity patterns

Methods:

Whenever a hyaena was being followed the number of minutes in each hour that it was active were recorded and expressed as a percentage of that hour. An animal was regarded as being active if it was standing or walking and as inactive if it was lying down, even though it might be suckling subs. Three basic types of activity were recognised:-

(1) Foraging, which includes actually looking for food, moving to known food sources and carrying food back to the cubs.

(2) Eating.

(3) Social activities.

Because of the method used in recording activity patterns, more observations were made during the hours of darkness, when the hyaenas were most likely to be active, than during daylight.

If, the following evening, an individual was found in the same place or close to where it had been left previously, it was assumed not to have been active in the intervening period and these hours were included as observation hours. If, however, it had moved before I returned in the evening as happened in nine of 46 (19,6 per cent) cases the observation period was taken to have ended when the individual was left and only commenced if and when it was found.

Results and discussion:

Figure 21 illustrates the activity rhythm of adult brown hyaenas observed during the study. Analysis showed that they were predominantly nocturnal, although in winter they were sometimes encountered during the day and

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were active on average for 42,6 per cent of the 24 h period. The amount of time spent active by brown hyaenas per 24 h period was the same for summer (42,7 per cent) and for winter (42,5 per cent), but in winter the hyaenas became active and lay up for the day earlier. This suggests that activity is initiated but not terminated by changes in light intensity, although Ashby (1972) reports that the entrainment of the daily rhythm in mammals appears to be caused by the periodicity of rapid changes in light intensity, that is dusk and dawn. No difference in activity at different intensities of night illumination was found, as is the case with several species of nocturnal mammals (Erkert 1974).

The three large cubs which were observed between July and September 1973 were more diurnal than the adults were (Fig. 22), but as these were the only cubs followed during the study, it is unknown if this behaviour was typical. As it was difficult to follow these animals at night, because no radio collars or beta lights were used on them, these results are biased towards the day and the cubs were probably more nocturnal than is illustrated.

Aschoff (1966) reports that most animals show a two-peak activity pattern in the 24 h period. This has been illustrated in both the spotted and striped hyaenas in East Africa (Kruuk 1972 and 1976 a) where the first peak is larger than the second and is called the bigeminus pattern by Aschoff (1966). This pattern is not apparent in the data presented in Fig. 21 although in summer there is a slight increase in activity between 04h00 and 05h00.

There are three reasons for a two-peak activity pattern being less evident in brown hyaenas of the southern Kalahari:-

(1) Most importantly, environmental conditions can modify an activity

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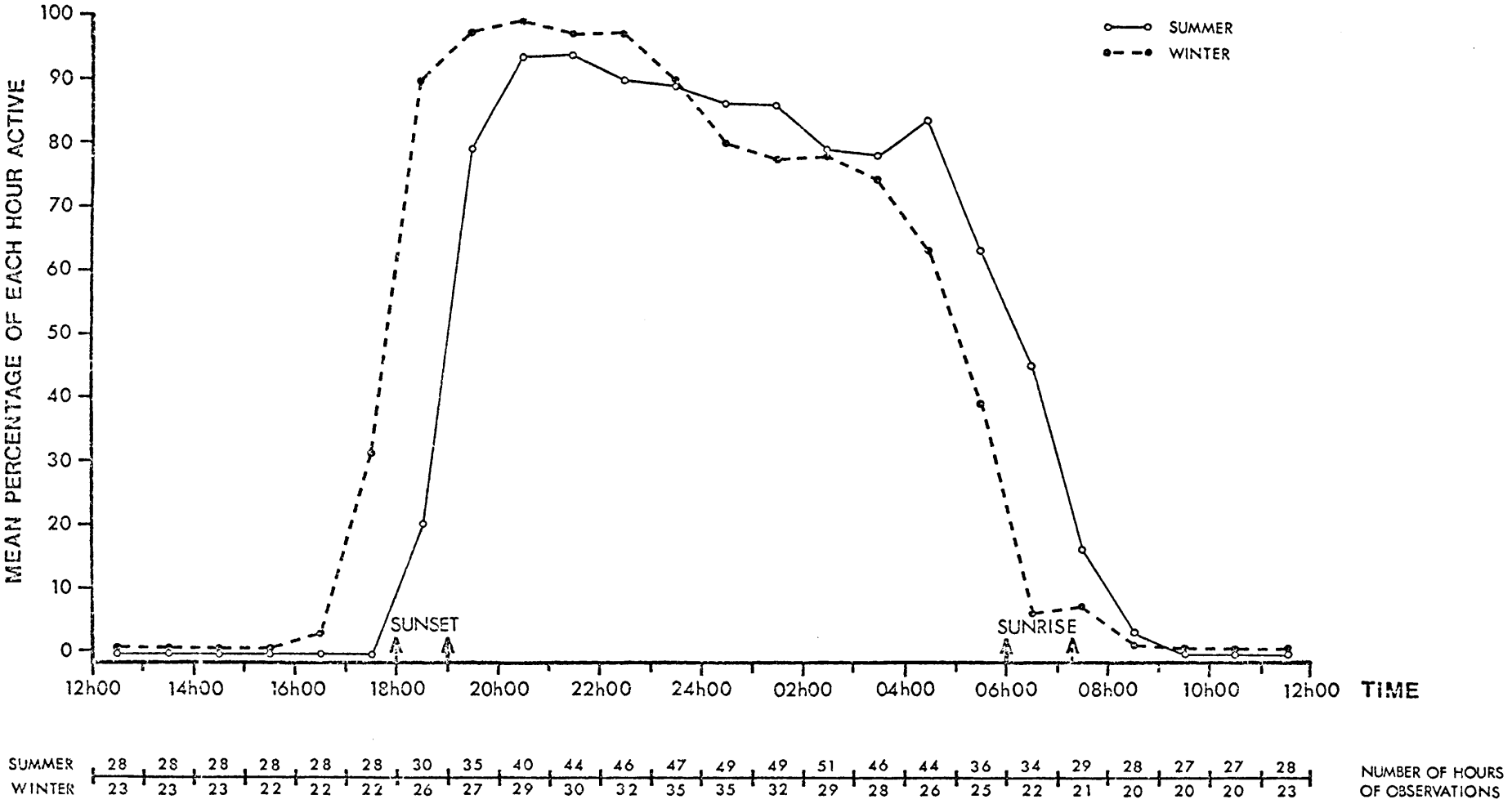


Figure 21. Mean percentage of each hour of the 24 h period that adult brown hyaenas (Hyaena brunnea) were active in the southern Kalahari; December 1974 - July 1976.

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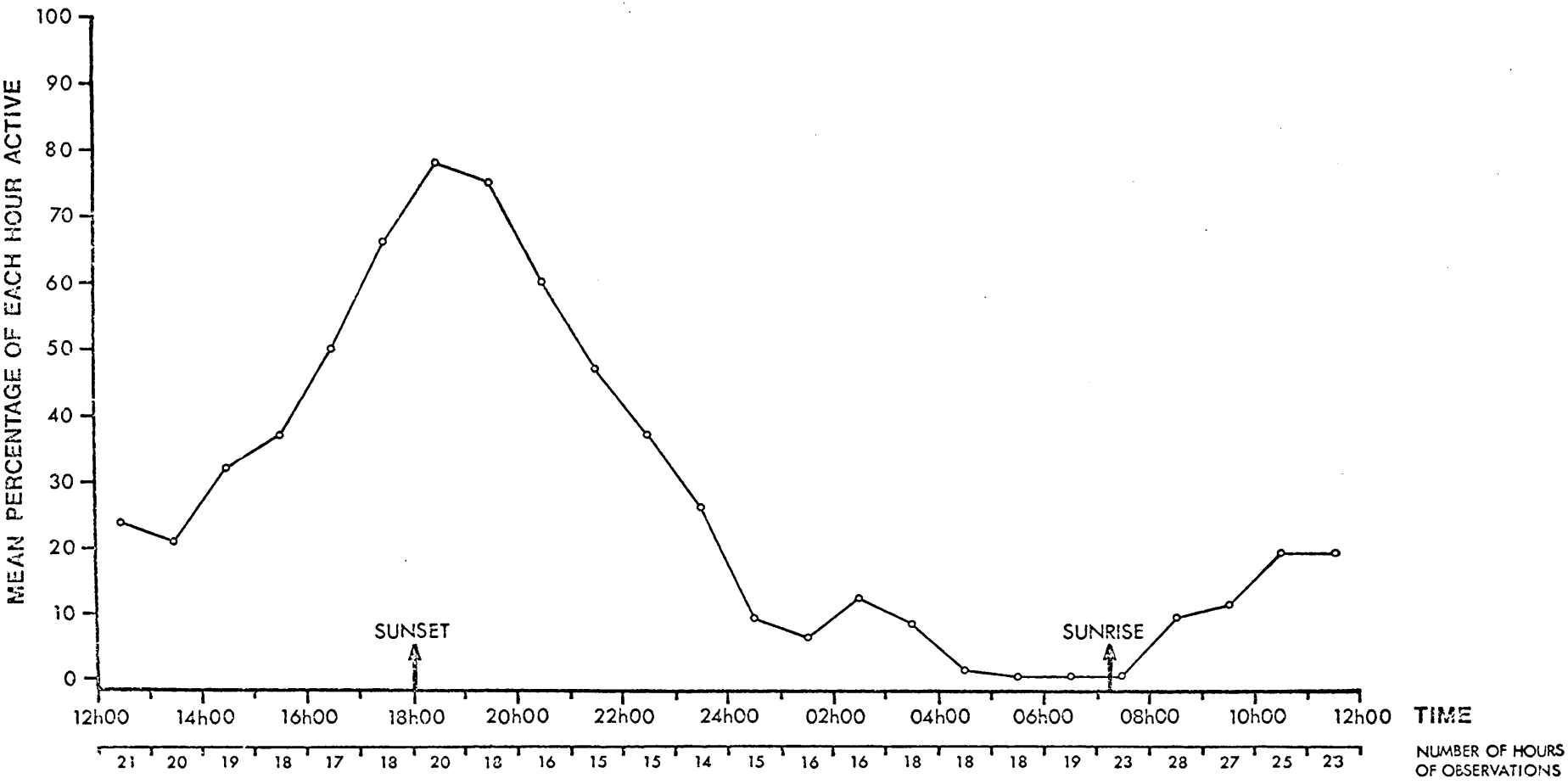


Figure 22. Mean percentage of each hour of the 24 h period that one year old brown hyaena (Hyaena brunnea) cubs were active in the southern Kalahari; June - September 1973.

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pattern. Brown hyaenas in the Kalahari are forced to spend significantly more of the night searching for food than the ecologically equivalent striped hyaenas are in the Serengeti (Kruuk 1976 a) (Mann-Whitney test; $U = 68,5$; $p < 0,05$), and therefore the quiescent stage between the two peaks is almost non-existant.

(2) As Aschoff (1966) points out, the second peak is often small, variable in position and of limited duration and may be obscured in graphs based on average values of many days, as is the case here. Of 42 continuous observations of hyaenas between 20h00 and 06h00 the animals rested once in 12 (28,6 per cent) of them and twice in three (7,1 per cent), although the times and duration were variable (Fig. 23).

(3) In at least some of the nine occasions when an individual had moved when I returned the next afternoon it is possible that it had exhibited a second peak of activity just before sunrise, as on six of these occasions the hyaena had lain down well before sunrise.

Figure 24 shows how brown hyaenas divide their time into four basic behaviour patterns. Of the active time they spend 88,2 per cent foraging, 4,2 per cent eating and 0,8 per cent on social activities.

Resting sites

A brown hyaena usually has no fixed resting site and instead spends the day in a suitably concealed place anywhere in the home range. There are, however, some general areas which will more often be selected for resting than others, such as near an area with a potential food source like the Nossob river-bed (Fig. 25). I never observed an adult to spend the day in the den and females with small cubs usually rested within a kilometre

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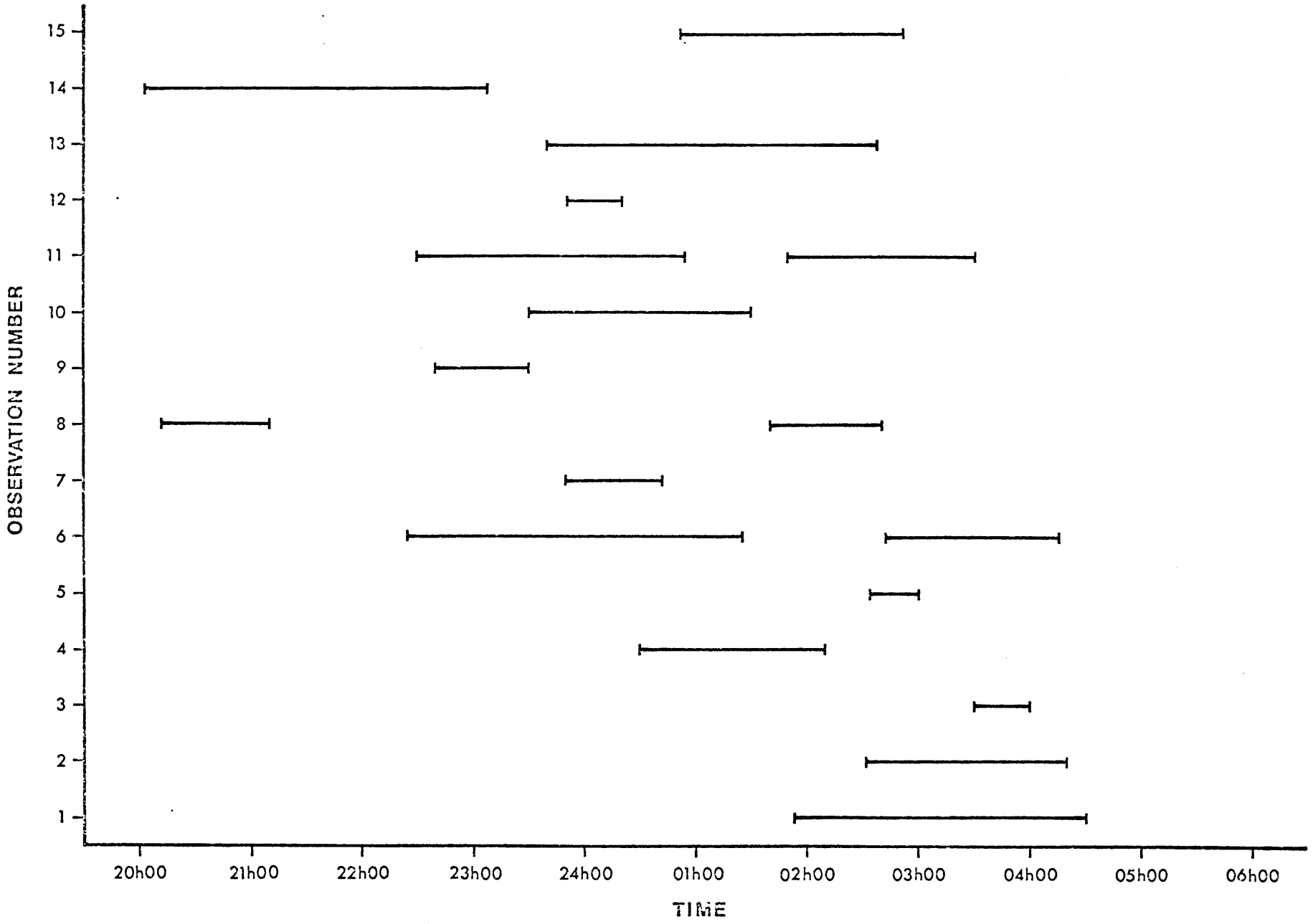


Figure 23. Time and duration of inactive periods between 20h00 and 06h00 of brown hyaenas (Hyaena brunnea) in the southern Kalahari; December 1974 - July 1976.

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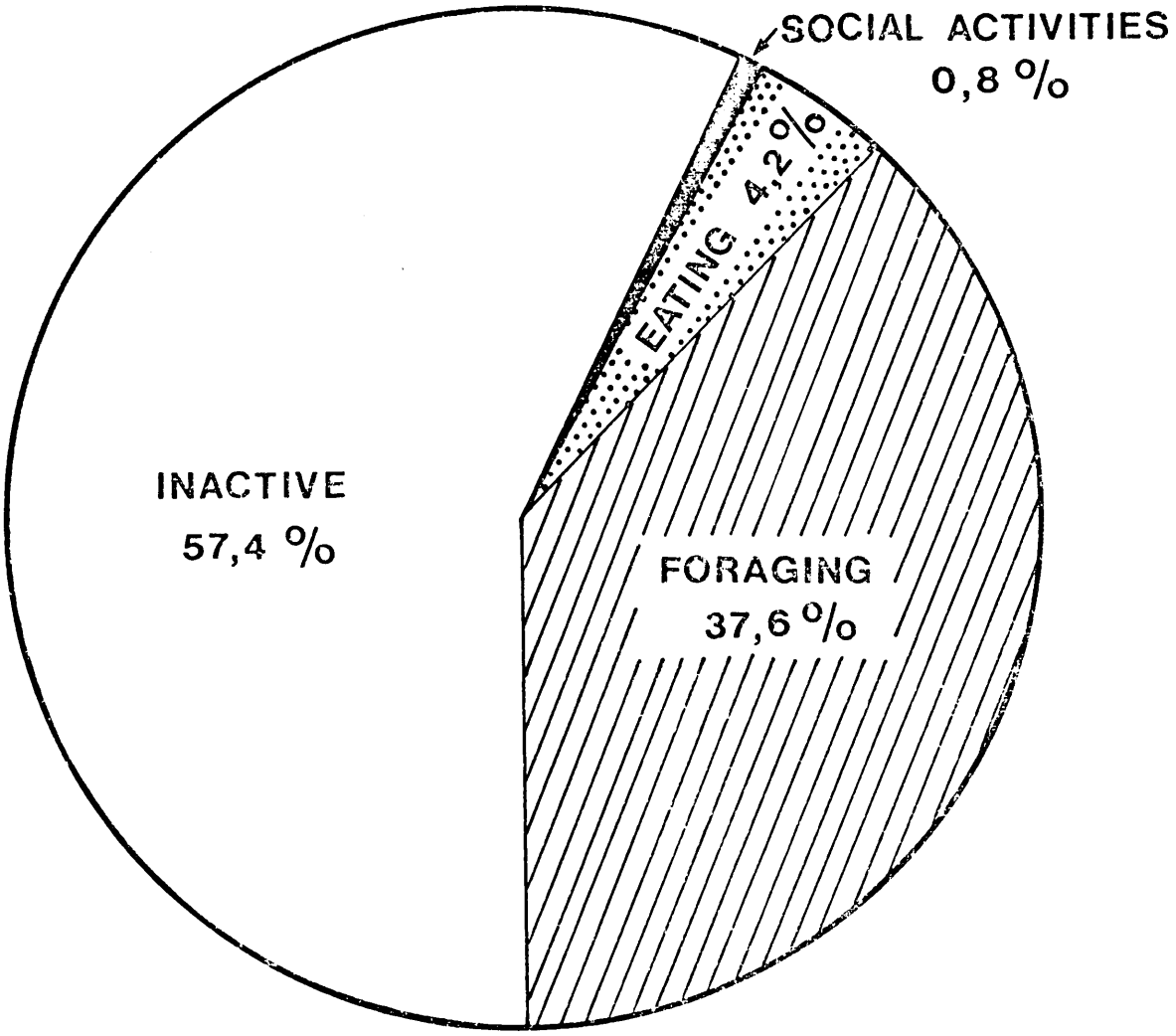


Figure 24. Relative time spent on various activities by brown hyaenas (Hyaena brunnea) in the southern Kalahari; December 1974 - July 1976.

