

THE SOCIO-ECOLOGY AND SOCIAL BEHAVIOUR OF THE BROWN HYAENA HYAENA
BRUNNEA, THUNBERG, 1820 IN THE SOUTHERN KALAHARI

by

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DEDICATED
TO
MY PARENTS

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by

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ABSTRACT

The brown hyaena in the southern Kalahari is predominantly a scavenger of mammal remains, supplementing its diet with wild fruits as well as other vertebrate remains, insects, birds' eggs and the occasional small animal which is killed. Brown hyaenas are solitary foragers, but most of them live in small groups which inhabit large territories. The rest of the population consists of dispersing subadults and nomadic adult

males. Territory size is mainly affected by the dispersion pattern of the food in the territory and group size by the "quality" of the food. Mating is carried out between nomadic males and group-living females and group-living males help with the feeding of cubs. Communication is carried out mainly through olfactory and visual means. Subadult recruitment and emigration are mainly responsible for group size regulation. Evolutionary trends in Hyaenid behaviour are briefly discussed as is the management of the brown hyaena in the southern Kalahari and other areas.

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CHAPTER 1 : INTRODUCTION

BACKGROUND TO THE STUDY AND THE MAIN AIMS

The brown hyaena Hyaena brunnea is listed in the I.U.C.N. Red Data Book of endangered species, where its status is given as vulnerable. The main purpose of the present study is to make a contribution to the conservation of the brown hyaena by documenting as much as possible of its behavioural ecology in the southern Kalahari.

The study was done in the Kalahari Gemsbok National Park, Republic of South Africa and the adjacent Gemsbok National Park, Republic of Botswana. These parks form one of the largest conservation areas in Africa. The present study forms part of continuing research aimed at building up an understanding of the ecology of this area, so that any future management decisions which might have to be taken can be done so from a sound basis.

A close relationship between social behaviour and organisation, and diet and distribution of the food supply, has been established for many species of animals in a number of taxa: in birds by Crook (1964, 1965); in antelopes by Jarman (1974); in primates by Crook and Gartlan (1966), Crook (1970), Struhsaker (1975) and Clutton-Brock and Harvey (1977); in bats by Bradbury and Vehrencamp (1976 a and b), and in carnivores by Kruuk (1972, 1975, 1976 a and 1978 a), Camenzind (1978), Mills (1978 a), Macdonald (1979 a), Bekoff and Wells (1980) and Kruuk and Parish (In press). The main aim of the present study was to investigate this relationship in the brown hyaena, as it is important from both the conservation and theoretical viewpoints to understand how the population is affected by its food supply and the effect that this has on its social

system.

In the present study, therefore, the most important questions which I attempted to answer were:-

1. What is the diet of the brown hyaena?
2. How does it procure its food?
3. How is the food supply distributed?
4. What is the social system of the brown hyaena?
5. How is the social system related to the food supply and any other environmental factors?
6. How is the social system maintained through behaviour?
7. How does the behaviour of the brown hyaena compare with that of other members of the Hyaenidae?
8. What steps need to be taken in the southern Kalahari to ensure the survival of the brown hyaena in this area?
9. What recommendations can be made for the conservation of this species in other areas?

Other studies on the brown hyaena

The brown hyaena is one of four species in the family Hyaenidae. When the present study started little was known about the brown hyaena. Apart from some studies on its anatomy (Murie 1871, Ewer 1954 and De Boom 1957) and some observations on breeding behaviour in captivity (Lang 1958 and Schultz 1966), the available information on the brown hyaena was either of incidental nature, or had been passed on by the indigenous inhabitants of Africa to the early naturalists and scientists. Much of the latter was more traditional fancy than fact (Sclater 1900, Shortridge 1934, Stevenson-Hamilton 1947, Roberts 1954, Pienaar 1969, Smithers 1971 and others).

During the last few years several studies on the brown hyaena have been published. Von Richter (1972), Eaton (1976) and Skinner (1976) reviewed the distribution of the brown hyaena, with the last mentioned author documenting various aspects of its ecology in agricultural areas of the Transvaal, particularly with regard to its feeding habits. From studies of the brown hyaena in captivity Shoemaker (1978) has published a studbook, Yost (1980) has published notes on activity and breeding behaviour and Eaton (1981) has discussed aspects of ethology, behaviour and husbandry. In the central Kalahari, Owens and Owens (1978, 1979 a and b) have studied various aspects of the ecology, behaviour and social organisation of the brown hyaena.

Previous publications arising from the present study include a preliminary one on ecology and behaviour (Mills 1976), three on the diet and the foraging behaviour (Mills 1977, Mills 1978 b and Mills and Mills 1978), and one on scent marking (Mills, Gorman and Mills 1980). In addition a paper on the comparative socio-ecology of the Hyaenidae (Mills 1978 a) places particular emphasis on the brown hyaena. A paper on the analysis of bones collected at brown hyaena and spotted hyaena Crocuta crocuta dens in the southern Kalahari (Mills and Mills 1977) is of particular interest to paleontologists and taphonomists.

Basic features of the ecology and behaviour of the brown hyaena in the southern Kalahari

The brown hyaena is essentially an inhabitant of the south-west arid and adjacent drier parts of the southern savanna biotic zones of Africa (Von Richter 1972). It is a scavenger of all kinds of vertebrate remains, supplementing its diet with wild fruits, insects, birds' eggs and the occasional small animal which it manages to kill (Mills and Mills

1978). A brown hyaena covers large distances alone each night in its search for food (Mills 1978 b).

As will be shown in this dissertation brown hyaena home ranges are large, but vary in size and each is shared by a varying number of mostly closely related individuals. Group members sometimes come together at large carcasses or at the den, but do not forage together. Home ranges are regarded as territories because they overlap little, when members from different groups meet, particularly if they are of the same sex, they normally behave aggressively towards each other, and the members of the group regularly deposit various kinds of scent marks throughout their territory.

Brown hyaena cubs are raised at a den to which they remain attached until they are 15 months old, although the cubs begin to forage partially for themselves when they are nine months old. All members of the group assist in raising the cubs by carrying food back to the den for them.

Apart from group-living hyaenas, a segment of the population is nomadic. These nomads are either dispersing young animals of either sex which have left their natal home ranges, or they are mature males. The mature nomadic males are responsible for mating with the females, but do not, as far as is known, play any role in raising the cubs.

THE STUDY AREA

A detailed description of the study area has been given in Mills (1977). As it would be superfluous to duplicate this information here, only a brief summary incorporating some additional meteorological information is given.

Location

The study was done in the adjacent Kalahari Gemsbok (South Africa) and Gemsbok (Botswana) National Parks, which together cover an area of 36 190 km², of which the Kalahari Gemsbok National Park comprises 9 590 km². These two National Parks lie between 20°00' and 22°15' E and 24°08' and 26°30' S. Within this vast area the majority of my observations were confined to an area of approximately 2 750 km² centered around Nossob Camp in the Kalahari Gemsbok National Park (Fig. 1).

The unfenced boundary between the two National Parks is formed by the dry bed of the Nossob river. The western and south-western boundaries of the National Parks are separated from adjoining stock farming areas by a game deterrent fence. The short southern boundary has a jackal-proof stock fence separating it from stock farming areas. The other boundaries are unfenced and mainly adjoin controlled hunting areas (Von Richter and Butynski 1973).

Climate

The southern Kalahari is an arid region having an irregular rainfall and experiencing large temperature fluctuations both on a daily and seasonal basis. Three basic ecological seasons are recognised:-

1. The hot, wet season: January to April, when the mean monthly temperature is 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

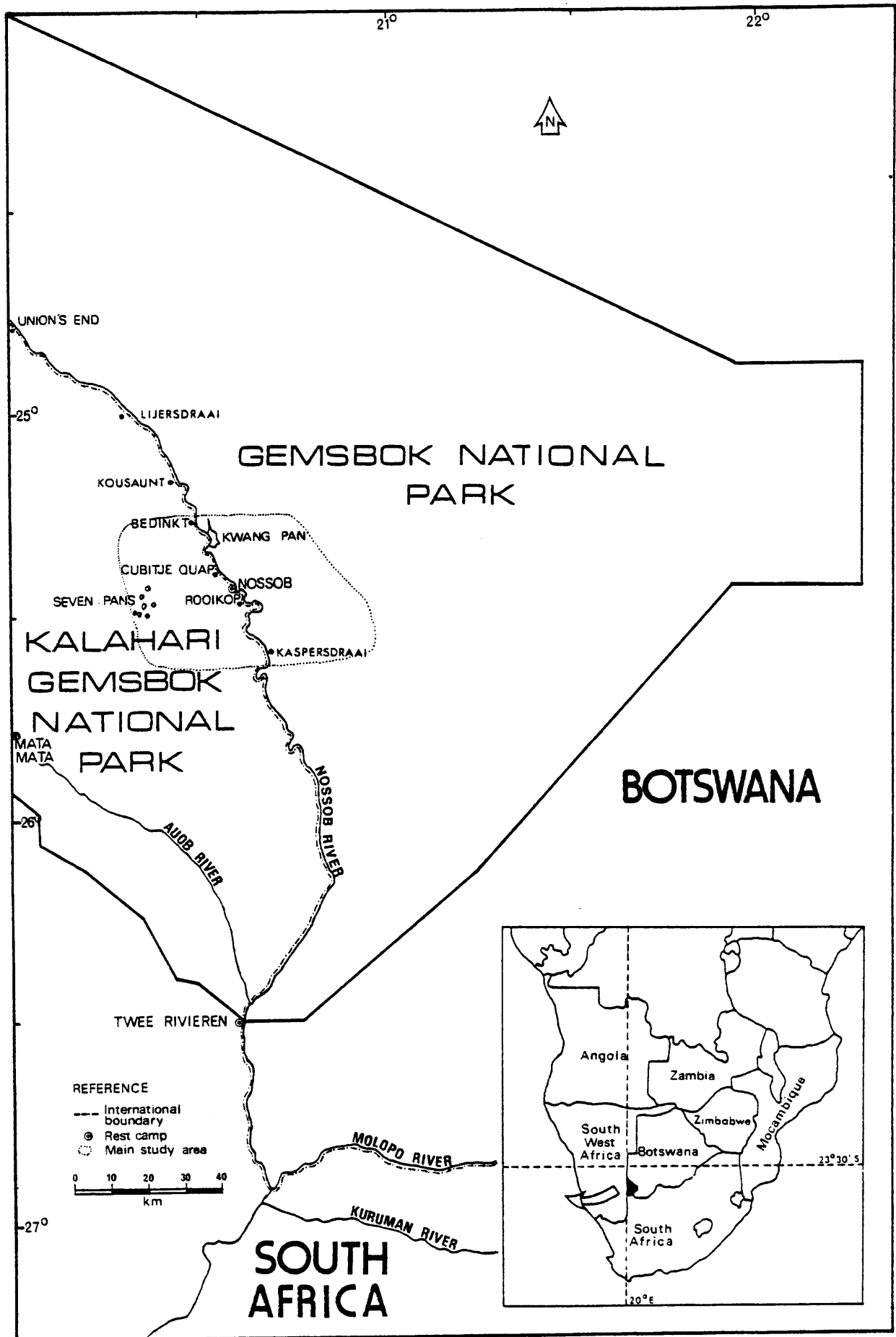


Figure 1: The Kalahari Gemsbok and Gemsbok National Parks, showing the main study area and other places mentioned in the text.

temperature is above 20° C and on average not more than 20 per cent of the annual rain falls.

The mean annual rainfall and standard deviations for the three weather stations in the area are as follows; Twee Rivieren (1961 - 1980) $230,3 \pm 120,35$ mm, Mata Mata (1962 - 1980) $242,3 \pm 155,60$ mm and Nossob (1967 - 1980) $256,3 \pm 144,85$ mm. Figure 2 gives the monthly rainfall at Nossob Camp for the entire study period i.e. 1972 - 1980.

As it receives on average less than 255 mm annual rainfall (and experiences high temperatures and low humidity) the southern Kalahari falls within the most commonly accepted limits for desert areas (Köppen 1931 and Cloudsley-Thompson 1975).

Geomorphology, physiography and geology

The Kalahari is the largest sandveld area in the world (King 1963), and in the southern Kalahari the sand deposits are arranged in a series of long, roughly parallel longitudinal dunes. Most of the Kalahari Gemsbok and Gemsbok National Parks lie more than 900 m above sea level. Four rivers which drain southwards run through the area, but they are almost always dry, only flowing for short periods during abnormally wet years. A large number of shallow, flat depressions or pans are scattered unevenly throughout the southern Kalahari (Wellington 1955, Parris 1976 and Parris, Bothma, Waanders and Boshoff 1977).

Beneath the sand lies a vast sheet of calcareous or silicified sand or sandstone which is exposed at places along the river courses and in a number of pans (Du Toit 1954, Smit 1964, Louw 1964 and Leistner 1967).

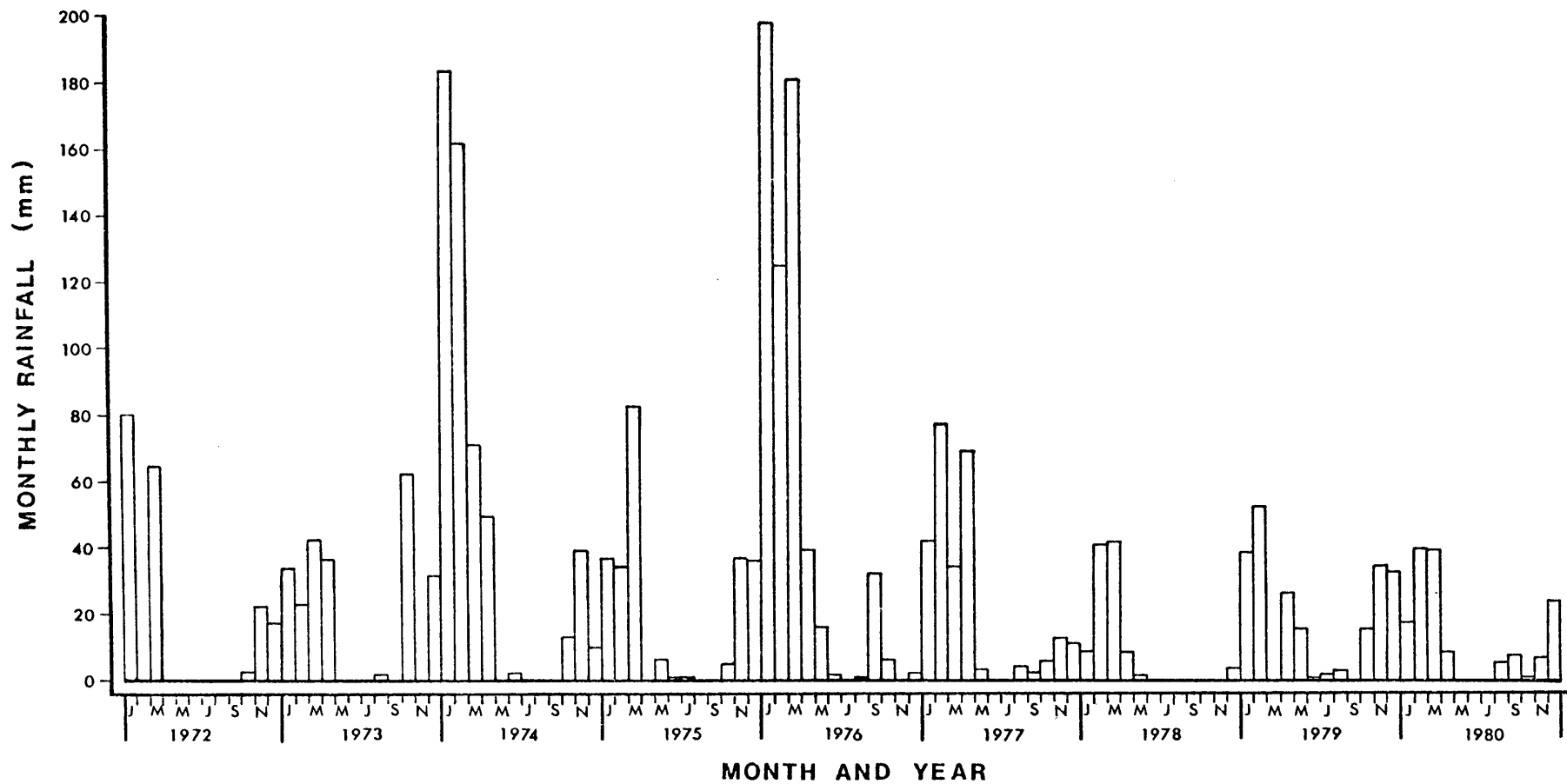


Figure 2: Monthly rainfall for Nossob Camp, Kalahari Gemsbok National Park, South Africa; January 1972 - December 1980.

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, 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, however, two habitats are recognised (Fig. 3); the river-beds and immediate environs, and the adjacent dune areas, including pans.

The former, which make up less than 10 per cent of the study area, are dominated by large Acacia erioloba and Acacia haematoxylon trees, the shrub Acacia mellifera subsp. detinens, grasses such as Panicum coloratum and Eragrostis bicolor and, after good rains, by the annual grasses Chloris virgata and Schmidtia kalahariensis. Large limestone flats dominated by the short perennial grass Stipagrostis obtusa and the dwarf shrub Rhigozum trichotomum form a significant part of this habitat type.

The dunes are areas of extremely open shrub or tree savanna dominated by smaller Acacia erioloba and Acacia haematoxylon trees as well as Boscia albitrunca, and by tall perennial grasses such as Eragrostis lehmanniana, Asthenatherum glaucum, Aristida meridionalis and Stipagrostis amabilis. Pan vegetation resembles that of river areas, with Stipagrostis obtusa and Rhigozum trichotomum and the dwarf shrub Monechma incanum common on the edges (Leistner 1967).

Fauna

Apart from Insectivora, Chiroptera and small rodents, 35 mammal species have been recorded from the area (Mills 1977). Of the large ungulates the gemsbok Oryx gazella is the most sedentary and widespread species, whereas the blue wildebeest Connochaetes taurinus, red hartebeest Alcelaphus buselaphus and springbok Antidorcas marsupialis are for the most part migratory, although resident populations of blue wildebeest do occur along the river-beds. All the above mentioned ungulates reach their highest densities along the dry river-beds and around pans, after rains. Eland Taurotragus oryx are usually rare, becoming more common to the east. Steenbok Raphicerus campestris are common and widespread, being found mainly in the dune areas, and common duiker Sylvicapra grimmia exclusively inhabit the dunes, but are uncommon (Eloff 1959 a and b, 1961, 1962 and 1966, Bothma 1971 a, 1972, Bothma and Mills 1977 and personal observations).

Several species of small carnivores inhabit the area with the black-backed jackal Canis mesomelas and the bat-eared fox Otocyon megalotis being particularly common. Rodents, in particular springhares Pedetes capensis and porcupines Hystrix africaeaustralis, both of which are eaten by brown hyaenas, are common throughout the area. Ground nesting birds such as the ostrich Struthio camelus, kori bustard Otis kori, black korhaan Afrotis afra and the red-crested korhaan Eupodotis ruficrista are all common and widespread and are eaten by brown hyaenas, as are insects such as termites (Isoptera) and beetles (Coleoptera) (Mills and Mills 1978 and personal observations).

Large carnivores are well represented in the southern Kalahari although none reach high densities. Besides brown hyaenas, lions Panthera leo, leopards Panthera pardus, cheetahs Acinonyx jubatus and spotted

hyaenas are all residents. Wild dogs Lycaon pictus are rare visitors to the area (personal observations).

The distribution and abundance of many of the above mentioned animals are discussed more fully in Chapter 2.

MATERIALS AND METHODS

Introduction

Some of the materials and methods used during the present study have been described and discussed elsewhere (Mills 1977). For the sake of completeness, however, it is necessary to summarize those which are relevant here and to describe in detail new ones.

Although the study was spread over nine years (1972 - 1980), field work was carried out intermittently in the following manner:-

1. April 1972 to November 1974: Tracking spoor, making observations at dens and catching and marking animals.
2. December 1974 to September 1975; January to July 1976; July 1977 to August 1978: Following radio-collared individuals, catching and marking animals, and to a lesser extent making observations at dens.
3. September 1978 to December 1980: Irregular observations, mainly at carcasses, catching and marking a few animals and documenting the reproductive condition of the two females of the main study group (the Kwang group).

All non-parametric statistical tests used are taken from Siegel (1956) and all parametric statistical tests from Bailey (1959).

Percentages are given to one decimal place in tables but are rounded off in the text. Time periods are inclusive e.g. January to July 1976 means from January up to and including July.

Tracking spoor

With the aid of a bushman tracker approximately 1 200 km of brown hyaena spoor were followed in the soft Kalahari sand. This method, however, had severe limitations because of the long distances travelled by the hyaenas, their erratic movements, and because it was impossible to follow their spoor in the Nossob river-bed.

If the spoor originated from or came to a den it could be established to which group the tracked hyaena belonged. Frequently, however, a spoor did not pass a den, and unless the hyaena could be caught up with to check if it was marked or not, it was impossible to determine the originator of the spoor. Because of the soft sand it was impossible to use measurements of footprints reliably for identifying individuals as has been done in several other carnivore studies; for example civets Viverra civetta (Randall 1977), bears (Klein 1959), leopards (Smith 1977) and pumas Felis concolor (Koford 1978). In 1972 and 1973, therefore, I fitted radio collars (C.S.I.R., Pretoria) to certain individuals in the hope that they could be located regularly and their spoor followed. These radios, however, were unreliable and of little value (Mills 1977).

As an alternative to radio tracking I attempted to mark the spoor of certain individuals by removing a claw, in the hope that the missing claw could be seen from the spoor. This technique has been used successfully to identify the tracks of individual coyotes Canis latrans

in snow (Andelt and Gipson 1979). I removed one claw from a hindfoot of one hyaena and one from a fore-foot of another. This was done by cutting off the claw at the base with a pair of bone forceps and then cauterizing the wound. Because of the soft sand, however, the prints were normally not clear enough to be able to determine if a claw had been removed or not. Only if the individual came into the road was it possible to identify a marked spoor, and as this rarely happened I abandoned this technique.

Later it became apparent that it was possible to follow certain brown hyaenas in a vehicle whereupon I gave up tracking spoor except in a few exceptional circumstances.

Direct observations

During the study approximately 2 500 h were spent observing brown hyaenas either as they moved around, or while they were at dens and carcasses. Nine individuals were fitted with radio collars (Dav-Tron Company, Minneapolis, Minnesota, U.S.A.) and beta lights (Saunders Roe Development Ltd., Hayes, Middlesex, England), and were followed for varying periods (Fig. 4), mainly at night, in a four-wheel drive vehicle. The transmitters in the collars operated in the 26 - 28 MHz range. Usually no headlights from the vehicle were used when following a hyaena, but a hand-held spotlight was switched on when I wished to observe specific details of an animal's behaviour. As far as I could ascertain the vehicle and spotlight had no effect on the behaviour of the hyaenas that I was regularly observing and they quickly became habituated to these objects. Some strange hyaenas were extremely wary of the vehicle and bolted on sight. Most, however, did not run away so long as I did

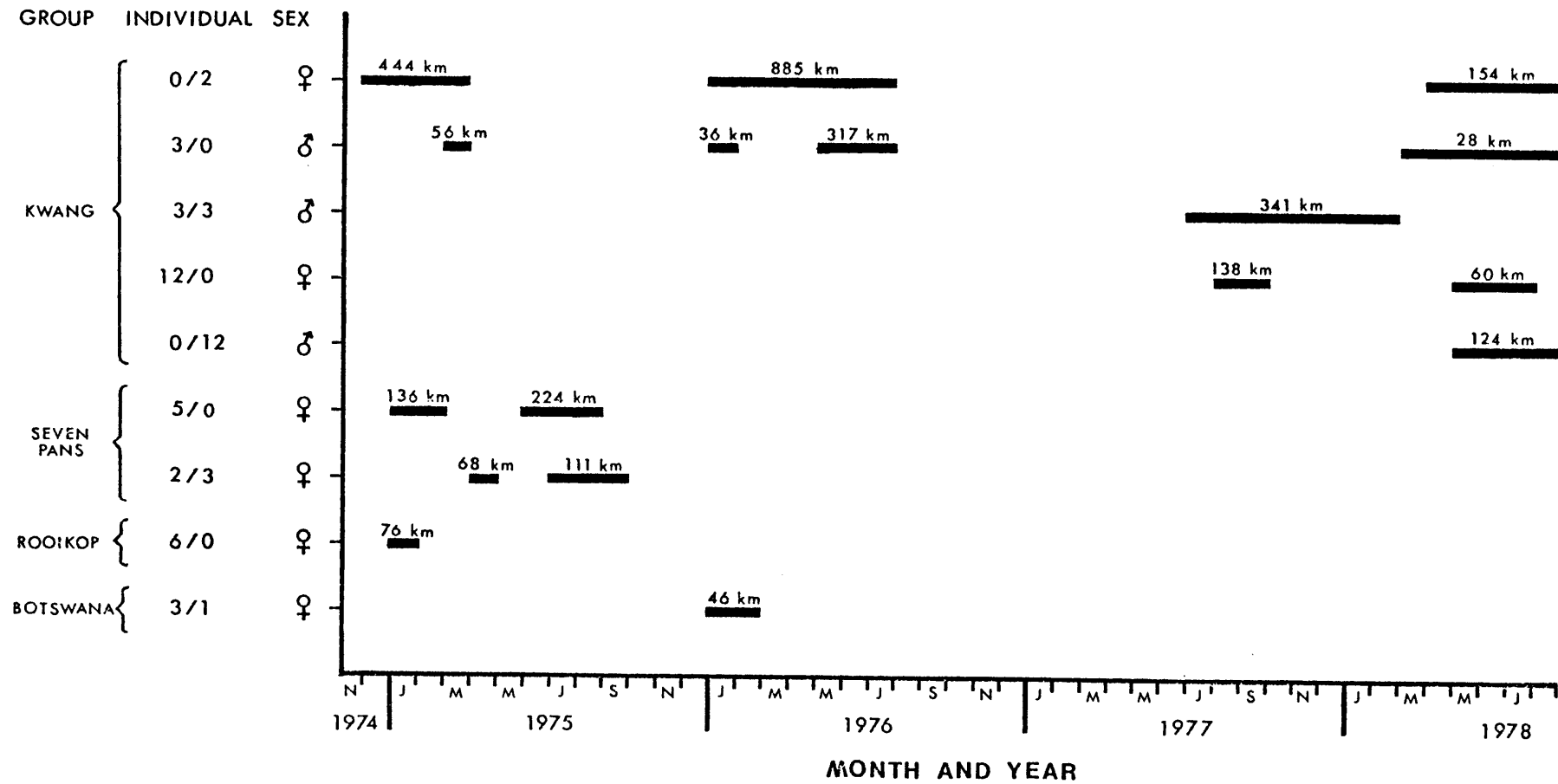


Figure 4: Periods and distances that radio-collared adult brown hyaenas were followed in the southern Kalahari; December 1974 - August 1978.

not attempt to start the engine or suddenly focus the spotlight onto them when they were within approximately 50 m of the vehicle.

Observations at dens and at carcasses were made from a stationary vehicle at varying distances from the hyaenas, depending on how close they would tolerate the presence of the vehicle. Normally this was approximately 20 m.

At the beginning of the study I had the use of a starlight scope to assist in making night observations. This, however, was of limited value as it was only effective at full moon and was too bulky to be used except from a stationary vehicle. A pair of 7 x 50 binoculars was adequate at full moon for my purposes. Furthermore the tolerance by the hyaenas to a spotlight enabled me to make frequent use of this apparatus.

Capture procedure

The reasons for catching brown hyaenas in the present study were:-

1. To fit, replace or remove radio collars.
2. To mark as many individuals as possible so that they could be recognised for population assessments and behavioural observations.
3. To age by tooth wear and to sex a random sample of hyaenas for gaining an insight into the population structure.
4. To weigh and measure animals for comparative purposes and in order to augment the observations in 3 above.
5. To gain an insight into the rate of tooth wear.

Most hyaenas were caught in a baited drop-door trap (Mills 1977). This was a successful method of capturing brown hyaenas, although it had the drawback of being non-selective in that some individuals were more likely to enter a trap than others were. For example, four hyaenas which

belonged to the same social group were caught 17, 11, 8 and 0 times respectively in 160 trap-nights between January 1976 and December 1978 ($\chi^2 = 16,67$; $df = 3$; $p < 0,01$). This propensity for some brown hyaenas to be more easily trapped than others did not appear to be linked to sex or age nor to the time elapsed since the last capture. Once, for example, I released a hyaena from one trap whereupon it immediately entered a second trap 500 m away.

Throughout the study I caught 29 different hyaenas 169 times, six lions and four leopards, in 666 trap-nights. This gives a success rate of one brown hyaena per 3,9 trap-nights (25,4 hyaenas per 100 trap-nights) and one previously untrapped hyaena per 23,0 trap-nights (4,3 hyaenas per 100 trap nights).

Smuts, Whyte and Dearlove (1977 a and b) reported that dragging a carcass in two to three directions from the capture site prior to putting it out improved the chances of lions and other carnivores coming to the bait. In the latter part of the present study, therefore, I dragged a carcass 1 - 2 km either side of the traps each time I began a trapping session with a new carcass. This increased the trapping success rate. For example, during one trapping session I caught four hyaenas 15 times in 39 trap-nights after dragging a carcass beforehand. Earlier and at the same trapping locations I had caught these four individuals 10 times in 60 trap-nights, without dragging a carcass beforehand. This difference is significant ($\chi^2 = 4,73$; $df = 1$; $p < 0,05$). Table 1 shows that the trapping success rate tended to get less on successive nights after the night that the carcass was dragged, although these differences were not significant ($\chi^2 = 2,10$; $df = 3$; $p > 0,05$).

A problem encountered with trapping was the tendency for some hyaenas to bite at the bars of the cage after being caught, occasionally damaging a tooth. After this had been discovered, I removed the cross

Table 1: Trapping success of brown hyaenas on successive nights after dragging a carcass for 1 - 2 km on either side of the trap in the southern Kalahari; June 1977 - August 1978.

TRAPPING SUCCESS	NIGHTS AFTER CARCASS WAS DRAGGED			
	1	2	3	4
Number of trap nights	55	34	29	11
Number of hyaenas caught	43	22	17	5
Per cent success	78,2	64,7	58,6	45,4

bars on the drop-door and the back of the cage and this alleviated the problem (Mills 1977). Still, however, some animals bit at the vertical bars on the door and so I fastened a piece of heavy duty conveyer belting on the inside of each door. This further improved the situation. Still it happened that particularly determined individuals bit at the vertical bars on the back and side of the cage, although no damage to these animals' teeth occurred. In retrospect it would have been better, although costlier, to have had the cages made from steel mesh instead of bars.