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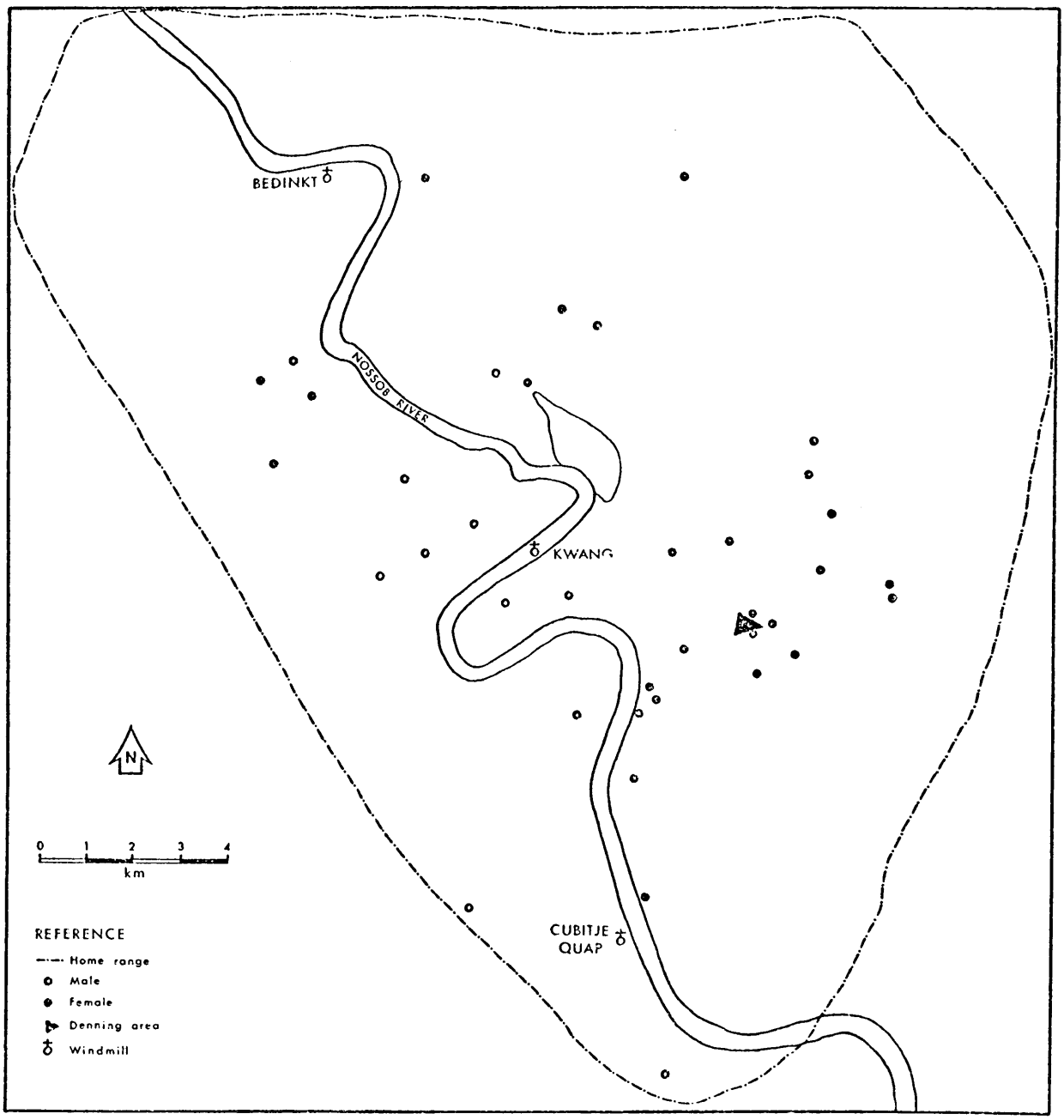


Figure 25. Location of resting sites used by a male and a female brown hyaena (Hyaena brunnea) in the southern Kalahari; December 1974 - July 1976.

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of it, sometimes in the same place. Thus brown hyaenas are similar to the striped hyaena in their resting behaviour (Kruuk 1976 a), and it is obviously advantageous for these animals to be independent of resting sites when their home ranges are so large.

The type of resting site used by brown hyaenas varied with the seasons (Fig. 26). In the hotter months, November to February, they would choose either a hole or a large "witgat" tree (Boscia albitrunca) with thick branches, especially close to the ground (Fig. 27 a). These trees are carefully selected and a hyaena would often inspect several before finally choosing one. Before settling down it would dig a hollow in which it would lie and during the course of the day would occasionally kick sand with its back legs onto its stomach (Fig. 27 b). As the temperature of the sand even 25 mm below the surface is 10° C lower than the temperature on the surface (Leistner 1967), this behaviour obviously helps to keep the animal cool.

In the months between summer and winter it is still usually fairly hot in the middle of the day and a cool resting place is sought. At this time, however, because the angle of the sun is more oblique, brown hyaenas can utilise a wider range of resting places and a less dense tree (Fig. 27 c) or a large thick bush can now provide shade all day, provided that the hyaenas move around as the sun's position changes, which they do.

In winter, keeping cool is no longer a problem and the hyaenas utilise a wide range of bushes. During a cold snap they will often rest in a patch of tall grass (usually Stipagrostis amabilis) (Fig. 27 d), warming themselves in the sun's rays.

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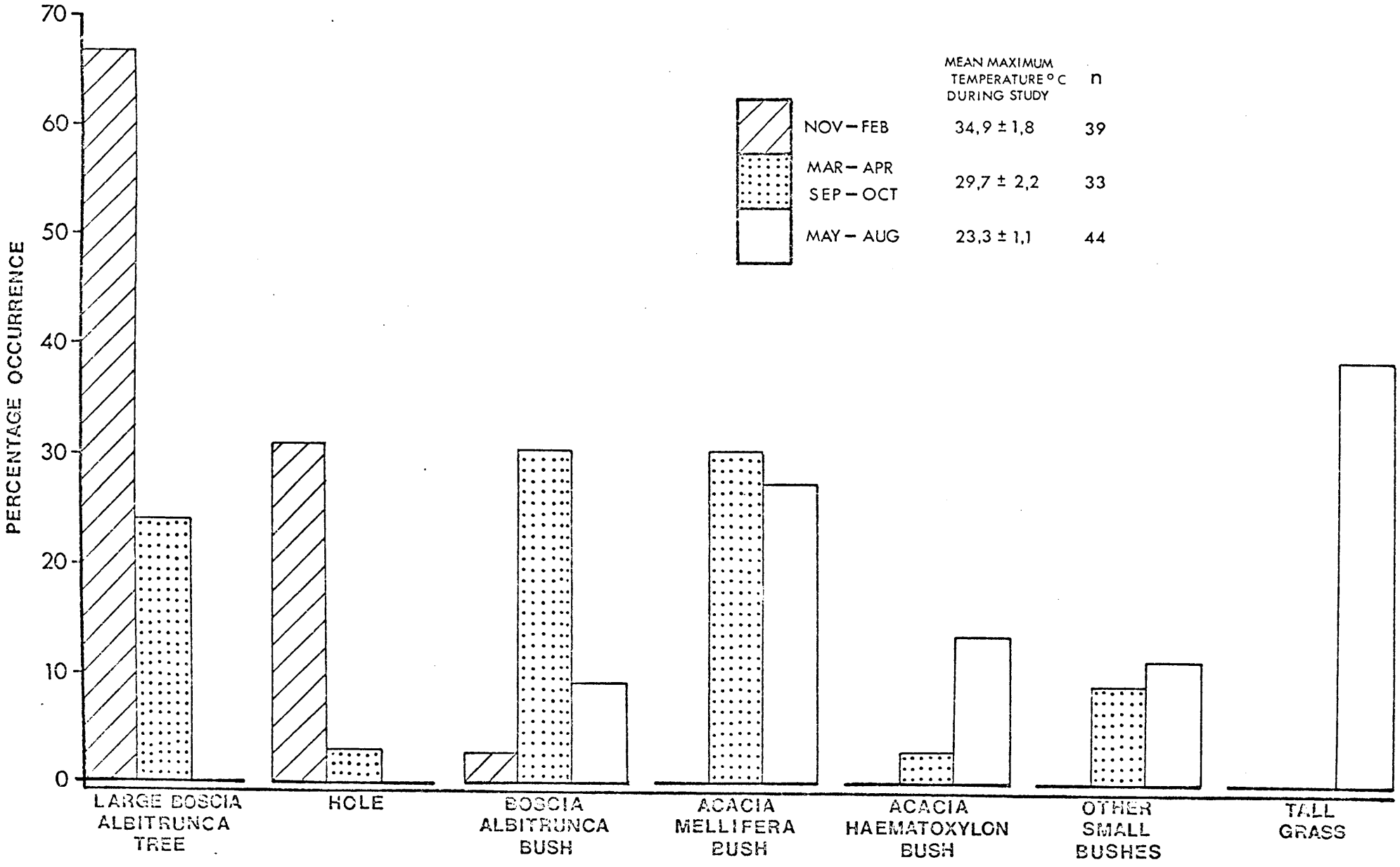


Figure 26. Percentage occurrence of different types of resting sites used by brown hyaenas (Hyaena brunnea) at different times of the year in the southern Kalahari; April 1972 - July 1976.

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(a)



(b)



(c)



(d)

Figure 27. Resting sites of brown hyaenas (Hyaena brunnea) in the southern Kalahari: (a) Summer resting site; a large Boscia albitrunca tree with thick branches close to the ground providing shade throughout the day. (b) Animal kicking sand with its forefeet onto its stomach in order to keep cool. (c) Animal resting in a typical spring or autumn resting site, September 1973; the branches near the ground need not be as thick as those of a summer resting site. (d) Winter resting site, a clump of tall grass, when protection from the sun is unnecessary.

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Searching

Brown hyaenas spend 37,6 per cent of their time searching for food (Fig. 24), and often travel long distances during a night (Fig. 28). The mean distance covered by the vehicle on 29 nights (three from spoor, the rest from direct observations), when a brown hyaena was followed from the time it became active until it lay up for the day, was 32,0 km (range 1,5 - 54,4 km). These are the minimum distances travelled as it was impossible to record all the small diversions and circling they do when forgaing. The mean distance differs substantially from the mean distance of 19 km covered during 10 nights by striped hyaenas in the Serengeti (Kruuk 1976 a).

The home range size of a brown hyaena is large and varies between 340 and 544 km^2 (Mills 1976 b) depending on the habitat. Individuals use different parts of their home ranges to varying extents, again depending on the quality of habitat which is reflected by the availability of food (Mills in prep.).

Brown hyaenas almost always forage alone (Fig. 29). Occasionally two might move together for a short distance, although then they are usually more interested in each other than in looking for food, and once I found three cubs of one year old moving together approximately 4 km away from their den.

When foraging, brown hyaenas move fairly quickly at a walk of approximately 4 km/h (on rare occasions they will lope), usually with the head held slightly down (Fig. 29) but sometimes with their nose to the ground, in a similar manner to the striped hyaena (Kruuk 1976 a). Although a large part of their foraging occurs cross country and is often characterised

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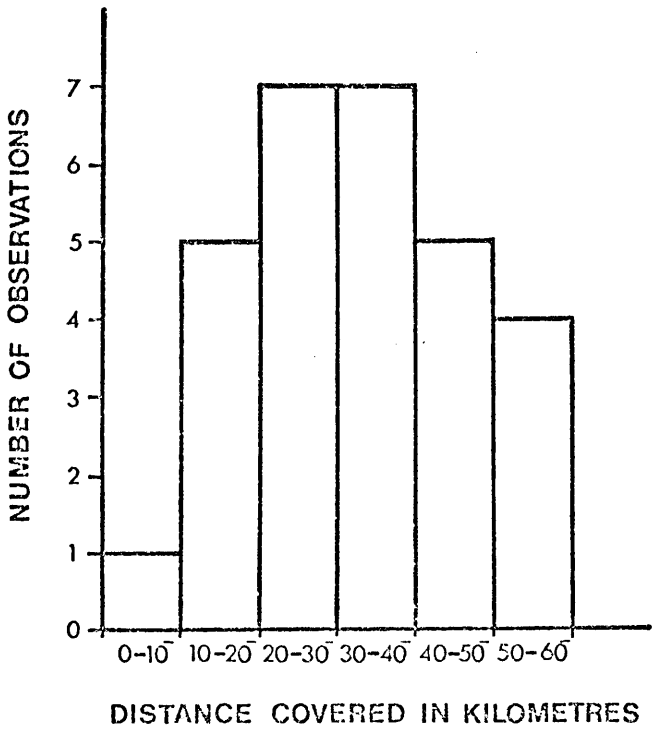


Figure 28. Frequency distribution of distances covered during one night's foraging by brown hyaenas (Hyaena brunnea) in the southern Kalahari; April 1972 - July 1976 (n = 29 nights).

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by erratic movements, they tend to use roads more often than striped hyaenas do (Kruuk 1976 a), being more like the spotted hyaena in this respect (Kruuk 1972). This was particularly so when animals were foraging in river habitat when they would often move up or down the river-bed along the road on the western bank. Brown hyaenas also differ from striped hyaenas in the Serengeti in that they do not spend as much time sniffing around at trees, bushes, holes and so on, although this is done occasionally.

On five occasions it started to rain farily hard while a foraging brown hyaena was being followed. On three of these the hyaena stopped foraging and lay up under a bush, becoming active again as soon as the rain stopped, while on two occasions it continued foraging. On another occasion a hyaena was feeding on a springbok carcass when it started raining but it was not deterred. Once a brown hyaena was lying in the open waiting for a lion to finish eating a springbok and did not take cover when it started raining hard. Kruuk and Sands (1972) comment that aardwolves cease foraging as soon as it starts raining, probably because it affects their foraging success. This may be true for brown hyaenas as well. Perhaps the intensity of the rain and accompanying wind conditions are of importance here, but I made no regular notes of these at the time, except on one occasion when the hyaena continued foraging, and then the rain was accompanied by a strong wind. Alternatively continued foraging might depend on some other factor such as the state of hunger of the hyaena.

Senses used when searching

Olfactory

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The most important sense used in finding food is almost certainly olfactory. Often when following an animal it would be observed to make an abrupt turn into the wind (upwind) and move a few metres to a food item, such as a small piece of bone, or occasionally to give chase after a prey. If the wind was coming from behind the animal it would walk right past the food item and then turn round, obviously having picked up the scent, and move back to it. Again this type of behaviour is characteristic of the striped hyaena (Kruuk 1976 a) and the aardwolf (Kruuk and Sands 1972).

Although the direction of the wind was not seen to be important in dictating the direction of movement of the hyaena, it certainly aided it in locating food. When foraging in conditions where there was a steady wind blowing from one direction, no matter how strong, a hyaena would repeatedly sniff the air by facing into the wind and lifting its head (Fig. 30). Then it would either continue on its original course or move further upwind, still sniffing, until it found something to eat or eventually reverted to its original course. Even when no wind was blowing the hyaena would still sniff the air at regular intervals.

These movements were different from the abrupt upwind turns of a few metres mentioned earlier, and might involve distances of over 1 km. For example, one night I was following a hyaena which was moving in an easterly direction towards Rooikop windmill. There was a fairly strong south wind blowing and she suddenly stopped and stood for 2 min sniffing upwind. She then changed direction and started moving south quite quickly, moved up over a high dune and 1,9 km from where she had first turned upwind, came to the fairly old, dry leg and shoulder of a gemsbok. Similar ability at sensing food, in this case live prey, from such long distances has been recorded in the wolf (Mech 1970) and in the spotted

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Figure 29. Brown hyaena (Hyaena brunnea) foraging in the southern Kalahari.



Figure 30. Brown hyaena (Hyaena brunnea) sniffing upwind in the southern Kalahari. Note the direction of the wind from the direction in which the grass is bent.



Figure 31. Brown hyaena (Hyaena brunnea) in the southern Kalahari cocking its ears and listening to a sound originating close by.

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hyaena (carrion) by Kruuk (1972) and Bearder (1977).

The frequency and orientation of sniffs made by a foraging brown hyaena were determined whilst following the three large cubs which foraged during the day, when I was able to count most, if not all, of these (Table 18). On days when there was a steady wind blowing they would average 3,1 sniffs per km and these were always upwind. In conditions where there was no wind blowing the same animals averaged 2,1 sniffs per km, but these were random and in all directions. Thus these cubs made significantly more sniffs when a steady wind was blowing than they made when no wind was blowing (Chi-squared = 6,48; df = 1; $p < 0,05$). There was no differnece in the direction of their sniffs when no wind was blowing in that they were just as likely to sniff either in a northerly, a southerly, an easterly or a westerly direction or even in various directions at one time (Chi-squared = 1,3; df = 4; $p > 0,05$).

A large number of the upwind sniffs and turns observed proved to be non-productive in terms of the location of food. I sometimes gained the impression that the hyaena was merely testing the wind for a possible scent, but it often looked just as if it had really picked up a scent as it moved quickly and in one direction, only to revert to its original course later without having found anything. Exactly what was happening under these circumstances is impossible to say, as our sense of smell is so poorly developed and it is impossible to measure accurately a brown hyaena's sense of smell.

Wind conditions, therefore, affect brown hyaenas' foraging efficiency in different ways. When there is a wind blowing brown hyaenas can detect food from down wind for long distances as in the example cited earlier. If, however, they happen to be upwind of a food source hyaenas will be

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Table 18. Frequency and orientation of sniffs made by three, one year old brown hyaena (Hyaena brunnea) cubs, under different wind conditions, during daylight in the southern Kalahari; July - September 1973.

OBSERVATION	WIND CONDITION	
	Steady wind	No wind
Distance followed (km)	95,4	30,2
Total number of sniffs	292,0	63,0
Sniffs per kilometre	3,1	2,1
Number of upwind sniffs	292,0	-
Number of other sniffs	0,0	63,0
North	-	15,0
South	-	18,0
East	-	8,0
West	-	14,0
Other	-	8,0

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unable to detect it even when close to it. For example, once a hyaena passed within approximately 250 m of a fresh springbok carcass hanging in a tree. The wind was blowing away from the hyaena and to the carcass and as he did not move over to investigate or show any interest in the carcass, I assumed that he did not detect that it was there. When the wind is still on the other hand, the hyaenas are able to detect a scent from all directions, although probably not from as far away as when the wind is blowing. They also then have difficulty in pin-pointing the direction from where a scent originates as the following example illustrates:-

> 2 February 1975. 19h43. I find a female brown hyaena on the air strip north of Cubitje Quap. She has obviously picked up a scent and is moving erratically with her nose on the ground but there is no wind blowing. She moves into the river-bed and runs up it (north) for approximately 500 m. Then she moves out of the river onto the eastern bank, still sniffing frequently, both in the air and on the ground. She circles around, moving over an area of approximately 0,5 km^2 in a more or less northerly direction, and passes a cheetah, but it does not appear to have a kill. She eventually crosses the river-bed again and at 21h00 moves off in a north-westerly direction having given up the search. After she has moved in this direction for 1,4 km the wind starts blowing. Almost immediately she turns round and starts moving back towards the air strip and comes back to almost the same place that she was originally found at. She crosses the river-bed again and starts moving south to south-west, upwind. She now begins to move quickly, moves back into the river-bed and finds a fresh springbok carcass.

In this example it is tempting to conclude that when the wind started blowing the hyaena was motivated to return to the area where she had earlier seemed to have been on a scent, the origin of which she could not pin-point. The fact that she had seen the cheetah in the vicinity

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earlier possibly strengthened this motivation. When I found her originally she was approximately 500 m north of the carcass, but moved away from it, only to find it quickly upon her return with the aid of a south-westerly wind.

Brown hyaenas are also good at following scent trails. Once, for example, one was observed to move 1,5 km at a fast walk, with her nose to the ground, until she found the back half of a springbok lamb. During this search she stopped thrice, circling around, usually with her nose still to the ground, then continued, once at least on a slightly different course. It seemed that from time to time the hyaena had lost the scent and would circle around until she had picked it up again.

Audtiory

Brown hyaenas are attracted by the sounds emitted by some other animals, as is illustrated in the following example:-

> 2 March 1976. 24h20. A female brown hyaena lies near the top of a dune near Kwang Pan. After 10 min she suddenly jumps up and runs down past the vehicle with her head up and her ears cocked. She runs off for 400 m, cross-wind, stops for a few seconds and then continues running for another 250 m. She then stops again and moves upwind for approximately 100 m, stops, sniffs around on the ground and moves quickly down wind for approximately 20 m and picks up a freshly killed springhare.

When being killed or injured springhares characteristically give vent to a cry, not unlike that of a human baby, and this sound attracts brown hyaenas and other carnivores, especially jackals. In the example cited above this is almost certainly what happened, but even though I was out of the vehicle when the hyaena first ran off, I heard nothing. The fact

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that the hyaena was cross-wind from the food source would seem to rule out any olfactory stimulus. Unfortunately I saw no other predator at the springhare carcass, but as it was in tall, thick grass a small predator could easily have run off without having been seen. To illustrate this attraction of brown hyaenas to a springhare cry, experiments were carried out on seven occasions by playing the recording of the cry of a springhare over the loudspeaker of a Uher 4 000 Report L tape recorder, when a brown hyaena was known to be in the vicinity. On five of these occasions the hyaena came running up to the vehicle within a few minutes.

Brown hyaenas are also attracted by the "mobbing" call of black-backed jackals. This call is a fairly high-pitched bark of short duration repeated several times (...wha...wha...wha...) interspersed with a series of short deep grunts and is directed at other carnivores, particularly leopards and occasionally caracals and brown hyaenas (see later). When they hear this call brown hyaenas often run off in the direction from which the noise eminates. On one occasion, for example, the hyaena ran 700 m to where two jackals were barking at a leopard which had a springbok carcass in a tree, and picked up some food scraps including a leg, under the tree (Fig. 37).

On four occasions a brown hyaena was observed to stand (one observation of 14 min) or lie down (three observations of 57, 61 and 67 min), from time to time lifting its head and cocking its ears. On three of these occasions there were large numbers of springbok around which were repeatedly giving the alarm whistle. I gained the impression that the hyaena was waiting for a springbok to be caught by some predator, thus possibly getting some food. Spotted hyaenas also employ a similar foraging strategy (Kruuk 1972).

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Foraging hyaenas are also attracted by short distance sounds as they will often stop and cock their ears in a certain direction (Fig. 31), sometimes prior to chasing, after obviously hearing something rustling in the grass.

Hearing, therefore, also plays an important role in the foraging pattern of the brown hyaena, particularly with regard to interspecific interactions and hunting.

Visual

Brown hyaenas obviously have good night vision. They would often stop and look at something which I would only be able to see through binoculars on moonlit nights, or with the aid of a spotlight on dark nights. The extent to which they use their sight to obtain food is, however, difficult to evaluate. It would seem that it is most often used in combination with auditory cues when hunting (either vertebrates or invertebrates) as they would often stop and look in a direction before chasing, and they also probably select prey animals visually (see later).

Scavenging

Scavenging is defined as the consumption by a carnivore of animal matter not killed by itself or a conspecific. It is found to a greater or lesser degree in nearly all carnivores (Ewer 1973). In Europe and North America the wolverine is probably the best adapted scavenger of the carnivores (Haglund 1966, Myhre and Myrberget 1975, Hornocker pers. comm.) and in

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M.G. Hornocker. Idaho Co-operative Wildlife Research Unit, University of Idaho, Moscow, 83843, U.S.A. April 1977.

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Asia and Africa the hyaenas, with their powerful jaws and teeth, and efficient digestive system, are the chief mammal scavengers. Recent studies have shown, however, that the spotted hyaena, for so long regarded as the dominant scavenger in Africa, is in fact an efficient hunter in its own right (Deane 1962, Eloff 1964, Hirst 1969, Pienaar 1969, Kruuk 1966 a and b, 1970 and 1972, Mills in press). One of the primary aims of this study, therefore, was to establish the extent to which the brown hyaena hunts as opposed to scavenges.

As I have mentioned 95,8 per cent of all vertebrate food items directly observed to be eaten by a brown hyaena in this study were scavenged. They also, however, utilise a range of other foods, particularly wild fruits, insects and birds' eggs. This figure, therefore, does not give a true picture of the actual contribution of scavenging to their diet. It would not, however, be accurate to include all these items listed above in a calculation of the scavenging contribution to the brown hyaena's diet, as it gives all items the same weight, which I have shown earlier should not be done. It is also biased to weigh all the vertebrate food items equally, as there is such variation in the size of the different items, and the figure of 95,8 per cent is merely presented as a rough guide. It can safely be concluded, however, that in the southern Kalahari, scavenging plays a major role in the brown hyaena's acquisition of food.

Many of the scavenged food items eaten were small pieces of bone, odd legs and skulls picked up in the course of an individual's foraging and which were found scattered throughout its home range. It was impossible, therefore, to determine the origin of these pieces of carrion and this could only be done in a few cases when the hyaenas found a fresh carcass. Even then, however, it was difficult. The carcasses were usually found at night when it was difficult to search for clues of other carnivores

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and the carcasses were, furthermore, often picked clean (Fig. 32) by vultures and jackals which had also often obliterated the signs of the predator. Another problem was that I usually could not spend too much time looking around when the hyaena moved off as I did not want to lose it. Table 19, however, presents the data which I could collect and shows that from fresh carcasses the most utilised animals were springbok, steenbok, hartebeest and black-backed jackals. The smaller species would be more likely to be carried back to the den for the cubs to feed on as well, and the larger species would be more likely to attract more than one hyaena.

When a brown hyaena found a large herbivore carcass it had difficulty in breaking off and consuming the large bones as the following example illustrates:-

> 17 January 1975. 02h30. Approximately 5 km north-west of Cubitje Quap windmill a female brown hyaena finds a fresh hartebeest carcass consisting of the head, backbone and ribs, two legs and skin. She begins to chew on the broken head of a tibia, but after 16 min gives up without much success. She then goes to the ribs and eats for 5 min, easily cracking and swallowing them. She then picks up another leg, which has already been broken off from the carcass, holds it upright with her forefeet and chews on the proximal head of the tibia, licking it vigorously before biting it, and using her neck muscles in pushing down and sideways as she struggles to break the bone (Fig. 33). After 49 min she finally breaks the head of the bone and starts eating it, moving onto the shaft which she consumes easily. She then picks up a piece of hide, shakes it vigorously and chews on it for 5 min. Finally, at 04h07, after trying for 12 min, she breaks off a radius and ulna and carries it off.

Ewer (1954) has shown that of the three hyaenas the spotted hyaena has the most specialised dentition, followed by the brown and then by the

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Table 19. Cause of death of fresh carcasses on which brown hyaenas (Hyaena brunnea) were observed to be feeding in the southern Kalahari; April 1972 - July 1976. The figures refer to the total number of hyaenas of all ages known to have eaten from each type of carcass.

CARCASS TYPE	CAUSE OF DEATH									
	Lion	Leopard	Cheetah	Jackal	Caracal	Man	Martial eagle	Non-violent	Unknown	Total
Steenbok	0	0	0	4	3	0	0	2	9	18
Springbok (adult)	0	2	1	0	0	0	0	5	8	16
Hartebeest (adult)	10	0	0	0	0	4	0	0	0	14
Black-backed jackal	0	1	0	0	0	0	0	0	9	10
Springbok (lamb)	0	0	0	3	0	0	1*	0	3	7
Gemsbok (adult)	5	0	0	0	0	0	0	0	1	6
Springhare	0	0	0	1	1	0	0	0	4	6
Gemsbok (calf)	1	2	0	0	0	0	0	0	0	3
Domestic cow (calf)	3	0	0	0	0	0	0	0	0	3
Small rodent	0	0	0	3*	0	0	0	0	0	3
Porcupine	0	0	0	0	0	0	0	0	2	2
Secretary bird	0	0	0	0	0	0	0	0	2	2
Wildebeest	0	0	0	0	0	1	0	0	0	1
Hartebeest (calf)	0	0	1	0	0	0	0	0	0	1
Duiker	0	0	0	0	0	0	0	0	1	1
Cape fox	0	0	0	0	0	0	0	0	1	1
Bat-eared fox	0	0	0	0	0	0	0	0	1	1
Brown hyaena	0	0	0	0	0	0	0	0	1	1
Suricate	0	0	0	0	0	0	0	0	1	1
Pangolin	0	0	0	0	0	0	0	0	1	1
Korhaan	0	0	0	0	0	0	0	0	1	1
Mole snake	0	0	0	0	0	0	0	0	1	1
Unidentified small bird	0	0	0	0	0	0	0	0	1	1
Total	19	5	2	11	4	5	1	7	47	101

Note. * Evidence not conclusive but strongly suspected.

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Figure 32. Brown hyaena (Hyaena brunnea) feeding on the remains of a springbok (Antidorcas marsupialis) in the southern Kalahari. The carcass has been picked clean by vultures and black-backed jackals (Canis mesomelas).



Figure 33. Brown hyaena (Hyaena brunnea) eating a long bone of a red hartebeest (Alcelaphus buselaphus) in the southern Kalahari. Note the animal has started by chewing on the head of the bone.

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striped hyaena. This particularly applies to the carnassial sheer, which is used for cutting through hide and tendons, and to the size of one of the principle bone crushing teeth, P^3. This was borne out by the above and similar observations which showed that brown hyaenas struggle to break off and consume large bones, whereas the larger spotted hyaenas have little trouble in doing so (Kruuk 1972, Bearder 1977 and personal observations). Furthermore, more than one hyaena feeding on a large carcass makes it easier for them to break it up as they pull on it from different directions, and here too the more social spotted hyaena has an advantage over the brown hyaena. These facts, plus the spotted hyaenas' superior hunting ability, suggest that spotted hyaenas are better adapted to consuming large ungulates than brown hyaenas are.

Smaller carcasses such as that of the springbok in Fig. 32 were consumed more easily and rapidly than larger ones. In this particular example the hyaena finished eating the carcass, except for the head which another hyaena ate, in 1 h 23 min, beginning with the ribs, which still had a little meat on them, then the vertebral column and finally the legs.

When feeding on the last remains of a carcass which had obviously been fed on by other scavengers and where the pieces were widely scattered, a brown hyaena would often spend much time moving around in ever increasing circles with its nose to the ground, searching for the last few bone chips and other scraps.

Frequently brown hyaenas would find an old piece of hide, often stored under a bush, and would spend up to an hour licking and chewing on it. In these cases, however, only a small piece of the hide was broken off and ingested, and little benefit seemed to have been derived from this activity, although it might be useful when other food is scarce.

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The largest complete carcass that a brown hyaena found during the study was an adult springbok and this observations is described in detail:-

> 2 July 1976. 21h09. Approximately 6 km north of Kwang Pan a male brown hyaena comes to the untouched carcass of an adult female springbok. He opens up the carcass through the stomach and pulls out the innards which he consumes. Then, after being at the carcass for 18 min, he breaks off the haunches and legs and carries them off for 400 m putting them down in a patch of tall grass. He returns to the carcass and eats for another 21 min. At 22h15 he breaks off a small piece and carries it off, at which four black-backed jackals which have been around all the time, start feeding. At 22h24 a second hyaena comes running up to the carcass with her hair up and scatters the jackals. She immediately picks up the carcass and carries it off for 100 m when she is joined by a third hyaena, her two year old daughter. The two struggle with the food and at one stage the younger hyaena manages to get hold of the whole carcass and tries to run off with it, but the mother easily catches up with her. They then settle down, eating quickly (Fig. 34) with no noise and only a little pushing and pulling. This continues for a few minutes until the daughter breaks off a piece of the front leg and moves off with it. The adult female feeds for another 3 min then picks up the remains (Fig. 35) and carries them back to her den which is 7,3 km away.

Thus five hyaenas (the female had two cubs of approximately seven months old) fed on this carcass. When I returned to the place where the male had left the back portion of the carcass it was gone, but it was impossible to determine what animal had taken it. The behaviour of the brown hyaenas at this carcass was similar to that of spotted hyaenas feeding on a carcass, where the stomach and soft parts are eaten first, and pieces are carried off for undisturbed consumption away from the carcass (although sometimes the animal doing so will be chased by the others) and where competition is expressed in the speed of eating (Kruuk 1972). The important difference between these two hyaenas lies in the fact that the brown

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Figure 34. Two brown hyaenas (Hyaena brunnea) feeding together on a springbok (Antidorcas marsupialis) carcass in the southern Kalahari.



Figure 35. Brown hyaena (Hyaena brunnea) in the southern Kalahari carrying off part of a springbok (Antidorcas marsupialis) carcass to its den.

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hyaenas, like striped hyaenas (Kruuk 1976 a), carried off large parts of the carcass to be stored close by or to be taken to the den.

Smaller whole carcasses were usually fed on by only one hyaena unless the animal carried part or all of it back to the den. On three occasions when something the size of a springhare was scavenged or killed the hyaena ate the carcass head first (Fig. 51). A striped polecat killed by a brown hyaena cub was eaten (Figs. 52 b and 52 c) in 57 min (mass approximately 0,6 kg) and two springhares, both killed by adults, were eaten in 30 and 76 min respectively (approximate mass 2,7 kg (Smithers 1971)). The large time difference here might be due to the old age of the hyaena that took 76 min.

Scavenging from and interactions with other carnivorous animals

Brown hyaenas scavenge from a wide range of meat eaters (Table 19) and in the following section the extent to which they do so and the way in which the different species interact with brown hyaenas, particularly over food, is discussed. A more detailed discussion on the way that these interactions affect the brown hyaena population in the southern Kalahari will be presented elsewhere (Mills in prep.).

Lion

Table 19 shows that more brown hyaenas were observed scavenging from the fresh remains of lion-killed herbivores than from herbivores that had died from any other cause. The relative importance of lions is, however, exaggerated in Table 19, as it was easier to find signs of lions around the carcasses than of any other agents. On the other hand, most of the other large mammal remains that were eaten were almost certainly the

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left-overs from lion kills. Thus brown hyaenas were provided with a substantial amount of food by lions.

If, during its foraging, a brown hyaena locates lions feeding on a kill, it will usually move off returning from time to time until the lions have abandoned their food. Once, however, a brown hyaena waited for 8 h in vain for a lioness to finish feeding on a springbok. They will usually approach no closer than 50 m from the feeding cats and often stand down wind looking at them for a few minutes before moving off. Sometimes a lion will move towards the hyaena and chase it for a short distance and once a lioness all but caught a hyaena in this way.

Leopard

The leopard's habit of taking its kills into trees is a most effective way of preventing all but another leopard, or perhaps a lion, from scavenging from them. On several occasions, when following a brown hyaena it came to a tree in which a leopard kill was hanging and spent some time sniffing around the base of the tree, sometimes picking up scraps that had fallen from the carcass. Once a brown hyaena attempted to reach a carcass 2,5 m up in the fork of a tree by standing on its hind legs (Fig. 36).

Only twice was a brown hyaena directly observed to get a reasonable meal from a leopard kill. The first incident was described earlier (Fig. 37) where the hyaena obtained a leg as well as other scraps of a springbok, and the second was when the hyaena found the fresh legs, head, ribs, vertebrae and skin of a springbok. While it was eating it suddenly jumped back and raised its mane, upon which I saw a leopard approximately 50 m away. The leopard, which by its appearance had obviously just had a good

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meal, took no notice of the hyaena which soon continued eating.

Cheetah

Schaller (1968 and 1972) and Kruuk (1972) have reported how other large carnivores steal kills from cheetahs, usually with no resistence from the cheetahs, except occasionally against spotted hyaenas (Schaller 1972). The following observation shows that even the rather timid brown hyaena is capable of dislodging a cheetah from its kill, although it is doubtful whether it would do so if a group of large cheetahs were feeding:-

> 28 July 1973. Langklaas. Just after dark a brown hyaena is seen approaching a springbok carcass on which a female cheetah and her three small cubs are feeding. The hyaena circles around down wind from the carcass, and the adult cheetah, on seeing it moves towards the hyaena, at which the cheetah cubs run off in the opposite direction. As the cat approaches the hyaena, the hyaena retreats a few metres. Then the hyaena tunrs around and, with mane and tail erect, runs towards the cheetah. They clash, the cheetah slaps at the hyaena and then turns around and runs off, abandoning the carcass to the hyaena (Fig. 38).

On one other occasion I was able to determine that a brown hyaena was feeding on an abandoned cheetah kill and on several others I suspected that cheetahs had been the killers of a carcass being fed on by a brown hyaena.

Spotted hyaena

Spotted hyaenas were rare in the study area and during the time I was following the radio-collared brown hyaenas I never saw the two species interact. The only observation that I have of direct competition over food between these two species was when a group of seven spotted hyaenas

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Figure 36. Brown hyaena (Hyaena brunnea) in the southern Kalahari standing on its hind legs in an attempt to reach a springbok (Antidorcas marsupialis) carcass in the tree.



Figure 37. Brown hyaena (Hyaena brunnea) (bottom right) in the southern Kalahari feeding on the scraps of a springbok (Antidorcas marsupialis) carcass which a leopard (Panthera pardus) has dragged into the tree. Note the leopard lying in the tree (top left) and the remains of the springbok (top centre).



Figure 38. Brown hyaena (Hyaena brunnea) in the southern Kalahari at a springbok (Antidorcas marsupialis) carcass which it had just stolen from a female cheetah (Acinonyx jubatus) and her three small cubs.

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came to a brown hyaena den when the cubs were away, and ate the remains of a carcass which an adult brown hyaena had brought the night before. Eaton (1976) and Skinner (1976) have speculated on the amount of competition that exists between these two species, and hopefully more data on this important relationship will be collected in the future.

Black-backed jackal

Black-backed jackals are common in the Kalahari both in the rivers and dunes. They appear to be efficient predators in this region, preying on springbok lambs and steenbok (personal observations), springhares (Ferguson pers. comm.), and other small mammals, especially rodents, as well as taking birds, reptiles, arachnids, insects, wild fruits and carrion (Bothma 1966, Smithers 1971). Thus their diet to a large extent overlaps that of the brown hyaena.

On three occasions brown hyaenas were observed to chase jackals off kills: a steenbok (from spoor), a springbok lamb and a springhare (both from direct observations), and three times a brown hyaena was seen to find a small dead rodent which had possibly been cached by a jackal. Ferguson (pers. comm.) twice saw a brown hyaena chasing jackals off springhare kills, once with success but the other time the jackals managed to escape with the remains.

Brown hyaenas are always alert to the activities of black-backed jackals, paying particular attention to the "mobbing" call as was illustrated earlier. Also they often move over to jackals which they have seen, probably to check if they have any food, and if so, to try and steal it. In addition brown hyaenas will readily eat jackals (Table 14) and occasionally were observed to try and catch one (see later).