Black-backed jackals were the only carnivores that regularly interfered with the traps. The jackals would enter a trap and pull at the meat, causing the gate to close, then escape through the bars. This behaviour was usually confined to certain individuals and the best thing to do if a trap was regularly interfered with in this way was to move the trap at least 1 km away.

I managed to capture some of the trap-shy brown hyaenas that I needed to by firing a dart from a carbon-dioxide powered Cap-Chur pistol (Palmer Chemical and Equipment Co., Atlanta, U.S.A.) at the animal from a stationary vehicle whilst it was feeding at night. I caught seven unmarked brown hyaenas and four marked ones by this method. As long as I could get to within 10 m of the animal this was successful and the hyaena never ran off more than 100 m after being darted in this manner.

Immobilisation

Brown hyaenas were immobilised with three immobilising drugs; phencyclidine hydrochloride (Sernylan, Parke-Davis), ketamine hydrochloride (Vetelar, Parke-Davis) and a 1 : 1 combination of the

anaesthetic tiletamine hydrochloride and the tranquilizer zolazepam hydrochloride (CI-744, Parke-Davis).

Sernylan, together with the tranquilizer Combellem, was used when it was necessary to immobilise a hyaena for over an hour. A satisfactory dosage rate to achieve this was 0,5 - 0,9 mg/kg of Sernylan. If the animal became difficult to work with as a result of the effect of the drug wearing off, it was given a booster injection of ketamine as described in Mills (1977).

Short duration immobilisation was achieved with ketamine mixed with Combellem. Dosage rates of between 10 - 20 mg/kg of ketamine were administered (Mills 1977).

CI-744 was used to immobilise 11 brown hyaenas during the latter part of the study (Table 2). On three occasions I initially injected a brown hyaena with CI-744 and later administered a booster injection of 300 mg ketamine with satisfactory results.

The advantages of this CI-744 over Sernylan have been discussed by Bertram and King (1976) and Smuts et al. (1977 b). The time taken for an animal to recover from CI-744 is much faster than it is for Sernylan, yet prolonged anaesthesia can be maintained by additional doses of CI-744 with no obvious harmful effects to the animal. Furthermore CI-744 does not cause convulsions which Sernylan may do.

Another advantage of CI-744 over Sernylan is the shorter induction period of the former drug. For Sernylan the mean induction period until brown hyaenas became recumbant was $19,1 \text{ min} \pm \text{s.e. } 2,68$ (Mills 1977), whereas with CI-744 it was $4,5 \text{ min} \pm \text{s.e. } 1,15$ ($d = 5,004$; $df = 24$; $p < 0,01$). This is important when free-ranging carnivores are being darted, especially at night, as they are then less easily lost if they run away.

Table 2: Dosage rates and reaction times for brown hyaenas immobilised with CI-744 in the southern Kalahari; June 1977 - August 1978.

MASS (kg)	SITE DART ENTERED	DOSAGE RATE (mg/kg)	TIME (min) RECUMBANT	TIME (h) OF FIRST SIGNS OF RECOVERY	TIME (h) FULLY RECOVERED
± 32	Neck	$\pm 8,9$	2	1,3	?
± 38	Neck	$\pm 3,6$	2	0,9	?
37,5	Rump	9,4	5	2,0	?
30,0	Rump	4,5	4	0,6	?
43,0	Neck	4,7	4	1,5	8,0
42,0	Rump	8,4	6	0,8	?
27,0	Shoul.	7,4	2	1,0	?
± 40	Rump	$\pm 5,0$	5	?	11,0
43,2	Neck	6,9	3	1,0	?
35,0	Rump	8,6	2	1,5	?
47,5	Rump	4,2 ⁺	15	2,3	?

⁺ Never became tractable, 21 min after being darted injected with 400 mg ketamine.

1124843
1096067

Ketamine is a more satisfactory drug to use on brown hyaenas than CI-744 when a short immobilisation period is desired. A dosage of 15 mg/kg usually restrains a hyaena sufficiently for an hour, giving a researcher time to carry out routine procedures such as taking body measurements and clipping ears.

If a period of anaesthesia longer than an hour is needed, then CI-744 becomes more practical to use on brown hyaenas. The drug is sufficiently potent for the dose to be accommodated in a 3 ml dart. Both ketamine and CI-744 have rapid induction periods until the animals become recumbant; the mean for ketamine being $4,5 \text{ min} \pm \text{s.e. } 0,62$ (Mills 1977), the mean for CI-744 being $4,5 \text{ min} \pm \text{s.e. } 1,15$ ($t = 0,001$; $df = 21$; $p > 0,05$). Both are therefore suitable for use on free ranging brown hyaenas.

For carnivores larger than brown hyaenas, CI-744 is more practical to use than ketamine for short duration immobilisation because of its increased potency, thus enabling a strong enough dosage to be accommodated in a 3 ml dart. Bertram and King (1976) and King, Bertram and Hamilton (1977) recommend the use of CI-744 on lions and leopards and I have had good results with it on spotted hyaenas (Mills in prep.).

Marking

It was essential to be able to recognise individual study animals. With brown hyaenas the stripe patterns on the forelegs vary between individuals and it is possible, but difficult, to recognise certain individuals by this method. Furthermore some brown hyaenas have distinct natural nicks or tears in their ears which makes it possible to recognise these individuals.

It was decided, however, that the most reliable and convenient method of recognising individuals was to mark, wherever possible, those that had no easily recognisable natural marks. Brown hyaenas have large pointed ears and often stop and look at an approaching vehicle with their ears cocked. Thus I marked them by cutting small triangular pieces out of their ears at different positions (Fig. 5), in a similar manner to Kruuk's (1972) method with spotted hyaenas. The pieces were removed with a pair of surgical scissors and the wound was treated with Surgispray (Novo Industries, Johannesburg) to facilitate healing.

I experienced little trouble in seeing whether a hyaena was marked or not and, if it was marked, what its mark was. If a hyaena would not allow a close enough approach, I could often attract it by imitating the yell (see vocalisations). This would make it stop and look at the vehicle and sometimes even cause the hyaena to move closer. Alternatively a recording of the distress call of a springhare would invariably cause the hyaena to come closer. Of 527 encounters with brown hyaenas during the study, I was unable to see in 10 cases (2 per cent) whether the animal was marked or not.

Where necessary individual animals are referred to in the text with their marking code. For example, the animal marked in position 2 on its left ear has the code 0/2, the animal marked in position 2 on the right ear and 3 on the left ear has the code 2/3 etc. Known animals whose ears were not cut were assigned codes above 4 in the order of first sighting e.g. 5/0, 6/0 etc.

Ageing techniques

No information on ageing in the brown hyaena is available and no

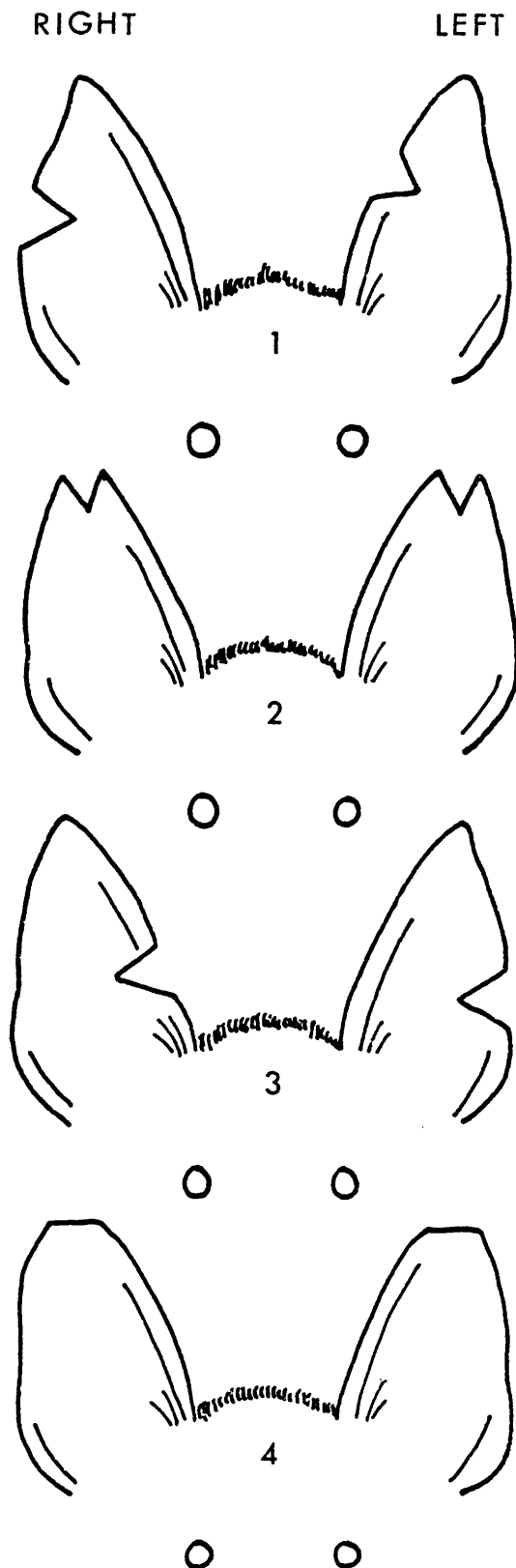


Figure 5: Positions from which pieces were removed from the ears of brown hyaenas in the southern Kalahari to individually identify them: April 1972 - December 1980.

known-age skulls of brown hyaenas were available for examination during the study. I therefore aged animals on the basis of tooth eruption and wear, particularly with regard to the wear on P_3 , in a similar manner to Kruuk's (1972) method with spotted hyaenas. The dental formula for adult brown hyaenas is as follows:-

$$I_{\frac{3}{3}}^{\frac{3}{3}}, C_{\frac{1}{1}}^{\frac{1}{1}}, P_{\frac{4}{3}}^{\frac{4}{3}}, M_{\frac{1}{1}}^{\frac{1}{1}} = 34$$

Brown hyaenas are apparently born without teeth, the incisors having appeared by the fourth week of life (Anderson In litt.). The youngest animal that I immobilised was approximately seven months old. I_1^1 , I_1^2 and I_2 had erupted and i_3^3 and i_3 were either loose or had fallen out. All the deciduous premolars had fully erupted and the molars had broken through the gums (Fig. 6 a). Two approximately 10-month old animals had I_3^3 erupting and I_3 fully erupted. The permanent premolars and the molars were erupting, P_1^1 , P_4^4 , P_4 , M_1^1 and M_1 being almost fully erupted. The other permanent premolars were not as far advanced and could be seen below the deciduous premolars. By 12 months the permanent canines begin to erupt and P_1^1 , P_2^2 , P_4^4 , M_1^1 , P_2 , P_4 and M_1 have completely erupted. The third premolars and the canines are the last teeth to erupt completely, and at approximately 15 months of age a brown hyaena has its full permanent dentition (Fig. 6 b).

Brown hyaenas with erupting teeth were placed into age-class 1 and considered as cubs. The dentition of animals in the remaining four age-classes are illustrated in Figs. 6 b, c, d and e.

I have regarded brown hyaenas as subadults from the time that they

J.L. Anderson. Natal Parks, Game and Fish Preservation Board, Umfolozi Game Reserve, P.O. Box 19, Mtubatuba, 3935. 11 September 1979.

receive their full permanent dentition until they are 30 months old, after which they are considered adults. At 30 months they reach full size (see Appendix A). It is sometimes possible, therefore, to differentiate age-class 2 animals into subadults (age-class 2 a) and adults (age-class 2 b).

From long-term observations on the dentition of certain known individuals it has been possible to obtain an indication of the absolute ages of some of these age-classes.

Brown hyaenas move from age-class 2 to age-class 3 in their fourth year. A female which was just placed in age-class 3 in February 1973 was still in this age-class in December 1974. In January 1976 she was placed in age-class 4. Thus she passed into age-class 4 when she was approximately six years old.

These observations agree with those of Kruuk (1972) for spotted hyaenas in East Africa. Kruuk says that East African spotted hyaenas pass into age-class 5 at 16 years of age. Whether this is the same for brown hyaenas or not remains to be established. It is possible that differences in the amount of bone chewing done by the two hyaena species causes different tooth wear patterns. Alternatively the abrasive action of the sand on the teeth during feeding could cause the teeth of the Kalahari hyaenas to wear down more rapidly. Smuts, Anderson and Austin (1978) recorded that the incisors of lions in the Kalahari wear down more rapidly than they do in other areas and suggest that this might be caused by the sand inadvertently ingested during feeding.

Once in age-class 5 the premolars of a brown hyaena wear down rapidly. Figures 6 e and f are photographs of the same brown hyaena's teeth taken three years apart, Fig. 6 f being taken after he was found dead. The premolars in the upper jaw have worn considerably in the three-year period and P^2 and P^3 have become non-functional. Another brown

hyaena which was in age-class 4 when I caught her was found dead five years later. Her premolars in the upper jaw were also badly worn and non-functional. She had spent approximately four years in age-class 5.

Shoemaker (1978) records many brown hyaenas living 12 - 15 years in captivity and Crandall (1964) records longevities of over 20 years.

Mapping of movements and measurement of territory size

Data on movements of brown hyaenas were obtained either from tracking spoor or from direct observations. When a spoor or animal was first located the vehicle's odometer reading was noted and, if possible, its position relative to a known fixed point was established, for example, 3 km up the Nossob river-bed from Cubitje Quap windmill.

The direction which the spoor took was determined with a compass by moving at least 10 m from the vehicle and taking a reading on the tracker as he disappeared from view. The vehicle was then driven as straight as possible along the bearing until the point that the tracker disappeared was reached. The odometer reading was again recorded and the next compass reading was taken when the tracker again disappeared from view.

In the case of direct observations the direction in which the animal was moving was ascertained by using the sun, moon and certain constellations of stars, particularly the Southern Cross, Orion and the Scorpion as reference points, and by dividing the points of the compass into 16 divisions; N, NNE, NE, ENE, E etc. Whenever the hyaena made a direction change and maintained the new direction for more than 50 m, the new direction and the odometer reading at the point of change were noted.

Whenever the spoor or the hyaena passed a known fixed point the odometer reading was also noted. At the termination of the observation period the odometer reading was noted and the vehicle was driven on a fixed compass reading until a known point was reached, when the odometer reading was again noted. At a later date each movement was plotted on a 1 : 10 000 map.

The methods used for plotting the movements, particularly those from direct observations, are crude and great accuracy was obviously not achieved. If, after being plotted, the end of a movement between two points did not correspond with the second point on the map, an adjustment was made in order to bring the movement to the fixed point. This was accomplished by adjusting the entire movement so that it ended at the correct place (Fig. 7). No plotted movement ended more than 10 per cent of the total distance moved away from the second point on the map.

Territory size was calculated for those social groups for which 300 km or more movement data were collected during a particular observation period. Territorial boundaries were delineated by the smallest convex polygon method and the size measured with a planimeter. In the case of tracking spoor, any brown hyaena's spoor which passed a particular den was assumed to be a member of the group which used that den, even if it was impossible to catch up with the hyaena and identify it. In none of these cases did the spoor move out of an area with a radius of more than 15 km from the den. Tracked spoor which did not pass a den was only included if I knew which individual's spoor was being followed. The social groups whose movements were mapped and particulars of the data collected for each group, are listed in Table 3.

The various techniques for evaluating home range and territory size have recently been reviewed and discussed by Macdonald, Ball and

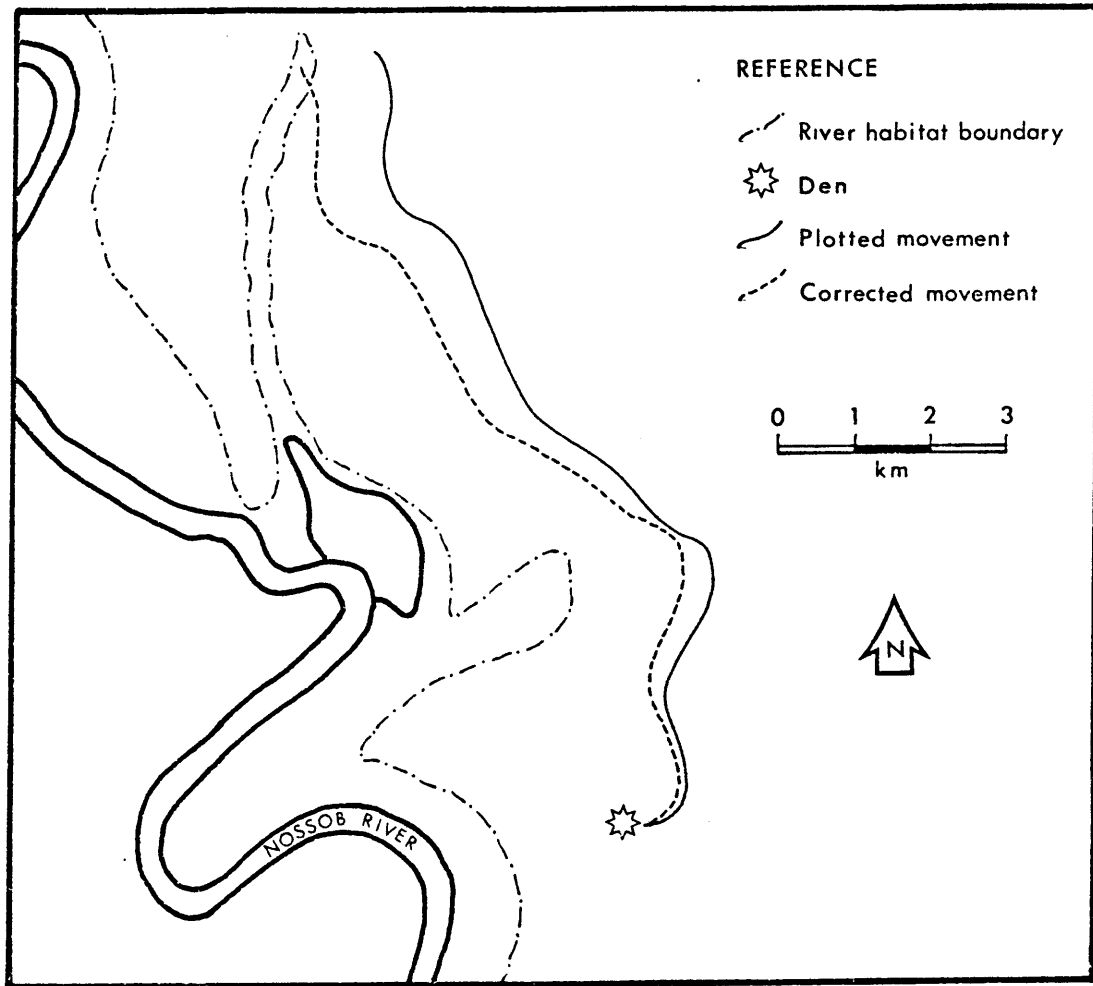


Figure 7: An example of how the movement of a brown hyaena in the southern Kalahari plotted from inaccurate data was subjectively adjusted. The hyaena left its den and moved mainly north for approximately 4 km, then mainly north-west for a further 8 km before reaching a narrow belt of river habitat. At this point the plotted movement lay approximately 1 km to the east of the river habitat. Without moving the starting point the entire plotted movement was moved to the west on this axis until the end point reached the river habitat. The corrected movement was then redrawn as shown.

Table 3: Some particulars of the data collected from certain brown hyaena social groups whose movements were mapped in the southern Kalahari; April 1972 - August 1978.

NAME OF SOCIAL GROUP	START OF OBSERVATIONS	MONTHS OBSERVED	METHOD OF OBSERVATION	DISTANCE (km) TRACKED OR FOLLOWED	NUMBER OF INDIVIDUALS TRACKED OR FOLLOWED
Cubitje Quap	June 1972	8	Spoor	235	4
Botswana	April 1972	16	Spoor	124	?
Kaspersdraai	October 1972	7	Spoor	442	1
Rooikop	May 1973	8	Spoor and direct	302	2
Seven Pans	January 1975	9	Direct	539	2
Kwang 1	December 1974	4	Direct	500	2
Kwang 2	January 1976	7	Direct	1 235	2
Kwang 3	July 1977	14	Direct	865	5
Total		-		4 242	≥ 15

Hough (1980). These authors conclude that provided there are sufficient observations, a technique such as the one used in the present study is superior to the more sophisticated quantitative techniques which are available. Since I followed the hyaenas for long periods of time, often for two or more complete nights at a time, I am confident that my observations comprise a representative sample of the total movements made by the hyaenas concerned.

Movement data from the Kwang 2, Seven Pans and Kaspersdraai territories were further analysed by means of the computer programmes SYMAP and SYMVU (Laboratory for computer graphics, Harvard University, U.S.A.) by Gorman (pers. comm.). These programmes graphically display spatially distributed quantitative data, first as a two-dimensional contour map and then as a three-dimensional map. In the present study the first two dimensions represent the surface area of a hyaena territory. The third (vertical) dimension reflects the density of movements within each part of the territory.

In order to perform the analysis, a grid matrix was overlayed on each hyaena territory, each grid covering an area of 2,5 x 2,5 km. The map for the Kwang 2 territory (Fig. 8) is used as an example. The total distance moved within each grid square in each territory was measured, and the distances per square were analysed by the SYMAP programme. This produced a contour map of movement densities over the surface area of the hyaena territory. The SYMAP programme grouped the movement density values into 10 class intervals of equal size, covering the range 0 - 88 km per square in the Kwang 2 territory, and 0 - 27 km per square in the

M.L. Gorman. Department of Zoology, University of Aberdeen, Aberdeen, Scotland. March 1981.

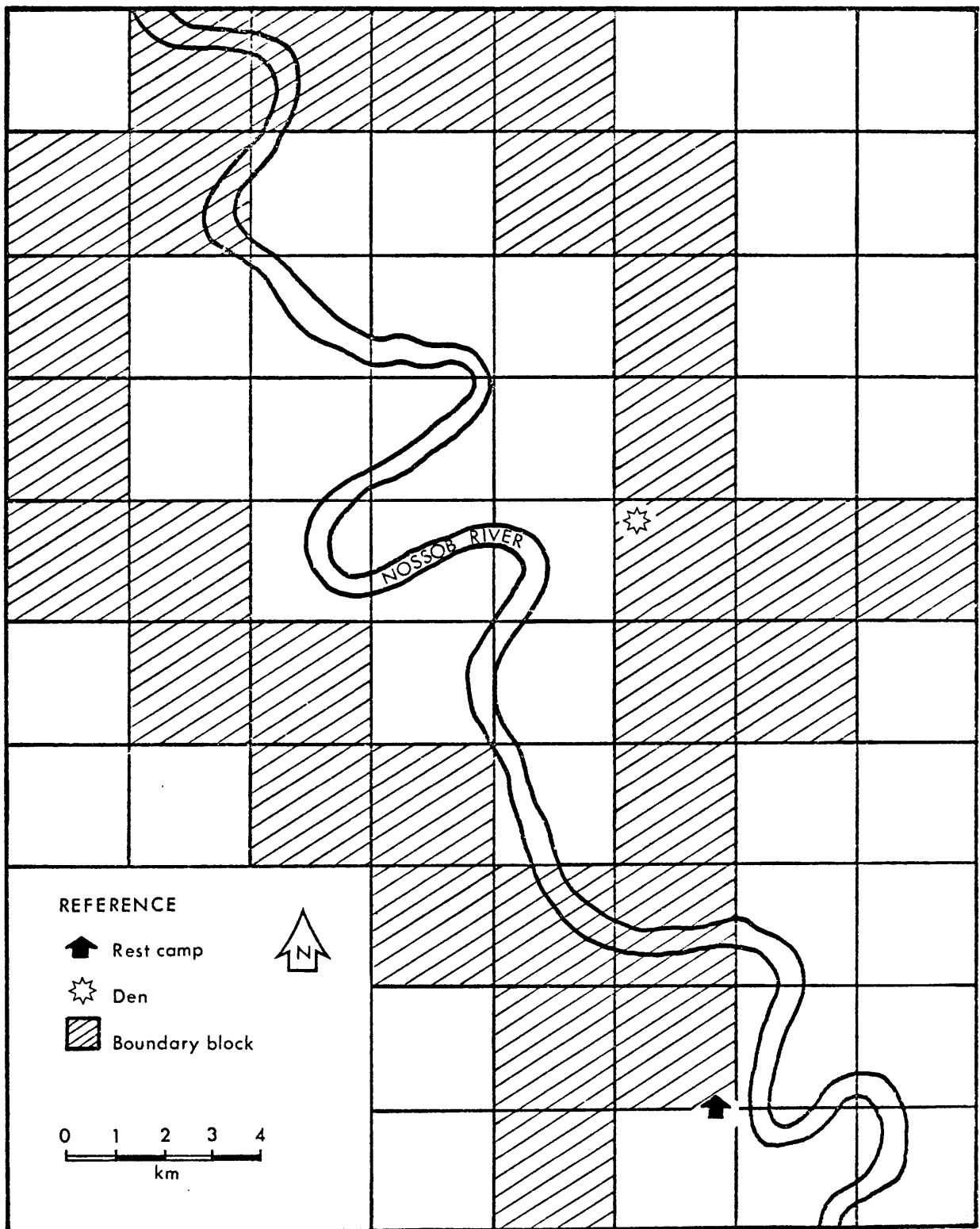


Figure 8: A 2,5 x 2,5 km grid covering the area of the Kwang 2 brown hyaena territory in the southern Kalahari; January - July 1976.

Seven Pans and Kaspersdraai territories.

The contour matrix generated by SYMAP was then used to compute the three-dimensional SYMVU plots (Chapter 3). These maps are displayed as if seen from the south-east at an altitude of 35° above the horizontal. Figure 9 shows a map of the Kwang 2 territory viewed from this angle in order to orientate the reader. In the three-dimensional SYMVU plots the peaks represent areas of the territory in which high movement densities were observed.

Scent marking

Mapping of latrines and pasting points

Each time that a brown hyaena being followed passed a latrine or stopped to paste (Chapter 5) the vehicle's odometer reading was noted. These points were plotted onto a 1 : 10 000 map together with the movement data. The data for both the positions of latrines and pasting points for the Kwang 2 and 3 territories were also analysed by means of SYMAP and SYMVU computer programmes. In these cases the quantitative data reflected in the vertical dimensions of the SYMVU maps were the density of latrines or pasting points. The density values in the SYMAP programmes were divided into 10 class intervals of equal size covering the following ranges: for latrines, 0 - 7 per square in the Kwang 2 territory and 0 - 11 per square in the Kwang 3 territory; for pastings, 0 - 190 per square in the Kwang 2 territory and 0 - 204 per square in the Kwang 3 territory.

In each territory those 2,5 x 2,5 km grid squares containing movements of hyaenas from that territory which were not completely

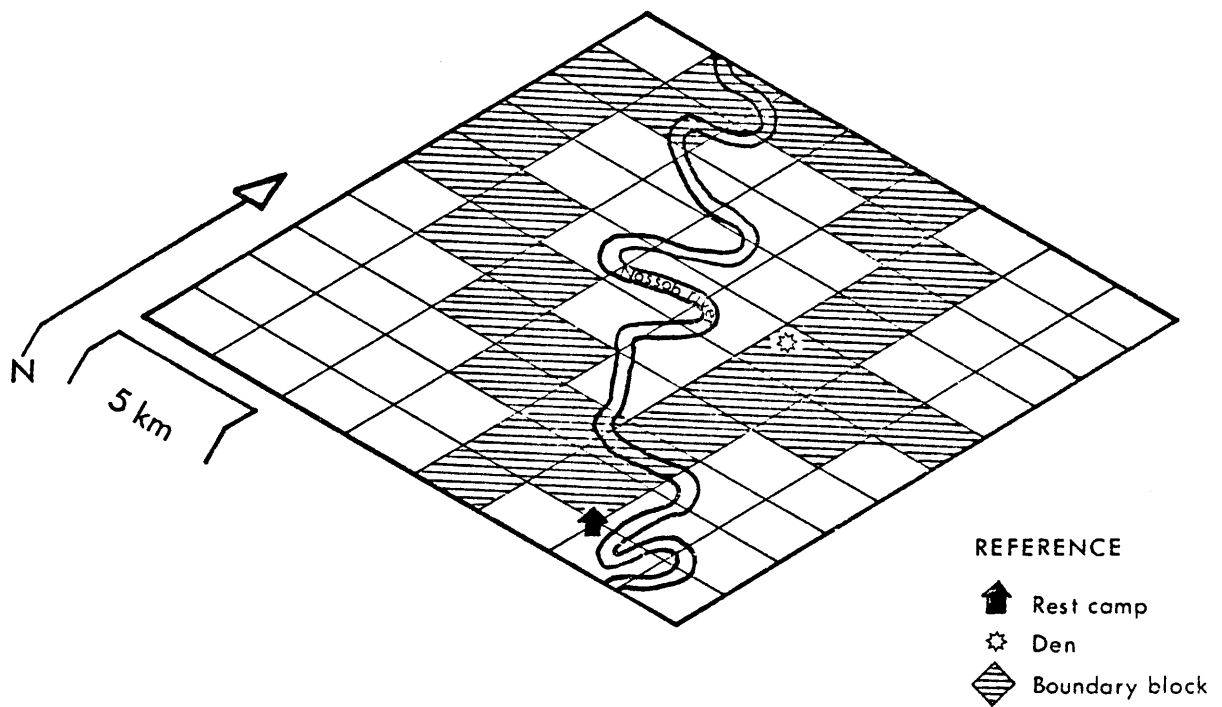


Figure 9: A map of the Kwang 2 brown hyaena territory in the southern Kalahari, as seen from the south-east and from an altitude of 35° above the horizontal, to serve as an orientation for reading the SYMVU maps of the Kwang territory.

surrounded by other squares containing movements of hyaenas from that territory were designated border squares. The other squares containing movements of hyaenas from that territory were designated internal squares (Fig. 8).

Histological analysis of the anal scent pouch

The anal scent pouches from two freshly killed brown hyaenas, one male and one female, were removed and quickly frozen. Several months later they were fixed in 10 per cent buffered formal-saline. Representative pieces of tissue from the areas of the pouch producing the black (apocrine tissue) and white (sebaceous tissue) secretions (Chapter 5) were dissected, washed, dehydrated in ethanol, cleared in methyl benzoate and embedded, under vacuum, in paraffin wax. Ten μm sections for general descriptive histology were stained in haematoxylin and eosin or in Mallory's trichrome stain. Paraffin sections and 20 μm frozen sections were subjected to certain histo-chemical procedures which are listed together with the reactions, in Table 26 (Gorman pers. comm.).