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Black-backed jackals derive benefit from brown hyaenas and were observed scavenging around brown hyaena dens (two observations), licking the dregs from ostrich eggs which had been opened and eaten by a brown hyaena (one observation), and picking up scraps of bones after a brown hyaena had eaten (numerous observations). On many occasions I noticed that, when a brown hyaena began feeding, one or more jackals would appear (possibly attracted by the sound of the bones being cracked) and wait around (Fig. 39) until the hyaena moved away. Then they would immediately go up to investigate the area, sometimes picking up a few food scraps. Sometimes the jackals, by persistent pestering, would cause the hyaena to move away a few metres with its food, allowing the jackals to pick up some scraps that the hyaena could not take with it and which, if left in peace, it would probably have eaten. A similar behavioural pattern between jackals and spotted hyaenas has been reported by Kruuk (1972) and Bearder (1975) and I have observed it in the Kalahari as well. In all these cases, however, the benefit derived by the jackal is hardly detrimental to the hyaenas, but presumably it is of some significance to the jackals.

Frequently when following a brown hyaena a jackal would be observed to come up to the hyaena and to follow it for some distance, usually for 20 - 50 m (nine occasions) but sometimes for a few hundred metres (four occasions) and once for 2 km. When this happens the brown hyaena usually does not take much notice although it sometimes does raise its hair, flick its tail and hurry off, and if the jackal should approach too close, turns on it and chases it away a few metres.

Occasionally, however, the jackal will attack the hyaena, barking at it (Fig. 40) and often nipping at its back legs, causing the hyaena to run off with its hair raised and retaliating from time to time by turning

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around and snapping at the jackal should it continue the attack. This was observed six times; twice the brown hyaena concerned was a large cub and four times it was an adult. Kruuk (1972) records similar behaviour towards spotted hyaenas when a hyaena ventures near a jackal den, although he makes no mention of the jackal barking at the hyaena. In none of the above observations do I know whether the jackal had a den in the vicinity, and in one of the cases involving a hyaena cub, which occurred in July, this is unlikely. Of the others, one occurred in September, one in December, and three in January and it could well be that there was a jackal den in the vicinity as this is when they have their pups (Bothma 1971 c and personal observations).

Jackals are more successful at getting meat from large carnivores' kills than brown hyaenas are. Often the former are able to snatch a few morsals when the predators are still in attendance, and they are usually first onto the kill after the killers have left and can quickly dispose of the last pieces of meat. In this respect they can deprive brown hyaenas of a substantial amount of food on some occasions.

In summary, it is apparent that there is a fair degree of competition between brown hyaenas and black-backed jackals, far more so than between spotted hyaenas and jackals (Kruuk 1972, Bearder 1975). Both brown hyaenas and black-backed jackals benefit by the presence of the other and both are deprived of food by the other, although it is difficult to say to what extent. Kruuk (1976 b) says that there is most aggression between carnivores that overlap significantly in food habits. This is why there is so much confrontation between brown hyaenas and black-backed jackals, although the large difference in size probably inhibits excessive overt aggression. The relationship between these two species is also somewhat different from that between most other carnivore competitors

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in that one (the jackal) is a favoured food item of the other (the brown hyaena).

Caracal

On four occasions (two from spoor and two from direct observations) a brown hyaena chased a caracal off its kill. The two encounters observed from spoor involved steenbok and in at least one of them the hyaena must have obtained a good meal as I found him the next day approximately 1 km away, lying under an Acacia mellifera bush with the hindquarters of the steenbok still uneaten (Fig. 50 a). One of the direct observations was made with Ferguson when the hyaena chased a caracal off a springhare kill, which the caracal had earlier taken from three jackals. In the fourth observation the hyaena scavenged an African wild cat from the caracal. In all these observations the hyaena merely came up to the kill and the caracal ran off without putting up any resistance.

Man

During the course of day to day management in the Kalahari Gemsbok National Park a small number of herbivores are shot, either for rations, occasionally for research purposes, or if they are sick or injured. These activities provide some food for brown hyaenas, especially around the rest camps. Once, for example, a hyaena that I was following near Nossob Camp found a fresh piece of hide of a wildebeest which had been shot for rations. Furthermore the trapping exercise I carried out provided some food for brown hyaenas and, as mentioned earlier, a few individuals were caught several times, each time getting a meal of 2 - 3 kg of bait.

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Figure 39. Black-backed jackal (Canis mesomelas) in the southern Kalahari approaching a brown hyaena (Hyaena brunnea) feeding on the innards from a dead blue wildebeest (Connochaetes taurinus). Note that the hyaena's hair is slightly raised.



Figure 40. Black-backed jackal (Canis mesomelas) in the southern Kalahari barking at a large brown hyaena (Hyaena brunnea) cub which is moving away with its hair raised.

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The rubbish dumps at the rest camps attract brown hyaenas which regularly visit them and rummage around, picking up all sorts of edible scraps (Fig. 14). Most of the hyaenas that I followed did not come to the rest camp and I only once followed an animal that went to the rubbish dump where it spent 50 min picking up several small food scraps. It was, however, a good place to go to when looking for spoor to follow.

In the Gemsbok National Park the activities of poachers from time to time provide brown hyaenas with substantial amounts of food. These activities, however, sometimes work against the hyaenas when they themselves get caught in gin traps.

Birds of prey

The larger eagles, and in particular the martial eagle (Polemaëtus bellicosus) which is common in the Kalahari, catch a range of small mammals, game birds and snakes (McLachlan and Liversidge 1966) and on three occasions I found a martial eagle eating a springbok lamb. The remains of these prey items (Fig. 41) will obviously be eaten by brown hyaenas should they find them, and on one occasion a hyaena ate a springbok lamb, the condition of which closely resembled that of the one shown in Fig. 41. I came back the next day but could not find any clue of a predator except for a small feather, although I could not say from what species of bird it had come.

On three occasions I saw a chanting goshawk (Melierax musicus), an abundant bird in the area, with a dead mole snake (Pseudaspis cana). On another I found a half consumed mole snake with only the soft parts eaten, which from the tracks around it appeared to have been killed by a small raptor. Cases such as these will also provide brown hyaenas

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and other scavengers with an occasional small meal.

Vultures are uncommon in the main study area, although in other parts of the southern Kalahari, particularly further up the Nossob river, there are fairly large numbers of white-backed (Gyps africanus) and lappet-faced vultures (Torgos tracheliotus). I have never seen brown hyaenas reacting to vultures descending on a kill as spotted hyaenas do (Kruuk 1972), probably because of the nocturnal habits of brown hyaenas and the low density of vultures. Once, just before sunset, a brown hyaena approaching the Nossob river-bed, was moving towards a group of vultures sitting in some trees. Soon after I had noticed the vultures, some jackals began howling from the same direction and the hyaena immediately showed interest, so I was unable to determine whether it was the vultures, the jackals or both which had attracted the hyaena's attention.

Mundy and Ledger (1976) have suggested that griffon vultures collect bone fragments to supply their chicks with calcium, and that they get these from carcasses after hyaenas have been eating. Figure 42 illustrates the remains of a hartebeest calf that a hyaena had been feeding on, showing that these bone chips are available to the vultures unless another hyaena or jackal finds and consumes them. On the other hand, as mentioned earlier, vultures together with jackals usually consume the last pieces of meat at a predator kill before the brown hyaenas get to it.

Other sources

On three occasions a brown hyaena found a completely uneaten ungulate carcass; once an adult springbok, once a springbok lamb and once a steenbok. These carcasses showed no signs of having been killed by a

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Figure 41. Remains of a springbok (Antidorcas marsupialis) lamb killed by a martial eagle (Polemaëtus bellicosus) in the southern Kalahari and which might provide a meal for a brown hyaena (Hyaena brunnea).



Figure 42. Bone chips left by a brown hyaena (Hyaena brunnea) after eating the remains of a red hartebeest (Alcelaphus buselaphus) calf in the southern Kalahari. These might be taken by white-backed vultures (Gyps africanus) to feed their chicks. The lenght of the horn on the left is approximately 200 mm.

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carnivore and it is assumed that they died non-violently. This food source was uncommon in the study area, although in the Auob river it is more common to find a dead herbivore, especially a springbok.

Afterbirths of ungulates are another food source which brown hyaenas would be expected to utilise by scavenging, particularly from those species which have peaks in their breeding cycles: wildebeest, hartebeest and springbok.

Foraging for fruits, fungi and birds' eggs

Tsamas and gemsbok cucumbers

The two most common fruits utilised by brown hyaenas in the southern Kalahari are the tsama and gemsbok cucumber (Tables 11, 12 and 13). These fruits are widely distributed throughout the area, although not evenly so, and grow in patches of varying sizes containing from a few to several hundred fruits. Kruuk (1976 a) has shown that striped hyaenas know where their favourite fruit trees (*Balanites aegyptica*) are fruiting in their home range and make special trips to these. It is likely that under more normal conditions brown hyaenas would know where large patches of tsamas or gemsbok cucumbers are, although I could not prove this during the study, as the good rains (Fig. 2) produced abundant and widespread tsama and cucumber crops.

Usually a brown hyaena would apparently come upon a patch of tsamas of gemsbok cucumbers by chance, but sometimes it would first move upwind for distances of up to 50 m. Tsamas would invariably be plucked off the vine and carried off a few paces before being consumed. The hyaena would put it down and open it up by biting off a chunk with its canines (Fig.

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43), sometimes steadying the melon with its forefeet. Using the incisors and tongue the flesh would be scraped out and if necessary more chunks would be bitten off so as to get at the flesh. When the hyaena had finished eating there would be three or four large pieces of rind and a few pips left (Fig. 44). The smaller gemsbok cucumbers were eaten in a similar manner, although they were usually only bitten into two pieces (Fig. 45).

The mean number of tsamas eaten during each feeding bout was 2,0 ± 0,18 (range 1 - 11) (Fig. 46) and the mean number of cucumbers was 1,4 ± 0,11 (range 1 - 6) (Fig. 47), although on most occasions only one of either fruit was eaten during each bout. On five occasions a brown hyaena opened up a gemsbok cucumber and then left it, and twice it did so with a tsama. This was most probably because the fruits were not quite ripe (four occasions) or had been damaged by frost (three occasions).

The mean time taken by an adult brown hyaena to eat a tsama was 2,6 min ($n = 84$) and by a year old cub 10,2 min ($n = 12$), a significant difference (Mann-Whitney test; $z = 5,037$; $p < 0,01$). These cubs had trouble in opening up tsamas, particularly large ones, and were more inclined to eat tsamas that had already been opened (four out of 12 (33,3 per cent) observations), than adults were (one out of 84 (1,2 per cent) observations) (Chi-squared = 15,9; df = 1; $p < 0,01$). Also the cubs were not nearly as proficient at scraping out the flesh as the adults were, taking much longer to accomplish this task. Adults were never observed to bring any fruits to the den.

Other fruits and fungi

Eight feeding bouts by brown hyaenas were observed on *Grewia flava*

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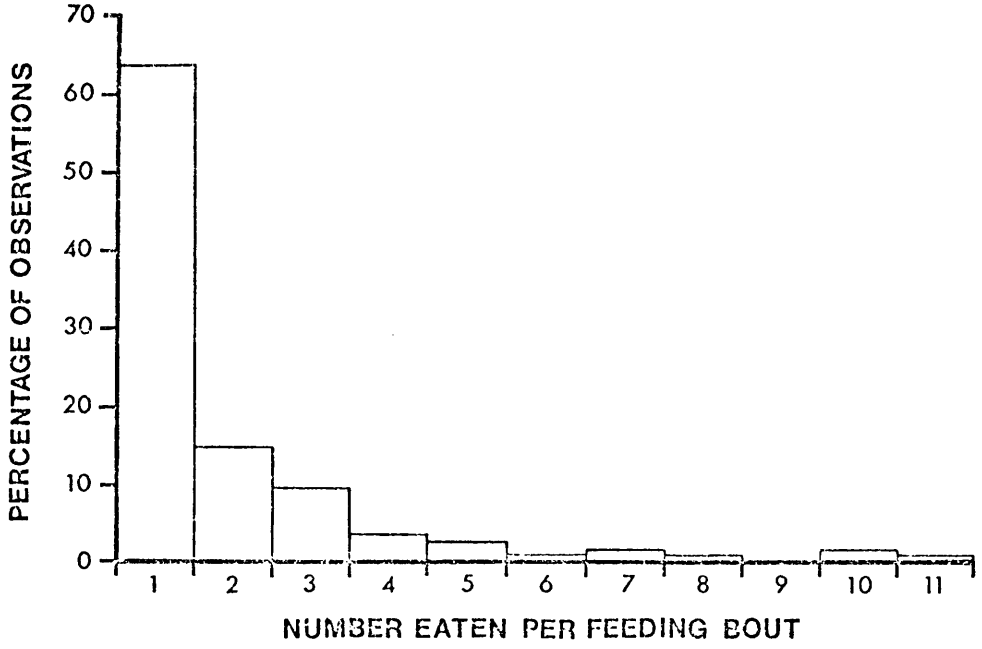


Figure 46. Number of tsamas (Citrullus lanatus) eaten per bout by brown hyaenas (Hyaena brunnea) in the southern Kalahari; April 1972 - July 1976 (n = 115 bouts).

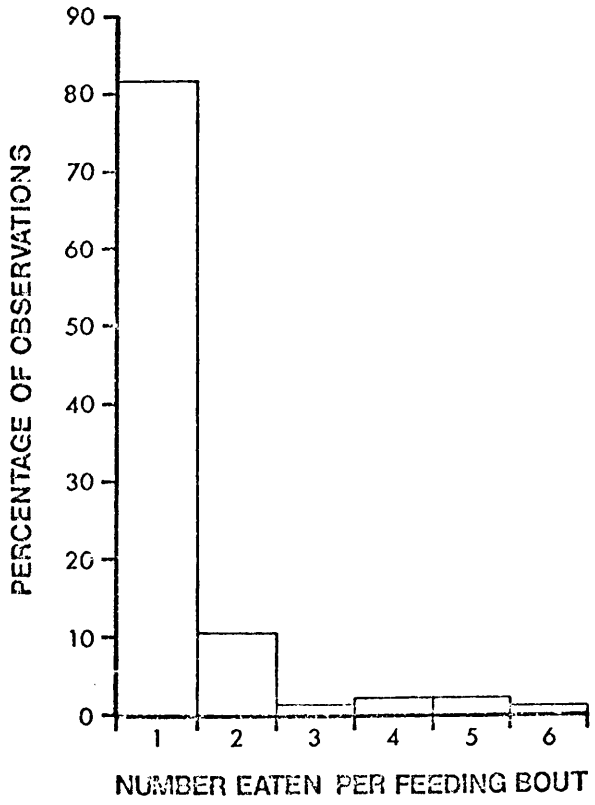


Figure 47. Number of gemsbok cucumbers (Acanthosicyos naudianus) eaten per bout by brown hyaenas (Hyaena brunnea) in the southern Kalahari; April 1972 - July 1976 (n = 83 bouts).

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Figure 43. Brown hyaena (Hyaena brunnea) eating a tsama (Citrullus lanatus) in the southern Kalahari.



Figure 44. Typical remains of a tsama (Citrullus lanatus) eaten by a brown hyaena (Hyaena brunnea) in the southern Kalahari.

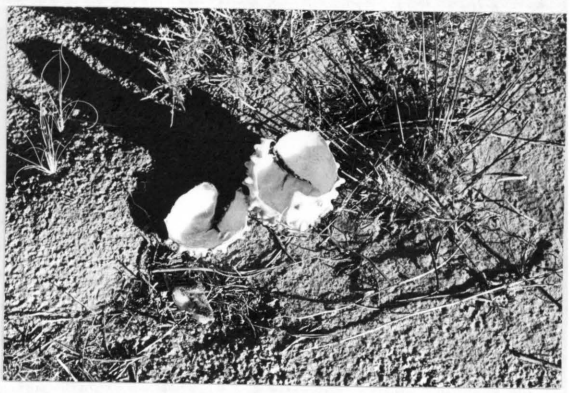


Figure 45. Typical remains of a gemsbok cucumber (Acanthosicyos naudianus) eaten by a brown hyaena (Hyaena brunnea) in the southern Kalahari.

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berries lasting between 15 sec and 15 min. As far as I could tell, the bushes, which are widely distributed and common throughout the area, were encountered by chance.

On three occasions the same brown hyaena was observed to feed on the fruits of Merremia tridentata for 10, 15 and 34 min. This plant is a prostrate annual which grows in large patches and the hyaena would move slowly and erratically through a patch with its head down, picking off individual fruits.

Although seven (1,8 per cent) scats contained the seeds of the wild cucumber (Table 13), I never observed a hyaena actually eating any, either from direct observations or when tracking spoor.

On 21 occasions in two nights (in April 1975) a brown hyaena was observed to dig for a few seconds in the sand and then to eat something small, but I could never identify the food item. On at least seven of these occasions the digging was preceded by an upwind turn of up to 200 m. All of these incidents took place in areas of calcareous soil alongside or near two small pans and I am confident that the animal was eating the fungus Terfezia pfeilii. This fungus, related to the European truffle, is regarded as a delicacy by the local inhabitants of the Kalahari and gives off an odour rather like that of a cooked mealie. It is found during April and May after late summer rains in calcareous, sandy soils, a few centimetres below the ground (Leistner 1967).

Birds' eggs

Ostrich eggs are prized food items of brown hyaenas and like all eggs are highly nutritious. The most striking observation I made in this

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regard was when a female brown hyaena found an unattended nest containing 26 eggs (Fig. 48 a). For about half an hour before she had found the nest, the hyaena had been moving slowly with her nose to the ground, occasionally lifting her head up, then putting it down again, in a purposeful manner as if on a scent trail. From time to time she would move upwind for a short while but basically her movements did not appear to be wind orientated. I do not know where the incubating bird was, and it is possible that it was frightened off by the vehicle, although Sauer and Sauer (1966) report that ostriches do sometimes leave the nest site, particularly before all the eggs have been laid and incubation commences. Two other instances when ostrich eggs were found appeared to be the recovery of eggs which the hyaena had stored itself, and once the animal moved upwind approximately 30 m to one which did not appear to have been stored.

When eating an ostrich egg at the nest, the hyaena mentioned above, after sometimes raking one out from the clutch with her forefeet, bit a small opening in the top of it using her premolars. She then lapped up the contents with her tongue (Fig. 48 b). As the level in the egg dropped she bit the egg open further, continuing in this way until she had finished. Any of the contents that spilled onto the sand were lapped up, but on the whole she was careful not to spill any, as are foxes when eating eggs (Ewer 1973). In contrast to some spotted hyaenas observed by Kruuk (1975 b) in East Africa, which were unable to either open or pick up an ostrich egg, brown hyaenas accomplish this easily and can even carry an ostrich egg for some distance (one observation of 6,8 km) without breaking it or putting it down to rest.

Cubs, on the other hand, are unable to open an ostrich egg. Several times I observed cubs trying to do so by attempting to bite the eggs, digging

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around them and kicking them vigorously with their forefeet through their hindlegs. Similar behaviour in opening eggs has been described in several carnivores, for example, in skunks (Stebler 1938, In: Ewer 1973, Van Gelder 1953) and in many viverrids (Ewer 1973), where eggs and other hard food items are thrown through the back legs against a hard object such as a stone, and broken. Furthermore, Kruuk (1975 b) has a photograph of a golden jackal (Canis aureus) with its forefeet on an ostrich egg, in a position which suggests that the animal was about to kick it backwards. In a region like the Kalahari where stones are rare this behaviour would hardly pay, unless perhaps one egg broke against another. It is unlikely that this pattern of behaviour evolved separately, and it is most probably a relict of a primitve behavioural pattern which has almost been lost amongst the hyaenas and other carnivores, but has undergone further specialisations in the viverrids, reaching its highest form in the banded mongoose (Mungos mungo) (Eisner and Davis 1967, Rood 1975).