Chemical analyses of pastes

A series of grass stalks on which two known male brown hyaenas had just pasted were collected. The pastes of each individual were collected within a period of 72 h for each individual. The black and white secretions were separated and were deep frozen a maximum of 6 h after being collected and three months later extracted in 1 ml redistilled dichloromethane. Later the extracts were centrifuged and the supernatant reduced to 250 μl under nitrogen.

GLC separations were carried out on a Pye-Unicam 104 gas chromatograph equipped with a flame ionisation detector and using N₂ as carrier gas. The analyses were performed on a 25 m (I.D. 0,23 mm) WCOT column coated with a 0,21 µm film of methyl silicone gum (SE30). The injected samples were split 1 : 100 and passed through the column with nitrogen at 1,5 ml/min. The analysis was temperature programmed from 100° to 200° C at 4° C/min. Injector and detector were maintained at 275° C. Peak areas were measured with a LDC308 computing integrator (Gorman pers. comm.).

Vocalisations

In the description and analysis of the vocal repertoire of the brown hyaena I followed the method used by Struhsaker (1975) in his analysis of the vocalisations of red colobus monkeys Colobus badius. A repertoire of the vocalisations of the brown hyaena was constructed on the basis of the way they sounded to me. Whenever possible tape recordings of the vocalisations, accompanied by notes on the stimulus situations of each recording and the name that I had given to the vocalisation were recorded. The recordings were then analysed in the laboratory by spectrographic analysis. Where I was unable to record what sounded to be a different vocalisation, I merely recorded the stimulus situation and the name I had given it.

Ideally, large numbers of vocalisations should have been recorded and analysed, particularly as the vocalisations of the brown hyaena are graded, so that accurate descriptions and measurements could have been made and the vocalisations objectively categorised. This, however, was beyond the scope of the present study. I have therefore chosen sections of the various vocalisations which sounded typical to me and have used

these to illustrate the typical features of a vocalisation. This analysis is, therefore, rudimentary.

The vocalisations were recorded on a Uher 4000 Report L tape recorder and a Uher dynamic reporter's microphone with a windshield. The tape speed was 19 cm/s. Tapes were analysed with a Kay Sonagraph 7029A Spectrum Analyser using a wide band filter with a resolution of 300 Hz within the frequency range 40 - 4 000 Hz or 80 - 8 000 Hz. The Automatic Gain Control was set on 0. Measurements of the sonograms were made with a frequency and time scale generated by the internal calibration signals of the sonagraph (Passmore pers. comm.).

Food availability

Large and medium-sized ungulates

For the purposes of this study a large herbivore is regarded as one with an adult mass of more than 80 kg and a medium-sized herbivore as one with an adult mass of 12 - 80 kg.

Between April 1972 and December 1980, 73 counts of ungulates were done from a vehicle along the road that runs beside the Nossob river-bed from Nossob Camp to 40 km north of that camp.

Counts in the dunes were irregular and of varying lengths. They were carried out whenever I happened to drive through dune areas. All the relevant ungulates seen during all of the counts were included.

N. Passmore. Department of Zoology, University of the Witwatersrand, Johannesburg, 2001. November 1980.

Visibility along the generally flat river-bed is better than in the undulating dunes, causing the count data to be biased towards the river-bed areas. No attempt was made to measure the extent of this bias, but visibility is never more than twice as good along the river-bed as in the dunes.

Small animals

Any animal with an adult mass of more than 1 kg and less than 12 kg is regarded as a small animal in the present study. Counting small animals, many of which are nocturnal, is difficult. One method which was used was to drive around slowly at night with an observer standing on the back of the truck holding a spotlight and scanning with it through an angle of approximately 270° . I carried out 10 counts of 20 km each in this manner, five along the river-bed and five in the dunes.

Along the river-bed and environs, where the grass was usually short, this method was effective and I could detect small animals, such as springhares, from approximately 250 m. In the dunes, however, where the grass was normally tall, the detection distance was reduced and variable. If the animal was on the side of a dune it might be detectable from 200 m, whereas if it was in a dune street it might be missed even if it was 50 m away. Thus in comparing the number of small animals seen in these two habitats, it must be remembered that the data are generally biased in favour of the river habitat and cannot be statistically compared.

The time of night that a count is conducted is also probably of importance. Nocturnal animals typically have a two-peak activity rhythm, being most active in the early part of the evening and then again just before sunrise (Aschoff 1966). I therefore carried out the counts in the early part of the evening, starting not later than 21h00.

An alternative method of censusing small animals was by the use of spoor counts which were carried out between July 1973 and November 1976. One hundred randomly chosen strips of 200 m were driven in a vehicle, and in each strip the area between the tracks made by the vehicle was swept clean of spoor. The next day I examined the strips with the help of a bushman tracker, and recorded the different species' spoor that had crossed the strips. It was impossible to accurately record the number of animals that had entered the strip and the species were merely noted on a presence or absence basis.

Several sources of bias are inherent in this method. Social species are under-represented. For example, bat-eared foxes usually forage in small groups of two to six individuals and black-backed jackals often forage in pairs, whereas the Cape fox Vulpes chama forages singly (personal observations). Thus, even though Cape fox spoor was encountered more often than that of the other two canids (Table 9), it does not necessarily mean that Cape foxes were more common. Furthermore, the distances covered by the various species between the time that a strip was cleared and the time that I returned to check the spoor may also have affected the results. Far-ranging species would have a better chance of crossing a strip, and thereby of being counted, than would species that do not move extensively. Finally, the data for the river habitat could not be collected in the river-bed itself as the ground is too hard for a spoor to be made and strips could only be counted on the side of the river-bed. This limitation is particularly severe in the case of springhares which show a preference for the river-bed as opposed to the sides (personal observations). Springhare occurrence in river habitat, therefore, is higher than shown by the spoor data and no statistical comparison between the frequency of springhare spoor in the two different habitats could be performed (Table 9).

Tsamas and gemsbok cucumbers

The abundance of tsama Citrullus lanatus and gemsbok cucumber Acanthosicyos naudianus fruits were monitored irregularly between 1976 and 1979 by counting the numbers found in a series of strips of 100 x 10 m. The strips were chosen randomly, but were mostly in the same general area each year. For each fruit counted it was recorded whether it had been eaten or not, but when eaten no attempt was made to identify which animal had eaten it. Eaten fruits were more difficult to detect than uneaten ones were, as their skins dry out and tend to disintegrate.

Counts were carried out in July and November 1976, February, May and July 1977, May 1978 and July 1979. Gemsbok cucumbers are highly susceptible to frost. Counts carried out in May of any year, therefore, are more accurate indicators of the gemsbok cucumber crop of that year than counts carried out in July are. Tsamas on the other hand are more frost resistant. July counts of tsamas, therefore, give a more accurate indication of the size of the crop of that year than July cucumber counts do.

CHAPTER 2 : FEEDING ECOLOGY

INTRODUCTION

Food has been shown to be the primary factor affecting the density of many species of birds (Lack 1966), as well as some carnivores such as wolves Canis lupus (Mech 1970 and Peterson 1977), spotted hyaenas (Kruuk 1970, 1972), lions (Hanby and Bygott 1979) and European badgers Meles meles (Kruuk and Parish In press). The close relationship that exists between the social organisation and food supply of many animals has already been commented on, and it is the main subject of investigation in the present study. The feeding habits of the brown hyaena and the manner of food dispersion are, therefore, of crucial importance here.

Although the diet and foraging behaviour of the brown hyaena have been discussed in detail elsewhere (Mills 1977, 1978 b, Mills and Mills 1978) it is necessary to summarize the main points of these publications and to augment them with subsequent observations.

Most of the effort invested in documenting food availability was done so in the area between Nossob Camp and Bedinkt windmill (Fig. 1). I looked for details in food availability in this area on an annual basis so that the relationship between aspects of food availability and the size of the main brown hyaena group inhabiting that area, the Kwang group, could be investigated. In addition, comparisons between the distribution and abundance of food in the two main habitats, river and dunes, are made.

DIET AND FORAGING BEHAVIOUR

In a previous study, Mills (1977) and Mills and Mills (1978) have shown that mammal remains are the brown hyaena's most important food in the southern Kalahari. Not only did they comprise 39 per cent of all food items observed to be eaten, but they are also the largest sized food items eaten. Wild fruits, mainly the tsama and the gemsbok cucumber, were the next most frequent food items observed to be eaten (29 per cent), but they are a low energy food (Mills and Mills 1978) and their contribution to the brown hyaena's diet cannot be directly compared with that of mammal remains. Insects, birds' eggs and other vertebrate remains are of lesser importance, either because of their size (insects and reptiles) or because of their low incidence (birds and their eggs) in the diet. Killed prey forms a small part of the brown hyaena's diet (4 per cent of all vertebrate food items observed to be eaten) and consists of small animals such as springbok lambs, springhares, bat-eared foxes and korhaans (Mills 1978 b).

Table 4 records those food items which were present in 10 per cent or more of faeces from adults or cubs which were collected between April 1972 and September 1974. These data were collected from the Kaspersdraai Rooikop, Cubitje Quap and Botswana territories. The table only records frequency of occurrence, thus small food items such as insects and Grewia flava berries are given an inflated status as far as their actual contribution to the diet is concerned. Bearing this in mind, it can be seen from Table 4 that large mammals, fruits and small mammals were the most important food items found in adults' faeces, and small mammals and insects the most important found in cubs' faeces.

Table 5 lists the frequency with which food items were observed to be found by individual members of the Kwang group during the three

Table 4: Food items found in more than 10 per cent of the faeces of adult and cub brown hyaenas from the southern Kalahari; April 1972 - September 1974. (Data taken from Mills and Mills 1978).

FOOD ITEM	ADULT (n = 143)		CUB (n = 240)	
	Number of scats	Per cent	Number of scats	Per cent
Coleoptera	50	35,0	151	62,9
Small carnivores ⁺	44	30,8	99	41,3
Gemsbok	74	51,7	49	20,4
Tsama	68	47,6	55	22,9
Steenbok	12	8,4	70	29,2
Reptiles	33	23,1	43	17,9
Isoptera	12	8,4	62	25,8
Red hartebeest	39	27,3	33	13,8
Birds	22	15,4	34	14,2
<u>Grewia flava</u> berries	21	14,7	26	10,8
Gemsbok cucumber	26	18,2	10	4,2
Blue wildebeest	22	15,4	13	5,4
Springhare	17	11,9	11	4,6
Cape hare	15	10,5	4	1,7

⁺ Mainly bat-eared fox and black-backed jackal

Table 5: Food eaten by brown hyaenas of the Kwang group in the southern Kalahari during direct observations; December 1974 - March 1975, January - July 1976, July 1977 - August 1978.

FOOD CATEGORY	PERIOD AND DISTANCE FOLLOWED					
	December 1974 - March 1975		January - July 1976		July 1977 - August 1978	
	500 km		1 235 km		865 km	
	Number eaten	Per cent frequency ⁺	Number eaten	Per cent frequency ⁺	Number eaten	Per cent frequency ⁺
Total mammal remains	39	42,4	130	53,1	98	54,4
Large mammals	14	35,9	25	19,2	46	46,9
Medium-sized mammals	5	12,8	51	39,2	13	13,3
Small mammals	7	17,9	8	6,2	10	10,2
Very small mammals	0	0,0	2	1,5	0	0,0
Unidentified mammals	13	33,3	44	33,8	29	29,6
Bird remains	1	1,1	7	2,9	2	1,1
Vertebrate kills	1	1,1	6	2,4	2	1,1
Fruits	30	32,6	55	22,4	6	3,3
Others ⁺⁺	21	22,8	47	19,2	72	40,0
Total	92	-	245	-	180	-

⁺ Per cent frequency for mammals are expressed as a percentage of total mammal remains. Per cent frequency for total mammal remains and all other items are expressed as a percentage of the totals of all food items.

⁺⁺ Items such as reptiles, birds' eggs, insects, carnivore faeces and small unidentified pieces of food.

observation periods between December 1974 and August 1978 referred to in Chapter 1. The most important food categories were mammal remains, consisting of carcasses or odd pieces of bone, followed by wild fruits.

The relative frequencies with which different food items were utilised varied in the three periods. Large mammal remains were particularly well utilised in the 1977 - 1978 period, less so in the 1974 - 1975 period and least of all in the 1976 period. The main contributor to the high incidence of mammal remains fed on in the 1977 - 1978 period was blue wildebeest, which comprised 55 per cent of the identifiable large mammal remains fed on in this period. This compared with 19 per cent for gemsbok, 16 per cent for red hartebeest and 10 per cent for eland.

Medium-sized mammals, 98 per cent of which were springbok, were most frequently eaten in the 1976 period, but less so in the other two periods.

Small mammal remains were more important in the 1974 - 1975 period than during the other periods. These comprised a variety of animals; steenbok, black-backed jackal, bat-eared fox and springhare being the most important.

Finally, wild fruits were commonly eaten in the 1974 - 1975 and 1976 periods, but hardly at all in the 1977 - 1978 period.

Although the data in Table 5 were not collected evenly throughout the year, these differences in diet are not only a result of seasonal variation in food availability as they also reflect annual or even longer term changes in the distribution and abundance of food. This will be discussed further in the next section.

In the southern Kalahari the brown hyaena is a solitary forager. Individuals cover large distances ($\bar{X} = 32$ km) at night in their search

for food, often seeming to search randomly. The olfactory sense is most important in locating food, especially carrion, which, provided that the hyaena is downwind of the food source, can be detected from at least 2 km away. Large food items may be shared by several brown hyaenas (Figs. 11 and 13) or the excess may be stored, usually under a bush. Fresh small and medium-sized carcasses with meat are often carried back to the den for the cubs. Except for the odd halfhearted attempt at catching adult springbok, brown hyaenas direct all their hunting attempts at small animals. Of 88 hunting attempts directed at mammals, five (6 per cent) were successful and of 16 hunting attempts directed at birds five (31 per cent) were successful (Mills 1978 b).

FOOD AVAILABILITY AND RELATIONS WITH OTHER CARNIVOROUS ANIMALS

Only the availability of those food items found to be frequently eaten by brown hyaenas (Tables 4 and 5) was assessed, but no attempt was made to count the smaller ones; insects, reptiles and Grewia flava berries, as their actual contribution to the diet was relatively unimportant because of their small size. Korhaans were the only birds counted, as these were the most important bird species in the brown hyaena's diet (Mills 1978 b and Mills and Mills 1978).

Large and medium-sized animals

Several papers on the movements and numbers of the ungulates in the southern Kalahari have been published in recent years (Eloff 1959 a and b, 1961, 1962 and 1966, Bothma 1971 a, 1972, Bothma and Mills 1977).

The general tendency is for gemsbok, red hartebeest, blue wildebeest and springbok to concentrate in and around the dry river-beds after the rains and then, as conditions become progressively drier, for these ungulates, in particular gemsbok and red hartebeest, to move away from the river-beds into the dune areas where they often become widely scattered. Pans, which are irregularly distributed throughout the dunes and are rare in the study area except for the Seven Pans area (Fig. 1), provide a habitat similar to that of the river-beds and also support concentrations of ungulates during the rains. The river-beds and environs cover less than 2 per cent of the southern Kalahari.

Despite the fact that visibility is better in the river-bed areas than the dunes, it is clear from Tables 6 and 7 that during the present study the river habitat in the study area supported a far higher biomass of ungulates throughout the year than did the dunes. Even when numbers of large ungulates were low along the river-bed, the density in the dunes was still considerably lower. Taking, for example, those months when the density of large ungulates along the 40 km stretch of river-bed in the Kwang territory was less than 250 per 100 km (Fig. 10), the mean density in this habitat was 125 large ungulates per 100 km driven. In the dunes of the study area the mean density for the same months was 29 large ungulates per 100 km driven.

Figure 10 records the number of ungulates counted from April 1972 to December 1980 in the area of the Nossob river-bed referred to above. The number of large ungulates fluctuated in the expected pattern between 1972 and 1975, with similar numbers being present each year. In early 1976 the number of large ungulates greatly increased and remained high for the entire year as they did in 1977. Blue wildebeest were mainly responsible for this increase (Table 6). In 1978, 1979 and 1980 the number of large ungulates again fluctuated in the typical pattern, but with a larger

Table 6: Average annual density of ungulates along a 40 km strip of the Nossob river-bed, southern Kalahari, from Nossob Camp northwards; 1972 - 1980.

YEAR	DISTANCE. (km) TRAVELLED	NUMBER OF UNGULATES COUNTED PER 100 km DRIVEN						
		Springbok	Gemsbok	Red hartebeest	Blue wildebeest	Eland	Steenbok	Duiker
1972	160	473	119	58	62	0	1	0
1973	200	1 247	66	98	118	0	0	0
1974	320	1 459	43	115	99	0	0	0
1975	400	1 028	75	88	69	0	1	0
1976	240	2 745	147	186	311	0	0	0
1977	360	2 273	159	278	431	0	3	0
1978	400	1 230	56	166	486	0	6	0
1979	440	1 523	43	121	441	0	2	0
1980	400	1 330	59	111	319	0	3	0
Mean		1 479	85	136	260	0	2	0
Standard error		$\pm 223,3$	$\pm 14,9$	$\pm 21,9$	$\pm 57,8$	$\pm 0,0$	$\pm 0,7$	$\pm 0,0$

Table 7: Average annual density of ungulates in the dunes of the study area in the southern Kalahari; 1972 - 1980.

YEAR	DISTANCE (km) TRAVELLED	NUMBER OF UNGULATES COUNTED PER 100 km DRIVEN						
		Springbok	Gemsbok	Red hartebeest	Blue wildebeest	Eland	Steenbok	Duiker
1972	678	9	13	3	0	0	14	1
1973	534	0	15	11	12	3	11	0
1974	259	0	7	12	0	35	6	2
1975	527	0	31	6	0	0	10	0
1976	413	0	17	13	0	0	16	0
1977	189	11	16	13	0	0	12	2
1978	212	0	24	0	0	0	11	1
1979	101	2	67	27	64	0	28	8
1980	495	4	79	2	0	2	13	0
Mean		3	30	10	8	4	13	2
Standard error		$\pm 1,4$	$\pm 8,5$	$\pm 2,7$	$\pm 7,1$	$\pm 3,8$	$\pm 2,0$	$\pm 0,9$

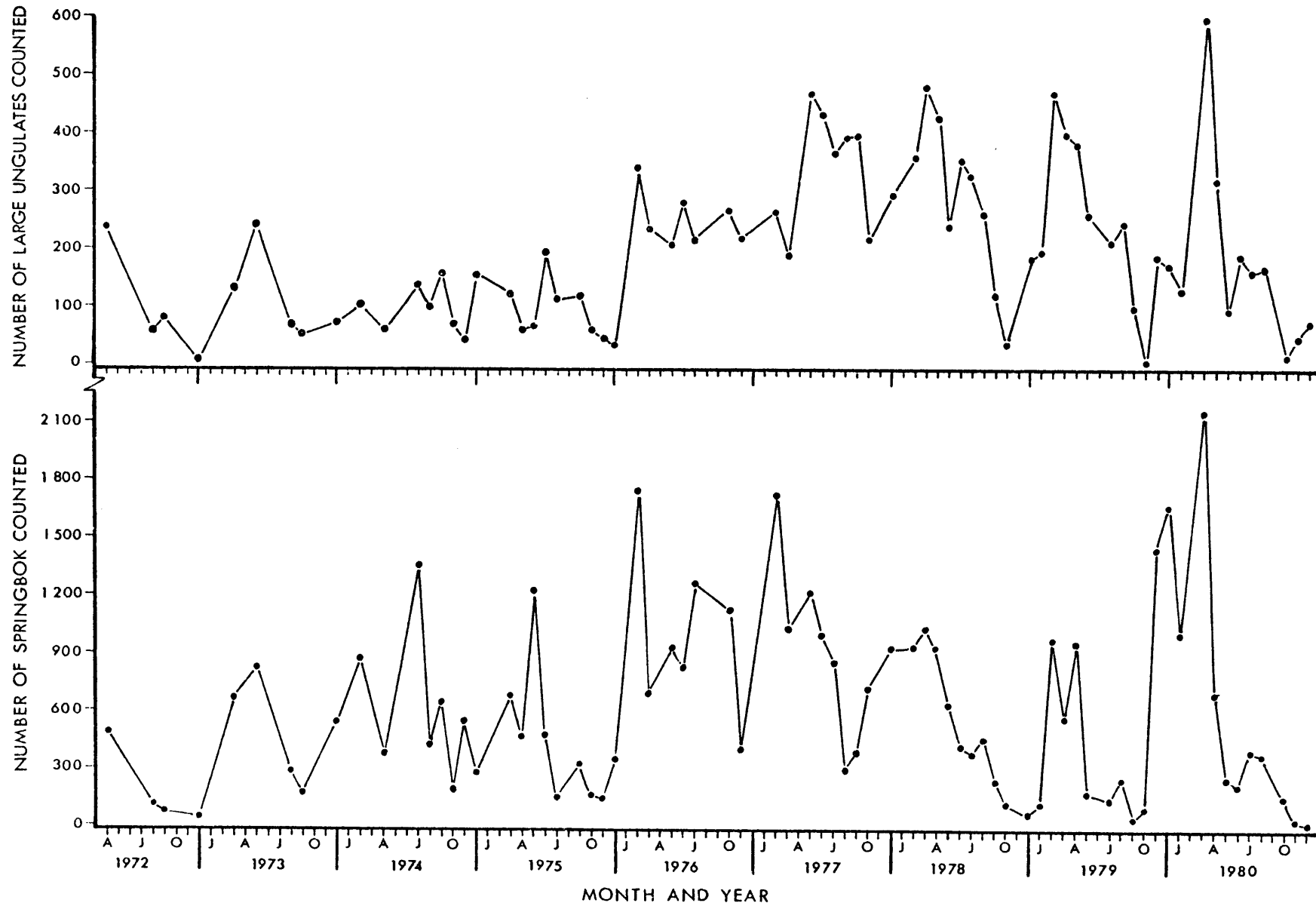


Figure 10: Numbers of springbok and large ungulates counted along the Nossob river-bed, southern Kalahari, between Nossob Camp and a point 40 km along the road to the north; April 1972 - December 1980.

amplitude than previously. The blue wildebeest was again the most common large ungulate in this area in these years (Table 6).

Figure 10 shows that springbok numbers followed a similar pattern to that of the large ungulates between 1972 and 1975. In 1976 they remained relatively high for the entire year and in 1977 for longer than normal. In 1978, 1979 and 1980 they reverted to the normal pattern, although in November and December 1979 they were again high due to abundant but localised rains falling in the study area. Rainfall (Fig. 2) and the resultant condition of the vegetation is thought to be the most important factor in regulating these movements in and out of the river-bed (Bothma 1971 a, 1972 and Bothma and Mills 1977).

As far as brown hyaenas are concerned there is a fundamental difference between a springbok carcass and a large ungulate carcass. Figures 11 and 12 show that a springbok carcass usually only provides a meal for one hyaena, whereas the remains from a large ungulate often provides an equal sized meal for several brown hyaenas (Figs 11 and 13). This difference is statistically significant ($d = 4,013$; $f = 19$; $p < 0,001$).

Are actual numbers of animals present in an area a valid means of assessing food availability for a scavenger, as the animals eaten have to succumb to some other agent of mortality before they become available to the scavengers? It is known that predators kill more often and utilise a carcass less efficiently during times of relative food abundance (Schaller 1972, Kruuk 1972 and personal observations). Lions were regularly encountered in the Kwang area throughout the study. It seems reasonable to assume, therefore, that the larger the ungulate concentrations in this area, the higher the kill frequency of lions. Cheetahs were irregular visitors to the Kwang area during the study, individuals or small groups usually spending approximately two weeks in the area before moving on. During these visits, however, a regular supply of springbok carcasses

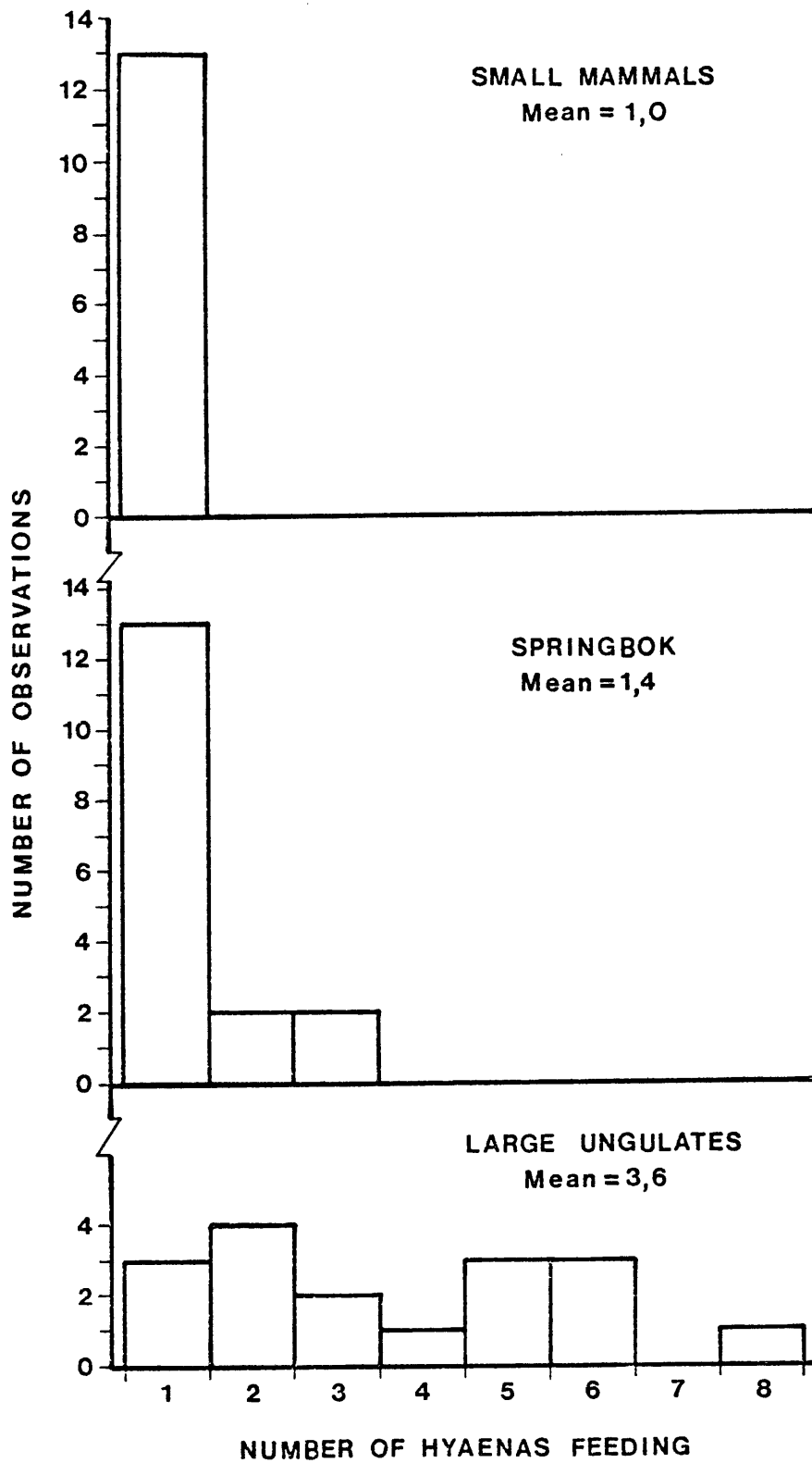


Figure 11: The number of brown hyaenas feeding on different sized carcasses in the southern Kalahari; 1975 - 1980.

were available to the scavengers in the area. Leopard kills were normally unavailable to scavengers as the leopards took their food into trees.

Despite a regular supply of carcasses, however, competition from other scavengers could severely reduce the chances of a brown hyaena being able to utilise all of the carcass. For brown hyaenas the most important potential competitor is the spotted hyaena as it is the only other species which is able to crush the large bones of large and medium-sized animals, and is considerably larger than the brown hyaena (personal observations). A brown hyaena living in the Ngorongoro Crater, Tanzania, where there is an extremely high year-round density of ungulates, for example, would find little to eat as the large numbers of spotted hyaenas utilise the carcasses to the full (Kruuk 1972).

To measure the amount of competition that existed between brown hyaenas and spotted hyaenas over fresh carcasses in the area covered by the Kwang brown hyaena group, I waited at fresh carcasses of ungulates that had either died naturally or which I had specifically put out, between 1978 and 1980. Of nine springbok carcasses, eight were consumed by one or more brown hyaenas and one was consumed by two spotted hyaenas. Of 17 large carcasses (blue wildebeest, gemsbok or red hartebeest), 14 were first found by one or more brown hyaenas and three by one or more spotted hyaenas. Of the 14 cases where brown hyaenas found the carcass first, they were twice dislodged, at least for a time, by a single spotted hyaena (Fig 14), although in one of the cases a brown hyaena came back to the carcass and fed with the spotted hyaena for 3 min before the brown hyaena broke off a piece of the carcass and carried it away. In one of the three cases where a spotted hyaena found the carcass first, the spotted hyaena moved off without consuming everything and later a brown hyaena came and fed off the carcass.

Apart from the above observations I only twice observed brown hyaenas

which found a large carcass while I was following them, being displaced by spotted hyaenas; on one occasion by two and on the other by one.

The extent to which brown and spotted hyaenas in the Kwang area competed for food, therefore, was small, with spotted hyaenas only occasionally depriving the brown hyaenas of food.

In another area of the southern Kalahari, around Kousant windmill, where spotted hyaenas were known to be more common than they were in the Kwang area, the situation was different. Although I only waited at a carcass on five occasions (one springbok, three blue wildebeest and one eland) in this area, the carcass was consumed each time by spotted hyaenas only. If these observations are compared with those from the Kwang area and even if those occasions where spotted hyaenas as well as brown hyaenas fed on the carcass are scored in favour of spotted hyaenas only, the difference in the utilisation of carcasses in these two areas by these two species is significant (Fisher exact probability test $p = 0,003$; one-tailed). I only once saw a brown hyaena feeding on a fresh carcass (a springbok) in the Kousant area and then it was driven off by a spotted hyaena. The spotted hyaenas were quick to locate fresh carcasses in this area and to utilise them fully (Mills in prep.). Here, therefore, it was likely that the spotted hyaenas were depriving brown hyaenas of a significant amount of food.

Brown hyaenas might be able to derive some food from spotted hyaenas when the spotted hyaenas are not utilising their kills to the full. This can be expected in areas of low spotted hyaena density. Kruuk (1972) has shown that in the Serengeti, Tanzania, where the spotted hyaena density is lower than in Ngorongoro, the spotted hyaenas are not so likely to consume their kills completely whereas in the Ngorongoro they invariably do so. Of 15 kills which I observed spotted hyaenas feeding on in the high density Kousant area, they utilised 14 of them completely. Of four

kills they made away from this area, three were under-utilised. The sample size is again small, but this difference is significant (Fisher exact probability test $p = 0,016$; one-tailed). This was because when some members of the spotted hyaena clan made a kill in the high density area, other clan members quickly joined them on the kill. On the other hand when some members of the clan moved into a less utilised area, only those hyaenas which participated in the hunt fed from the carcass (Fig. 15).

Another potential competitor of the brown hyaena is the black-backed jackal. Black-backed jackals were common in the Kwang area and because of their ability to find a carcass quickly they were often able to deprive the brown hyaenas of substantial amounts of meat. Even after brown hyaenas have found a carcass, jackals continue to feed from it (Fig. 13). The impact of jackals on this aspect of the brown hyaena's food supply, however, is limited as jackals are unable to consume any but the smallest bones.

Similarly, vultures are able to locate and dispose of the meat of a carcass quickly (Houston 1974 a and b and Richardson 1980). The white-backed vulture Gyps africanus was common in the Kwang area and these birds deprived brown hyaenas of much potential food, particularly from carcasses of animals which died non-violently. Even more so than jackals, however, vultures are unable to crush bones. Vultures are diurnal and brown hyaenas are nocturnal. One of the reasons why brown hyaenas are nocturnal may be that in this way they avoid competing with vultures and improve their chances of finding those animals that die at night before the vultures become active the next day.

During the present study, therefore, large numbers of ungulates in the Kwang area with its moderate density of lions and other predators, but low density of spotted hyaenas, could be taken as an indication of

a good food supply for the brown hyaenas. This assumption is strengthened when considering the mean distance travelled by the brown hyaenas of the Kwang group before finding certain types of food (Fig. 16). Here it can be seen, for example, that in 1976 when springbok numbers were high the brown hyaenas found medium-sized mammal remains significantly quicker than they did in 1974 - 1975 and 1977 - 1978 when springbok numbers were lower (Fig. 10). Similarly they found large mammal remains significantly quicker in 1977 - 1978 than they did during the other periods.

Another important consideration when looking at food availability is the amount of food available over an extended period. Bertram (1973) makes the point that a good year for lions would be one in which there were comparatively few months of food shortage, rather than one in which there was overall a high number of prey animals present.

The ends of 1978, 1979 and particularly 1980, produced a sharp reduction in the number of ungulates along the Nossob river-bed in the Kwang area (Fig. 10) even though the overall densities for the years were high (Table 6). There was, however, a high non-violent mortality of large ungulates, mainly blue wildebeest, during the dry parts of these years. In those months of the years 1978 to 1980 when less than 200 large ungulates were counted along the relevant 40 km of river-bed (Fig. 10), 14 large ungulate carcasses were recorded in the Kwang area, at least nine of which had died non-violently. This compared with a total of 40 large ungulate carcasses found in the same area during the remainder of the study, of which eight had died non-violently ($\chi^2 = 7,49$; $df = 1$; $p < 0,01$).

Although high numbers of ungulates appear to signify a good food supply for brown hyaenas, low numbers might not necessarily mean a poor food supply. There might, even with low numbers, be a high mortality due to disease or hunger, as apparently occurred in the Kwang group's

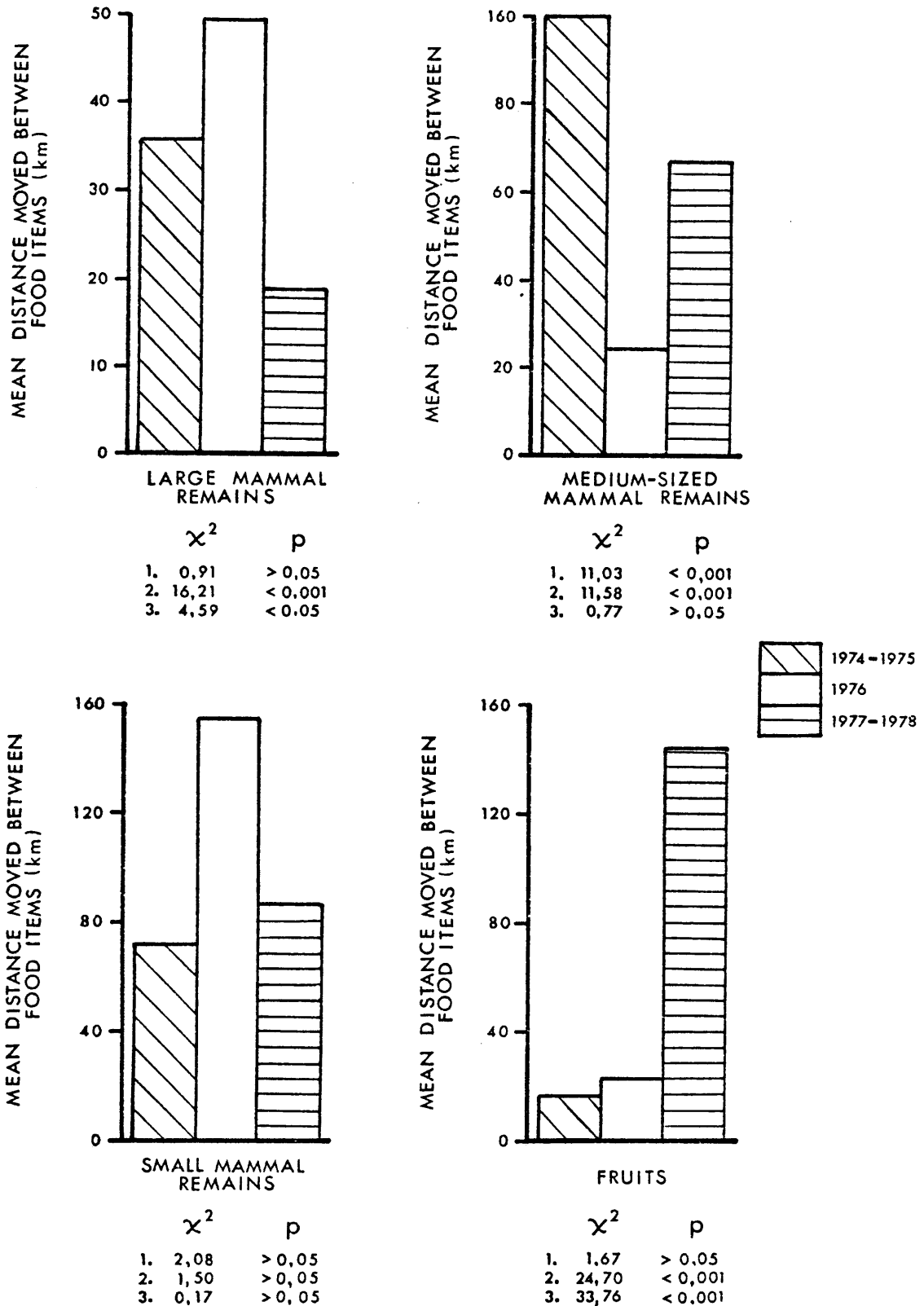


Figure 16: The mean distances which brown hyaenas of the Kwang group in the southern Kalahari were observed to move before finding various food items in three time periods; December 1974 - March 1975, January - July 1976 and July 1977 - August 1978. The χ^2 values compare the number of each food item eaten (taking into account the distance moved) for each pair of time periods; 1. 1974 - 1975 v 1976; 2. 1976 v 1977 - 1978; 3. 1974 - 1975 v 1977 - 1978.

territory between 1978 and 1980.

Apart from the number of ungulates present in an area their distribution within that area is important. Along the river-bed the distribution of ungulates at times was uneven and there were some rapid and drastic changes in their distribution. In Fig. 17 some examples of the distribution of ungulates along the 40 km strip of river-bed are given. Although there are no quantitative data from the dunes, the distribution of ungulates in this habitat was apparently more even. Thus when the ungulates moved out of the river-bed they tended to move into the dune areas outside the study area.

Small animals

The results of the small animal counts are given in Tables 8 and 9. Bearing in mind the limitations of the census techniques as discussed in Chapter 1, the following conclusions on the occurrence of the more important small animals in the brown hyaena's diet (Table 4) can be drawn. Steenbok and Cape hare Lepus capensis show a clear preference for the dune areas (see also Tables 6 and 7 for steenbok), and are common in their preferred habitat. Of the small canids, black-backed jackals prefer river habitat and bat-eared foxes show no preference for either habitat from the spoor counts and the suggestion of a preference for river habitat from the night counts. These last two mentioned species are also relatively common. The Cape fox is rarely eaten by brown hyaenas (Mills and Mills 1978) and, because of the Cape fox's solitary nature, it is probably not as common relative to the other two more social species as the spoor data suggest (see Chapter 1). This is borne out by the night counts. Springhares are common in both habitats, the night

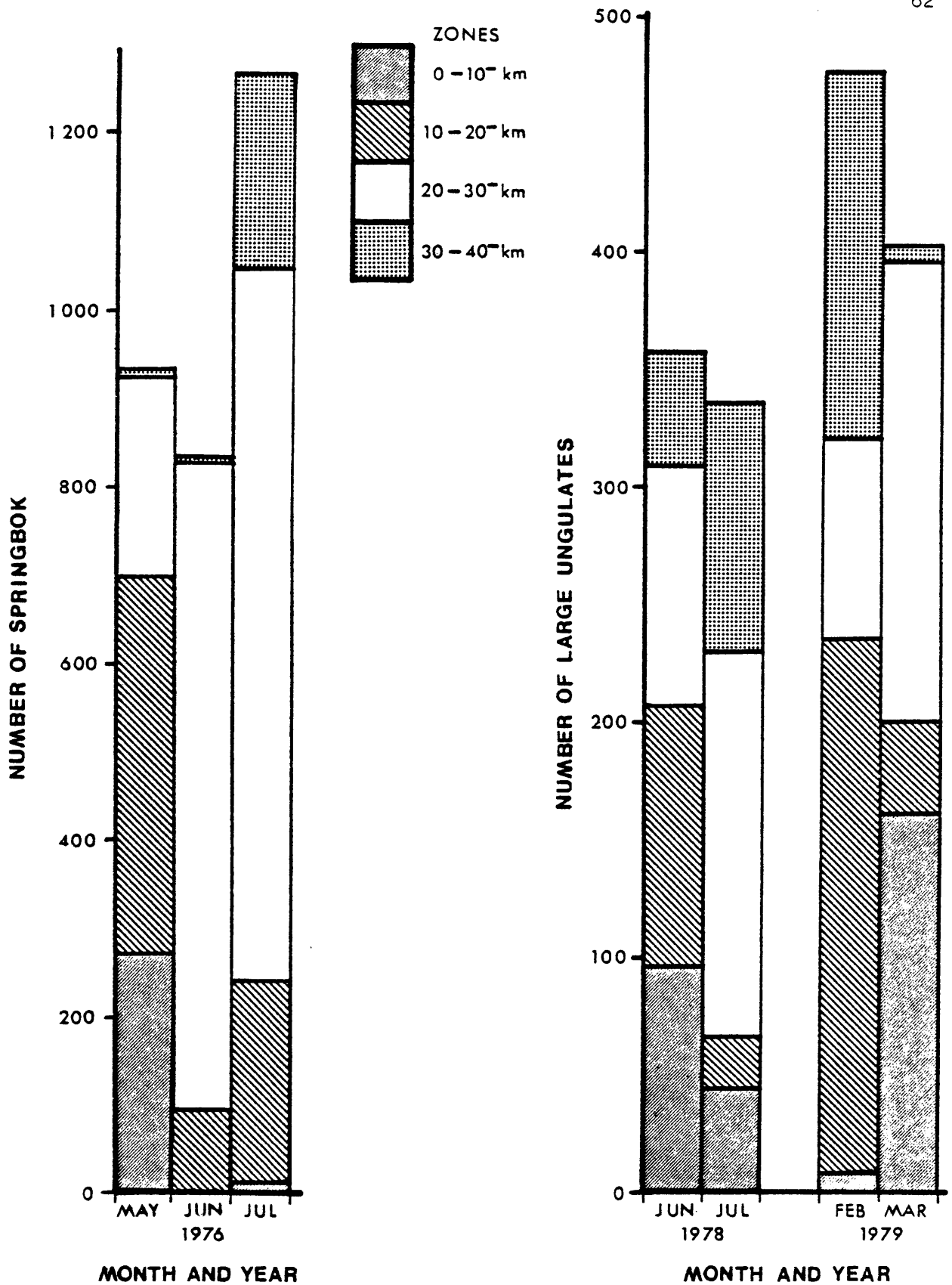


Figure 17: Three examples of the monthly changes in distribution of ungulates in four 10 km zones along a 40 km stretch of the Nossob river-bed in the southern Kalahari.

Table 8: Mean number and standard error of small animals counted in 10 night counts of 20 km each in the southern Kalahari; July 1973 - October 1977.

ANIMAL	RIVER	DUNES
Springhare	69,4 \pm 23,35	25,6 \pm 5,89
Korhaan ⁺	0,0 \pm 0,00	23,0 \pm 12,46
Bat-eared fox	8,8 \pm 2,63	0,4 \pm 0,25
Steenbok	1,0 \pm 0,55	6,2 \pm 2,01
Black-backed jackal	2,8 \pm 0,80	1,6 \pm 0,51
Cape hare	1,0 \pm 0,45	2,4 \pm 1,69
Cape fox	1,8 \pm 1,11	0,8 \pm 0,49
African wildcat	1,0 \pm 0,77	0,4 \pm 0,40
Aardwolf	0,0 \pm 0,00	0,6 \pm 0,60
Porcupine	0,0 \pm 0,00	0,4 \pm 0,40
Striped polecat	0,4 \pm 0,24	0,0 \pm 0,00
Caracal	0,0 \pm 0,00	0,2 \pm 0,20

⁺ Seen and heard.

Table 9: Frequency of occurrence of spoor of different animals in 10 strips of 200 x 1,5 m located in river and dune habitats in the southern Kalahari; July 1973 - March 1976.

ANIMAL	HABITAT					
	River (n = 20)		Dune (n = 80)		River vs dune	
	Frequency	Per cent	Frequency	Per cent	χ^2	p
Steenbok	13	65,0	71	88,8	8,60	<0,01
Cape hare	7	35,0	53	66,3	7,88	<0,01
Yellow mongoose	5	25,0	52	65,0	12,14	<0,001
Korhaan species	1	5,0	51	51,8	24,54	<0,001
Springhare	8	40,0	34	42,5	*	*
Cape fox	7	35,0	31	38,8	0,32	>0,05
Black-backed jackal	11	55,0	22	27,5	4,30	<0,05
Common duiker	0	0,0	22	27,5	8,74	<0,01
Bat-eared fox	3	15,0	16	20,0	0,69	>0,05
African wildcat	5	24,0	9	11,3	1,50	>0,05
Striped polecat	1	5,0	8	10,0	1,29	>0,05
Porcupine	1	5,0	3	3,8	0,15	>0,05
Ground squirrel	2	10,0	2	2,5	0,80	>0,05
Caracal	0	0,0	3	3,8	2,60	>0,05
Suricate	0	0,0	2	2,5	2,58	>0,05
Aardvark	0	0,0	2	2,5	2,58	>0,05
Pangolin	0	0,0	1	1,3	3,09	>0,05
Small-spotted genet	0	0,0	1	1,3	3,09	>0,05
Black-footed cat	0	0,0	1	1,3	3,09	>0,05
Honey badger	0	0,0	1	1,3	3,09	>0,05
Tortoise	0	0,0	1	1,3	3,09	>0,05

* Invalid - see page 40.

counts pointing to a possible preference for river habitat.

A common small animal of the dunes is the yellow mongoose Cynictis penicillata (Table 9), but it rarely occurs in the brown hyaena's diet (Mills and Mills 1978), perhaps because it is predominantly diurnal and also because it is so small that predators do not leave any remains for the hyaenas.

Korhaans were the most frequently observed animal to be killed by brown hyaenas (Mills 1978 b and subsequent observations). This was partly due to an idiosyncrasy of one hyaena, but not exclusively so. Korhaans are mainly restricted to the dunes where they are common.

The smaller carnivores, particularly caracals Felis caracal and black-backed jackals, provide food for brown hyaenas directly when the hyaenas eat them (Mills and Mills 1978) and, probably more importantly, brown hyaenas also scavenge from their kills.

In spite of the rareness of the caracal in the southern Kalahari (Tables 8 and 9), it is noteworthy that on eight occasions I observed a brown hyaena appropriate a kill from one. Each time the hyaena, on sensing the food, merely moved quickly towards it and the caracal withdrew without any resistance. The food stolen by brown hyaenas from caracals is of value because the carcasses invariably contain a large proportion of meat. I once saw a caracal up a tree with its springhare kill. In light of the apparently high loss of kills to brown hyaenas, it is strange that they do not do this more often.

Only six observations of a brown hyaena appropriating black-backed jackal kills were made, despite the higher density of jackals than caracals (Tables 8 and 9). I have also mentioned that jackals can on occasions deprive brown hyaenas of substantial amounts of meat. The relationship between brown hyaenas and black-backed jackals, therefore,

is not as beneficial to brown hyaenas as is their relationship with caracals.

In general I have little information on the fluctuations of populations of small animals during the study. I did get the impression that Cape hares were more common in the early years of the study, 1972 - 1974, than they were between 1975 and 1977, and that their numbers began to build up again in 1978.

Bat-eared fox numbers, too, apparently fluctuated markedly along the Nossob river-bed between 1976 and 1980. These canids often forage diurnally during the winter months (Nel 1978 and personal observations) and therefore I carried out a number of daytime counts of bat-eared foxes between May and September from 1976 to 1980, along the aforementioned 40 km of river-bed. Figure 18 records the number counted for each 100 km driven in each year. The data show that bat-eared fox numbers were considerably higher along this stretch of river-bed during 1977 than they were in any of the other years.

Tsamias and gemsbok cucumbers

Tsama and gemsbok cucumber fruits are important food items for brown hyaenas (Tables 4 and 5), both as a source of moisture and for their limited food value (Mills and Mills 1978). Brown hyaenas are not, however, the only animals that eat these fruits. They are utilised by a wide range of other animals, particularly rodents and ungulates (Leistner 1967 and personal observations) and also by bushmen (Story 1958).

The crops of both fruits become available from about March each year, although the perennial cucumbers appear slightly earlier than the

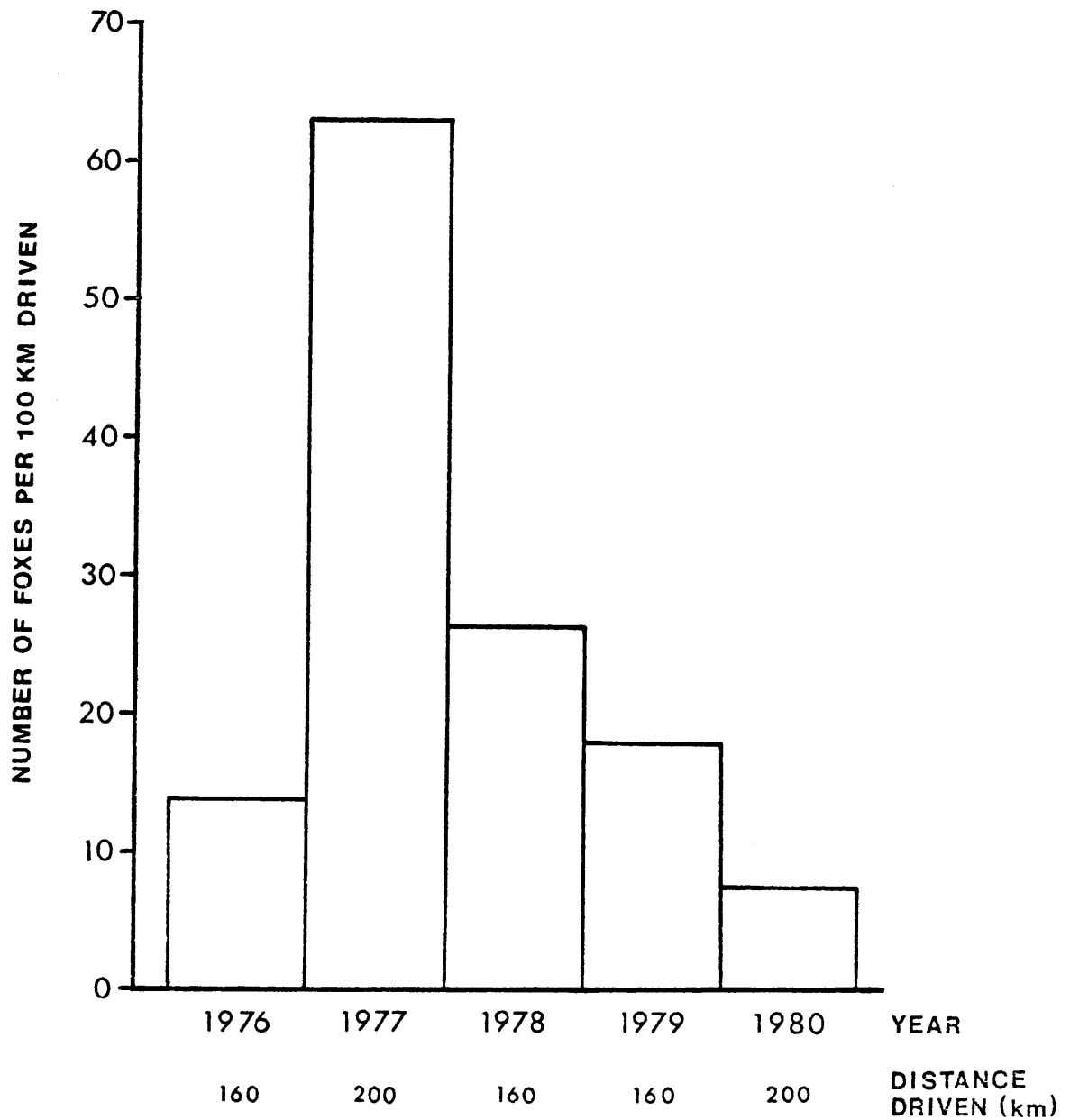


Figure 18: Number of bat-eared foxes counted per 100 km driven along the Nossob river-bed, southern Kalahari, between Nossob Camp and a point along the road 40 km to the north. All counts were made during the day between the months May - September 1976 - 1980.

annual tsamas do. Tsama fruits are practically frost resistant and can last for over a year, gemsbok cucumbers on the other hand are susceptible to frost and the bulk of the crop has usually disappeared by July.

Both tsamas and gemsbok cucumbers grow almost exclusively in the dunes (Fig. 19). In 30 strip counts carried out in river habitat only 29 tsamas and no gemsbok cucumbers were counted, whereas in 90 strip counts carried out during the same period in the dunes 2 807 tsamas and 2 070 gemsbok cucumbers were counted. The sizes of the crops vary annually (Fig. 20), although the conditions responsible for this phenomenon could not be definitely identified. The fluctuations are not related just to the total annual rainfall (Fig. 2), but the distribution of the rainfall is probably also important.

As far as tsamas are concerned, 1976 was an exceptionally good year, 1979 was also good, but 1977 and 1978 produced hardly any tsamas (Fig. 20). Although I did not carry out any surveys between 1972 and 1975, nor in 1980, there was a good crop in the first mentioned years, but an extremely poor tsama crop in 1980. The utilisation rate of tsamas in July 1979 was proportionally higher than it was in July 1976 (Fig. 20), no doubt because of the abundant crop in 1976 and also because of a large number of blue wildebeest, which also eat tsamas, in the area in June 1979. Figure 19 shows that even in good tsama years, although the fruits are widely distributed, this distribution is irregular. This was particularly so in 1979.

The data for the gemsbok cucumber (Fig. 20) are affected by this fruit's susceptibility to frost (Chapter 1), the May 1977 and May 1978 counts giving the most accurate picture of their abundance in any of the years sampled. Both the 1976 and 1979 data under-represent the gemsbok cucumber crop because the counts were done later in the year. During those years that no counts were done, my distinct but subjective

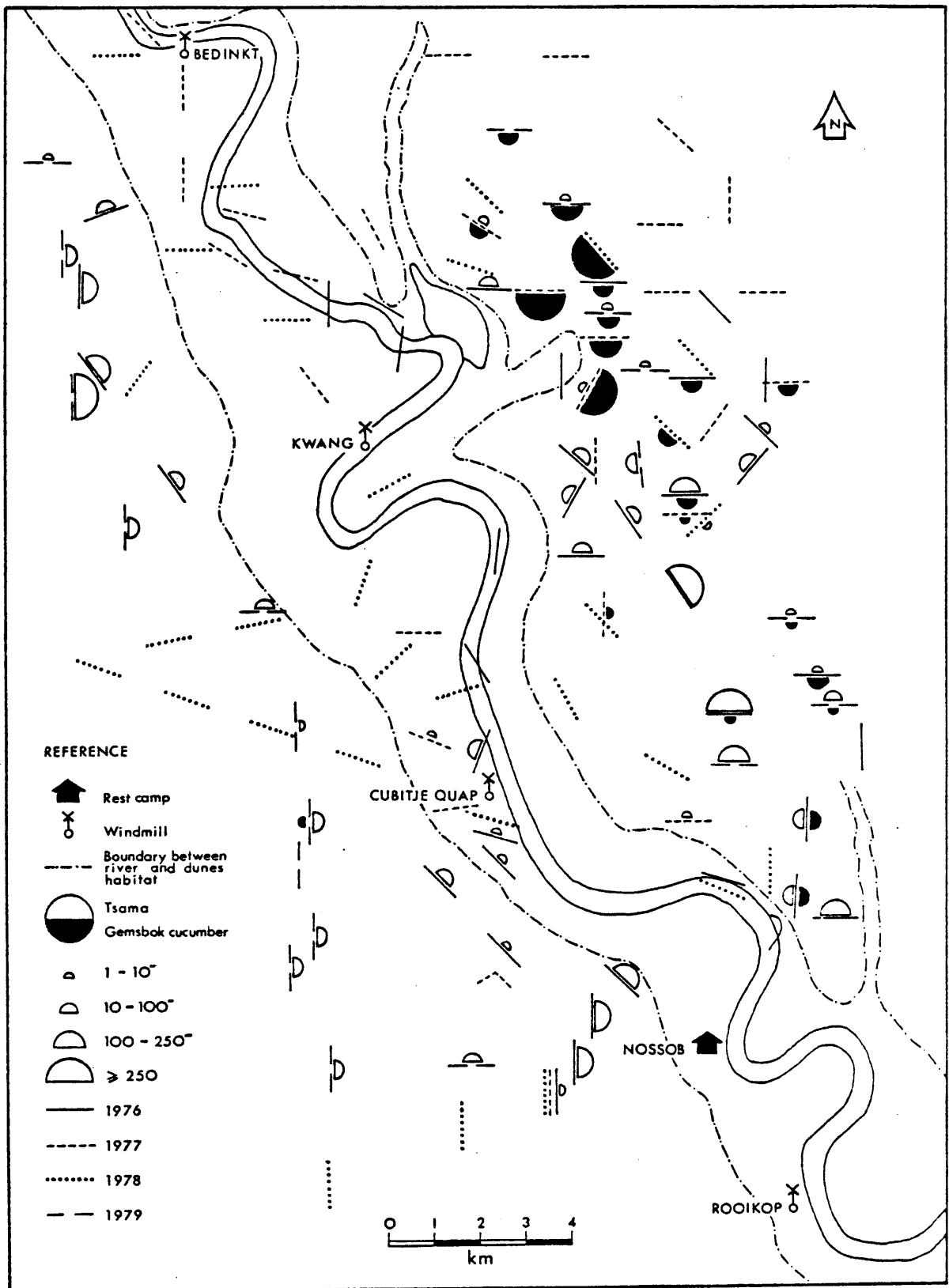


Figure 19: Distribution and size of tsama and gembok cucumber patches in a part of the southern Kalahari; 1976 - 1979.

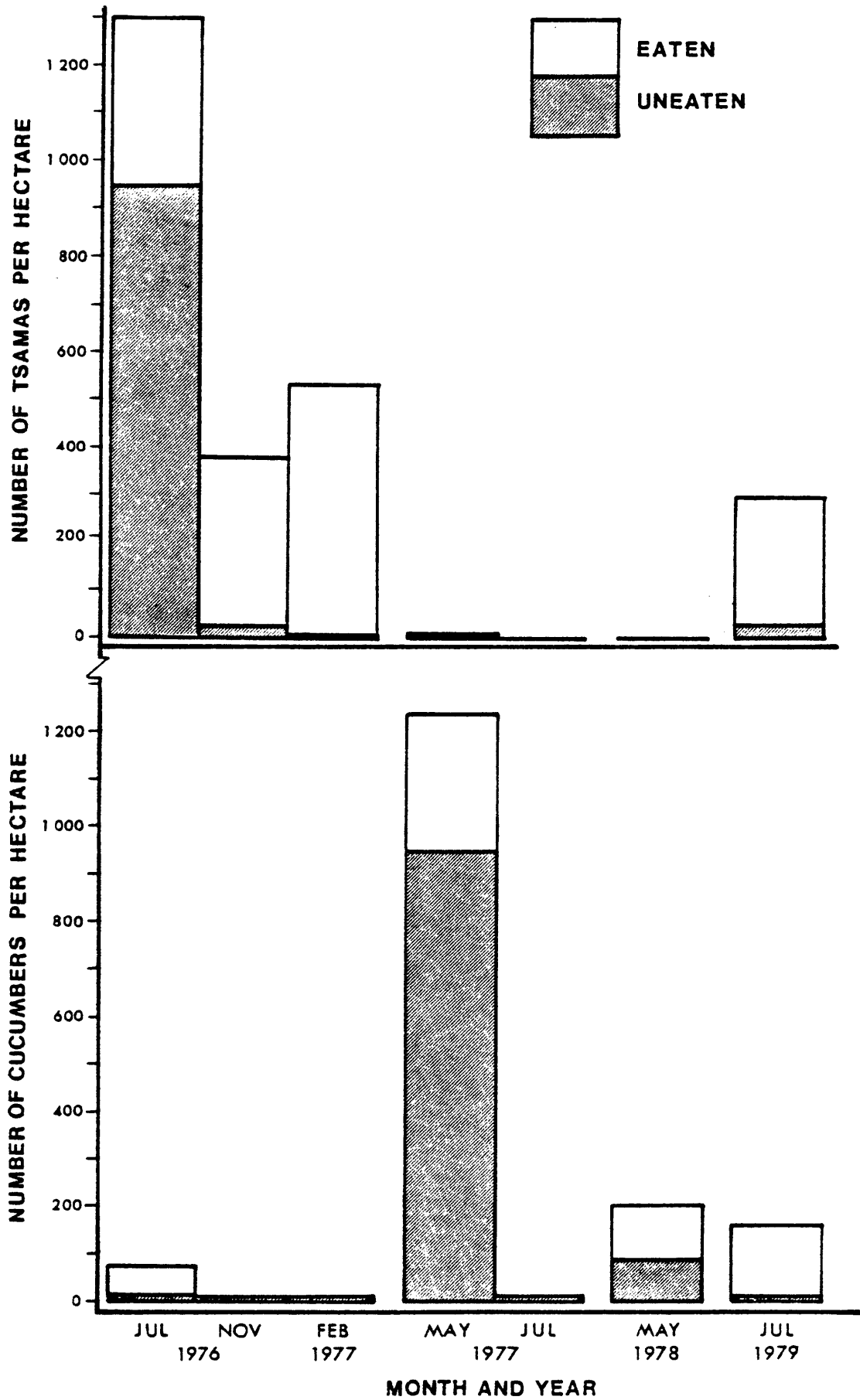


Figure 20: Abundance and amount of utilisation of tsamas and gemsbok cucumbers in the dunes of the southern Kalahari as determined by strip counts; 1976 - 1979. The February 1977 count was of the 1976 crop.

impression was that gemsbok cucumbers were common in all years from 1972 to 1975, but less common in 1980. Overall, therefore, it seems that the gemsbok cucumber, although given to large annual fluctuations, is a more reliable, albeit shorter lasting fruit than the tsama is.