Although several pieces of shell from broken ostrich eggs were found at brown hyaena dens (Table 14), I never saw an adult open one for the cubs. Once a female came to a den and, after suckling her cubs, picked up an ostrich egg which the cubs had previously tried to open and carried it off out of sight. A few minutes later she returned to the den without the egg and one of the cubs moved off in the direction she had come from, possibly getting some of the egg's contents

On another occasion, as a hyaena bit open an egg, there was a loud explosion and a most unpleasant odour was emitted. This did not deter the hyaena which ate the entire contents.

The only other time that a brown hyaena was seen to eat a bird's egg was early one morning when a black korhaan flew up approximately 5 m

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away from a foraging hyaena. She went over to investigate, found an egg and consumed it, leaving the shell.

Food storing

When a brown hyaena finds a large amount of food, the excess is often stored as is described in the following example:-

1 August 1975. 20h05. The brown hyaena I am following near Seven Pans finds an ostrich nest with 26 eggs in it (Fig. 48 a) and no adult birds present. After sniffing at the eggs for a few seconds she picks one up and carries it off approximately 50 m where she puts it down in the open (1 in Fig. 49) and runs back to the nest. She then eats two of the eggs and at 20h25 picks up another and moves off with it but I do not follow her. At 20h45 she returns to the nest, picks up another egg (5 in Fig. 49), carries it off in a north-easterly direction for 450 m and puts it down in the middle of a clump of Stipagrostis amabilis, a tall, thick grass. She comes back to the nest and again carries off an egg (6 in Fig. 49) in a northerly direction for 600 m before putting it down under a Grewia bush and returning to the nest. She carries off another 10 eggs in different directions for distances varying between 150 m and 600 m and hides them under various bushes or in grass clumps. At 23h36 she eats another egg at the nest, then carries one off for 600 m, drops it rather casually in a Stipagrostis amabilis clump (18 in Fig. 49) and at 00h12 lies down close by. At this stage there are eight uneaten eggs in the nest.

The next afternoon when I return to the nest at 16h45 there are only two broken eggs remaining (Fig. 48 c). I find the hyaena and a second one close by, both eating eggs, after which the original hyaena moves to a Grewia bush (6 in Fig. 49), picks up the egg stored there and carries it off for 2,1 km before putting it down in some long grass. She then moves away from the nest area and forages until 02h00 when she again returns to the vicinity of the nest. She finds and eats two more of

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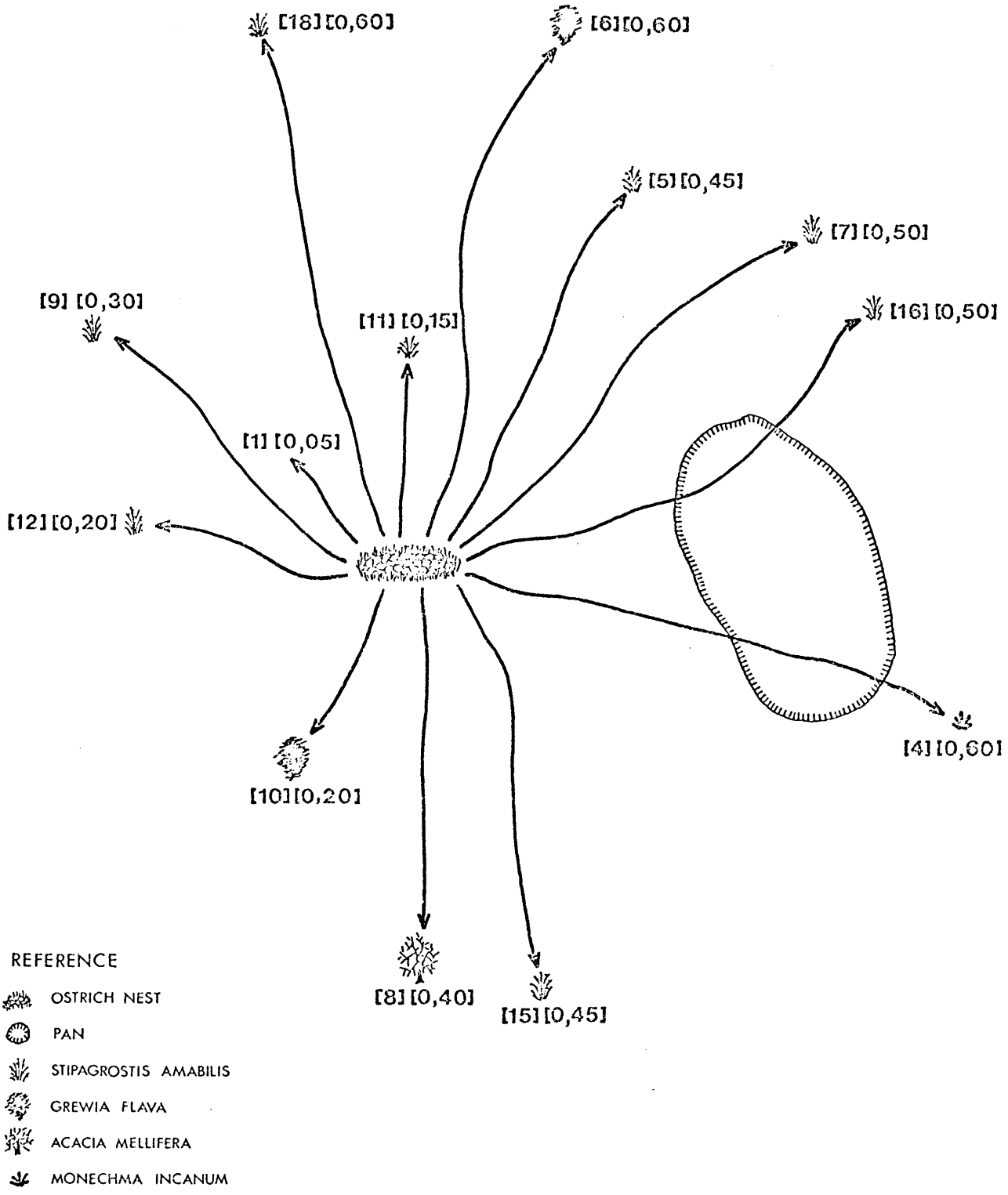


Figure 49. Diagrammatic representation of storing of ostrich (Struthio camelus) eggs by a brown hyaena (Hyaena brunnea) in the southern Kalahari; September 1975. The numbers in the first brackets refer to the sequence in which the eggs were dealt with by the hyaena, missing numbers referring to eggs that were either eaten at the nest or to occasions when the hyaena was not followed when it carried off an egg. Numbers in the second brackets refer to the distance of removal away from the nest(km).

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(a)



(b)

Figure 48. Brown hyaena (Hyaena brunnea) raiding an ostrich (Struthio camelus) nest with 26 eggs in it, in the southern Kalahari: (a) Standing at the nest shortly after finding it. Twenty one eggs are visible, the rest are to the right slightly apart from the main clutch. (b) Lapping up the contents of an egg. A small opening has been bitten in the egg so that the contents are not spilled onto the sand. (c) The nest the next day after all the eggs had either been eaten or carried away for storage.



(c)

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the stored eggs, goes to an Acacia mellifera bush (8 in Fig. 49), picks up a third egg and carries it off for 0,9 km and places it in a Monechma bush. She then moves over to an Acacia haematoxylon bush where there is another egg, eats this and lies down at 03h21.

A comparable observation was made when following another hyaena when she moved straight to a bush out of which she produced an ostrich egg which she ate. She then began circling around, investigating several bushes and after approximately 40 min of this behaviour found another egg under a bush and ate the egg. Approximately 1 km further on she passed an old ostrich nest with a few broken pieces of egg shell scattered around it. The next night she came back to the same area and after casting around for a short while found another two stored eggs.

Examples of red foxes "scatter hoarding" eggs have been given by Kruuk (1964) and Tinbergen (1965), and Macdonald (1976) has illustrated this behaviour experimentally with tame red foxes storing mice. All these authors conclude that the function of this type of storing is to minimise the risk of wholesale losses of a food source to other scavengers.

During my study, 65 food items were observed either to be stored, or to be recovered from storage by brown hyaenas. These stored food items were hidden either under bushes (Fig. 50 a), in clumps of tall grass (Fig. 50 b) or rarely down holes (Table 20). Furthermore, at dens food was often taken underground by the cubs or placed in the hole by the adults, and in fact was often consumed in the den by the cubs.

Of these 65 instances I was able to follow up the subsequent behaviour 12 times, not including the case involving the ostrich eggs related above. Four times the hyaena came back within 6 h and four times within 24 h to recover the food. Once 48 h and once 72 h later, the food was gone when

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Table 20. Food items stored by brown hyaenas (Hyaena brunnea) in the southern Kalahari; April 1972 - July 1976.

ITEM STORED	LOCATION						Total
	Bush		Clump of tall grass		Hole		
	Number	Per cent	Number	Per cent	Number	Per cent	
Herbivore leg	10	55,6	8	44,4	0	0,0	18
Ostrich egg	8	44,4	10	55,6	0	0,0	18
Piece of hide	2	28,6	5	71,4	0	0,0	7
Other meat or bone	15	68,2	5	22,7	2	9,1	22
Total	35	53,8	28	43,1	2	3,1	65

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(a)



(b)

Figure 50. Examples of food storing by brown hyaenas (Hyaena brunnea) in the southern Kalahari: (a) The hindquarters of a steenbok (Raphicerus campestris) under a bush from which the hyaena was flushed. (b) The leg of a gemsbok (Oryx gazella) stored in a clump of tall Stipagrostis amabilis grass.

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I returned and fresh brown hyaena tracks were found in the vicinity, although there was no way of knowing whether the same hyaena that had stored had also retrieved the food. Once, when I returned 72 h later, the food, in this case the hindquarters of a steenbok, had been taken at some time by a leopard. The twelfth case was the longest observed period of food storing and involved a complete black-backed jackal carcass which I found neatly pushed under a small Boscia albitrunca tree when tracking spoor on 12 April 1973. When I returned on 14 April 1973 the carcass had been moved approximately 200 m away by a brown hyaena and dropped in a Stipagrostis amabilis clump. Most of the hair had fallen out and the carcass was crawling with maggots and beetles and stank. On 18 April 1973 a hyaena was observed to come to her den with half a stinking jackal carcass at 22h10 and the next morning, on back tracking the spoor, I found that she had come from the place where this carcass had been stored.

Seven observations were made of brown hyaenas coming to a bush or a clump of grass, pulling out an old piece of hide, chewing on it and then putting it back in the same place. I never, however, saw an animal come to the same place to do this more than once, although it seems that they have a supply of this food source which they can draw on when other food is scarce. A comparable observation was made by Macdonald (1976) when a red fox came back six times to an apple core stored in a clump of grass, chewed on it briefly before returning it and continued on its way.

The brown hyaena's food storing behaviour is again similar to that of the striped hyaena (Kruuk 1976 a) except that the latter appears to store the food near the den most of the time, whereas only four (6,2 per cent) of the brown hyaena's food items were stored within 1 km of a den. Both these species store food more often than spotted hyaenas

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do, possibly because the latter are more social and therefore can ward off most other scavengers (Macdonald 1976). Spotted hyaenas also usually store their food in water (Kruuk 1972).

Food storing behaviour is not as advanced in the hyaenas as it is in many of the canids (Kruuk 1964, Tinbergen 1965, Macdonald 1976) or the mustelids, especially the wolverine (Ewer 1973), where the food is buried. The way in which a brown hyaena will come directly to an area and then cast about, searching from bush to bush, until it finds what it has stored, described above for ostrich eggs and also observed when recovering other kinds of stored food is, however, similar to the way in which these authors describe the recovery of cached food by foxes.

As described earlier, when a carcass with a large amount of meat is found, a brown hyaena will usually break off a large piece and store it close by before coming back to the carcass to feed again, perhaps carrying off more pieces short distances. These are temporary caches, presumably made to maximise the time spent on a food supply that might only be available for a short period (Macdonald 1976), as there is always the possibility that another scavenger might dislodge the hyaena.

Food storing by African carnivores is typically of short duration. The Hyaenidae usually return within 24 h to recover their food (Kruuk 1972 and 1976 a, this study) as do black-backed jackals (Wyman 1967) and leopards (personal observations). This is in contrast to northern hemisphere carnivores such as the red fox, and especially the Arctic fox (Alopex lagopus) and wolverine, where long-term storing occurs, particularly in winter (Ewer 1973). The African climate and numerous invertebrate scavengers do not allow meat to be preserved for long, and of course there are many other vertebrate scavengers which will steal

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cached food and eat it.

What then is the value of food storing to brown hyaenas? Much of the food that they store, such as leg bones, old pieces of hide and ostrich eggs, are reasonably immune to the harsh climate and scavengers other than hyaenas. It is beneficial, however, to remove the food item from its original source, such as a kill site, which would be expected to attract other scavengers, to a place further away under a bush or in some tall grass. Here the chances of it being discovered would be lessened.

Hunting behaviour

Hunting mammals

Prey selection and hunting success rate

Several authors including Mech (1970), Schaller (1972) and Kruuk (1972 and 1976 a) emphasise the fact that considerable caution must be exercised when analysing the efficiency of a predator's hunting behaviour, as it depends so much on what is defined by the observer as an attempt. All the species of hyaena, for example, sometimes run at potential prey in order to make them run, presumably to assess by the gait if an individual in the group is unfit and thus a suitable quarry. If not they will not give chase and it is sometimes difficult to judge if the animal was testing in this manner or in fact chasing with the intent to kill. Furthermore, brown hyaenas sometimes chance upon a small mammal which they will inevitably try to catch, either by lunging at the animal as it runs off, or by giving chase to it. Here again it is sometimes difficult to decide if the act should be included as a hunting attempt,

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or if it was merely a response to the proximity of a potential prey. Nor does it help to include only those cases where the hyaena ran more than a certain minimum distance after a prey species, as the distances that they chased their mammal prey in successful hunting attempts varied from 1 - 1 100 m.

With these limitations in mind I have endeavoured to assess the hunting efficiency of the brown hyaena in catching mammals (Table 21), although some attempts may have been included which were mere tests to assess the prey's potential. With the exception of one of the successful springhare kills, where two hyaenas were involved, all of these observations were of single hyaenas.

In spite of this possible bias the results show how few mammals are caught by brown hyaenas, with five of 88 (5,7 per cent) attempts being successful. The data also show that all hunting is directed towards small mammals. The large number of unknowns is due to the fact that on dark nights and in tall grass areas like the dunes and the river-bed, I was often unable to discern what species of prey the hyaena was running after. I am certain, however, that it was always a small animal, as after the hunt had been terminated, on scanning around with a spot= light, no large or even medium-sized mammal was seen in the vicinity. On some of these occasions the hyaena might have been hunting a bird. Their method of hunting mammals and birds was, however, noticeably different (see later), so this possibility seems unlikely.

In addition to the observations in Table 21, which all concern adult brown hyaenas, large cubs of approximately one year old were observed hunting on six occasions. On five of these I was unable to identify the prey item and on the sixth the animal caught and killed a striped polecat

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Table 21. Analysis of aspects of hunting attempts made on mammals by brown hyaenas (Hyaena brunnea) in the southern Kalahari; April 1972 - July 1976.

MAMMAL	NUMBER OF ATTEMPTS	NUMBER SUCCESSFUL	PER CENT SUCCESSFUL	CHASE DISTANCES (METRES)		
				Mean	Standard error	Range
Bat-eared fox	12*^	1	8,3	112	19,6	5 - 200
Springbok adult	1	0	0,0	50	-	-
Springbok lamb	11	1	9,1	192	57,9	1 - 1 100
Springhare	7	2	28,6+	92	9,0	10 - 150
Black-backed jackal	3	0	0,0	23	13,3	10 - 50
Steenbok	1	0	0,0	10	-	-
Duiker	1*	0	0,0	50	-	-
Aardwolf	1*^	0	0,0	-	-	-
African wild cat	1	0	0,0	150	-	-
Honey badger	1	0	0,0	15	-	-
Hare	1*^	0	0,0	45	-	-
Small rodent	1	1	100,0	20	-	-
Unknown	47	0	0,0	97	14,2	1 - 500
Total	88	5	5,7	-	-	-
Mean	-	-	-	71	7,6	5 - 400

Notes. * One observation from spoor. ^ One observation of attempting to dig the prey out of a hole.
+ But some of the unknowns were thought to be springhares, see text.

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(Fig. 52 a).

The flight distance of large herbivores from a brown hyaena is short and I gained the impression that brown hyaenas were more concerned in avoiding large herbivores than the reverse, although generally they ignored each other. Occasionally, if a large herbivore or group of herbivores was encountered by a brown hyaena, it would stand still for some time while looking at them and then it would move on, often changing course slightly so as to avoid them.

Shortridge (1934) maintains that the brown hyaena will kill injured and new-born small and medium-sized mammals in South West Africa and Roberts (1954) and Skinner (1976) say that normally brown hyaenas will not kill, although under certain circumstances they can become small stock killers. Smithers (1971) is of the opinion that the brown hyaena in Botswana is primarily a carrion eater, but says that it has been reported to kill young domestic stock such as sheep and goats. All these observations are in accordance with those of this study.

My observations, on the other hand, disagree with those of Stevenson-Hamilton (1947) and Pienaar (1969), who maintain that in the Kruger National Park brown hyaenas, hunting in small packs, attack a wide range of large mammal prey including kudu, waterbuck, impala and zebra (Equus burchelli). Although it is admittedly dangerous to extrapolate from one area to another, I feel that it is unlikely that brown hyaenas would overpower such large animals.

The Kruger National Park conclusions were drawn from data collected from two indirect sources; from reports by ranger staff (Pienaar 1969) and by analysing the food items found at dens (Stevenson-Hamilton 1947), and

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assuming that these were killed by the hyaenas. During a visit to the Kruger National Park in June and July 1974, I had the opportunity of questioning several of the experienced ranger staff in the Park and I am satisfied that most of them do not know the difference between the spoor of a brown and a spotted hyaena. Furthermore many of them agreed that spotted hyaenas do not hunt anything larger than an impala lamb, but that brown hyaenas will attack large herbivores. Pienaar (1969) believes that spotted hyaenas in the Kruger National Park do kill large herbivores and Kruuk (1972) has shown how capable they are at accomplishing this is East Africa.

I therefore believe that because of this preconceived opinion, the rangers, on finding a large herbivore killed by hyaenas, assume that it was killed by brown hyaenas, when it is more likely to have been killed by spotted hyaenas, or alternatively if brown hyaena spoor was found round the carcass then it was a case of scavenging. Stevenson-Hamilaton's (1947) conclusion that the remains he found at dens were killed by brown hyaenas is also open to question, as my study has revealed that all large herbivore remains found at dens, and the origins of which could be traced, were scavenged. Pienaar (pers. comm.) is also of the opinion that more conclusive evidence is needed before the true nature of the brown hyaena's hunting behaviour in the Kruger National Park can be established.

Hunting bat-eared foxes

On 11 occasions a brown hyaena was judged to have made an attempt to

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U.deV. Pienaar. Department of Nature Conservations, Privat Bag X404, Skukuza, 1350. September 1976.