Furthermore, the data suggest that the gemsbok cucumber is even more patchily distributed than the tsama is. In the area in which the fruits were monitored, the area to the east of Kwang Pan can be seen as the main gemsbok cucumber area (Fig. 19) in all years except 1976. The 1976 counts in this area, however, were carried out in November, long after the crop had disappeared. Gemsbok cucumbers may, therefore, have been present in this area earlier in the year.

SUMMARY

The brown hyaena is a solitary forager and predominantly a scavenger of mammal remains, with wild fruits an important secondary food. River habitat normally provides far more food for brown hyaenas than the dune habitat does. Of the most heavily utilised food items by brown hyaenas, only wild fruits and some small animals are found in equal or greater quantities in the dunes than they are in river habitat.

River habitat is subject to large-scale fluctuations in animal numbers, both in the short and long term. The ungulates in the river-bed may be concentrated in a small area one month and move to another area the next. At other times they may be more thinly distributed along a large stretch of river-bed. In the dunes these large-scale fluctuations in ungulate numbers and distribution are less common. Wild fruits which are found almost only in the dunes, fluctuate markedly in

abundance from year to year and are patchily distributed. Gemsbok cucumbers show a tendency to be found in the same relatively confined area each year.

In the Kwang area the majority of carcasses were available to brown hyaenas as their chief competitors, spotted hyaenas, were rarely encountered in this area. Black-backed jackals and vultures did, however, on occasions deprive brown hyaenas of substantial amounts of meat by locating carcasses before the hyaenas did. They could not, however, consume many of the bones.

In total quantity of food in the Kwang area during the present study, 1976 was a considerably better year than the previous four years had been. This concerns the number of ungulates throughout the year in the Nossob river-bed only. This trend continued into 1977 which was an even better year than 1976, as large ungulates, mainly blue wildebeest, were plentiful and provided most of the hyaenas' food. The year 1978 was as good, if not better than 1977, as even though ungulate numbers dropped towards the end of the year, there was a high non-violent mortality, particularly amongst blue wildebeest. The hyaenas were, therefore, gaining access to a number of untouched large ungulate carcasses. In 1979 and 1980 food was again abundant even when a drastic drop in ungulate numbers along the river-bed occurred, as non-violent mortality was again prevalent in the few large ungulates which stayed. The wild fruit crops were good in all years up to 1976 and again in 1979. In 1977, 1978 and 1980 tsamas in particular, were practically non-existent.

CHAPTER 3 : THE SOCIAL SYSTEM

INTRODUCTION

Although brown hyaenas are solitary foragers, most of them live in fixed territories which they share with a number of other, usually related, brown hyaenas. The size and composition of these territories and groups vary. It is important to know how much they vary and how this is brought about. Using data collected over a seven-year period from the Kwang group and supplementary data collected from five other groups, the structure and dynamics of brown hyaena groups, the land tenure system and the factors which affect them are described in this chapter.

Besides group-living animals and dispersing subadults, the southern Kalahari brown hyaena population contains a number of far-ranging adults, most, if not all, of which are males. A section of this chapter is devoted to a discussion on the numerical importance of these sections of the population and their possible origins.

Finally, using some of the data presented in the chapter, a population estimate of brown hyaenas in the southern Kalahari is made.

GROUP STRUCTURE

Figure 21 shows the structure of the Kwang group at six-monthly intervals between January 1975 and January 1981. The size of the group changed markedly during this period from five individuals in January

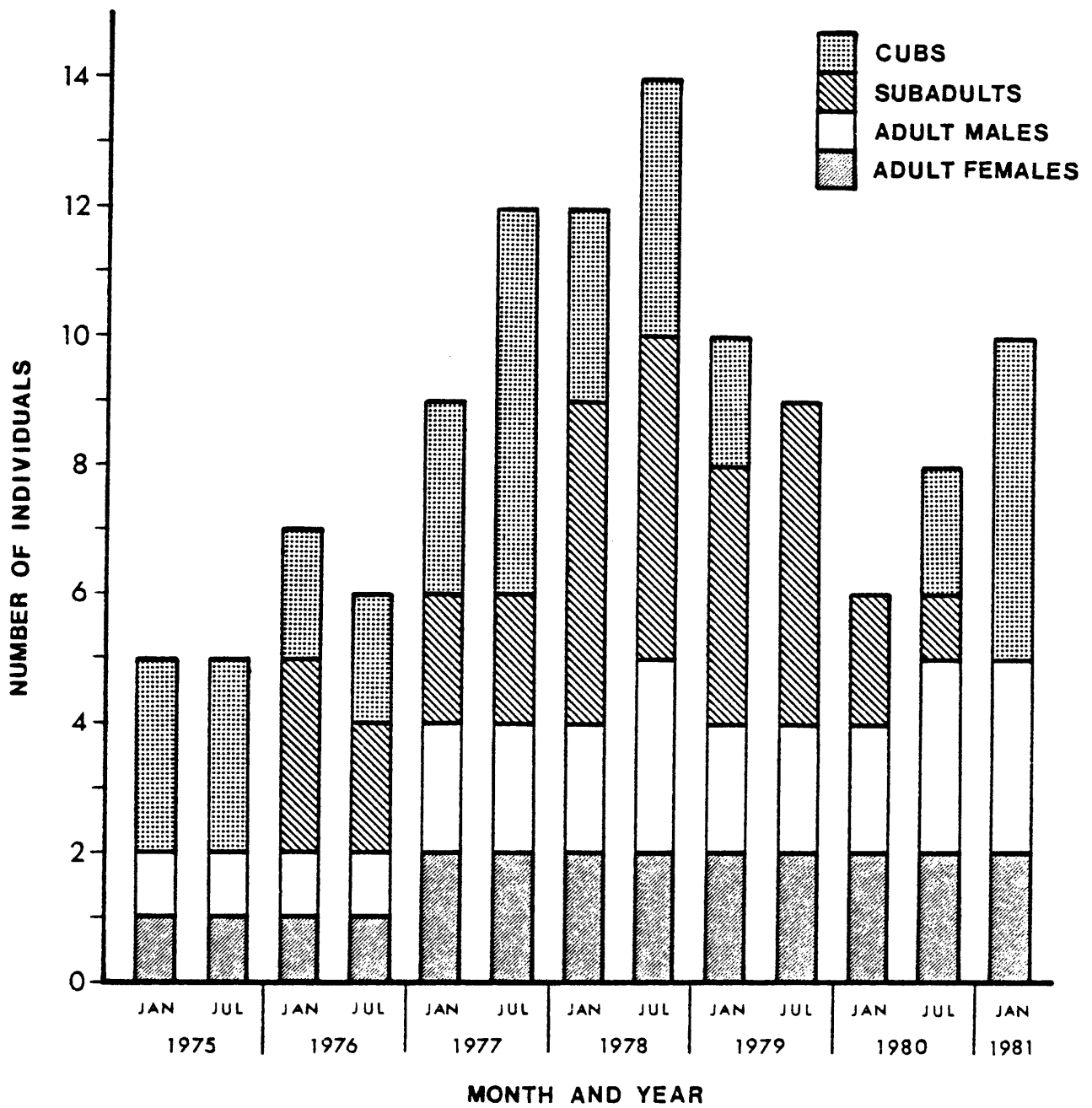


Figure 21: Structure of the Kwang brown hyaena group at six-monthly intervals in the southern Kalahari; January 1975 - January 1981.

1975 to 14 in July 1978, before falling again to six in January 1980. This fluctuation in group size was brought about mainly by the birth rate and the rate at which subadults disappeared from the group. The number of adults in the group did not fluctuate to the same degree as did the number of subadults and cubs.

Table 10 records the structure of five other groups as far as these could be established. The Kaspersdraai group was different from all the others in that no adult males were recorded living in the group. The sex ratio of the adults for all groups combined was 1,4 males per female ($n = 19$) and therefore close to parity (Binomial $p = 0,648$; two-tailed).

Figure 22 compares the relationship between the size of the Kwang group and certain aspects of food availability in the territory each year between 1975 and 1980. The only aspect of food availability which was found to be significantly correlated (Spearman rank correlation coefficient) with group size was the mean number of blue wildebeest counted along the Nossob river-bed in the territory each year (Fig. 22 a).

Figure 23 plots the relationship between group size and the frequency with which hyaenas followed in those groups found mammal food items. No significant Spearman rank correlation coefficient was found.

GROUP DYNAMICS

Recruitment

During the seven-year period (1974 - 1980) a minimum of 20 cubs from seven litters were born to two females in the Kwang group (Fig. 24),

Table 10: The composition of five brown hyaena groups in the southern Kalahari; August 1972 - December 1980.

GROUP	DATE	ADULTS		SUBADULTS		ADULT OR SUBADULT OF UNKNOWN SEX	CUBS	TOTAL
		M	F	M	F			
Cubitje Quap	August 1972	1	1	0	0	0	2	4
Kaspersdraai	May 1973	0	1	0	0	0	3	4
Rooikop	December 1973	1	1	0	0	1	2	5
Seven Pans	May 1975	?	2	1	0	2	1	6
Botswana	May 1975	2	1	0	2	0	1	6

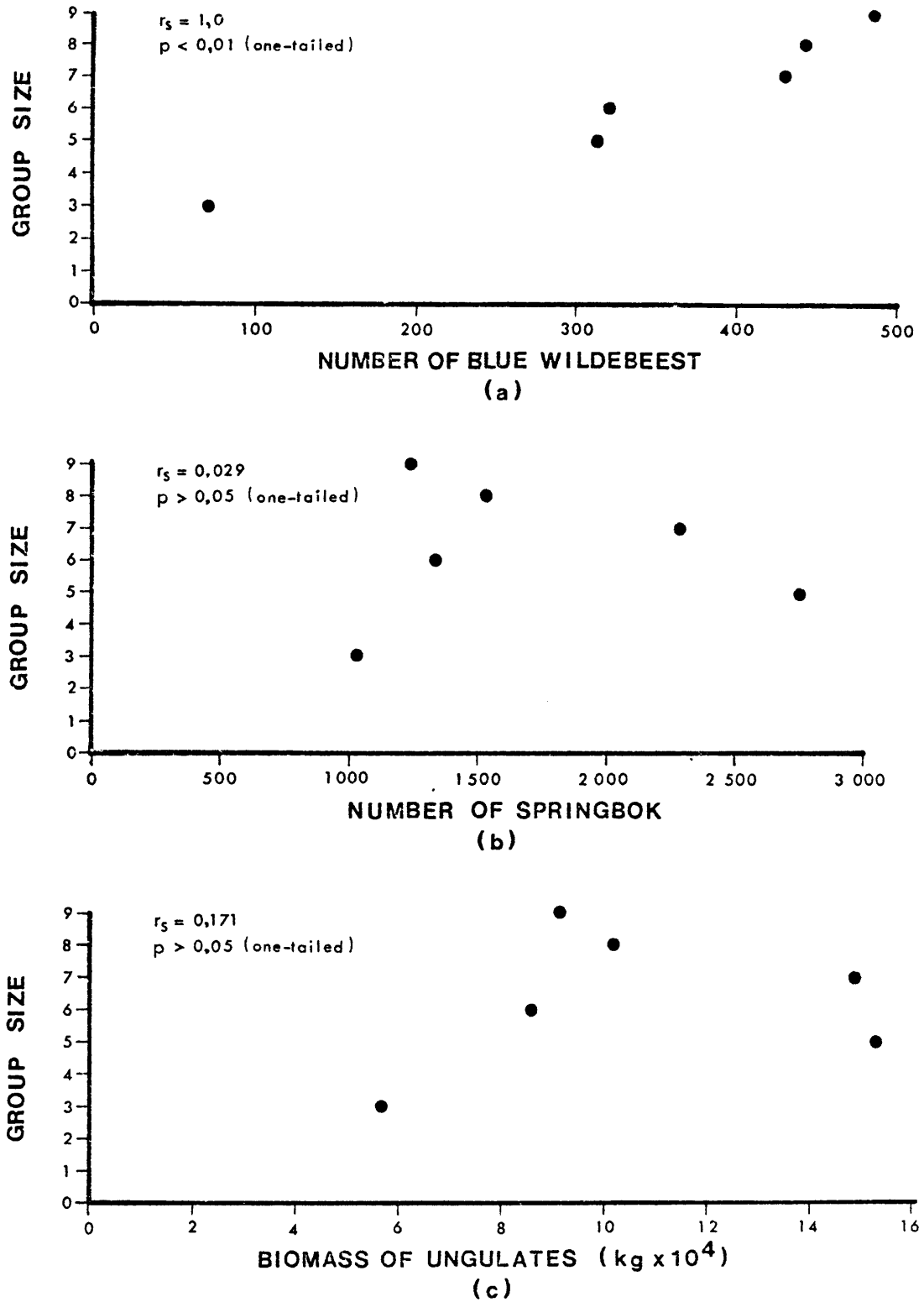


Figure 22: The relationship between the size of the Kwang brown hyaena group and certain aspects of food availability in the territory each year in the southern Kalahari; 1975 - 1980. Group size is the mean number of adults and subadults in the group each year. Food availability is (a) the mean number of blue wildebeest counted per year along a 40 km strip of the Nossob river-bed running through the territory, (b) the mean number of springbok counted per year and (c) the mean number of large ungulates and springbok counted per year converted to biomass (one springbok = 40 kg, one large ungulate = 200 kg).

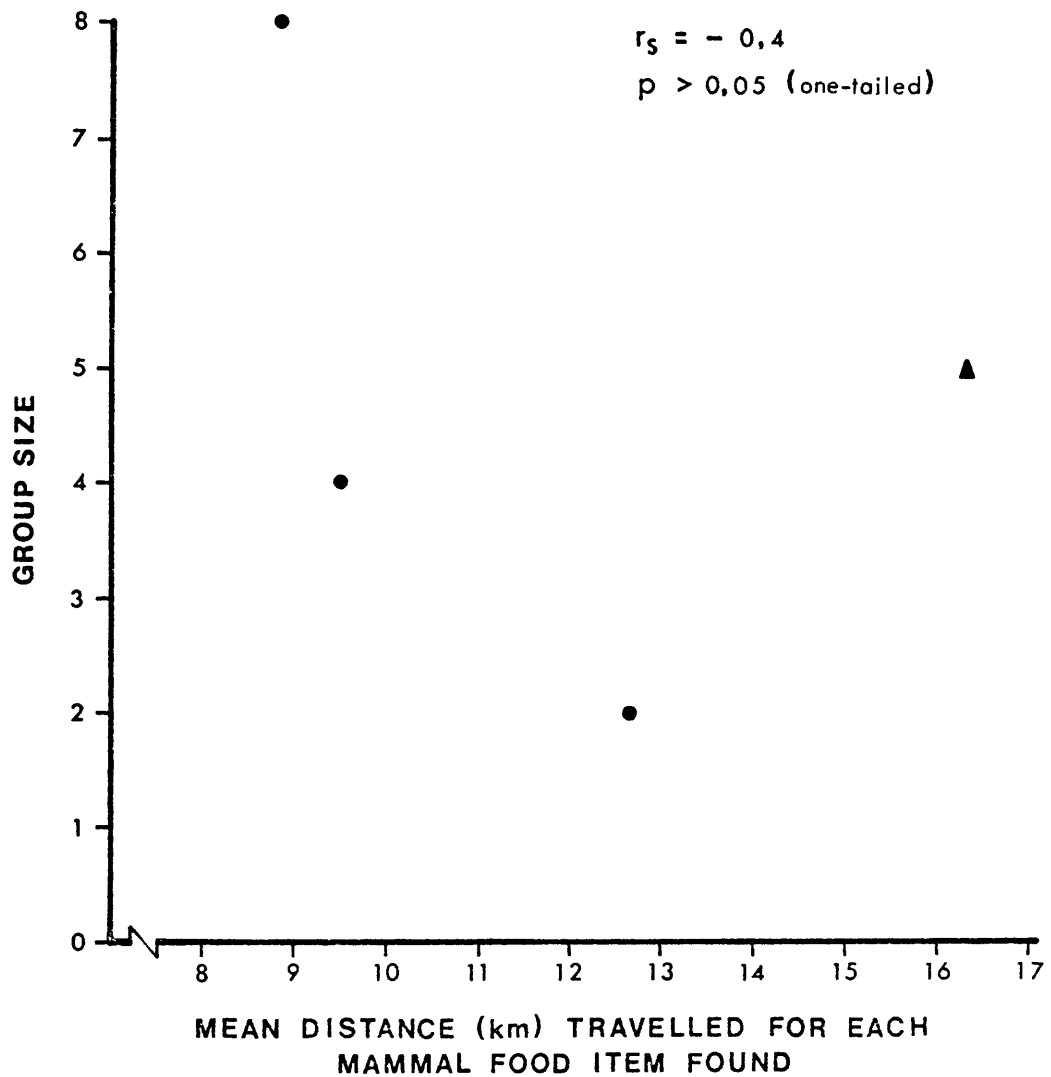


Figure 23: The relationship between brown hyaena group size in the southern Kalahari and the mean distance travelled by members of those groups between mammal food items. (●) Kwang group 1974 - 1975, 1976, 1977 - 1978; (▲) Seven Pans group 1975. Group size is the number of adults and subadults in the group during the time that the hyaenas were being followed.

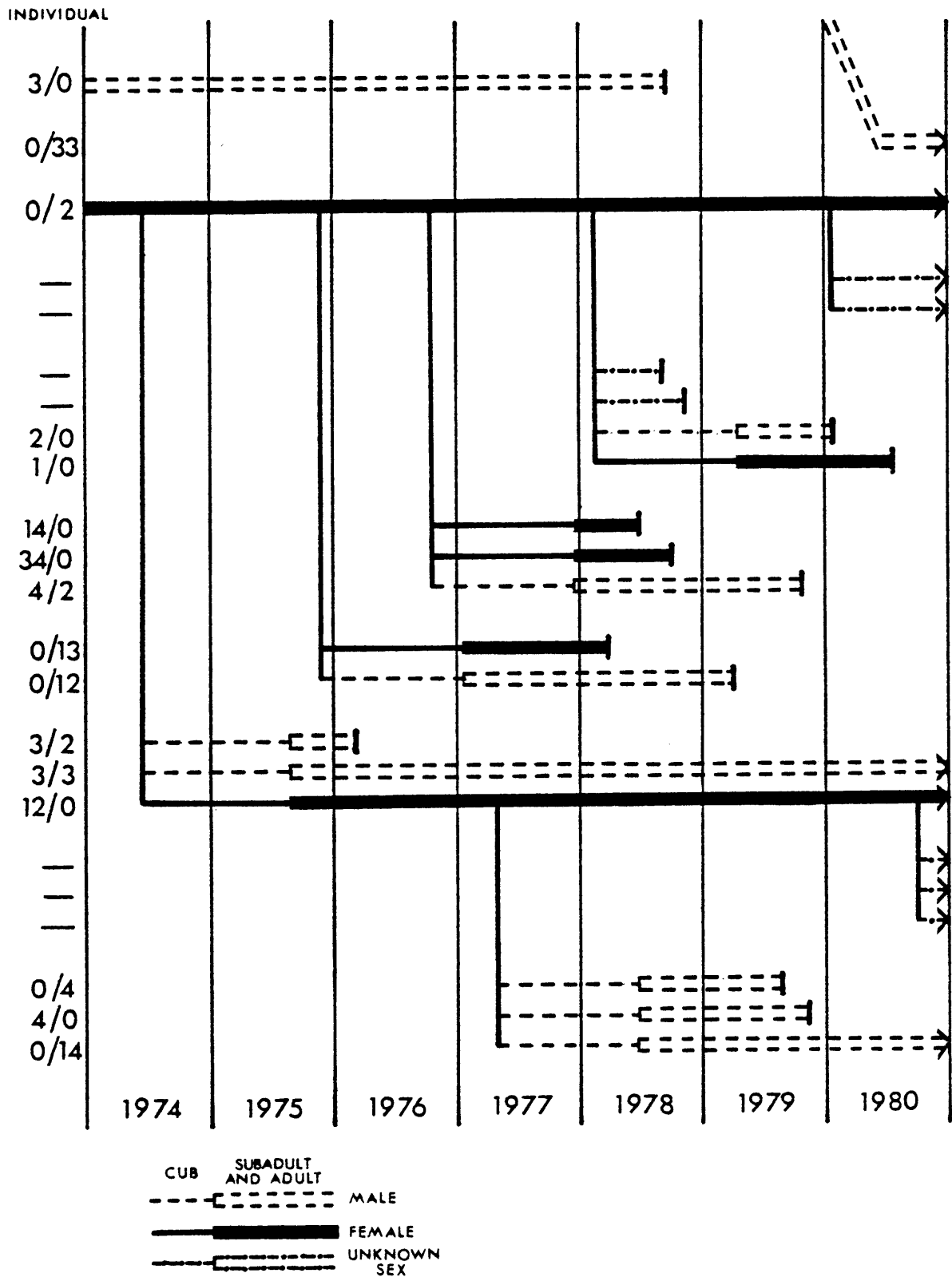


Figure 24: Summary of the reproductive history of the Kwang brown hyaena group in the southern Kalahari; 1974 - 1980. Birth of a litter is shown by a vertical line descending from the female's line. The ending of a horizontal line by one short vertical line denotes either death or emigration from the territory. The oblique line denotes immigration.

giving a mean litter size of $2,9 \pm$ s.e. 0,26. It is possible that in some of these litters some mortality occurred before I discovered the litter, particularly in two of them where the cubs were 10 months old when first found. This litter size, therefore, is possibly lower than the actual litter size at birth.

The sex ratio of 13 of the 20 cubs born into the Kwang group was 1,6 males per female and did not differ significantly from parity (Binomial $p = 0,582$; two-tailed). Combining these data with data on five cubs from other groups also gives a sex ratio of 1,6 males per female (Binomial $p = 0,480$; two-tailed).

No seasonality in births was found (Fig. 25), and the periods between births fluctuated markedly. The older female in the Kwang group (0/2) produced cubs at intervals of 18, 12, 17 and 23 months respectively. Her eldest daughter (12/0) produced her first litter when approximately 35 months old and then did not produce another litter for 41 months. A female from the Cubitje Quap group gave birth to cubs 13 months apart. Twice between her two litters 12/0 was observed mating without producing young. Unsuccessful matings have also been recorded in captivity at two to four month intervals (Lang 1958, Shoemaker 1978 and Eaton 1981).

Brown hyaena females are, therefore, polyoestrous and there is a lactation anoestrous. Eaton (1981) records an average gestation period of 96 days from five pregnancies recorded in captivity.

The important factors controlling the number of cubs born into a group are the number of females breeding in the group and the time interval between litters. Litter size does not appear to be as important. During the present study the two females in the Kwang group did not produce the number of litters that they were potentially capable of doing. Taking 12 months as the minimum interval between successfully raised litters, the two females produced seven (64 per cent) of a

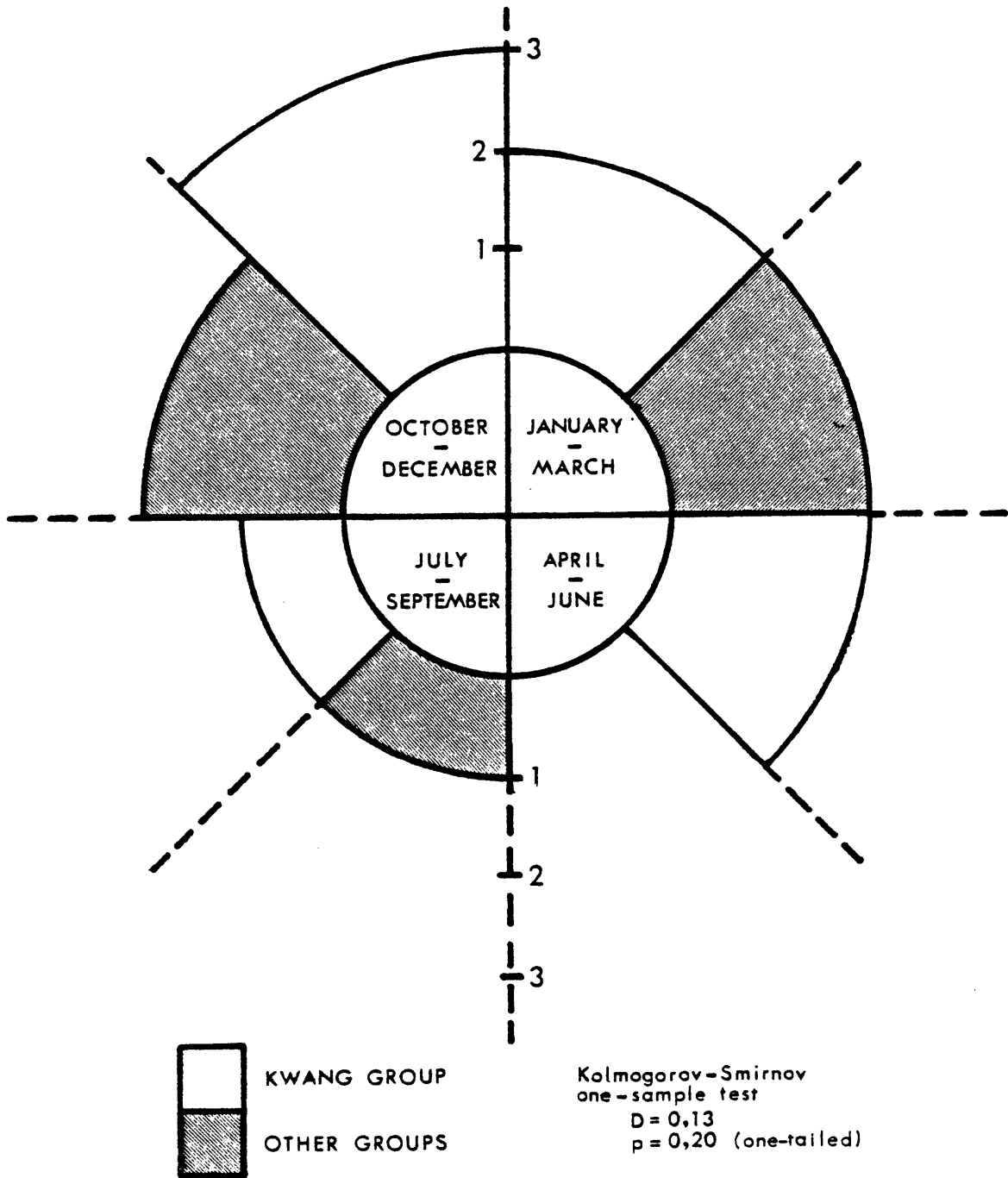


Figure 25: The quarterly distribution of brown hyaena births in the southern Kalahari; 1972 - 1980. The scale shows the actual number of litters born.

possible 11 litters in the $6\frac{1}{2}$ -year period between June 1974 and December 1980.

Immigration

Immigration does not appear to be an important aspect in brown hyaena group dynamics. During the seven-year period of study only one animal was observed to join the Kwang group (Fig. 24), an age-class 3 male (0/33), who was first recorded in the group in June 1980.

Emigration and mortality

Cub mortality in the present study was apparently low. Of 15 cubs known to be born into the Kwang group and which could be monitored until they reached subadulthood, two (13 per cent) died before they became subadults. Of another seven cubs from three groups which were under 10 months old when first found, all survived until they became subadults.