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catch a bat-eared fox by chasing it, and on one occasion it was successful (Table 21). Twice the fox ran into a hole and on the other occasions the brown hyaena gave up the chase after running distances ranging from 5 - 200 m after the fox, often in a series of large circles. The twelfth hunting attempt occurred when a brown hyaena dug for 7 min at a bat-eared fox den and then gave up the attempt. On another 10 occasions a brown hyaena showed definite hunting behaviour towards a single bat-eared fox or group of foxes, but did not appear to chase with the intent to kill.

Rejecting one of the hunting attempts which was discerned from spoor, 21 occasions were therefore directly observed of brown hyaenas showing definite predatory interest towards bat-eared foxes. Of these attempts only one took place in dune habitat, although approximately equal time (54,5 per cent in the dunes, 45,5 per cent in the river) was spent observing the hyaenas in river and dune habitat. In December 1975 I carried out two 20 km counts of nocturnal mammals using a vehicle and a handheld spotlight. Once count was made through the dunes and the other along the Nossob river-bed, both through areas which had recently been burnt and where visibility was the same. Eighteen bat-eared foxes were counted during the river-bed count and only one during the dune count, thus suggesting that the river habitat is more favoured by bat-eared foxes, which has also been shown by Smithers (1971). This explains the higher incidence of hunting-orientated behaviour towards bat-eared foxes by brown hyaenas in the river habitat.

The hunt was usually initiated when a hyaena encountered foxes, either after an upwind turn of a few metres, or after it had stopped and looked towards the foxes with its ears cocked. Then it chased them. The pursued animals would run off and any other foxes close by were immediately

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attracted to the activity, sometimes running over to the hyaena and following it with their tails held vertically, but bent over backwards at the tip so that the tail resembled an inverted U. This posture was observed by Kleiman (1967) during agonistic behaviour. When a hyaena abandoned the hunt the foxes usually followed it closely, jinking around it, sometimes uttering a high-pitched bark, and often causing it to run off with its hair raised. On nine other occasions bat-eared foxes followed a brown hyaena in a similar manner even though the hyaena had made no attempt to chase them. A similar behaviour by bat-eared foxes towards striped hyaenas is described by Kruuk (1976 a), and once I observed four foxes follow a leopard in this manner until it jumped into a tree, after the leopard had unsuccessfully attempted to catch one. These are seen as examples of "mobbing" behaviour, well known in birds and mammalian carnivores (Kruuk 1972) and probably have the effect of causing the hyaena to leave the area.

Hunting springbok

Twelve hunting attempts by brown hyaenas on springbok were witnessed and one was successful (Table 21). Once a brown hyaena which was foraging in steady rain moved quickly upwind to where an adult springbok was lying. As the springbok pronked off, the hyaena gave a determined chase for approximately 50 m after which it appeared to lose it. The hyaena then started moving back and forth quickly, located the springbok again and ran after it for a few metres before leaving it. This is the only occasion where a brown hyaena was observed to show definite hunting-orientated behaviour towards an adult springbok, despite the several hundred which occurred in certain areas well frequented by some of the hyaenas that I was observing.

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On the whole brown hyaenas ignored the springbok herds which would merely give way to an approaching walking hyaena when it was approximately 20 m away, in a similar manner that Thomson's gazelles (Gazella thomsonii) do to spotted hyaenas (Walther 1969, Kruuk 1972). On the few occasions, however, when for one reason or another a hyaena was observed to run towards a herd of springbok, they would move out of its way earlier and more rapidly, some of them even pronking. Again a similar behaviour pattern as observed by Kruuk (1972) with spotted hyaenas running towards Thomson's gazelles. Once a brown hyaena stood and looked intently for several minutes at a rutting adult male springbok which was running back and forth herding the females, and here it seemed likely that the hyaena was attracted by this rather striking behaviour.

Springbok in the southern Kalahari are prone to contracting sarcoptic mange, a condition which can severly reduce the mobility of an animal, and under these conditions it is possible that a brown hyaena could overpower the animal, although no observations in this context were made.

Between January and March 1976, however, when there were a large number of lambs in the study area, brown hyaenas showed a real interest in the springbok herds as the following example illustrates:-

> 7 January 1976. 20h05. I find a female brown hyaena amongst a large herd of springbok on the Stipagrostis plains south of Kwang. A lamb gets up 2 m away from her and runs off. The hyaena lunges at it but does not pursue. A little later she gives chase to another lamb for approximately 50 m but the lamb easily escapes. She then moves into the river-bed, proceeds up it in a northerly direction and after approximately 1 km she practically stumbles on a springbok lamb which runs off; again she lunges at it but does not pursue. She now moves out of the river-bed onto the

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plains and starts moving erratically, often with her nose to the ground. She runs off quickly after a springbok lamb over a rise and when I find her again approximately 300 m further on she is standing, looking around. Further on she does an upwind turn moving at a fast walk, then runs for approximately 15 m as a lamb pronks away, and sniffs around where the lamb had been lying. She stays on the plains until 23h00 and has two more chases at lambs, one of approximately 60 m, the other of 20 m, before moving off into the dunes.

The only successful hunt of springbok lamb occurred in the following manner:-

21 March 1976. Just after dark the hyaena being followed in the Nossob river-bed a few kilometres north of Kwang starts running in a north-westerly direction, but it is too dark to see what she is chasing. After 100 m she stops and sniffs around for a few seconds and then changes direction, moving at a fast walk in a southerly direction, changing to the south-east after 150 m. After another 150 m she starts running again at approximately 30 km/h, fairly straight but zig-zagging every now and then. She slows down momentarily after approximately 300 m and then goes hard for another 200 m until she catches and kills a two month old springbok lamb in a stand of tall Schmidtia kalahariensis grass.

This searching and hunting behaviour by brown hyaenas for springbok lambs is again similar to that of spotted hyaenas when searching and hunting for Thomson's gazelle lambs (Kruuk 1972), although brown hyaenas appear to use their noses more than spotted hyaenas do. A striped hyaena was also once observed by Kruuk (1976 a) to hunt a Thomson's gazelle lamb in the manner described above.

Hunting springhares

Springhares were abundant nocturnal mammals in the study area. During

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the counts referred to earlier, 145 springhares were counted in the river and 38 in the dunes. Yet I observed only nine attempts of brown hyaenas hunting springhares, two of which were successful. The low number of attempts observed might be due to the fact that many of the unidentifiable prey animals could have been springhares, as 7,3 per cent of the scats analysed contained springhare remains, showing that they are fairly frequently eaten by brown hyaenas.

One of the springhares was caught in the dunes after a chase of not more than 20 m, and the other in the river after the only hunting attempt I observed involving two hyaenas. In this instance the brown hyaena that caught the springhare did so after a chase of approximately 150 m when the springhare doubled back, passed the front hyaena and was easily caught by the second one which was 20 m behind. This animal then picked up the springhare and ran off with it, being chased by the first hyaena. It outran the first hyaena after a chase in large circles for a distance of approximately 300 m and ate it alone (Fig. 51).

Hunting black-backed jackals

Of all the other carnivores in the southern Kalahari brown hyaenas interact most often with black-backed jackals. On three occasions I gained the impression that a brown hyaena was trying to catch a jackal rather than merely to chase it away as a result of interspecific intolerance, but the hyaena failed in all cases. In addition Ferguson (pers. comm.) twice observed a brown hyaena to run up to a sleeping jackal, with the jackal jumping up and running off when the hyaena was a few metres away. In neither case did the hyaena pursue the jackal further.

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Figure 51. Brown hyaena (Hyaena brunnea) in the southern Kalahari with a half eaten springhare (Pedetes capensis) that it had killed. Note that the front half of the animal has been eaten first.

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Hunting striped polecats

Three interactions between brown hyaenas and striped polecats were observed. Once, whilst I was following a large cub in the moonlight, it suddenly ran approximately 10 m to its right. When I caught up with it, the hyaena was holding down a striped polecat with its forefeet and was biting it in the head. The polecat was at the entrance to a small hole into which it presumably had tried to escape. After a few minutes the polecat died and the hyaena carried it off for 10 m (Fig. 52 a) before devouring it (Figs. 52 b and 52 c).

On another occasion an adult brown hyaena (animal 6) was observed to stop, look ahead and then to run off quickly for 100 m to where there was a jackal. It stopped and the jackal backed away a little, then the hyaena went over to a small bush and appeared to sniff at it. A polecat jumped out from the bush and moved off but the hyaena left it alone. The jackal, however, looked interested in the polecat and followed it.

The third observation involved the same hyaena (animal 6) which, while moving down a road, moved over to a hump on the side of the road and lunged half-heartedly at something. A polecat emerged from this place into the road, turned around so that it was facing the hyaena and backed away from it with its tail up, curved forward over its back. It stopped approximately 3 m away from the hyaena, moved forward a short distance, then backed away again, in the manner described by Rowe-Rowe (1975 a), and then ran down the road right under the vehicle. The hyaena stayed in the same place for approximately 20 s before continuing on its course.

In both these incidents, which took place in open areas, the hyaena

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(a)



(b)



(c)

Figure 52. Large brown hyaena (Hyaena brunnea) cub in the southern Kalahari with a striped polecat (Ictonyx striatus) that it had killed: (a) Carrying it off approximately 10 m from the kill site before eating it. (b) Eating it. (c) Finishing off the tail. All that remained of the polecat were a few hairs and a patch of blood in the sand.

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was in a good position to catch the polecat, which cannot move as fast as a hyaena can. Yet the hyaena made no attempt to do so. The cub that caught the polecat was one of three whose mother was dead and which were therefore not getting much food, as the adults particularly the mother, provide the cubs with some food until they are approximately 15 months old. It is possible, therefore, that striped polecats are not highly sought after food items and are only eaten when other food is scarce. The adult in the above examples, on the other hand, was enjoying a good supply of food when these incidents took place. Furthermore only one (0,3 per cent) of the scats analysed contained polecat hair which also suggests a low preference rating for this mammal by brown hyaenas. Alternatively the effect of other antipredatory mechanisms of polecats, apart from flight, such as chemical defense, might be highly efficient in warding off brown hyaenas.

Hunting other mammals

Once a brown hyaena was seen to catch a small rodent after stopping, looking to its right and then running around in small circles for approximately 10 s. Other mammals that were seen to be hunted once were an African wild cat, which took refuge in a tree after being chased for approximately 150 m, a steenbok that was chased for approximately 10 m, and a honey badger (Mellivora capensis) which escaped under an Acacia mellifera bush after a short chase of 10 - 20 m from whence it faced the hyaena, emitting a grating, rattling sound as described by Sikes (1964).

From spoor it was possible to reconstruct chases after a hare and a duiker (Sylvicapra grimmia) as well as the one after the bat-eared fox mentioned earlier. Once a brown hyaena was tracked to an aardwolf den

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where it had tried to dig out two large cubs, but it gave up after digging approximately 1 m into the den. On four other occasions from direct observations, three after hard chases of 20, 100 and 150 m, the other when the hyaena suddenly sprung to its right, it was seen to dig briefly at a fairly large hole, and these too might have been aardwolf dens.

On three occasions I watched a foraging brown hyaena encounter porcupines which are sometimes eaten by them (Table 13 and 14). On none of these occasions, however, did the hyaena show much interest in the porcupines and they in turn were not unduly concerned by it. For example, once when following a brown hyaena that was moving down a road, two porcupines were seen ahead moving in the same direction. The hyaena was moving faster than the porcupines and soon caught up with them. As he passed them they moved over to the right-hand side of the road and watched him pass well over on the left-hand side. The hyaena merely glanced at them as he passed.

Hunting birds

Sixteen observations of adult brown hyaenas attempting to catch birds were made (Table 22). Apart from kori bustards and korhaans these were apparently merely chance affairs when the hyaenas flushed the birds whilst foraging, and lunged at them. On one of these occasions the brown hyaena snapped up a small bird and on another it flushed a black korhaan which had a chick(s) and ate it (them). Once a hyaena ran 25 m towards a kori bustard approximately 60 m away, which flew off. On two other occasions short chases were also made, but again the bustards flew off.

Korhaans (black and red-crested) are common in the dune areas and I

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Table 22. Analysis of aspects of hunting attempts made on birds by brown hyaenas (Hyaena brunnea) in the southern Kalahari; April 1972 - July 1976.

BIRD	NUMBER OF ATTEMPTS	NUMBER SUCCESSFUL	PER CENT SUCCESSFUL	CHASE DISTANCES (METRES)	
				Mean	Range
Korhaan sp.	5	3	60,0	6	3 - 12
Black korhaan chicks	1	1	100,0	-	-
Unidentified small bird	4	1	25,0	-	-
Kori bustard	3	0	0,0	10	1 - 25
Cape dikkop	2	0	0,0	-	-
Crowned plover	1	0	0,0	-	-
Total	16	5	31,3	-	-

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observed five attempts by brown hyaenas to catch one, three of which were successful. Four of these attempts were made when the hyaena stopped, turned sharply (I was unable to determine if this was upwind) and then moved quickly, perhaps running a few paces but usually at a fast walk, with its head down, until either the korhaan flew up or the hyaena caught it. All these attempts were made by the same individual (animal 6), and the first attempt which was observed on 30 March 1976 was successful. Up to that time she had been followed for approximately 550 km through the dunes and had never been observed to try and catch an adult korhaan. After that, until the end of July 1976, from 60 km of following, I observed four more attempts by this animal to catch a korhaan, two of which were successful. None of the other brown hyaenas observed during the study ever made an attempt to catch a korhaan (three of them were followed for a total distance of 274 km through the dunes between April and July, mainly in 1975) and it appeared that this female had learnt a technique for catching korhaans during the study. I do not believe that conditions had altered significantly between these two years as korhaans were common in the dune areas throughout the study. In view of the high success rate achieved by this female in catching korhaans and the fact that they are so common, it is strange that brown hyaenas do not hunt these birds more regularly.

Hunting frequencies in river and dune habitat

Of the 104 attempts by adult hyaenas to catch mammals or birds signif= icantly more (66,3 per cent) took place in river habitat than in the dunes (33,7 per cent) (Binomial; $p = 0,0086$). Furthermore, if the hunting frequencies of animal 6, which often used the river habitat to forage in (53,1 per cent of the time) are compared with those of two other females (animals 11 and 20) which mainly used the dunes (95,8 per cent of the

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time), the first individual made one chase for every 17,5 km followed, whereas the others made one chase for every 36,0 km followed respectively (Chi-squared = 7,52; df = 2; $p < 0,05$) (Table 23). There was no signif= icant difference between the hunting frequencies of any of these animals in the dunes (Chi-squared = 2,7; df = 2; $p > 0,05$) which suggests that the observed difference was not due to an individual difference in hunting behaviour. One of the main reasons for this discrepancy is the fact that the three main prey mammals of the brown hyaena, springbok lambs, bat-eared foxes and springhares, show a preference for river habitat and are less concentrated in the dunes, except around pans.

In terms of biomass (figures taken from Smithers (1971) for bat-eared fox, springhare and mouse, Skinner and Van Zyl (1971) for springbok lamb, and Kemp (pers. comm.) for birds) the total from kills in the river was approximately 13,4 kg and from the dunes 5,2 kg. Taking into account the relative times that hyaenas were observed in these two habitats (see earlier) these figures show that hunting is more productive for brown hyaenas in river than in dune habitat (Chi-squared = 5,20; df = 1; $p < 0,05$).

The brown hyaena's vertebrate hunting behaviour and comparison with other hyaenas

The vertebrate hunting behaviour of the brown hyaena appears to be similar to that described by Kruuk (1976 a: 103) for the striped hyaena, i.e. "a 'primitive' chase and grab affair", where mammalian and bird prey forms a small contribution to the diets of both species. The only time that I could detect any sort of specialisation in the brown hyaena's hunting behaviour, when it purposefully looked for potential prey, was when hunting springbok lambs.

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Table 23. Frequency of hunts by three individual brown hyaenas (Hyaena brunnea) followed in river and dune habitat in the southern Kalahari; December 1974 - July 1976.

ANIMAL'S NUMBER	TOTAL DISTANCE (KM) FOLLOWED	PER CENT OF TIME SPENT IN RIVER	DISTANCE (KM) MOVED PER HUNT IN RIVER	PER CENT OF TIME SPENT IN DUNES	DISTANCE (KM) MOVED PER HUNT IN DUNES	COMBINED FREQUENCY OF HUNTS (KM PER HUNT)
6	1 300	53,1	11,3	46,9	46,9	17,5
11	360	4,5	-	95,5	34,4	36,0
20	178	3,7	-	96,3	34,3	35,6
11 and 20	538	4,2	-	95,8	34,3	35,8

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Although I have only one observation of two individuals hunting together, I did get the impression that this enhanced the chances of success. Only one of the hyaenas, however, derived any benefit from the hunt and it is clearly not beneficial for brown hyaenas to hunt small animals in groups. This hunt was, moreover, almost certainly a chance occurrence as before the hunt commenced these two, litter mates of approximately two years old, were indulging in social activities and were certainly not foraging seriously. Only when one of them saw the springhare approximately 20 m away did the chase start.

Kruuk (1976 a) comments on the way that a striped hyaena raises its mane during pursuit, suggesting that this behaviour seems maladaptive in that it must slow the animal down. Brown hyaenas also often raise their manes, particularly in inter- and intraspecific interactions, but during hunting this was less obvious. Neither was the action of shaking when killing small animals, found in both the spotted and striped hyaenas (Kruuk 1976 a) noticed in this study. The only time that I was in a good position to observe this behaviour, however, was when the cub killed a polecat and then it did not occur. Stalking, which also occurs occasionally in the other two hyaenas (Kruuk 1976 a) was never observed.

As mentioned earlier, brown hyaenas hunting springbok lambs resembled spotted and striped hyaenas hunting Thomson's gazelle lambs (Kruuk 1972 and 1976 a). Assuming that these two prey species are ecological equivalents and that spotted hyaenas in the Kalahari hunt springbok lambs, which it appears they do (Eloff 1964 and 1975, personal obser= vations), this is where there is most overlap between the hunting behaviour and prey selection of the brown and spotted hyaenas. Even here, however, brown hyaenas appear to be rather inefficient, with a 9,1 per cent success rate for springbok lambs as compared with a 36,0

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per cent success rate for spotted hyaenas hunting Thomson's gazelle lambs (Kruuk 1972).

The contribution to the diet of a brown hyaena of animals actually hunted and killed is clearly small. These data were collected from approximately 2 400 km of following adults which, given that on average a brown hyaena moves 32 km per night, is equivalent to 75 nights. The average daily consumption of a brown hyaena has been calculated as 2,8 kg of food and the biomass of killed animals in 75 nights as 18,6 kg. However, not all this killed prey was eaten by the hyaena. The entire bat-eared fox and approximately half the springbok lamb were taken back to the den for the cubs, which makes the total biomass of prey killed and eaten by one hyaena approximately 12,2 kg. Therefore in 75 nights a brown hyaena consumes approximately 2,8 x 75 = 210 kg of food of which 5,8 per cent is killed. This, however, cannot be taken as an absolute indication of the contribution of killed prey to their diet as this food source is one of the highest in caloric value they receive, and it is therefore more important than would appear from these figures.

Hunting insects

Although insects form an important component of the diet of the brown hyaena (Table 13) I have few direct observations of hyaenas eating them. As suggested earlier, many of the "unidentifieds" in Table 12, when an individual spent a comparatively short period eating something off the ground, or snapped at something, were insects.

Apart from termites, the only insect that I observed to be eaten by a hyaena was a locust which was snapped off a tall grass stalk as the hyaena passed it. On two other occasions an individual was observed to

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YUNIBESITHI YA PRETORIA

move slowly in an erratic manner for several minutes with its nose to the ground, and on moving off a number of large black ants on one occasion, and dung beetles on the other, were seen. Although I never saw the hyaena actually ingest anything it was almost certainly feeding on these insects. Sometimes at a den when I was observing the hyaenas with a spotlight they would snap at an insect attracted by the light, but these observations have been excluded from Table 12. Brown hyaenas were never observed to run and then to jump into the air to catch a flying insect as striped hyaenas do (Kruuk 1976 a).

The only animals observed eating termites were the three large cubs. Ten such feeding bouts were observed, of which two lasted for less than 0,5 min, four from 1 - 5 min, two for 10 min, one for 26 min and one for 48 min. Termites were located apparently fortuitously or after an upwind turn. Once, for example, a cub was lying on the mound in front of its den when it got up and with its ears cocked moved quickly upwind to a Grewia bush. Around this bush was a colony of termites which it began feeding on, and it was clear that from where it was lying the hyaena had heard them generating a noise. Sound has also been mentioned as an important aid in detecting termites for aardwolves (Kruuk and Sands 1972).

When feeding on termites a hyaena would walk slowly amongst them with its nose close to the ground and its ears cocked, licking the termites up. It was not determined what caused a hyaena to terminate a feeding bout as there were always termites visible when it moved off. It was not caused by a chemical mode of defence as has been suggested by Kruuk and Sands (1972) to be the cause for aardwolves terminating their feeding bouts on Trinervitermes, as Hodotermes do not secrete distasteful

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chemicals (Coaton pers. comm.)

W.G.H. Coaton. Department of Agricultural Technical Services, Private Bag X116, Pretoria, 0001. December 1976.

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CHAPTER 5 : DISCUSSION AND CONCLUSIONS

Methods of investigating the diet of the brown hyaena

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 habits of the brown hyaena this technique does not yield satisfactory results. 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 b).

However, the brown hyaena's trapability and tolerance to immobilising drugs, and its large size, making it possible to fit a large and power= ful 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. The fairly simple method of keeping a record of food items found at brown hyaena dens gives a good picture of the type of food the cubs are fed by the adults, but does not reveal how the hyaenas acquired this food.

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A comparison of the diets of the four species of the Hyaenidae

The observations of Ewer (1954) regarding the dentition of the three hyaenas, where the spotted hyaena has the most specialised dentition followed by the brown and then the striped hyaena (see earlier), and the greatly reduced dentition of the aardwolf, are reflected in the diets of each of the species of the Hyaenidae (Table 24).

The aardwolf is the most specialised feeder of the family with 91,8 per cent of the food items found in faeces collected in the Serengeti being insects (Table 24), the large majority of which were a single species of termite, Trinervitermes bettonianus (Kruuk and Sands 1972). In addition Smithers (1971) found that Isoptera occurred in all 20 stomachs of aardwolves collected in Botswana, of which the vast majority were T. rhodesiensis, and Bothma (1971 a) found T. trinervoides to form the bulk of the stomach contents of eight aardwolves collected in the Transvaal and northern Natal.

Ninety per cent or more of the food items found in spotted hyaena faeces in the Serengeti and the Ngorongoro Crater (East Africa) were from large and medium-sized mammals (Kruuk 1972), and in the Timbavati, Transvaal, South Africa, a woodland area, from very large, large and medium-sized mammals (Bearder 1977) (Table 24). Furthermore, in the southern Kalahari spotted hyaenas have been observed to feed on large mammals on 23 (71,8 per cent) occasions, on medium-sized mammals on eight (25,0 per cent) and an ostrich once (3,1 per cent), and the seeds of wild fruits were found in 24 of 149 (16,1 per cent) of their faeces which were examined (Mills in press). In the Namib Desert (South West Africa), the approx=imately 20 spotted hyaena faeces that were locked at all contained gemsbok hair and a few, large insect remains (Mills and Kruuk 1976).

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Table 24. Percentage occurrence of various food categories in the faeces of spotted (Crocuta crocuta), brown (Hyaena brunnea) and striped (Hyaena hyaena) hyaenas and the aardwolf (Proteles cristatus) from different areas in Africa.

FOOD CATEGORY	SPOTTED HYAENA			BROWN HYAENA	STRIPED HYAENA	AARDWOLF
	Serengeti[1]	Ngorongoro[1]	Timbavati[2]	Southern Kalahari[3]	Serengeti[4]	Serengeti[5]
Very large mammals (>400 kg)	0,6	0,8	38,3	0,0	0,0	0,0
Large mammals (80-400 kg)	63,0	87,5	19,1	24,7	8,9	0,0
Medium-sized mammals (12-80 kg)	35,7	10,9	39,7	3,3	19,0	0,0
Small mammals (1-12 kg)	0,2	0,0	0,7	16,5	6,8	0,0
Very small mammals (<1 kg)	0,0	0,0	0,5	1,5	1,7	0,0
Birds	0,4	0,0	0,5	4,0	12,3	0,0
Reptiles	0,0	0,0	0,1	6,0	11,1	0,0
Insects	0,0	0,0	0,0	16,8	28,5	91,8
Fruits and vegetable matter	0,0	0,0	0,0	21,0	11,7	8,2
Unidentified hair	0,2	0,8	1,1	6,0	0,0	0,0
Total number of items found	658	530	794	547	179	196
Number of faeces analysed	401	348	527	143	50	79

Notes. 1 = Kruuk 1972. 2 = Bearder 1977. 3 = This study. 4 = Kruuk 1976 a. 5 = Kruuk and Sands 1972.

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Here too spotted hyaenas have been recorded to eat wild fruits (Stuart 1976). Spotted hyaenas, therefore, select most of their food from two or three of the categories in Table 24, but are also capable of utilis= ing others.

The brown and striped hyaenas have the most varied diet with 90 per cent or more of the remains found in faeces coming from six categories (Table 24). In addition to the categories in this Table, brown hyaenas also readily eat birds' eggs. In the Transvaal scavenged large domestic stock, small mammals and vegetable matter make up the bulk of the brown hyaena's diet (Skinner 1976). On the coastal plain of the Dead Sea in Israel, offal, dead chickens and other abattoir waste, specially put out at a carnivore feeding site by the Nature Reserve Authority, form the bulk of the striped hyaena's diet, with hyrax and fruits also being eaten (Macdonald 1977).

There is most overlap in diet, therefore, between the brown and striped hyaenas and both these species' diets overlap with that of the spotted hyaena, and to a small extent with that of the aardwolf. There is no known overlap in the diets of the spotted hyaena and the aardwolf.

An important consideration, particularly when dealing with hyaenas, is how the vertebrate food was obtained. In the Serengeti 58,3 per cent, and in the Ngorongoro Crater 95,5 per cent, of carcasses that spotted hyaenas were observed feeding on were killed by the hyaenas themselves (Kruuk 1972). In Timbavati, where direct observations of spotted hyaenas foraging were impossible, it is inferred from indirect observations that the majority of the very large mammals (all giraffe (Giraffa camelopardalis)) were scavenged and that the medium-sized mammals (mainly impala) were killed by the hyaenas (Bearder 1977). The spotted

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hyaena observations from the Kalahari were also mainly of an indirect nature, where 28,1 per cent of the carcasses were definitely killed by them, 37,5 per cent were probably killed, 21,9 per cent were scavenged and 12,5 per cent were indeterminable (Mills in press).

Brown hyaenas in the Kalahari scavenged 95,8 per cent of the vertebrate food items they were observed to feed on and striped hyaenas in the Serengeti and Israel also scavenged nearly all of their vertebrate food (Kruuk 1976 a, Macdonald 1977). Both these species, moreover, direct their limited hunting behaviour towards the young of medium-sized mammals and other small animals.

Schaller and Lowther (1969) maintain that there is no ecological room for a total mammalian scavenger. Observations on the Hyaenidae support this statement as the two species which scavenge the most in this family (the brown and striped hyaenas) supplement their diets to a significant degree with wild fruits, insects and birds' eggs.

Some adaptations of the brown hyaena to its environment

The brown hyaena is well adapted physiologically, morphologically and behaviourally to exist on the food it does and in an arid region. It has a highly efficient digestive system and is able to digest the organic matter in bone. Its skull and dentition are modified for crushing bones and slicing through hide and tendons, although it is not as specialised in this respect as the spotted hyaena is, so that the brown hyaena can deal more efficiently with a wider range of food items. For example, the chopping function of the talanoid of M_1 against M^1 (Ewer 1954) may assist the brown hyaena when eating wild fruits (and possibly insects), as they would often appear to chew up the flesh of

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tsamas and gemsbok cucumbers with these teeth.

The well developed forequarters in comparison with the poorly developed hindquarters (Fig. 35) means that much of the brown hyaena's strength is in its neck and shoulder region, thus assisting it in twisting off and breaking large bones and also in carrying heavy food items long distances to cubs. There is no need for strong hindquarters in a species like the brown hyaena that does not have to run down fast moving prey over long distances, as does the spotted hyaena.

Endowered with an efficient olfactory system the brown hyaena is particularly adept at finding carrion. In addition it is able to cover vast distances at night, alone, and can therefore efficiently utilise the many small pieces of carrion that are scattered over its range. Thus it is not solely dependent for its carrion on the patchily distributed kills of other large carnivores. Should it procure a large amount of food, however, it is able to utilise it, often storing the excess. The large pinnae of the brown hyaena are part of an excellent hearing system and it is quick to act on auditory cues in its acquisition of food.

The almost exclusive nocturnal behaviour, besides being an adaptation for the conservation of water, might also have evolved in the Hyaenidae as a means of avoiding competition from the other dominant scavengers, i.e. vultures, which are almost exclusively diurnal.

The hunting behaviour of the brown hyaena, although fairly primitive, is important in providing individuals with the odd highly nutritious meal.

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Finally, brown hyaena social organisation, where individuals forage solitarily, but live in large territories which are shared with other, mostly closely related conspecifics, is correlated with the distribution and type of food it exploits (Mills in press and in prep.).

The brown hyaena is in fact better adapted than the spotted hyaena and the other large carnivores in southern Africa to live in an arid region like the southern Kalahari, where the large ungulates are thinly and erratically distributed.

The conservation of the brown hyaena; some suggestions for future management and research

It is essential for the well-being of this species in the southern Kalahari that management practices do not alter the characteristics of the habitat significantly, especially in so far as making it more suitable for other large carnivores, particularly spotted hyaenas. There is some evidence to suggest that an increase in the large carnivore population, especially that of the spotted hyaena, would have a detrimental effect on the brown hyaena population. This relation= ship should be more fully studied in the future.

This 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. As a start to overcoming this problem and because they are such important fruits to most of the animals inhabiting the Kalahari,

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a study of the abundance, distribution and utilisation of the tsama and gemsbok cucumber has been initiated. It would be useful to determine how important these fruits are to brown hyaenas, exactly how they derive benefit from them and how they cope when these fruits are in short supply. Few data were collected when these fruits were scarce, and all the hyaenas that were studied were within reach of artificial water.

The fact that brown hyaenas scavenge so much of their vertebrate food in the Kalahari does not necessarily mean that they will do so in other areas, as amongst the carnivores there is a large range of intraspecific variation in food ecology (Kruuk 1976 b). It would therefore be valuable, both from the academic and management points of view, to investigate the feeding habits of the brown hyaena in other areas. There is, however, some evidence that in the Transvaal agricultural areas brown hyaenas are predominantly scavengers and that stock killing is limited to individual hyaenas (Skinner 1976). The female in my study that was believed to become a korhaan specialist also suggests that individual brown hyaenas can become specialist hunters, and Kruuk (1976 b) mentions that this phenomenon is widespread amongst the carnivores.

It is suggested, therefore, that the brown hyaena may be well-adapted to live side by side with man in certain agricultural areas and that more research should be carried out into its feeding habits as well as means of protecting domestic stock from predation in such areas.

To achieve this latter goal methods which might prove successful include: removing the culprit in the case of an individual stock killer (Skinner 1976), the use of aversive conditioning with lithium chloride (Gustavson, Garcia, Hankins and Rusiniak 1974), the provision of temporary wire netting enclosures in camps to afford protection for

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lambs and calves (Rowe-Rowe 1975 b), the practice of shepherds sleeping with their flocks, and the provision of alternative food such as a wild ungulate or low value domestic animals (Mills 1976 b). In Israel, the establishment of a carnivore feeding site by regularly putting out all kinds of abattoir waste, has successfully led to the conservation of striped hyaenas and other carnivores (Macdonald 1977). This practice could also be attempted in South Africa.

I would also like to suggest that the brown hyaena may be a suitable animal to be kept on smaller game reserves. The provision of adequate fencing and the supply of extra food during times of food scarcity could help to keep the hyaenas on the reserve (Mills 1976 b), where the presence of the species would add to the ecological diversity and therefore to the stability of such a reserve.

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SUMMARY

The brown hyaena (Hyaena brunnea Thunberg, 1820), an endangered species, is essentially an inhabitant of the south-west arid and adjacent drier parts of the southern savanna biotic zones. Little is known about its life history and this study was initiated in order to define the limiting factors on the brown hyaena population in the southern Kalahari. With this information a management plan to help ensure its survival in this area will be drawn up. In this thesis the diet of the species is analysed and a description on the way it procures its food is given.

The study was carried out in the Kalahari Gemsbok National Park, Republic of South Africa and the adjacent Gemsbok National Park, Botswana; a semi-desert region having an irregular rainfall and experiencing large temperature fluctuations both on a daily and a seasonal basis.

The southern Kalahari is a large sand-filled basin in the west of the south African sub-continent. The sand deposits are arranged in a series of long, roughly parallel, longitudinal dunes, which are fixed by vegetation. Four dry rivers, draining southwards, run through the area and a number of pans are distributed amongst the dunes. Beneath the sand lies a sheet of calcareous or silicified sand or sandstone (calc) which is exposed at places along the river courses and in a number of pans. Underlying the calc lies blue shale with occasional intrusions of dolerite.

The vegetation of this area is defined as the western form of the Kalahari thornveld and for the purposes of this study two habitat types are recognised: river and dune.

Numerous invertebrates, reptiles, birds and mammals inhabit the southern

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Kalahari. It is particularly rich in small mammals, although large mammals are for the most part thinly and erratically distributed.

Data were collected from April 1972 until July 1976. Four methods were used: tracking spoor, direct observations on individual brown hyaenas fitted with radio collars and beta lights, faecal analysis and recording food items found at dens. Most hyaenas were caught in a baited drop-door trap and immobilised with Sernylan or Ketamine.

The brown hyaena has a varied diet. Mammals, most of which are scavenged, form the most important component of their diet and they were recorded feeding on 25 of the 35 (71,4 per cent) mammals (excluding small rodents, insectivores and bats) which inhabit the area. Small canids, gemsbok (Oryx gazella), steenbok (Raphicerus campestris) and red hartebeest (Alcelaphus buselaphus) were the most frequently found remains in faeces. Springbok (Antidorcas marsupialis), gemsbok, hartebeest and steenbok were most frequently observed to be eaten during the direct observations.

Birds, reptiles, insects (mainly Coleoptera and Hodotermitidae) and birds' eggs were also frequently eaten by brown hyaenas. Wild fruits, particularly the tsama (Citrullus lanatus) and gemsbok cucumber (Acanthosicyos naudianus) are important food items for brown hyaenas and, although the moisture provided by these fruits is of importance, they are also of nutritional value.

The diets of cub and adult brown hyaenas were found to differ significantly in certain respects. Cubs eat more small mammals and insects and fewer large mammals and wild fruits than adults do.

Two lactating female brown hyaenas were found to consume 2,8 kg of food

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per day, a relatively large amount, mainly because of the low nutritional value of much of their food.

Brown hyaenas are independent of permanent water but do sometimes use artificial boreholes to obtain water, and regularly drink from rain puddles when they are available.

Adult brown hyaenas were on average active for 42,6 per cent of the 24 h period, mainly at night. Because of the severe ecological conditions and therefore the comparative scarcity of food, they showed only a weak two-peak activity rhythm. Three large cubs from the same litter were found to be more diurnal than adults were. The choice of daily resting sites varied with the season, with a thick tree or a hole being used in summer, when keeping cool is most important, a bush or a small tree in spring and autumn, and a bush or a tall grass clump in winter. No fixed daily resting sites were used.

The mean distance covered in a night's foraging by a brown hyaena was 32 km and the animals nearly always foraged alone. The olfactory sense was the most important in locating food, especially carrion, although auditory and visual cues were also sometimes used. Much of the scavenged food eaten was small pieces of bone, odd legs and skulls, although large remains and a few untouched carcasses were found. Lions (Panthera leo) provided brown hyaenas with a substantial amount of food, but leopard (Panthera pardus) kills were usually unobtainable as they were stored in trees. Once a brown hyaena was observed to chase a cheetah (Acinonyx jubatus) and her three small cubs off a springbok kill and four times a brown hyaena chased a caracal (Felis caracal) off its kill. There is a fair amount of competition between black-backed jackals (Canis mesomelas) and brown hyaenas with both depriving the other of food on occasions. Brown

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hyaenas were also observed scavenging from some birds of prey and from man.

Wild fruits were apparently usually encountered by a brown hyaena by chance, or after a short upwind turn. The mean number of tsamas eaten per bout was 2,0 and the mean number of gemsbok cucumbers 1,4. Ostrich (Struthio camelus) eggs were the most frequently observed egg to be eaten and these were opened up easily, the hyaenas exercising care not to spill the contents of the egg onto the sand.

When a large amount of food was found the excess was usually stored by the hyaena, either under a bush, in a clump of tall grass or occasionally down a hole and most times it was recovered within 24 h. The advantage of this behaviour is seen as removing the food from a source which might attract other scavengers.

All hunting behaviour by brown hyaenas was orientated towards small animals, except once when an adult springbok was chased. Of 104 cases judged to be attempts 10 (9,6 per cent) were successful, the victims being korhaan (3), springhare (Pedetes capensis) (2), bat-eared fox (Otocyon megalotis) (1), springbok lamb (1), small rodent (1), black korhaan (Afrotis afra) chicks (1), and unidentified small bird (1). In addition a large cub was once observed to kill a striped polecat (Ictonyx striatus). Approximately 5,8 per cent of the biomass of food eaten by brown hyaenas was from brown hyaena-killed vertebrates.

Except for termites, observations on insect hunting by brown hyaenas were difficult to make as usually the insects were snapped up and not identified.

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It is concluded that a combination of direct observations and faecal analysis yields an accurate picture of the brown hyaena's diet in the southern Kalahari, although they do not reveal the exact importance of each item. The analysis of food items at dens represents accurately the type of food cubs are fed by adults, but tracking spoor has severe limitations.

Amongst the Hyaenidae the brown hyaena and striped hyaena (Hyaena hyaena) have the most varied diet and they are predominantly scavengers. The spotted hyaena (Crocuta crocuta) is a hunter-scavenger feeding mainly off large mammals, and the aardwolf (Proteles cristatus) is a highly specialised insect eater.

The brown hyaena is the best adapted of the larger carnivores in southern Africa to live in an arid region like the Kalahari and manage= ment practices should not alter the characteristics of the habitat by making it more suitable for other large carnivores, particularly spotted hyaenas. It is suggested that research should be carried out in some agricultural areas and smaller game reserves in order to investigate the extent to which the brown hyaena clashes with mans' interests in these areas, and ways of overcoming this problem.