A problem encountered during the present study was when to decide that a subadult or adult which had not been seen for some time had actually left the group. From Fig. 26 it can be seen that a period of six months or less elapsed between successive sightings of the same individuals of the Kwang group in 99 per cent of the cases. I have therefore made this the main criterion for deciding if an animal had left the group or not. If, as happened in four cases involving three individuals, more than six months elapsed between sightings, I assumed that the animals had remained in the territory all the time. It is possible that in these long periods of not being seen the animals had temporarily left the territory. In the case of a female which was not

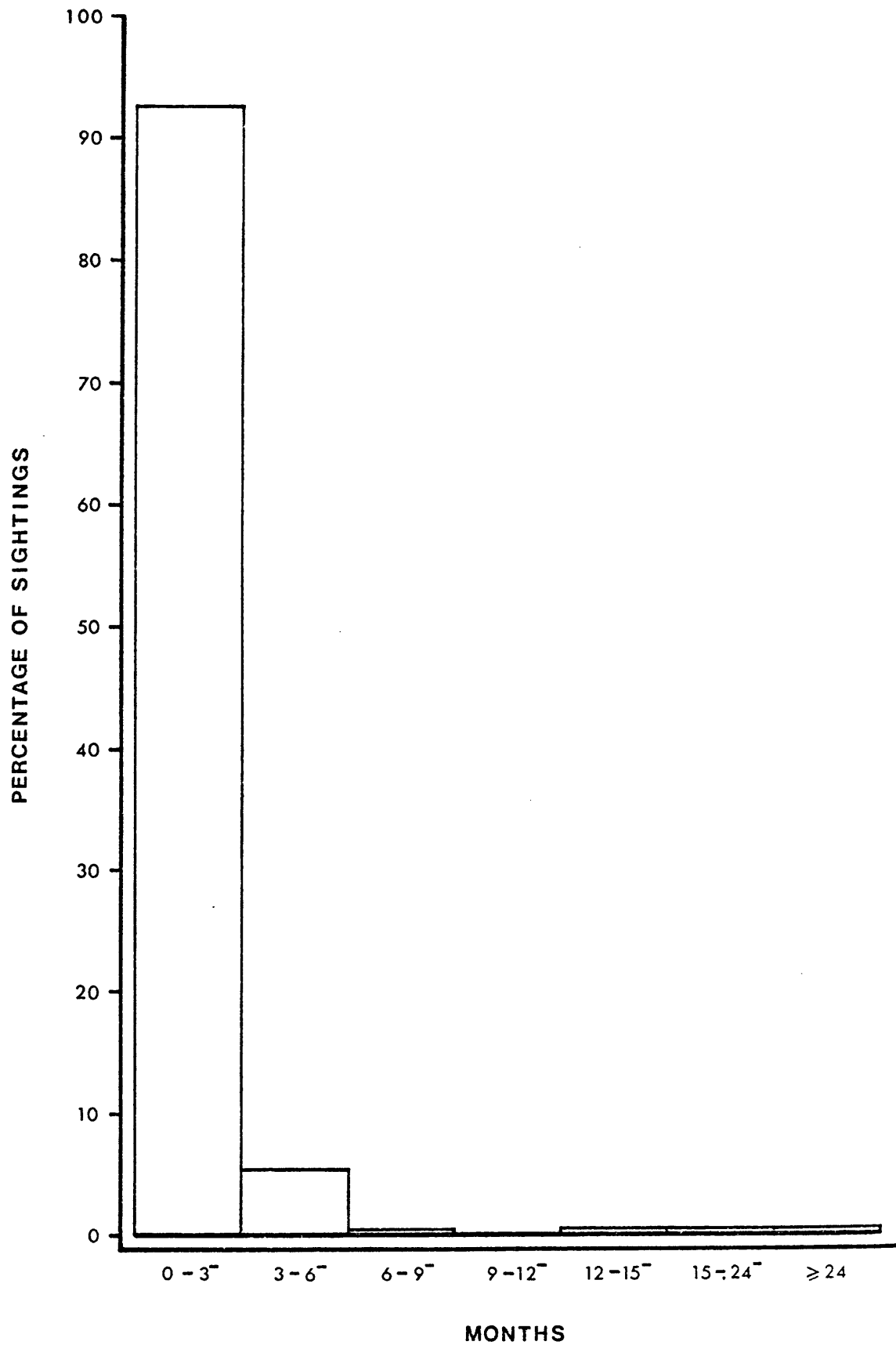


Figure 26: Time periods which elapsed between 293 successive sightings of individual brown hyaenas of the Kwang group in the southern Kalahari; December 1974 - December 1980.

seen for 13 months, however, I know that she had cubs in a den in the Kwang territory for practically the entire period. In her case at least, it was impossible for her to have been out of the territory for the entire period.

Of 17 brown hyaenas that had been members of the Kwang group between December 1974 and December 1979, 13 (76 per cent) had disappeared by December 1980. The sex ratio of 11 of these animals was 1,8 males per female which does not differ significantly from parity (Binomial $p = 0,548$; two-tailed). An age-class 5 male (0/2) and two unmarked cubs were known to have died. An age-class 2 b male (4/2), was three years old when he "disappeared", but he was seen again 13 months later 20 km to the south of the Kwang group's territory boundary. The fates of the rest were unknown. An age-class 2 male from the Seven Pans group which disappeared in early 1975 was seen six years later 40 km from where he was marked.

If the Kwang group data from age-class 2 are compared with those from age-classes 3, 4 and 5, there is a significant difference between the number of animals which disappeared from the group in the former category, compared with the number which disappeared from the group in the latter category, taking into account the mean number of animals which occurred in each category (Fig. 27) (χ^2 with Yates's Correction = 5,61; $df = 1$; $p < 0,02$).

In Fig. 28 I have attempted to document the age structure of the brown hyaena population. Here all age-class 2 or older animals caught for the first time between 1975 and 1978 have been included and the frequency with which each age-class occurred has been plotted. If a hyaena was caught as a cub (age-class 1) and again when its teeth had fully erupted (age-class 2 or 3) it was placed in the latter relevant age-class. This is because my data are only suitable for an analysis

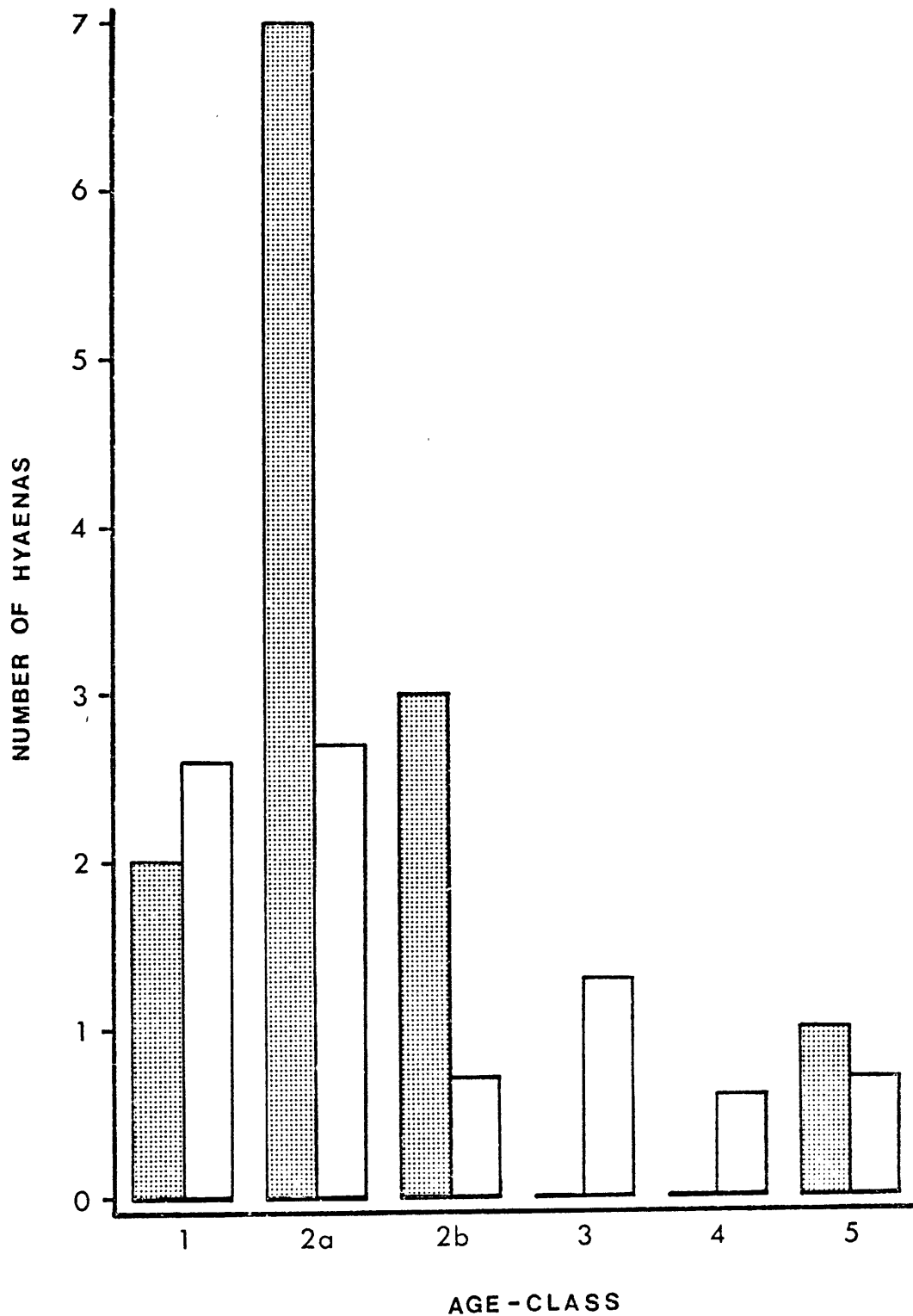


Figure 27: The number of brown hyaenas of different age-classes which disappeared from the Kwang group (dotted) and the mean number of animals in the group in each age-class (open) between December 1974 and January 1980 in the southern Kalahari. The mean values have been calculated from the composition of the group at six-monthly intervals.

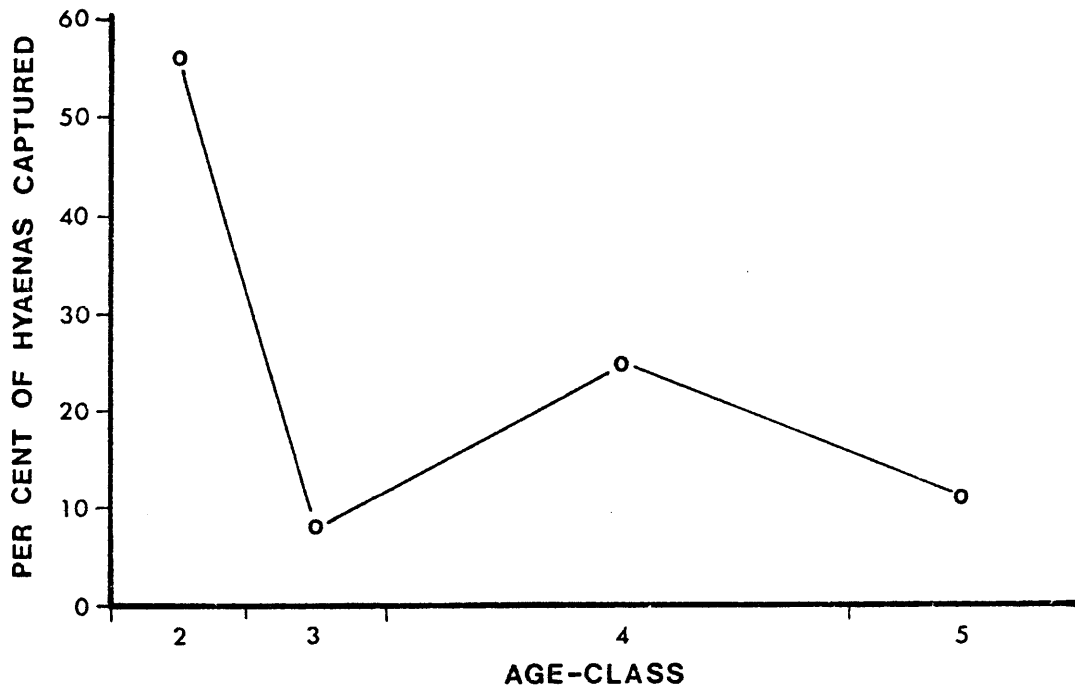


Figure 28: Age-class distribution based on tooth wear of 36 brown hyaenas caught in the southern Kalahari; 1975 - 1978. The age-class intervals are proportional to the time that animals spend in each age-class.

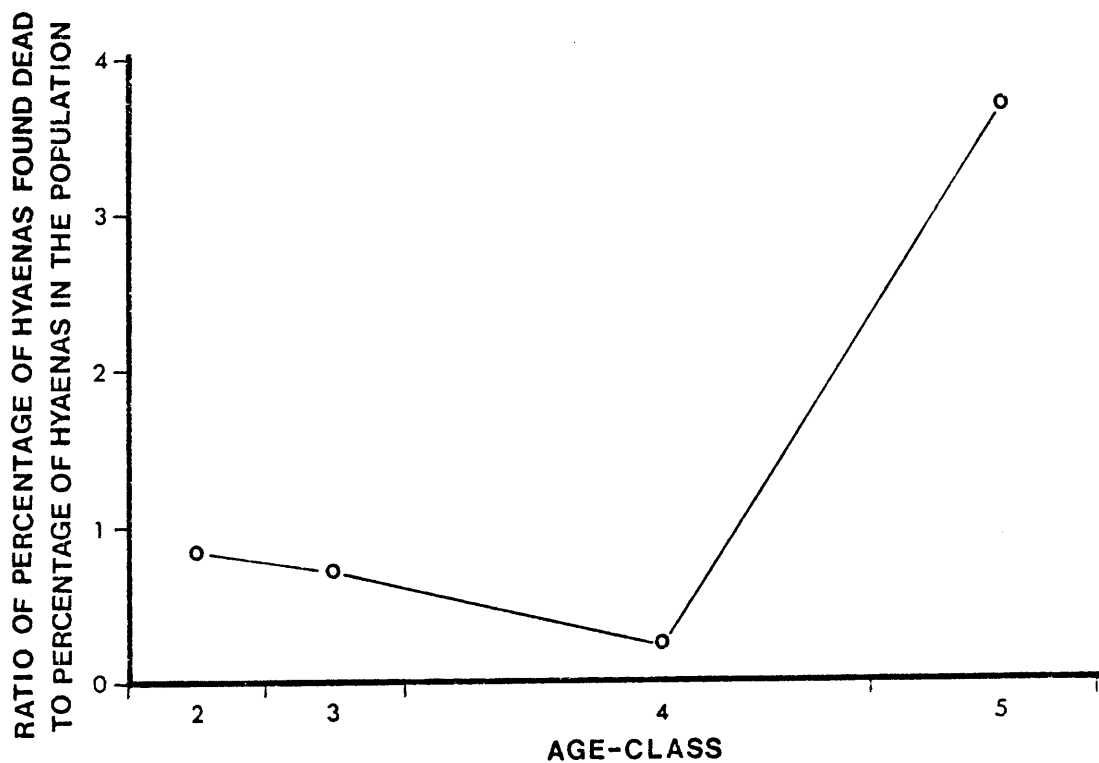


Figure 29: The ratio of the percentage of brown hyaenas found dead ($n = 17$) to the percentage of hyaenas in the population for different age-classes ($n = 36$) in the southern Kalahari; 1975 - 1978.

of the age-class 2 and above segment of the population. The chances of catching a cub were enhanced if the traps were set near their den and I often concentrated the traps around the dens. As I did not know where all the dens were in the study area during these years, however, the traps were not randomly distributed for cubs. I have, however, assumed that the chances of catching age-class 2 or older animals were the same for all age-classes and that the area in which I trapped was representative of the study area.

In Fig. 29 I have plotted the ratio of the percentage of brown hyaenas found dead to the percentage of hyaenas caught for each age-class. The number of known-age animals found dead is too small for any statistical analysis of the data. The apparent trend is that animals in age-classes 2 and 3 die in roughly the same proportions to which they occur in the population, whilst animals in age-class 4 are less likely and in age-class 5 more likely to die than the proportions in which they occur in the population.

Causes of mortality

In addition to the 17 hyaenas used to compile Fig. 29, I recorded the death of six cubs and seven subadults or adults of unknown age, the causes of which are recorded in Table 11.

The man-caused mortality relates to brown hyaena carcasses found either along the fence bordering the Kalahari Gemsbok or Gemsbok National Parks and farming areas in South West Africa/ Namibia, or to brown hyaenas killed on the adjoining farms (Le Riche and Meyer pers. comm.).

E.A.N. le Riche and I.J. Meyer. Kalahari Gemsbok National Park, P. Bag X5890, Upington, 8800. Throughout the study.

Table 11: Causes of mortality of brown hyaenas of different age-classes in the southern Kalahari; April 1972 - December 1980.

CAUSE	AGE-CLASS						ALL CLASSES	
	1	2	3	4	5	Unknown	Total	Per cent
Man	1	5	0	1	0	5	12	40,0
Violent	1	3	1	0	3	2	10	33,3
Starvation/ disease	2	0	0	0	0	0	2	6,7
Unknown but natural	2	0	0	0	4	0	6	20,0
Total	6	8	1	1	7	7	30	100,0

The dead animals found along the fence were presumed to have been poisoned by farmers, or were found caught in gin-traps set by the farmers. Although the mortality data are biased towards this type of mortality which, because of its concentrated nature, was easiest to record, the indications are that it was an important mortality factor during the study. There are indications too, that the majority of the animals killed in this way were age-class 2 animals (Table 11). I have already suggested that age-class 2 brown hyaenas are the most likely segment of the population to emigrate. It is probable, therefore, that the majority of the brown hyaenas killed by man on the boundaries of the two National Parks, are emigrating animals searching for an area in which to live.

In the 10 instances where a brown hyaena died violently through natural causes, the culprits were lions on three occasions and spotted hyaenas once. In none of these cases was a food dispute involved. In the other cases it could not be established what had attacked the brown hyaena.

Most of the wounds inflicted on brown hyaenas were along the back and around the hind region. One animal, for example, was found dead with its tail missing and part of its intestines hanging out. Such injuries were most probably caused by other species of large carnivore. Once, however, a brown hyaena was found with neck injuries and was unable to raise its head. It was kept in captivity for two weeks and, although it ate well, it showed no signs of recovering and remained listless and disorientated. It was eventually destroyed. Fighting between brown hyaenas, although usually inhibited, is directed at the neck (Chapter 5). Although I never saw an animal receive more than superficial wounds from such a fight, it is possible that the above-mentioned animal had been injured in an intra-specific fight. Tourists also once reported

seeing a brown hyaena in poor condition which had been badly mauled around the neck.

Not included in Table 11 is the case of a semi-immobilised brown hyaena which was attacked by a leopard. The leopard appeared to be "playing" with the hyaena before I drove it off. Later, still under the influence of the drug, this brown hyaena was attacked and killed by a pack of six spotted hyaenas (Mills 1977).

Violent mortality in the brown hyaena, therefore, is apparently mainly caused by other large carnivores, but may also sometimes result from intra-specific fighting. It was the most common form of natural mortality observed during the present study.

Eventually the bone crushing premolars of old brown hyaenas become so badly worn as to be non-functional (Chapter 1). The old male whose teeth are shown in Fig. 6 f, for example, was once observed to spend half an hour unsuccessfully attempting to crush the leg bone of a springbok, a feat which a young animal would have accomplished in less than five minutes. Three months after this observation this individual died. Old brown hyaenas therefore probably die from starvation or related factors.

Little is known about the roles which disease and parasites play in brown hyaena mortality. Rabies, which has been thoroughly researched in southern Africa, has not been recorded in the brown hyaena (Barnard 1979). The only published report that I could find of an identified parasite from a brown hyaena was of a captive animal which, on necropsy, was found to host nymphs of Armillifer armillatus, a wide ranging Pentastomid. This hyaena had also developed cataracts in one eye (Greve and Russel 1974). Schultz (1966) records that a two-week old cub which died in captivity was found to have underdeveloped lungs with the centres soft and macerated.

In the present study the most commonly found ectoparasite on brown hyaenas was a species of Hippoboscid biting fly. These were particularly numerous around any wounds which the hyaenas might have had. At dens fleas occasionally built up to such numbers that the hyaenas were forced to move to a new den (Table 21), and cubs in particular often spend long periods grooming themselves. The flea Echidnophada larina has been identified from a large brown hyaena cub from Zimbabwe (Peek In litt.). Ticks were rarely found on brown hyaenas. Two brown hyaenas were observed with a few small patches of sarcoptic mange, particularly around their heads, but these cleared up within a few weeks.

Two species of internal parasites were collected from the brown hyaena with neck injuries that was destroyed. These were the tape worm Taenia hyaenae and the nematode Spirocerca lupi (Du Preez In litt.). The former has also been recorded in the spotted hyaena (Kruuk 1972) and the latter is commonly found in canids (Du Preez In litt.).

NOMADIC MALES

In Fig. 30 I have recorded the number of times that I resighted all the adult brown hyaenas seen at least once in the territories of known groups, which were either marked or recognisable from natural marks, between December 1974 and December 1980. Only sight records of

J.R. Peek. The National Museums and Monuments, P.O. Box 240, Bulawayo, Zimbabwe. 10 April 1981.

P. du Preez. Department of Physiology, Pharmacology and Toxicology, P.O. Box 12580, Onderstepoort, 0110. 1 October 1980.

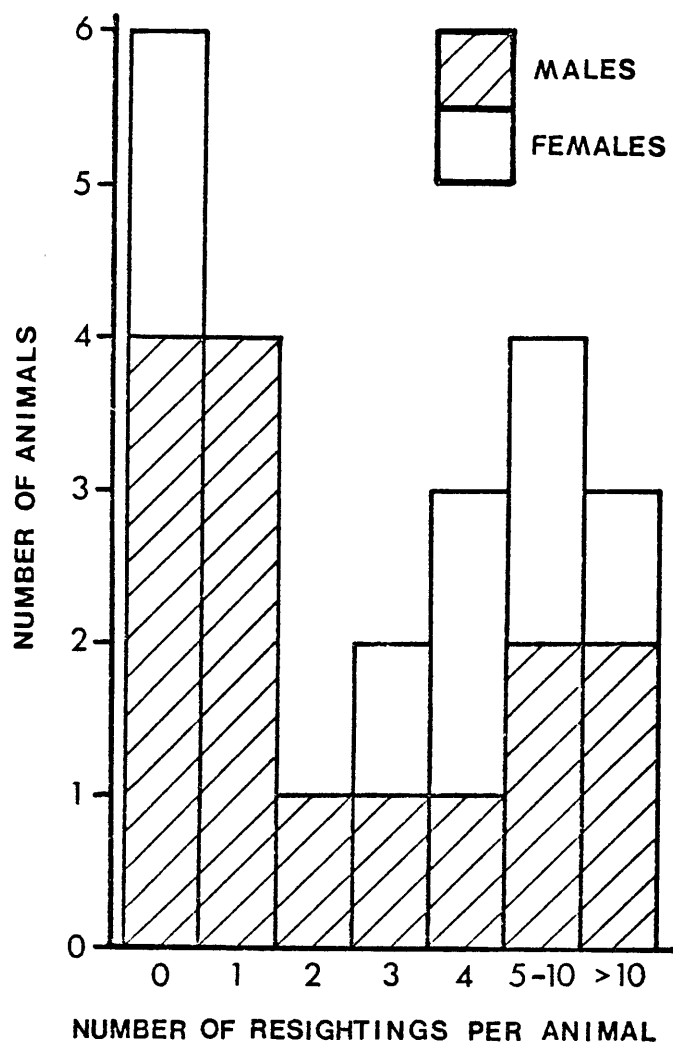


Figure 30: The number of times that 23 individually known adult brown hyaenas were resighted in the territories of known groups in the southern Kalahari during a six-year period (1975 - 1980), provided that they were seen for the first time before the end of 1979.

those animals which were first seen before 1 January 1980 have been included. Radio tracking and trapping data have been excluded. The figure shows a discontinuous distribution in the frequency with which different individuals were resighted. Comparatively many were never resighted or only resighted once, a few were resighted two or three times and more again were resighted four or more times.

Radio tracking, trapping data and observations at dens showed that all those individuals which were resighted four times or more remained in the territories that they were originally found in for at least one year, or were known to be born in that territory. All these animals, therefore, were assumed to be group-living animals. None of the animals sighted less than four times, however, fitted either of these criteria and it seems likely that many of them were not members of a group. A minimum period of one year was considered to be a reasonable time in which to establish whether an individual had remained in the general area where it was discovered or not, particularly as in the last year of the study (1980) I concentrated in looking for known animals and made 80 brown hyaena sightings in the relevant area.

The sex ratio of animals resighted less than four times was 3,3 males per female, a significant difference (Binomial $p = 0,046$; one-tailed). The sex ratio of animals resighted four times or more, however, was 1,0 male per female (Binomial $p = 0,623$; one-tailed). The sex ratio of 36 brown hyaenas of all ages which were caught (Table 12) and which I assumed to be representative of the population as a whole was 1,6 males per female and also did not differ significantly from parity (Binomial $p = 0,121$; one-tailed). These data strongly suggest, therefore, that there are some brown hyaenas that do not belong to a group and that most of these are adult males.

Further evidence for some adult male brown hyaenas not belonging

Table 12: The subsequent behaviour of 36 brown hyaenas in the southern Kalahari after they were captured and marked; December 1974 - August 1978.

SUBSEQUENT BEHAVIOUR	NUMBER OF ANIMALS	PER CENT	SEX AND AGE-CLASS			
			Class 2		Class 3-5	
			M	F	M	F
Remained in the area in which it was marked for at least one year	23	63,9	6	5	6	6
Disappeared within three months after being marked	13	36,1	7	3	3	0
Total	36	100,0	13	8	9	6

to a group is presented in Table 12 which analyses the behaviour of animals after they were caught and marked. These data show that animals of age-class 2 were prone to disappear from the area in which they were marked, but that few age-class 3 or older animals did. The only age-class 3 or older animals which behaved in this way were males and these comprised 8 per cent of all the animals caught. One of these males was fitted with a radio collar, but was never relocated.

One possible origin of these strange males is that they were animals from neighbouring groups, or even from groups further away, which periodically left their own territories to wander far afield. Radio tracking observations of group-living males, however, have not revealed such behaviour. Although there is a certain amount of overlap between the territories of neighbouring groups, and both males and females were occasionally observed to make short expeditions out of their own territories, these were of rare occurrence and only two such expeditions were observed in over 900 km of following radio-collared males. Furthermore these trips covered comparatively small distances (17 and 6,5 km) and appeared to be normal foraging expeditions (see later).

A second possibility is that these males were animals with extremely large home ranges which encompassed several family group territories. In that case certain individuals would have been seen regularly, albeit with longer periods between sightings than for group-living hyaenas, which were regularly seen at less than three-monthly intervals (Fig. 26). Of 10 males that were identifiable and which were not known to be group members (Fig. 30), four were never resighted and six were resighted at least once within one month of the original sighting. After one month four of the latter six were never seen again and two were resighted once each 14 and 27 months later. It seems unlikely, therefore, that they were moving in any sort of regular pattern.

A third possibility is that these males were nomadic with no fixed home range. The fact that the majority of resightings were made in the same area over a very short period, after which the animals usually were never seen again, makes this possibility the most likely one of the three.

I believe, therefore, that a component of the brown hyaena population consists of nomadic males. The data from captured animals suggest that these animals account for 8 per cent of the subadult and adult segment of the population, and 33 per cent of the adult male segment of the population (Table 12).

Whether any of the unknown adult females were nomadic was not established. If they were, they were obviously far less common than nomadic males. A female needs a den in which to keep her cubs for up to 15 months and this must depend on the animal possessing a fixed home range or territory. Thus it is unlikely that adult females would become nomadic, and if they did they would be unlikely to be able to raise cubs successfully, as is also the case with most nomadic female lions (Schaller 1972).

LAND TENURE SYSTEM OF GROUPS

Territories

Figure 31 shows the movements of hyaenas from four different dens as determined chiefly from tracking spoor and, in a few instances from direct observations, between April 1972 and December 1973. Figure 32 shows

similar data to those shown in Fig. 31 for two other groups between December 1974 and September 1975. All the data in Fig. 32 were obtained by means of direct observations. Figures 33 and 34 show the movement patterns from direct observations of hyaenas from the Kwang group from Fig. 32 for the periods January to July 1976 (Kwang 2) and July 1977 to August 1978 (Kwang 3).

The distances between neighbouring dens (Table 13) are not significantly different ($\chi^2 = 2,02$; $df = 4$; $p > 0,05$). Moreover, there is evidence that hyaenas from different dens inhabit largely exclusive areas (Figs. 31 and 32), with only a small amount of overlap between the areas inhabited by neighbouring groups (Table 13). In addition the areas are scent marked (Chapter 5) and hyaenas from neighbouring groups are often aggressive towards each other (Chapter 6). The land tenure system of group-living brown hyaenas, therefore, meets with the criteria laid down by most authors for a territorial system (Brown and Orians 1970, Wilson 1975 and Davies 1978).

Figures 31 and 32 show some changes in the distribution of territories between 1972 - 1973 and 1974 - 1975. The group inhabiting the Cubitje Quap territory (Fig. 31) comprised an adult female and an adult male with two male cubs. In October and November 1972, when the cubs were approximately 13 months old, the female and male were both accidentally killed by drug overdoses (Mills 1977). The two cubs survived in the area until March 1973, when they disappeared. By December 1974 the Kwang group comprising an adult male, an adult female and three six-month old cubs, had taken over the bulk of the vacated Cubitje Quap territory. The Seven Pans group, comprising at least two adult females and three one-year old cubs, had taken over the rest of the area (Fig. 32).

Both territory size and group size of brown hyaenas in the southern Kalahari fluctuate markedly (Table 14), although the two are not

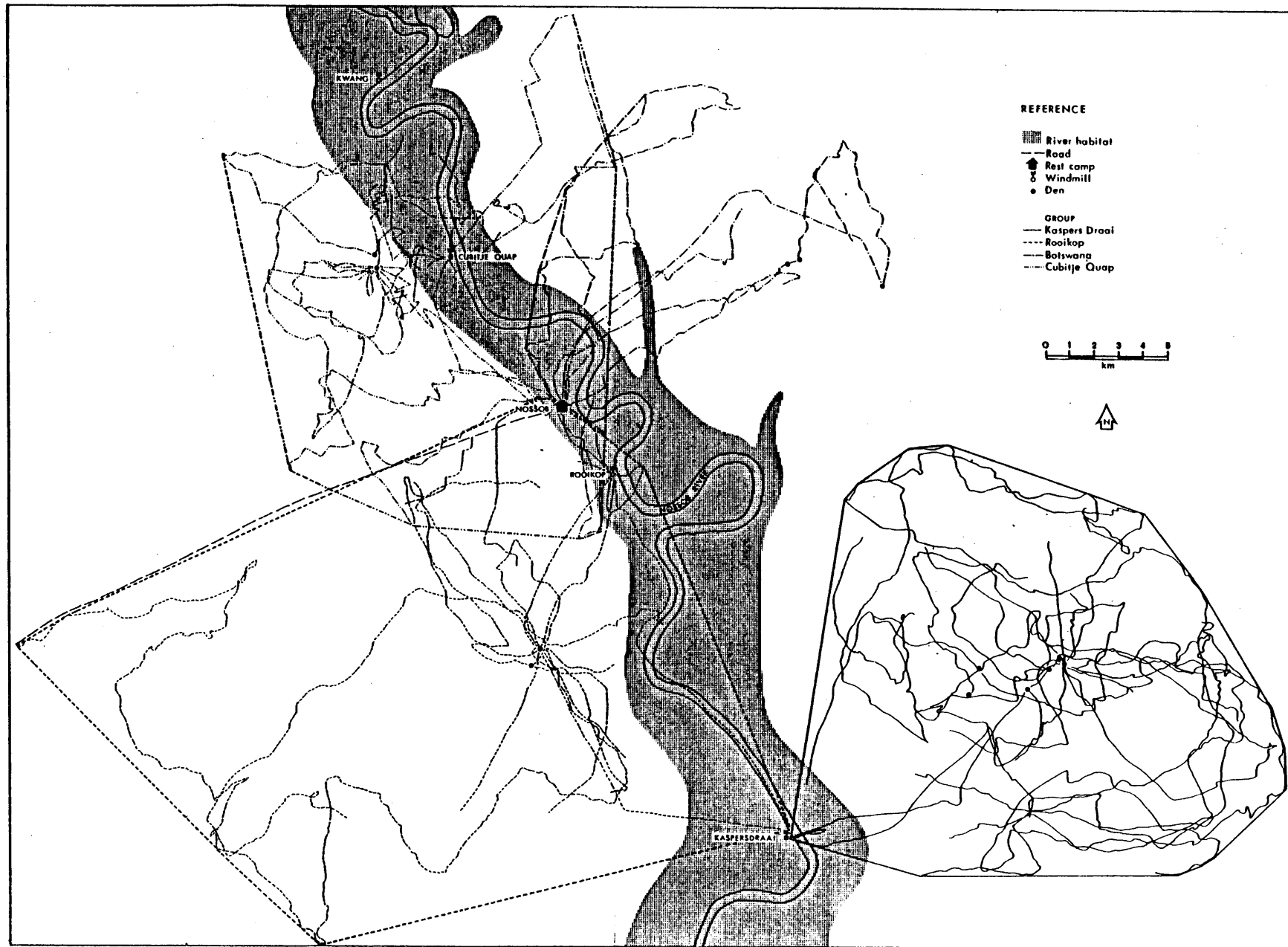


Figure 31: The observed movements of brown hyaenas from four groups in the southern Kalahari as determined from tracking spoor; April 1972 - December 1973.

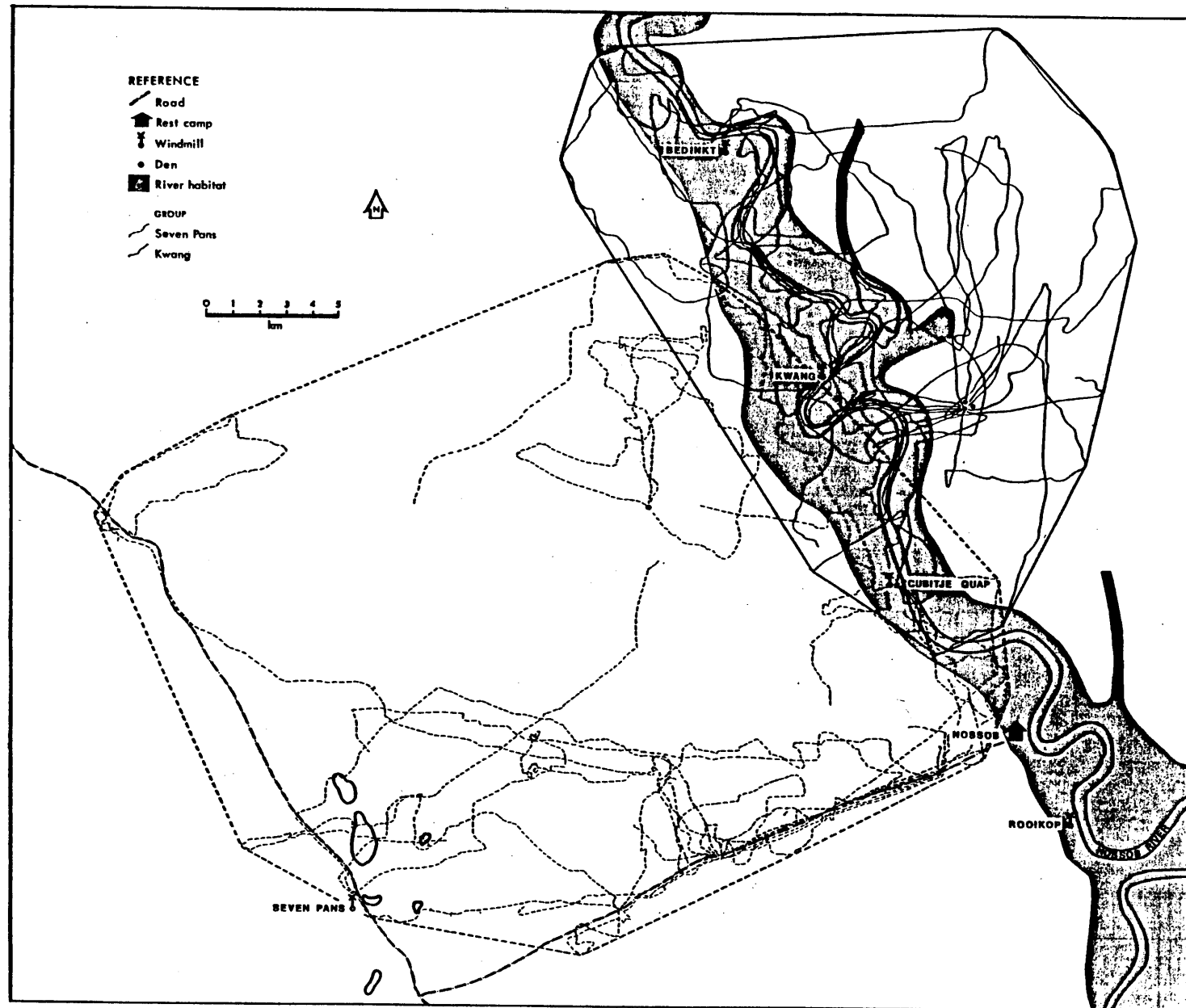


Figure 32: The observed movements of brown hyaenas from two groups in the southern Kalahari as determined from direct observations; December 1974 - September 1975.

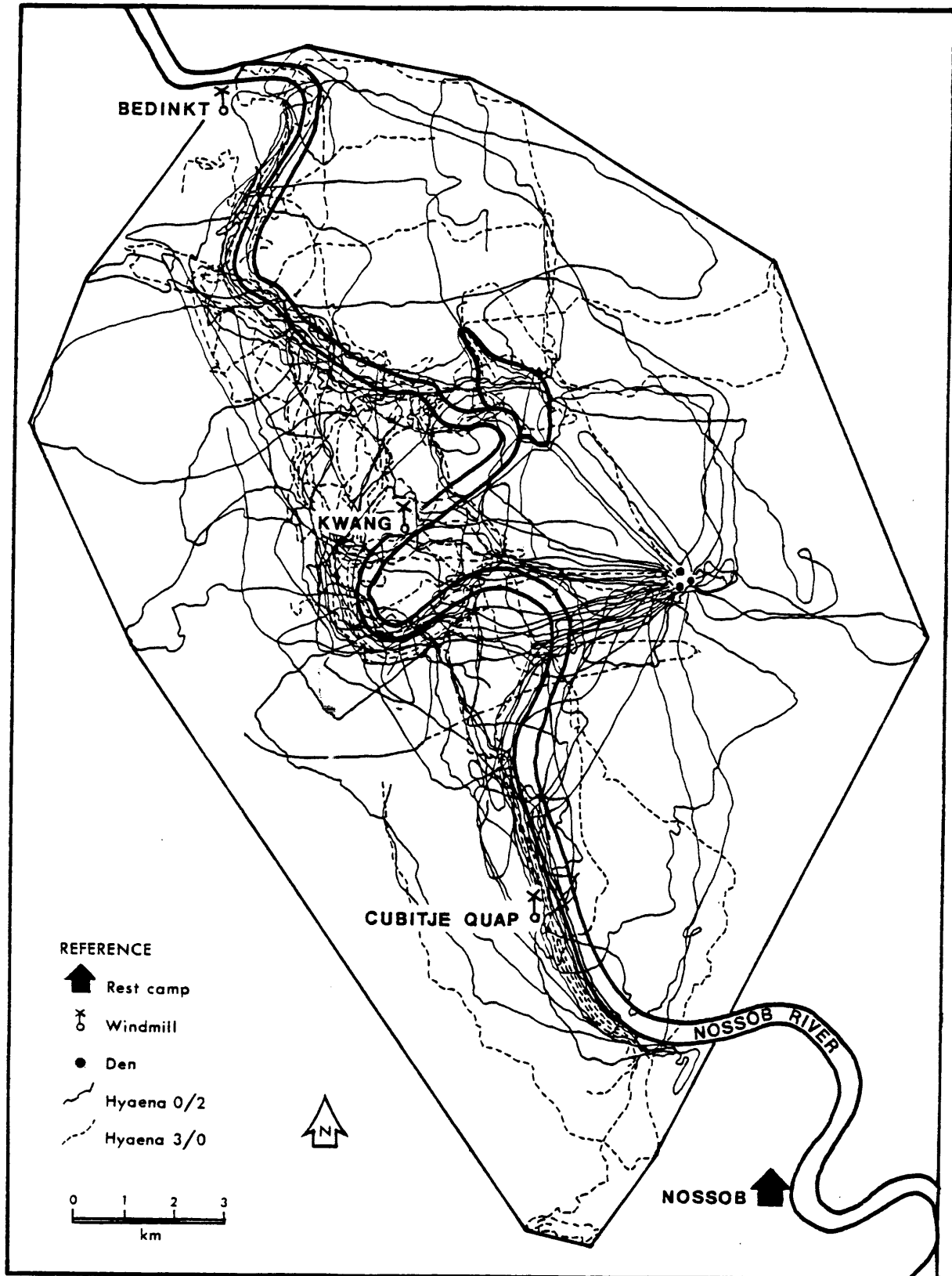


Figure 33: The observed movements of two brown hyaenas from the Kwang group in the southern Kalahari as determined from direct observations; January - July 1976.

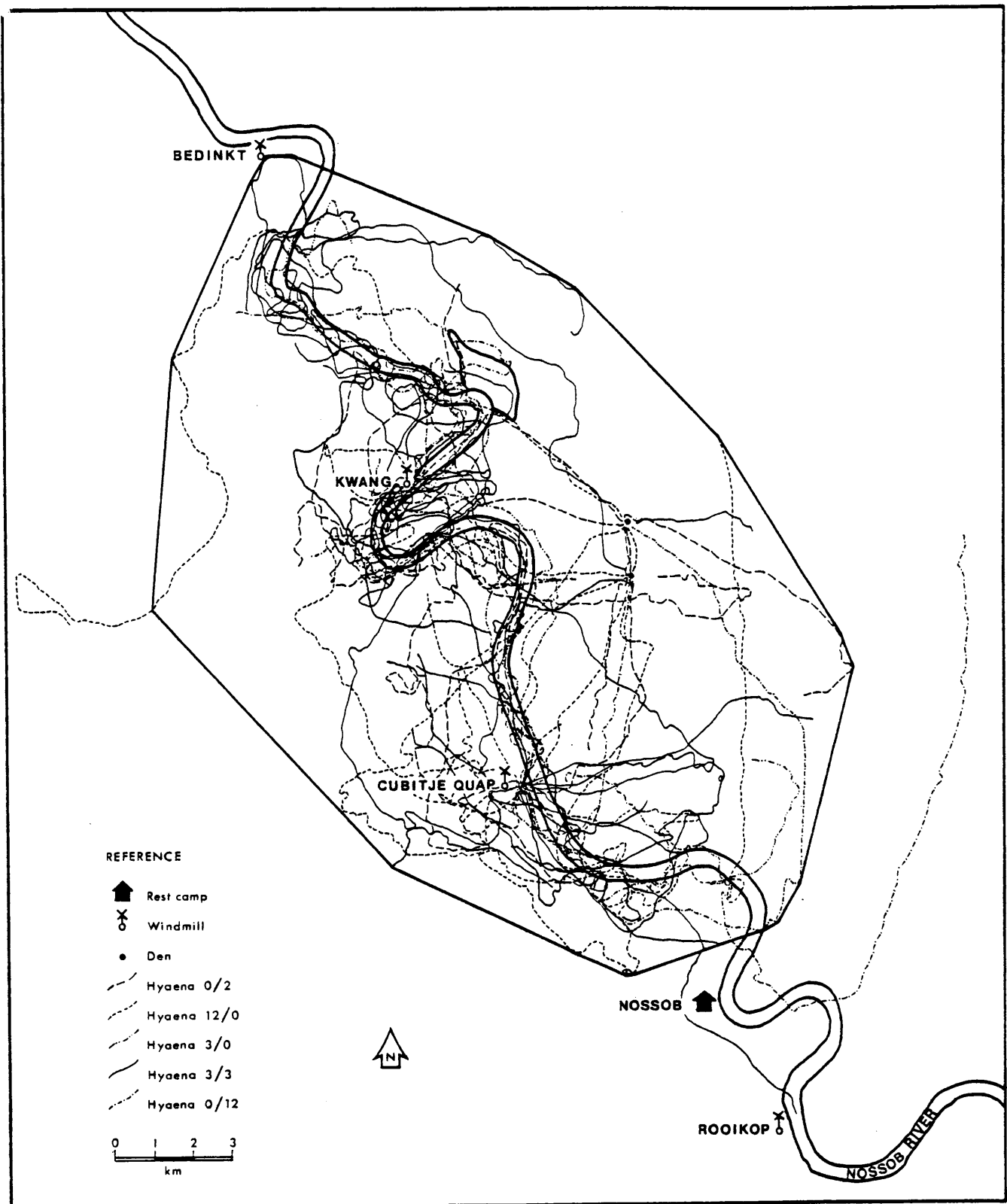


Figure 34: The observed movements of five brown hyaenas from the Kwang group in the southern Kalahari as determined from direct observations; July 1977 - August 1978.

Table 13: Distances between dens and the area of overlap between territories of neighbouring brown hyaena groups in the southern Kalahari; April 1972 - August 1978.

TERRITORY		DISTANCE (km) BETWEEN DENS	AREA (km ²) OF OVERLAP	PERCENTAGE OF TERRITORY 1 OVERLAPPING TERRITORY 2	PERCENTAGE OF TERRITORY 2 OVERLAPPING TERRITORY 1
1	2				
Kaspersdraai	Rooikop	20,0	0	0,0	0,0
Kaspersdraai	Botswana	18,7	-	-	-
Botswana	Cubitje Quap	19,2	27	-	-
Cubitje Quap	Rooikop	18,0	38	-	9,0
Kwang 1	Seven Pans	12,5	59	18,6	12,3
Mean		17,7	31	7,9 [*]	
Standard error		1,88	12,28	3,60 [*]	

* Mean and standard error of percentage overlap between all territories.

- No data.

Table 14: Brown hyaena territory size, habitat composition and group size in the southern Kalahari; April 1972 - August 1978

TERRITORY	SIZE (km ²)	PER CENT DUNES IN TERRITORY	PER CENT RIVER-BED IN TERRITORY	NUMBER OF ADULTS AND SUBADULTS IN THE GROUP
Kaspersdraai	276	97,1	2,9	1
Rooikop	424	84,1	15,9	3
Seven Pans	481	95,0	5,0	5
Kwang 1	317	67,8	32,2	2
Kwang 2	249	62,2	37,8	4
Kwang 3	235	58,3	41,7	8
Mean	330	77,4	22,6	3,8
Standard error	41,00	6,91	6,91	1,01

significantly correlated (Spearman rank correlation coefficient) (Fig. 35). Territory size is significantly correlated (Spearman rank correlation coefficient) with the mean distance travelled by the hyaenas in those territories between finding mammal food items (Fig. 36), although group size is not (Fig 23). These differences in territory sizes, moreover, decrease in close proportion to the decreasing mean distances travelled between finding the mammal food items (Fig. 36).

Insufficient data are available to determine the relationship between territory size and the number or biomass of any of the ungulates in the territory. There is, however, reason to believe that, unlike with group size (Fig. 22), no correlation exists. The Kaspersdraai territory, for example, had few large and medium-sized ungulates in it (Table 7 where the data for 1972 were mainly collected in this territory), yet it was smaller than the Kwang 1 territory, but larger than the Kwang 2 and 3 territories, all of which, because of the relatively large amount of river habitat in them, had higher ungulate numbers (Table 6). I am unable, however, to compare these data statistically.

Movement patterns

Influence of food dispersion

The movement patterns of brown hyaenas in different territories vary. The movements of individuals of the Kwang group tend to be clumped along the Nossob river-bed (Figs 32, 33 and 34). The movements of individuals of the Kaspersdraai, Rooikop and Seven Pans groups on the other hand, tend to be more evenly distributed throughout their territories (Figs. 31 and 32). These differences in dispersion pattern

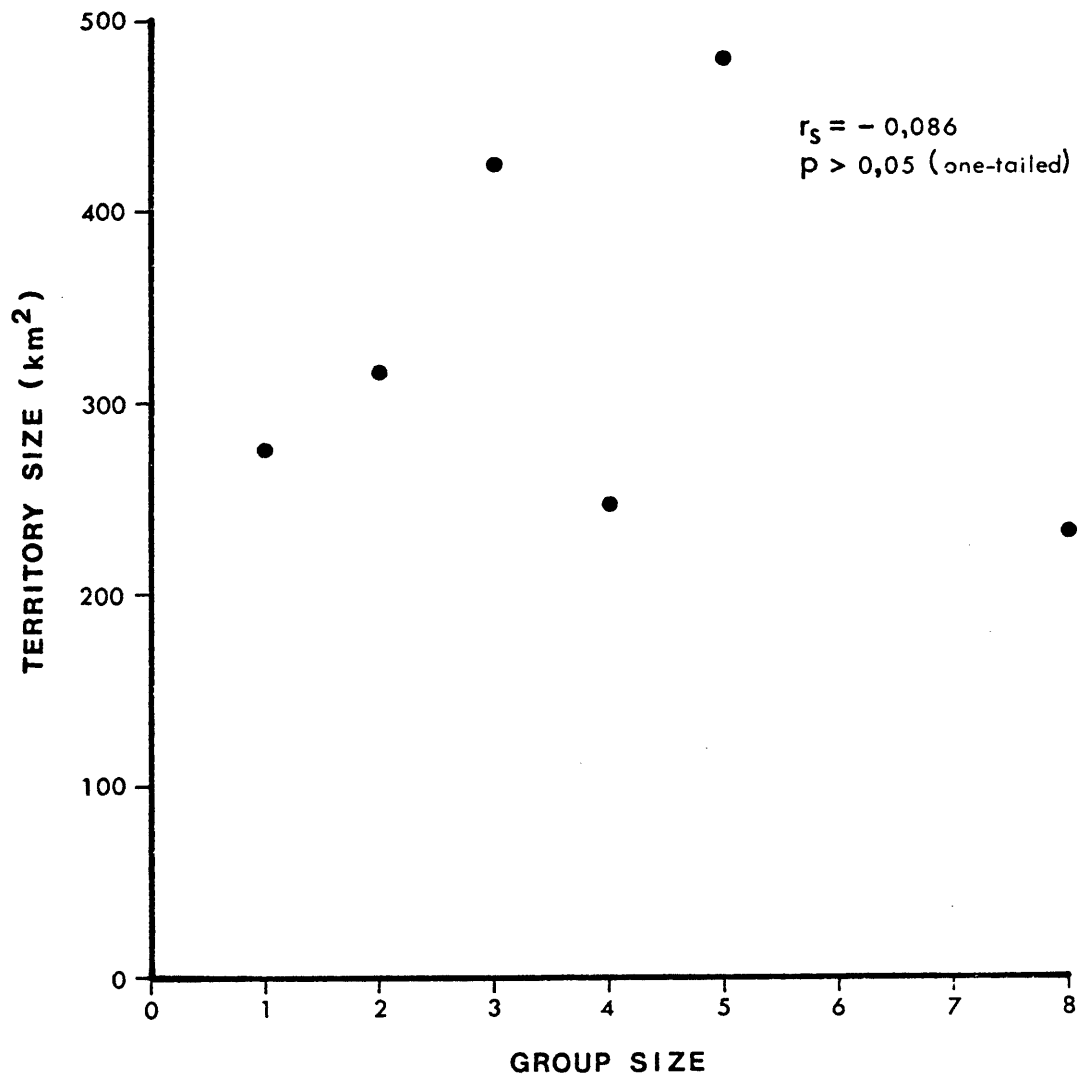


Figure 35: The relationship between territory size and group size of brown hyaenas in the southern Kalahari; April 1972 - August 1978. Group size is the number of adults and subadults in the group during the time that territory size was being measured.

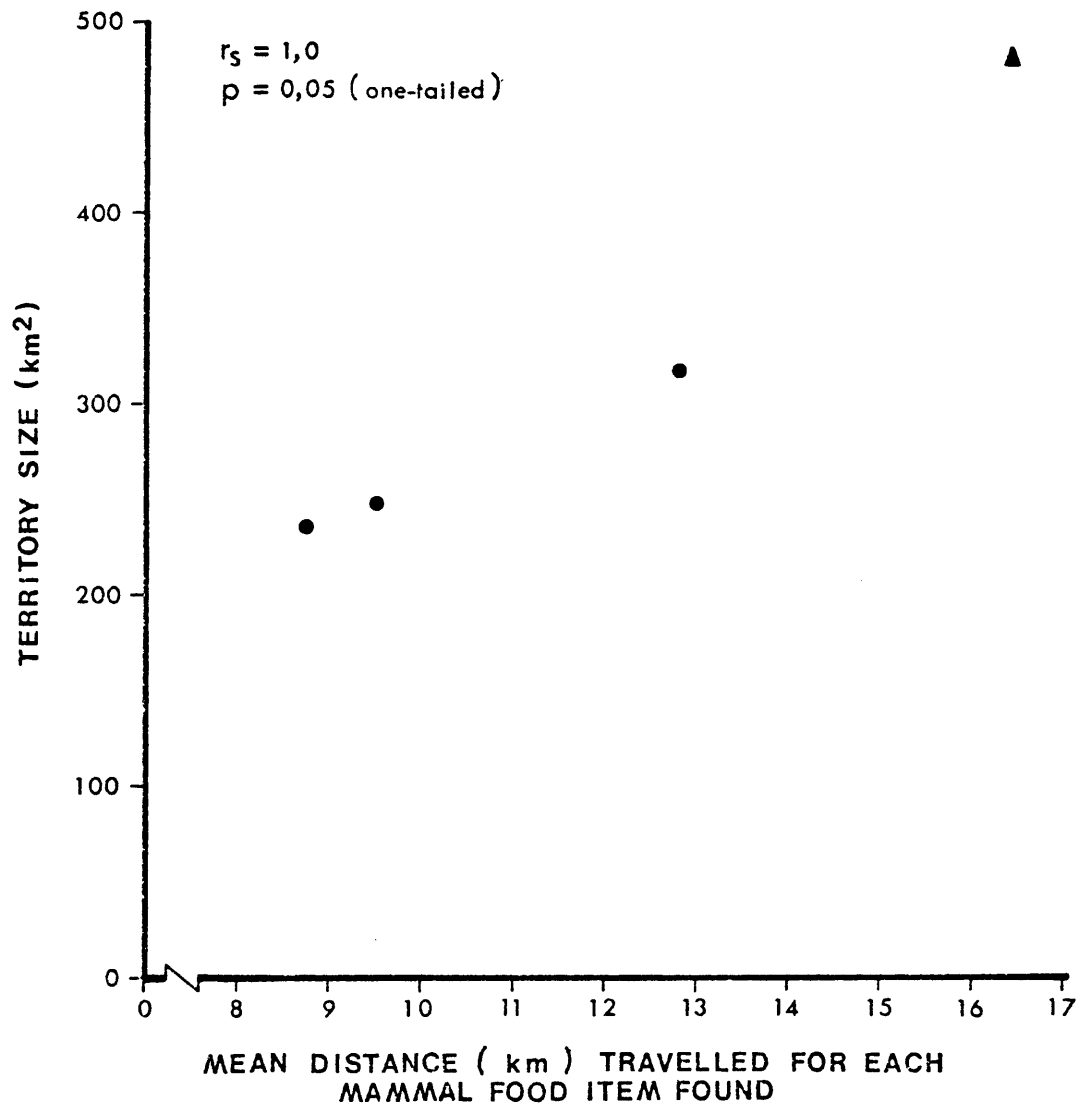


Figure 36: The relationship between territory size and the mean distance travelled by brown hyaenas in those territories between mammal food items in the southern Kalahari. (●) Kwang group 1974 - 1975, 1976, 1977 - 1978. (▲) Seven Pans group 1975.

are illustrated in three-dimensional SYMVU maps of the Kwang 2, Kaspersdraai and Seven Pans territories in Figs. 37, 38 and 39 respectively. The third, vertical dimension in these maps reflects the distances that members from each group were observed to move in each $6,25 \text{ km}^2$ block in the territory (Chapter 1). The movements of individuals from the Kwang group show a continuous peak along the Nossob river-bed and out to the den (Fig. 37), whereas individuals of the other two groups show a scattering of peaks throughout their territories (Figs. 38 and 39). The relatively large number of movements along the southern boundary of the territory of the Seven Pans group is due to one of the radio collared animals which was often trapped and then followed upon release in this area.

These differences in the movement patterns are probably due to differences in the distribution of the hyaenas' food. Hyaenas with a large amount of river habitat in their territories tend to forage extensively in this habitat as much of their food is concentrated there (Chapter 2). Animals which live mainly in the dunes, however, are faced with a more even distribution of food (Chapter 2) and therefore forage more evenly over their territories.

Influence of spotted hyaenas

The local density of spotted hyaenas may also influence the movement patterns of brown hyaenas. There was evidence that brown hyaenas avoid areas well frequented by spotted hyaenas. I recorded the numbers of both hyaena species that I observed whilst driving and searching with a spotlight along two different regions of the Nossob river-bed at night, between July 1979 and December 1980. The first region was between Nossob Camp and Bedinkt windmill (the Kwang area) and the second was

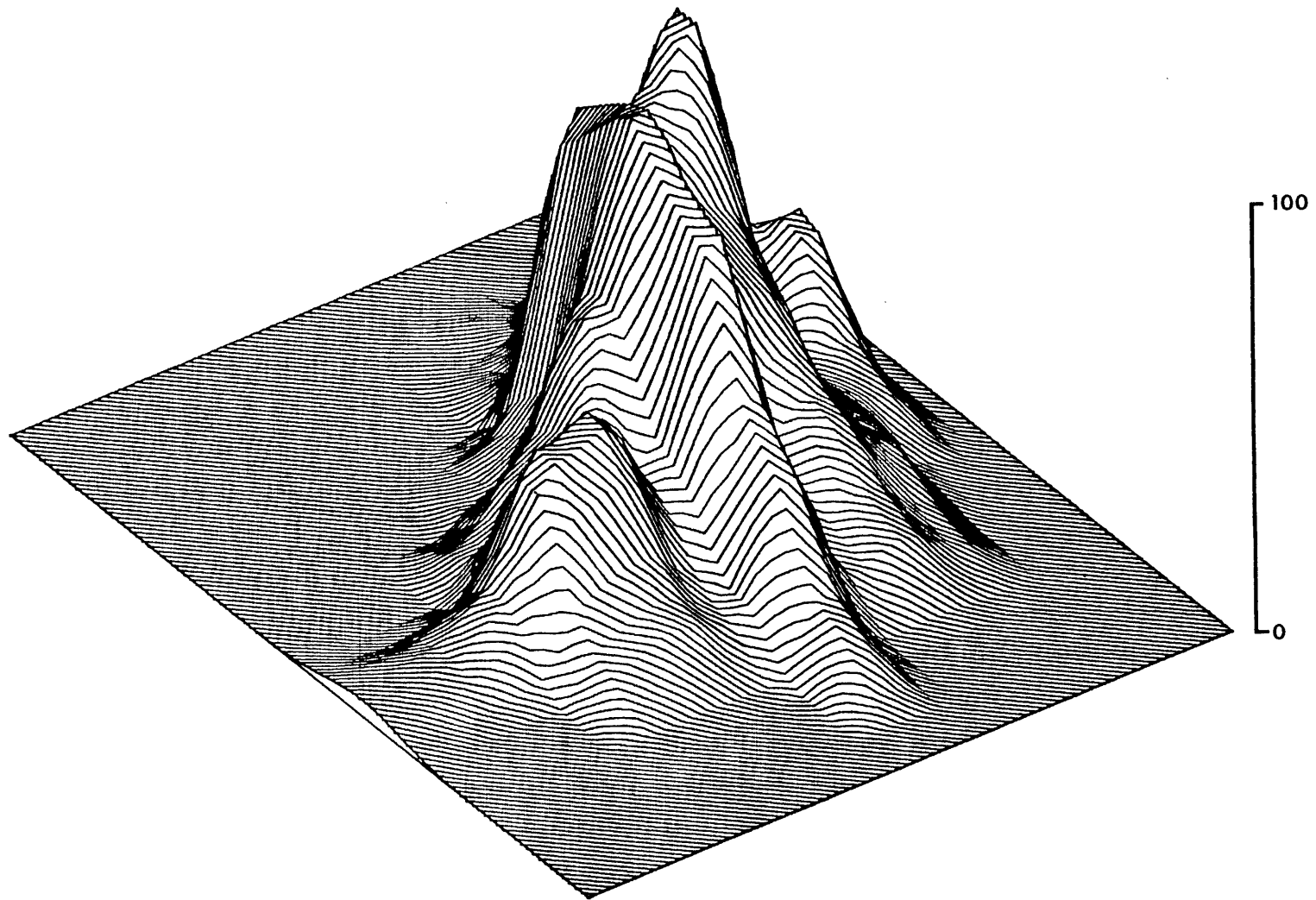


Figure 37: A three-dimensional map, generated by SYMVU, of the movement patterns of the members of the Kwang 2 brown hyaena group in the southern Kalahari; January - July 1976. The scale represents the distance that hyaenas were followed per 2,5 x 2,5 km square. The area covered by the map and the orientation are as in Fig. 9.