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OPSOMMING

Die bruinhiëna (Hyaena brunnea Thunberg, 1820), 'n bedriegde diersoort, is in wesse 'n inwoner van die droë suidwestelike en aangrensende droër dele van die suidelike savanna biotiese sones. Sy lewensgeskiedenis is nog feitlik onbekend en hierdie studie is van stapel gestuur met die doel om die beperkende faktore van die bruinhiënabevolking in die suidelike Kalahari te omskryf. 'n Bestuursplan sal op grond van hierdie inligting opgestel word om die voortbestaan van die bruinhiëna in hierdie gebied aan te help. In hierdie tesis word die dieet van hierdie diersoort geanaliseer en die metode van voedselverkryging beskryf.

Die studie is in die Kalahari-Gemsbok Nasionale Park, Republiek van Suid-Afrika, en die aangrensende Gemsbok Nasionale Park, Botswana, uitgevoer. Dit is 'n halfwoestyngebied met 'n ongereelde reënval, wat groot daaglikse en seisoenale temperatuurskommelings ondervind.

Die suidelike Kalahari is 'n uitgestrekte sandgevulde kom in die weste van die Suid-Afrikaanse subkontinent. Die sandneersettings vorm 'n reeks lang, min of meer parallele, lengteverlopende duine wat deur plantegroei bevestig word. Vier droë riviere, wat suidwaarts dreineer, deurkruis die gebied en tussen die duine is daar 'n aantal panne. Onder die sand lê 'n plaat kalkagtige of verkieselde sand of sandsteen (kalk) wat hier en daar in die rivierbeddings en by 'n aantal panne ontbloot is. Onder die kalk lê blou skalie met enkele dolerietintrusies.

Die plantegroei van hierdie gebied word as die westelike tipe van die Kalahari-doringveld beskryf en vir die doeleindes van hierdie studie word twee habitattipes erken: rivier en duin.

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Talryke ongewerweldes, reptiele, voëls en soogdiere bewoon die suidelike Kalahari, wat veral ryk aan klein soogdiere is, terwyl die groot soogdiere meesal yl en erraties versprei is.

Data is van April 1972 tot Julie 1976 versamel. Vier metodes is gebruik: spoorsny, direkte waarnemings van individuele bruinhiënas met radionek= bande en betaligte aan, misontledings en die aanteken van voedselitems wat by nesgate gevind is. Die meeste hiënas is in vanghokke met lokaas gevang en met Sernylan of Ketamine geimmobiliseer.

Bruinhiënas vreet 'n wye verskeidenheid voedselitems. Die belangrikste komponent van hul dieet is soogdiere, wat meesal geaas word. Daar is aangeteken dat hulle 25 (71,4 persent) van die 35 soogdiersoorte in die gebied (uitgesonderd klein knaagdiere, Insectivora en vlermuise) gevreet het. Die oorblyfsels van klein Canidae, gemsbok (Oryx gazella), steenbok (Raphicerus campestris) en rooihartbees (Alcelaphus buselaphus) was die volopste in die mis. Tydens direkte waarnemings is die vreet van springbok (Antidorcas marsupialis), gemsbok, hartbees en steenbok egter die meeste aangeteken.

Voëls, reptiele, insekte (hoofsaaklik Coleoptera en Hodotermitidae) en voëleiers is ook dikwels deur bruinhiënas gevreet. Wilde vrugte, veral die tsamma (Citrullus lanatus) en gemsbokkomkommer (Acanthosicyos naudianus) is belangrike voedselitems vir die bruinhiëna en alhoewel die vog wat hierdie vrugte verskaf belangrik is, het hulle ook voedings= waarde.

Die dieet van welpies en volwasse bruinhiënas verskil betekenisvol in sekere opsigte. Welpies vreet meer klein soogdiere en insekte en minder groot soogdiere en wilde vrugte as die volwassenes.

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Daar is vasgestel dat twee sogende bruinhiënawyfies 2,8 kg voedsel per dag verorber het, wat 'n groot hoeveelheid is, hoofsaaklik weens die lae voedingswaarde van baie van hul voedsel.

Bruinhiënas is onafhanklik van standhoudende water maar benut soms kunsmatige boorgate om water te verkry en drink gereeld van reënpoeletjies indien beskikbaar.

Volwasse bruinhiënas was gemiddeld vir 42,6 persent van die etmaal aktief, hoofsaaklik snags. Weens die strawwe ekologiese toestande en dus relatiewe voedselskaarste het hul aktiwiteit slegs 'n lae tweepiekritme getoon. Daar is bevind dat drie groot welpies van dieselfde werpsel meer dag= lewend as die volwassenes was. Die keuse van rusplekke bedags het met die seisoene gewissel. Gedurende die somer, wanneer dit belangrik was om koel te bly, is 'n dik boom of gat verkies, terwyl 'n bos of klein boompie in die lente en herfs en 'n bos of langgraspol in die winter benut is. Dieselfde rusplek is nie herhaaldelik gebruik nie.

Tydens kossoek snags met 'n bruinhiëna gemiddeld 32 km afgelê, terwyl die diere feitlik altyd alleenlopend was. Die reuksin was die belang= rikste in die opspoor van voedsel, veral aas, alhoewel die gehoor- en gesigsintuig ook soms gebruik is. Baie van die geaasde voedsel het uit beenstukkies, pote en skedels bestaan, alhoewel groot oorblyfsels en 'n aantal onaangeraakte karkasse gevind is. Leeus (Panthera leo) het 'n aansienlike hoeveelheid voedsel aan die bruinhiënas verskaf, terwyl die vangste van luiperds (Panthera pardus), wat in bome gestoor word, gewoonlik onbereikbaar was. Daar is een keer waargeneem hoe 'n bruinhiëna 'n jagluiperd (Acinonyx jubatus) en haar drie klein welpies van 'n springbokvangs verjaag en vier maal hoe 'n bruinhiëna 'n rooikat (Felis caracal) van sy vangs verdryf. Daar is taamlik kompetisie tussen

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rooijakkalse (Canis mesomelas) en bruinhiënas, waar beide mekaar per geleentheid van kos ontneem. Bruinhiënas het ook soms van roofvoëls en van die mens geaas.

Bruinhiënas het blykbaar gewoonlik toevallig op wilde vrugte afgekom, of hulle 'n kort afstand wind-op geruik. Hulle het gemiddeld 2,0 tsammas per keer en gemiddeld 1,4 gemsbokkomkommers per keer gevreet. Volstruis= eiers (Struthio camelus) was die volopste eiers wat gevreet is. Bruin= hiënas het hulle maklik oopgemaak, en was versigtig om nie die inhoud van die eier op die sand uit te stort nie.

As 'n groot hoeveelheid kos gevind is, het die bruinhiëna gewoonlik die oormaat onder 'n bos, in 'n langgraspol of soms in 'n gat gestoor. Dit is gewoonlik binne 24 h weer herwin. Die voordeel van hierdie gedrag lê moontlik in die verwydering van die voedsel van 'n bron, wat moontlik ander aasvreters mag aanlok.

Al die jaggedrag van bruinhiënas was op kleindiere gerig, behalwe in een geval, toe 'n springbok gejaag is. Van die 104 gevalle wat as jagpogings beskou is, was 10 (9,6 persent) suksesvol. Die slagoffers was korhane (3), springhase (Pedetes capensis)(2), bakoorjakkals (Otocyon megalotis) (1), springboklam (1), klein knaagdier (1), swartkorhaankuikens (Afrotis afra) (1), en 'n ongeïdentifiseerde klein voëltjie (1). Verder is daar een keer waargeneem dat 'n groot welpie 'n stinkmuishond (Ictonyx striatus) gevang het. Bykans 5,8 persent van die voedselbiomassa van bruinhiënas was afkomstig van werweldiere wat hulle self gevang het.

Met die uitsondering van termiete, was dit moeilik om waarnemings wan insekjag deur bruinhiënas te doem, aangesien die insekte gewoonlik opgeraap is en nie uitgeken kon word nie.

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Daar word tot die slotsom geraak dat 'n kombinasie van direkte waar=nemings en misontledings 'n noukeurige beeld van die bruinhiëna se dieet in die suidelike Kalahari weergee, alhoewel dit nie die presiese belang=rikheid van elke item uitbring nie. Die ontleding van voedselitems by nesgate verteenwoordig akkuraat die tipe kos wat die welpies deur die ouers gevoer word, maar spoorsny het ernstige tekortkomings.

Onder die Hyaenidae het die bruinhiëna en gestreepte hiëna (Hyaena hyaena) die mees variërende dieet en is oorwegend aasvreters. Die gevlekte hiëna (Crocuta crocuta) is 'n jagter-aasvreter wat in die eerste plek van groot diere lewe, en die maanhaarjakkals (Proteles cristatus) is 'n hoogs gespesialiseerde insekvreter.

Van die groter vleisvreters in suidelike Afrika is die bruinhiëna die beste aangepas om in 'n droë gebied soos die Kalahari te bestaan en bestuurspraktyke moet nie die kenmerke van die habitat verander om dit meer geskik vir ander groot vleisvreters, veral gevlekte hiënas, te maak nie. Navorsing in landbougebiede en kleiner reservate word voor=gestel om te ondersoek tot watter mate die bruinhiëna in hierdie gebiede met die mens se belange bots, en metodes om hierdie probleem te oorkom te vind.

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Note. Journal abbreviations taken from World List of Scientific Periodicals.

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Appendix A. Habitat and status of the mammals (except Insectivora, Chiroptera and small rodents) in the southern Kalahari. The number in the status column for each species is a reflection of the relative status of that species, with 1 indicating the rarest and 5 the most common.

SPECIES	HABITAT	STATUS
Order Primates		
Chacma baboon (Papio ursinus)	Dunes and river	1
Order Pholidota		
Pangolin (Manis temmincki)*	?	1
Order Carnivora		
Aardwolf (Proteles cristatus)*	Dunes and river	2
Brown hyaena (Hyaena brunnea)*	Dunes and river	4
Spotted hyaena (Crocuta crocuta)	Dunes and river, prefers river	2
Cheetah (Acinonyx jubatus)	Dunes and river	3
Leopard (Panthera pardus)	Dunes and river	4
Lion (Panthera leo)*	Dunes and river, prefers river	4
Caracal (Felis caracal)*	Dunes and river	4
African wild cat (Felis libyca)*	Dunes and river	4
Black-footed cat (Felis nigripes)	?	1
Bat-eared fox (Otocyon megalotis)*	Dunes and river, prefers river and pans	5
Black-backed jackal (Canis mesomelas)*	Dunes and river	5
Wild dog (Lycaon pictus)	Dunes and river	1
Cape fox (Vulpes chama)*	Dunes and river	4
Honey badger (Mellivora capensis)*	Dunes and river	3

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SPECIES	HABITAT	STATUS
Striped polecat (Ictonyx striatus)*	Dunes and river	4
Small spotted genet (Genetta genetta)	River	2
Suricate (Suricata suricatta)*	Dunes and river, prefers pans and river	5
Yellow mongoose (Cynictis penicillata)*	Dunes and river, prefers dunes	4
Slender mongoose (Herpestes sanguineus)	River	2
Order Tubulidentata		
Antbear (Orycteropus afer)*	?	2
Order Artiodactyla		
Warthog (Phachochoerus aethiopicus)	Dunes and river	1
Common duiker (Sylvicapra grimmia)*	Dunes	4
Steenbok (Raphicerus campestris)*	Dunes and river, prefers dunes	5
Kudu (Tragelaphus strepsiceros)	Dunes and river, prefers dunes, especially to the east	1
Springbok (Antidorcas marsupialis)*	Pans and river, partially migratory	5
Gemsbok (Oryx gazella)*	Dunes and river, prefers dunes except after rains	5
Eland (Taurotragus oryx)*	Dunes	3
Blue wildebeest (Connochaetes taurinus)*	Nomadic in dunes, tends to be more sedentary in river	5
Red hartebeest (Alcelaphus buselaphus caama)*	Dunes and river, prefers pans and river, migratory	5
Order Lagomorpha		
Hare (Lepus species)*	Dunes and river	4
Order Rodentia		
Porcupine (Hystrix africaeaustralis)*	Dunes and river	4
Ground squirrel (Xerus inauris)*	Pans and river	5

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SPECIES	HABITAT	STATUS
Springhare (Pedetes capensis)*	Dunes and river, prefers pans and river	5

Notes. 1. Scientific names taken from Smithers (1971).

2. * Recorded as being eaten by brown hyaenas during this study.

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Appendix B. Food items and approximate mass of each eaten by two female brown hyaenas (Hyaena brunnea) in 13 nights in the southern Kalahari; January, April and August 1975, January and February 1976.

DATE	ANIMAL'S NUMBER	ITEM	TIME TAKEN (MINUTES)	MASS (KILOGRAMS)
24 January 1975	6	Dove remains	3,00	0,050
		?	1,00	0,005
		?	1,00	0,005
		Tsama	2,00	0,540
		Tsama	3,00	0,540
		Tsama	3,50	0,540
		?	1,00	0,005
		Steenbok carcass (took part of it to the den)	30,00	1,800
		Total		3,485
25 January 1975	6	?	0,50	0,005
		Bones of baby wild cat	5,00	0,100
		Gemsbok cucumber	1,00	0,130
		?	0,25	0,005
		?	1,00	0,005
		?	0,25	0,005
		Bone	2,00	0,160
		Mouse	0,50	0,030
		Bone	2,00	0,160
		Bone	8,00	0,220
		Total		0,820

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DATE	ANIMAL'S NUMBER	ITEM	TIME TAKEN (MINUTES)	MASS (KILOGRAMS)
26 April 1975	20	Gemsbok cucumber	1,00	0,130
		Gemsbok cucumber	0,50	0,130
		Gemsbok cucumber	0,50	0,130
		Gemsbok cucumber	0,50	0,130
		Terfezia pfeilii	1,00	0,020
		Gemsbok cucumber	0,25	0,130
		Gemsbok cucumber	0,25	0,130
		Gemsbok cucumber	0,25	0,130
		Gemsbok cucumber	0,25	0,130
		Gemsbok cucumber	0,50	0,130
		Large ants?	27,00	0,005
		Tsama	4,33	0,540
		Tsama	4,33	0,540
		Tsama	4,33	0,540
		?	1,00	0,005
		?	2,00	0,005
		?	2,00	0,005
		Old bones	1,00	0,100
		Gemsbok scapula	3,00	0,150
		Bone	7,00	0,200
		Terfezia pfeilii	1,00	0,020
		Terfezia pfeilii	3,00	0,020
		Terfezia pfeilii	3,00	0,020
		Terfezia pfeilii	3,00	0,020
		Terfezia pfeilii	3,00	0,020
		Terfezia pfeilii	3,00	0,020
		Terfezia pfeilii	3,00	0,020

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DATE	ANIMAL'S NUMBER	ITEM	TIME TAKEN (MINUTES)	MASS (KILOGRAMS)
26 April 1975 cont.	20	Terfezia pfeilii	3,00	0,020
		Terfezia pfeilii	5,00	0,020
		Terfezia pfeilii	3,00	0,020
		Terfezia pfeilii	3,00	0,020
		Terfezia pfeilii	2,00	0,020
		Terfezia pfeilii	3,00	0,020
		Tsama	2,50	0,540
		Tsama	2,50	0,540
		Total		4,620
27 April 1975	20	Tsama	3,25	0,540
		Tsama	3,25	0,540
		Terfezia pfeilii	4,00	0,020
		Gemsbok bones	11,25	0,500
		Gemsbok cucumber	2,00	0,130
		Gemsbok cucumber	1,00	0,130
		Tsama	3,00	0,540
		Terfezia pfeilii	3,00	0,020
		Tsama	2,00	0,540
		Tsama	2,00	0,540
		Terfezia pfeilii	1,00	0,020
		Terfezia pfeilii	1,00	0,020
		Terfezia pfeilii	3,00	0,020
		Terfezia pfeilii	3,00	0,020
		Terfezia pfeilii	2,00	0,020
		Bone	1,50	0,100
		Base of horns	9,50	0,100

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DATE	ANIMAL'S NUMBER	ITEM	TIME TAKEN (MINUTES)	MASS (KILOGRAMS)
27 April 1975 cont.	20	Bone fragments	5,00	0,100
		Gemsbok cucumber	0,50	0,130
		Gemsbok leg	132,00	1,500
		Gemsbok cucumber	0,50	0,130
		Total		5,660
30 August 1975	20	?	0,50	0,005
		?	0,75	0,005
		?	1,00	0,005
		?	0,25	0,005
		Old bone	2,00	0,100
		?	0,25	0,005
		Small bone	1,00	0,100
		?	0,25	0,005
		?	0,25	0,005
		Total		0,235
31 August 1975	20	Termites?	3,00	0,005
		?	0,50	0,005
		Gemsbok cucumber	0,50	0,130
		?	1,00	0,005
		Insect?	1,50	0,005
		?	0,50	0,005
		Cape fox remains	3,00	0,900
		?	0,50	0,005
		Vertebrate of large herbivore	93,00	1,500

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DATE	ANIMAL'S NUMBER	ITEM	TIME TAKEN (MINUTES)	MASS (KILOGRAMS)
31 August 1975 cont.	20			
		Total		2,560
1 September 1975	20	Gemsbok cucumber	0,50	0,130
		Ostrich egg	9,00	0,735
		Ostrich egg	9,00	0,735
		Ostrich egg	9,00	0,735
		Total		2,335
6 January 1976	6	Hide	12,00	0,150
		Gemsbok cucumber	0,50	0,130
		Small bone	2,00	0,100
		Total		0,380
7 January 1976	6	Piece of bone	1,50	0,100
		Scapula of springbok lamb	1,00	0,100
		Small bone	0,50	0,100
		?	0,13	0,005
		?	0,13	0,005
		Bone	1,00	0,100
		?	0,13	0,005
		Mouse	0,50	0,030
		Small bone	2,00	0,100
		Mouse	6,00	0,900
		Total		1,455

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DATE	ANIMAL'S NUMBER	ITEM	TIME TAKEN (MINUTES)	MASS (KILOGRAMS)
21 January 1976	6	Springbok head	27,00	3,000
		Intestines	0,50	0,200
		?	0,13	0,005
		Bones of gemsbok calf	16,50	0,400
		Total		3,605
22 January 1976	6	Chews on gemsbok skull	5,00	0,100
		Ostrich carcass	14,00	0,500
		Total		0,600
18 February 1976	6	Tsama	2,00	0,540
		Tsama	2,50	0,540
		Tsama	2,50	0,540
		Tsama	1,75	0,540
		Tsama	4,00	0,540
		Tsama	4,00	0,540
		Scraps	0,50	0,050
		Bone etc.?	60,00	1,500
		Merremia tridentata	34,00	0,050
		Total		4,840
19 February 1976	6	Bone	3,50	0,100
		Jackal faeces?	1,00	0,005
		?	0,25	0,005
		Small bird	0,50	0,020
		Tsama	2,25	0,540

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DATE	ANIMAL'S NUMBER	ITEM	TIME TAKEN (MINUTES)	MASS (KILOGRAMS)
19 February 1976 cont.	6	Tsama	2,25	0,540
		Bones of large herbivore	113,00	0,900
		Tsama	3,00	0,540
		Tsama	4,50	0,540
		Tsama	2,50	0,540
		Tsama	3,50	0,540
		Tsama	2,50	0,540
		Tsama	2,25	0,540
		Tsama	2,00	0,540
		Total		5,890
Whole Period Total				36,485

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