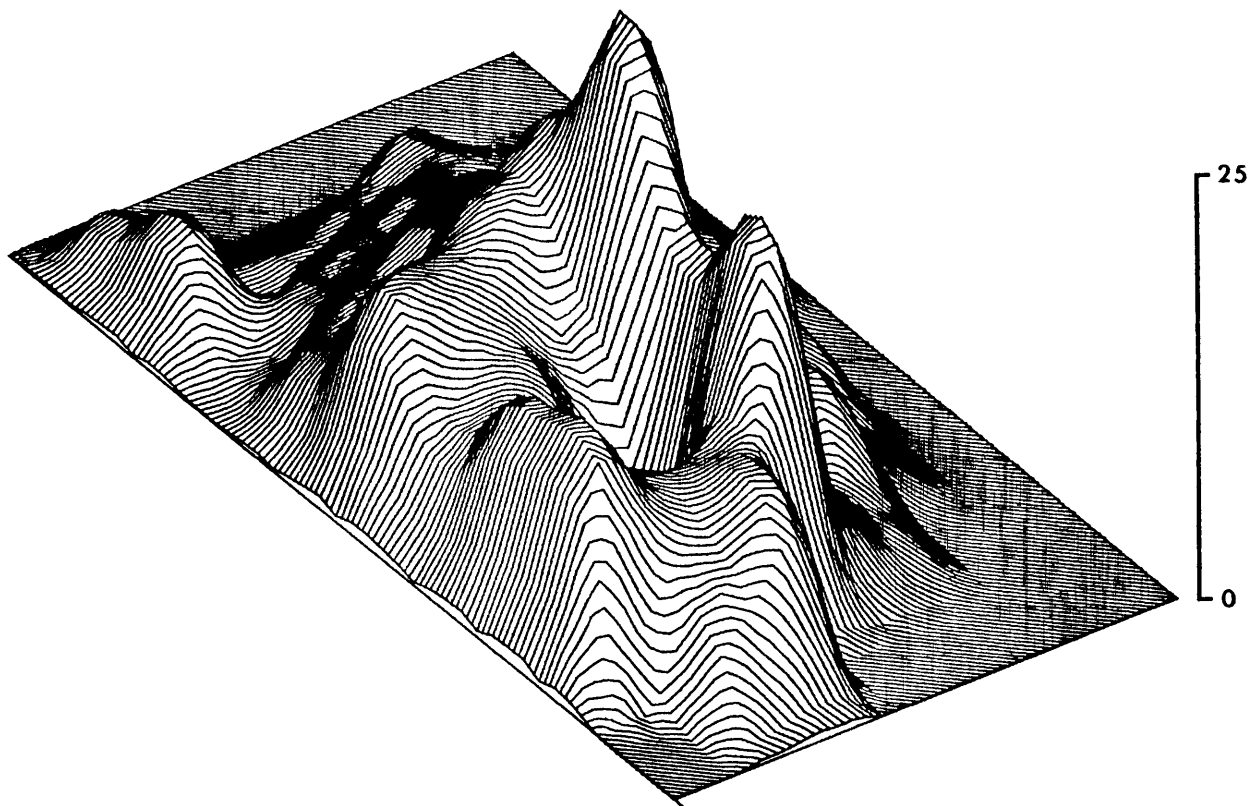


Figure 38: A three-dimensional map, generated by SYMVU, of the movement patterns of the Kaspersdraai brown hyaena in the southern Kalahari; October 1972 - April 1973. The scale represents the distance that the hyaena was followed per 2,5 x 2,5 km square. The area covered by the map is shown in Fig. 31. The orientation is from the south-east and from an altitude of 35° above the horizontal.

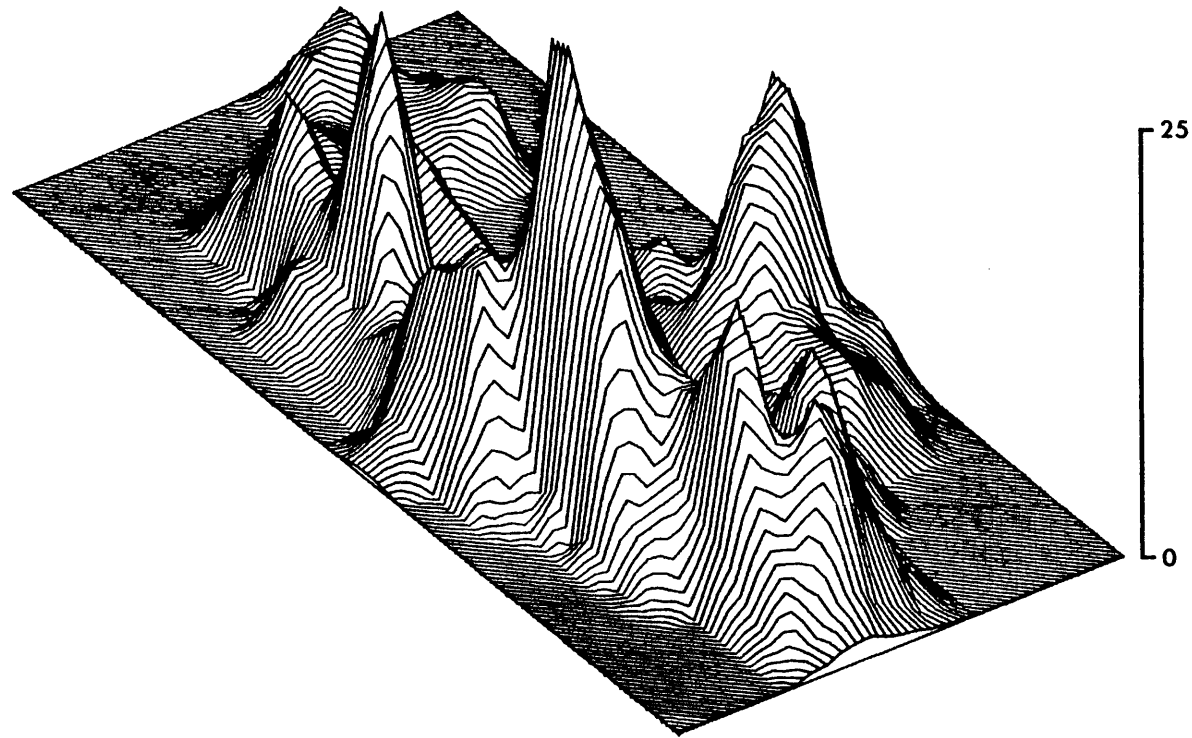


Figure 39: A three-dimensional map, generated by SYMVU, of the movement patterns of two of the brown hyaenas from the Seven Pans group in the southern Kalahari; January - September 1975. The scale represents the distance that the hyaenas were followed per 2,5 x 2,5 km square. The area covered by the map is shown in Fig. 32. The orientation is from the south-east and from an altitude of 35° above the horizontal.

between Bedinkt and Lijersdraai windmills (the Kousant area). Both regions were of similar size and habitat (Fig. 1). Table 15 shows that the frequency with which these two hyaena species occurred in the two areas differed significantly ($\chi^2 = 26,40$; $df = 1$; $p < 0,001$), with brown hyaenas being encountered more frequently in the Kwang area than in the Kousant area.

In Chapter 2 I have argued that the comparatively high density of spotted hyaenas in the Kousant area may have had a negative influence on the brown hyaena's food supply in this area and this is probably one of the reasons why brown hyaenas were seldom seen there. Additionally there is the possibility that direct antagonism exhibited by spotted hyaenas towards brown hyaenas also caused brown hyaenas to avoid this area.

During the study I observed brown and spotted hyaenas interact in the absence of food on 19 occasions. The results of these interactions are shown in Table 16 from which it is clear that spotted hyaenas are dominant over brown hyaenas, and that most encounters between these two species result in a harassing experience for the brown hyaena, occasionally leading to death.

The brown hyaena killed by the spotted hyaenas (Table 16) was a cub. This incident was reconstructed from spoor, thus the circumstances surrounding it were unknown. The spotted hyaenas had eaten little of the brown hyaena. Not included in Table 16 is the case when a group of six spotted hyaenas killed a half-drugged brown hyaena (Mills 1977).

A group of brown hyaenas which have had several clashes with spotted hyaenas in a certain area, may begin to avoid that area. This may necessitate an adjustment to the territory of the particular group and/or cause a decrease in the size of the group.

Table 15: Number and density of brown hyaenas and spotted hyaenas counted at night in two different parts of the Nossob river-bed, southern Kalahari; July 1979 - December 1980.

OBSERVATION	AREA	
	Kwang	Kousant
Kilometres driven	1 053	1 166
Brown hyaenas counted	20	6
Brown hyaenas per 100 km	1,9	0,5
Spotted hyaenas counted	10	50
Spotted hyaenas per 100 km	0,9	4,3

Table 16: Outcome of interactions between a brown hyaena and spotted hyaenas away from food in the southern Kalahari; April 1972 - December 1980.

BEHAVIOUR	OBSERVATIONS		NUMBER OF SPOTTED HYAENAS INVOLVED							
	Number	Per cent	1	2	3	4	5	6	7	?
Spotted hyaenas chase brown hyaena	14	73,7								
Spotted hyaenas catch up with brown hyaena	9	-	4	4	0	0	0	0	1	0
Spotted hyaenas fail to catch up with brown hyaena	5	-	2	2	0	1	0	0	0	0
Brown hyaena avoids spotted hyaenas	4	21,1	1	2	0	1	0	0	0	0
Spotted hyaenas kill brown hyaena	1	5,3	0	0	0	0	0	0	0	1
Total	19	100,1	7	8	0	2	0	0	1	1

Spotted hyaenas and also probably lions may influence the movement patterns of brown hyaenas in one other way. Brown hyaenas show a marked tendency to den in the dunes; 93 per cent of the 40 dens found in the present study were in the dunes. As 67 per cent of 24 dens of spotted hyaenas found were in river habitat (Mills in prep.), the absence of brown hyaena dens from the river-bed does not seem to be merely because there are few suitable dens there. Brown hyaena dens frequently have strong smelling carcasses scattered around them. This is the result of adults bringing food to the cubs and means that their dens may act as a strong attraction to potential enemies. Brown hyaenas may, therefore, locate their dens in the dunes in order to keep away from the main activity areas of the other large carnivores and therefore reduce the chances of being disturbed by them.

Lions were twice observed to investigate brown hyaena dens and once a group of seven spotted hyaenas was observed at a brown hyaena den eating a carcass that an adult brown hyaena had brought to the den the previous night. On another occasion two spotted hyaenas came to a brown hyaena den and chased and caught up with one of the brown hyaena cubs. The spotted hyaenas stood over the cub mouthing it, but as far as I could see, not biting it. After a few seconds the brown hyaena rolled free and darted into the hole unharmed.

Abnormal movements

During the 1977 - 1978 study period three movements were made by three different hyaenas of the Kwang group which I considered to be outside the group territory (Table 17). My criteria for regarding these movements to be outside the territory are two-fold. Firstly, they moved into areas well away from the areas usually frequented by members of

the group (Fig. 34) and secondly the rate of pasting dropped markedly. These movements appeared to be normal foraging expeditions.

POPULATION ESTIMATES

By utilising data from Tables 12 and 14 I have made some estimates (Table 18) of the number of brown hyaenas in the southern Kalahari. This was done in the following manner:-

1. From the capture data (Table 12) I have assumed that 64 per cent of the population comprises group-living animals, 28 per cent dispersing subadults and 8 per cent nomadic males.
2. From the direct observations and spoor tracking data I have calculated an average territory size of 330 km^2 and an average group size of 3,8 (Table 14) and have attached 95 per cent confidence limits to these two parameters.
3. From the average territory and group size figures I have calculated the number of group-living brown hyaenas in the Kalahari Gemsbok National Park and the number in it and the neighbouring Gemsbok National Park combined. From the 95 per cent confidence limit figures I have calculated a theoretical maximum number (assuming minimum territory size and maximum group size) and a minimum number (assuming maximum territory size and minimum group size) of hyaenas in the two areas.
4. Assuming that each of the calculations in 3 represent 64 per cent of the hyaenas in their respective population estimates, I have next calculated what 8 per cent and 28 per cent of each population would be and have added these figures to the relevant 64 per cent figures.

Table 18: Population estimates for brown hyaenas in the southern Kalahari; August 1978. The average territory size \pm 95 per cent confidence limits is $330 \pm 105 \text{ km}^2$. The average group size \pm 95 per cent confidence limits is $3,8 \pm 2,6$ individuals. Maximum and minimum group and territory sizes have been calculated from the 95 per cent confidence limits.

SOCIAL CLASS OF HYAENA	PER CENT OF POPULATION	NUMBER IN KALAHARI GEMSBOK NATIONAL PARK			NUMBER IN KALAHARI GEMSBOK NATIONAL PARK AND GEMSBOK NATIONAL PARK		
		Assuming average territory and group size	Assuming minimum territory and maximum group size	Assuming maximum territory and minimum group size	Assuming average territory and group size	Assuming minimum territory and maximum group size	Assuming maximum territory and minimum group size
Group living	64	110	273	26	417	1 029	100
Nomadic male	8	14	34	3	52	129	13
Dispersing subadult	28	48	119	11	182	450	44
Total		172	426	40	651	1 608	157
Hyaenas per 100 km^2		1,8	4,4	0,4	1,8	4,4	0,4

Thus I have made three estimates for the number of hyaenas in each area.

The data give a density of 1,8 brown hyaenas per 100 km² (0,4 - 4,4) for the Kalahari Gemsbok National Park. By way of comparison the lion density for this park has been calculated as 1,5 lions per 100 km² (1,1 - 1,9) (Mills, Wolff, Le Riche and Meyer 1978) and the spotted hyaena density as 0,6 spotted hyaenas per 100 km² (Mills in prep.).

The range of population estimates in Table 18 represents theoretical estimates within 95 per cent confidence limits, within which the population could fluctuate. It is most unlikely that conditions would ever be so good or so bad for either of the extremes to be reached.

SUMMARY

In this chapter I have shown that brown hyaenas in the southern Kalahari live in small groups of between four and 14 individuals, and that the size of the Kwang group, which was most intensively studied, was significantly correlated with the number of blue wildebeest in the territory each year. Fluctuation in group size is partially caused through changes in the birth rate, but mainly by the number of subadults which emigrate from the group. Immigration plays a small role in group dynamics.

In the study area mortality was highest amongst old animals. Violence on the part of lions and spotted hyaenas seems to be the main cause of natural mortality and starvation due to wearing down of the teeth may also be important. Young animals in particular are killed by man on the boundaries of the National Parks. These are probably mainly

dispersing subadult animals.

In addition to group-living animals and dispersing subadults, a segment of the brown hyaena population consists of adult males which have no fixed territories. These are called nomadic males and it was calculated that they comprised 8 per cent of the adult and subadult segment of the population.

Each brown hyaena group inhabits a large territory, these varying in size from 235 - 481 km². Territory size is not correlated with group size. There is a positive correlation between the mean distance travelled by brown hyaenas between finding mammal food items and the size of their territories.

The foraging patterns of brown hyaenas from different groups vary according to habitat, most probably because of differences in the distribution of their food. A high local density of spotted hyaenas may also influence the movement patterns of brown hyaenas in that area, necessitating an adjustment either to territory and/or to group size.

The brown hyaena density in the southern Kalahari is in the region of 1,8 hyaenas per 100 km². The indications are that this can fluctuate markedly depending on conditions, from a theoretical low of 0,4 hyaenas per 100 km² to a theoretical high of 4,4 hyaenas per 100 km².

CHAPTER 4 : BREEDING BEHAVIOUR

INTRODUCTION

Amongst carnivores mating systems usually entail either monogamous pairs, which may or may not be assisted in raising their offspring by a number of helpers, or polygyny. Polygyny is normally associated with dominance or territoriality on the part of the breeding males and a floating segment of the population of non-territorial, non-breeding males (Orians 1969 and Halliday 1978). The mating system of the brown hyaena as describe in the first part of this chapter, does not fit into this general pattern and it was, in fact, only the nomadic males which were observed to mate.

Cubs spend approximately 15 months at the den. The second part of this chapter describes the denning behaviour and development of the cubs, as well as the associated behaviour of the other group members. Of particular importance is the behaviour of the non-breeding males of the group, as it is here that a possible explanation for the way in which these animals maximise their inclusive fitness (Hamilton 1964) is found.

THE MATING SYSTEM AND MATING BEHAVIOUR

Table 19 shows that group-living male brown hyaenas show little sexual interest in females compared with the amount shown by strange males ($\chi^2 = 19,89$; $df = 1$; $p < 0,001$). Only three (6 per cent) of the interactions observed between group-living males and females included elements of sexual

Table 19: The frequency with which group-living and strange brown hyaena males in the southern Kalahari were observed in sexual encounters with group-living females, and the number of interactions observed between these animals where no sexual behaviour occurred; April 1972 - December 1980.

CATEGORY OF MALE	BEHAVIOUR			
	Sexual			Non-sexual
	Mounting	Foreplay	Sniffing female's vulva and/ or urine	
Group living	0	0	3	48
Strange	6	2	3	13

behaviour, when the males sniffed at the vulva and/or urine of a female and then exhibited flehmen.

In contrast 11 (46 per cent) of the interactions between group living females and strange males were classified as sexual, with mounting taking place on six (25 per cent) of the occasions. Five of these 11 males could be identified through natural markings on their ears; three were never seen again and two were seen twice each in the same area over periods of 12 and 33 days respectively. One of these last two was seen again once in the same area 27 months later.

All observed mating, therefore, was carried out by nomadic males. These males appeared to visit various groups, mate with any of the females which might be receptive and, as will be shown in Chapter 6, were usually tolerated by all the other members of the group.

The ratio of group males to strange males in a territory appeared to change when a group female was in oestrus. In the Kwang group there was a significant difference in the ratio of group males to strange males sighted in those months during which mating was observed, as opposed to those months when no mating was observed ($\chi^2 = 6,34$; $df = 1$; $p < 0,02$).

The females do not appear to scent mark more frequently during oestrus. A female was followed for a total of 34,3 km on two successive nights prior to being seen mating, and pasted 0,9 times per km. This compared with an average pasting frequency of 2,6 times per km for all animals observed during the present study. This suggests that a female's oestrous condition is not advertised through an increase in pasting, although it is possible that the paste-composition may change.

Three times a strange male was observed following a female closely until she stopped, when he immediately sniffed at her vulva. In this way it is possible that the nomadic males receive an indication of the

females' oestrous condition. Additionally, the behaviour of the female might also contribute in communicating her willingness to mate. Twice a male and female indulged in what is here termed as "foreplay" (Table 19). This behaviour was characterised by some aggression on the part of both animals and much mutual approaching and retreating. An increase in agonistic encounters has been suggested as a precursor to mating behaviour in brown hyaenas in captivity (Yost 1980).

The oestrous period of a female brown hyaena lasts several days. Yost (1980) recorded mating behaviour over at least a 15-day period between a pair of captive brown hyaenas, with a high incidence in mating activity being observed on the eight and fifteenth days. In the southern Kalahari, Ferguson (pers. comm.) saw the same female brown hyaena mating nine days apart, but could not be certain if the same male was involved both times. In between he saw the female on her own. My observations also suggest that during the oestrous period the male and female do not remain together all the time.

Table 20 shows some details of the six mating bouts which were observed during the present study. The mean duration and range of each mounting was considerably less than the 1,9 min (range 0,5 - 10 min) recorded by Yost (1980) for captive brown hyaenas, yet the frequency of mountings per observation period (Table 20) was higher than the peak of five matings in an hour observed in captivity.

Of the 35 mountings observed in the present study the male always moved over to the female first, mounted the female while she was standing 34 (97 per cent) times and while she was recumbant once (3 per cent). In

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July 1975.

Table 20: Details of six mating bouts between brown hyaenas in the southern Kalahari; April 1972 - December 1980.

DURATION OF OBSERVATION (min)	NUMBER OF MOUNTINGS	MEAN INTERVAL (min) BETWEEN MOUNTINGS	DURATION(s) OF MOUNTING			NUMBER OF TIMES ANIMALS PASTED DURING OBSERVATION	
			Mean	Minimum	Maximum	Male	Female
20	3	6,7	-	-	-	0	0
5	2	2,5	9	2	15	0	0
60	7	8,6	64	10	180	3	0
20	4	5,0	11	5	15	0	0
90	9	10,0	87	15	180	11	0
67	10	6,7	37	30	60	12	2
Mean		6,6	42	-	-	4,3	0,3
Standard error		1,08	15,1	-	-	2,3	0,3

this latter case the female immediately stood up and walked forward and the male fell off. When mounted (Fig. 40) the male typically rests his chin on the female's back, has his mouth open baring his teeth, his ears flattened out sideways and in at least three cases uttered a growl and a staccato sounding soft yell (see vocalisations). Once a male was also observed to softly bite at a female's back. The male clasps the female around her stomach with his forefeet. The female stands with her head held down (Fig. 40) and twice I could see that the female's tail was elevated. It was impossible to tell if intromission occurred at each mounting, although I gained the distinct impression that it did not. Pelvic thrusting was never observed, neither was it seen in captivity by Eaton (1981). Upon dismounting the male sniffed and licked at the female's vulva on nine (26 per cent) occasions, the two hyaenas stood with their hind regions close together, their heads held down and facing away from each other for 30 - 60 s on five (14 per cent) occasions, and immediately moved apart on 21 (60 per cent) occasions. In between mountings the hyaenas may groom themselves, but usually they keep moving with the female dictating the direction of travel. In two of the six mating bouts which I observed a second strange male brown hyaen was seen briefly in the vicinity of the mating couple, but no interaction between the strange male and the mating pair took place.

DEVELOPMENT OF CUBS AND THE ASSOCIATED ROLES OF THE OTHER GROUP MEMBERS

Dens

The prime function of a brown hyaena den is to provide protection

for the cubs for the long periods that the adults are away; the holes are small, large enough for the cubs, but not for an adult brown hyaena or any other large carnivore to enter, and are also deep enough to make the possibility of another carnivore digging the cubs out remote. If the cubs are frightened by anything they immediately run into the den.

The den is also the social centre of a brown hyaena family group. All the other members of the group visit the den from time to time even if they do not bring food. In this way the cubs get to know the other members of the group. The mound of sand at the entrance to the den is the focus of activity at the den. The cubs normally lie on it when out of the den, are suckled (Fig. 42), greet each other and the adults, and indulge in muzzle-wrestling on this mound.

Of 40 brown hyaena dens found during the present study 37 (93 per cent) had one entrance, two (5 per cent) had two entrances and one (2 per cent) had three entrances. This last mentioned den was unusual and by the time the hyaenas abandoned it there were seven entrances, although not all were inter-connected, i.e. there was more than one hole. Not all the entrances, and therefore probably the holes as well, were used at the same time. Often there were one or two minor dens at distances varying from 5 - 500 m from the main den, in which the cubs sometimes spent the day. However, they always returned to the main den in the evening.

Figure 43 is a diagram of a den that I dug up after the cubs had left it. The dimensions of this den are similar to those given by Skinner (1976) for a brown hyaena den in the Transvaal and by Watson (1965) and Kruuk (1972) for spotted hyaena dens in East Africa.

Brown hyaenas tend to den in a small area of their territory over a number of years. The Kwang group denned in as small an area as 1 km^2 between 1974 and 1980. The Kaspersdraai dens in 1972 and 1973 were spread out over an area of 5 km^2 . The denning area is not necessarily in the

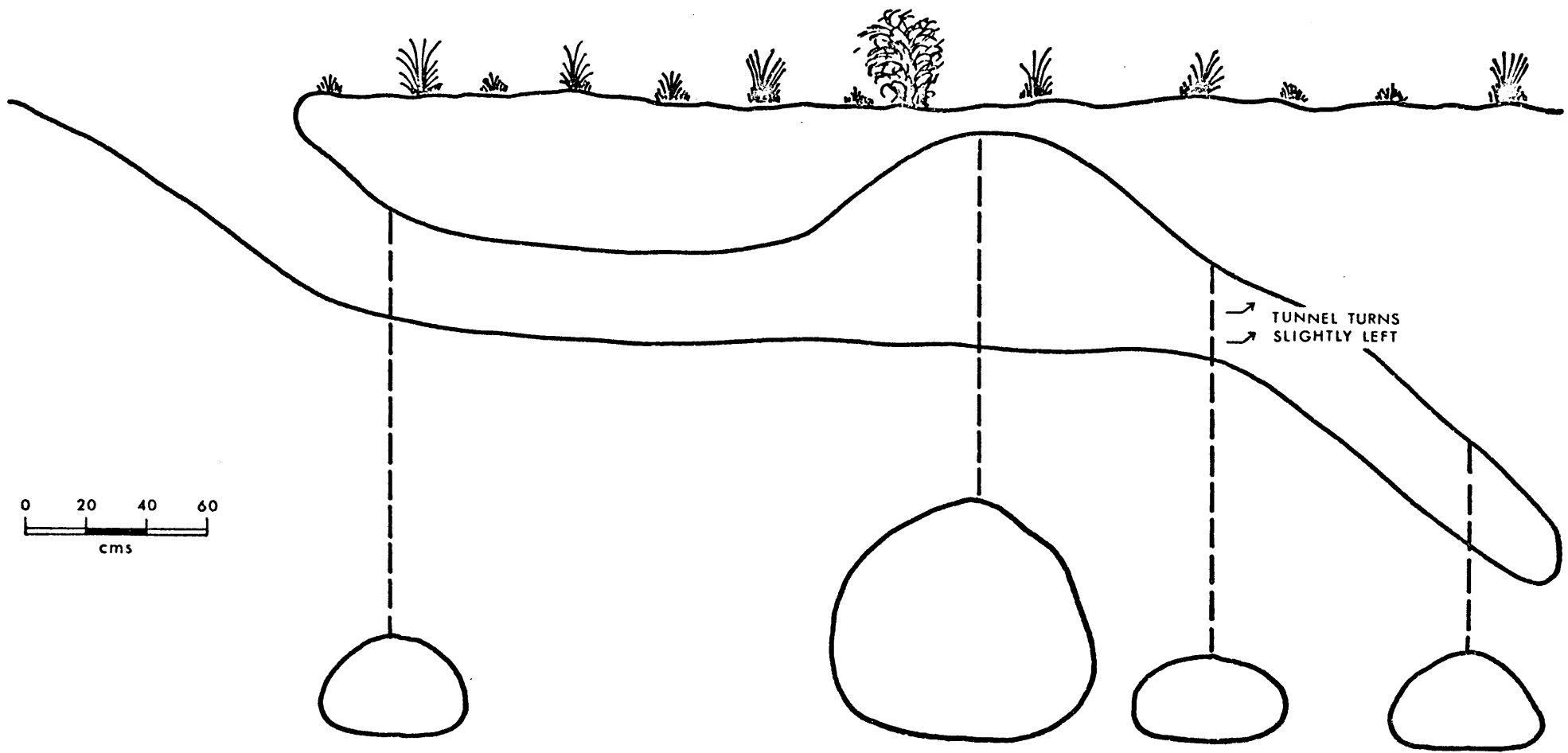


Figure 43: Diagrammatic representation of a brown hyaena den which was dug up near Rooikop in the southern Kalahari; September 1974.

centre of the territory (Figs 31, 32, 33 and 34). As mentioned earlier 93 per cent of the dens were in the dunes, probably in order to escape harassment from spotted hyaenas and lions.

During the course of their development the cubs may use several dens. When the cubs are under six months old, the movement to a new den is initiated by the mother, cubs under two months of age sometimes being carried by her. In the case of older cubs it is apparently often the cubs themselves that move to a new den.

Table 21 lists the number of dens used by 11 litters of cubs and, where known, the reasons for the hyaenas moving dens. At three (14 per cent) dens, with cubs under six months old, the hyaenas moved immediately after I discovered the den, and therefore almost certainly as a result of this. In one instance they moved a second time immediately after I relocated the new den. Spoor tracking data showed that the mothers never saw me at these dens and obviously my scent was enough to cause them to move.

On two (10 per cent) occasions the movement of a den was possibly a result of a build up of fleas at the den. Although I have no quantitative data, my impression was that the cubs were spending more time grooming themselves a week or two prior to their departure than they usually did. When I disturbed the sand at the entrance to these dens, numerous fleas were seen jumping in the sand. At the new dens no fleas were observed. In one of these instances the old den still had numerous fleas three months later, whereas the new one was still relatively free of them. Kilgore (1969) lists disturbance by man and an increase in ectoparasites around the den as two factors causing the swift fox Vulpes velox to move from a den.

On three (14 per cent) occasions a violent rain storm caused the entrance to a den to cave in and the hyaenas immediately left the den.

Table 21: Number of dens used and reasons for changing dens by brown hyaenas in the southern Kalahari; April 1972 - December 1980.

DEN	APPROXIMATE AGE (MONTHS) OF CUBS WHEN DEN WAS FIRST FOUND	MINIMUM NUMBER OF DENS USED	NUMBER OF MOVEMENTS	CAUSES OF MOVEMENTS			
				Disturbance by man	Den caved in	Build-up of fleas and ectoparasites	Unknown
Botswana	7	4	3	1	0	0	2
Cubitje Quap	12	1	0	0	0	0	0
Kaspersdraai 3	2	7	6	0	2	1	3
Rooikop	3	4	3	2	0	1	0
Kwang 1974 - 1975	5	2	1	0	1	0	0
Kwang 1976	2	4	3	1	0	0	2
Kwang 1977 - 1978	10+4*	3	2	0	0	0	2
Kwang 1978	4	2	1	0	0	0	1
Kwang 1980	11+3*	3	2	0	0	0	2
Total	-	30	21	4	3	2	12

* Two litters.

In 12 (57 per cent) cases the hyaenas changed their den for no obvious reason. Frequent moving of dens is common in spotted hyaenas (Kruuk 1972 and Mills in prep.) and in many other den-living carnivores such as black-backed jackals, bat-eared foxes and Cape foxes (personal observations). Brown hyaenas do not usually use the same den more than once; this was only observed three (10 per cent) times. Spotted hyaena dens, on the other hand, are sometimes used on and off for many years (Kruuk 1972 and Mills in prep.).

Cubs: 0 - 3 months old

Schultz (1966) recorded that brown hyaena cubs are born with their eyes closed, their ears bent sharply forward forming triangles and with the same body colour as an adult, but with shorter hair. The eyes begin to open at eight days of age and are completely open at approximately 14 days of age (Anderson In litt.). The ears start to become erect at an age of four weeks (Schultz 1966 and Anderson In litt.).

The youngest cubs that I found during the present study were two litters of six to eight-week old cubs. At this age the cubs rarely come out of the den except when their mother or another adult is there. For the first three months of their lives the cubs are regularly visited by their mother, normally at sunset and sunrise. They are suckled at each visit and the mother spends time grooming them. Occasionally, however, the mother may stay away from the den for several nights, the maximum period of absence observed being five nights.

When the mother (or another adult) comes to the den, it puts its head into the hole and at least on some occasions utters a very soft growl. The cubs soon emerge and, if the mother is not lying down, they

follow her around with their ears flattened out sideways and their mouths open (Fig 41) uttering a harsh whine, until she does lie down and allows them to suckle (Fig. 42). If the adult is not the mother of the cubs they follow it around in the same way and greet with it.

The cubs are normally suckled with the mother lying on her side with her uppermost hind leg slightly raised and with the cubs lying at right angles to her. They do not adopt the suckling position of the spotted hyaena (Kruuk 1972). They will rarely suckle while the mother stands. Normally a female suckles all her cubs at the same time. Suckling is usually terminated by the mother rolling over onto her stomach. The mean duration that cubs under three months old were suckled per 24 h period, on those nights that the mother came to the den, was $21,2 \text{ min} \pm \text{s.e. } 4,63$ ($n = 8$).

By six weeks of age the cubs indulge in muzzle-wrestling with each other or any of the other visitors to the den. They also go through the motions of pasting, although the anal scent gland is as yet inactive.

Cubs: 4 - 9 months old

From the beginning of the fourth month the visits to the den by the mother become less frequent. She usually only visits her cubs once during the 24 h period and is more likely to stay away for longer periods. Of 115 nights observations at dens in which there were cubs of 4 - 9 months old, the mother visited the den on 86 (75 per cent) nights. The duration of suckling per 24 h period (if the mother does visit the den) is significantly longer than in the 0 - 3 month old period, the mean duration being $40,6 \text{ min} \pm \text{s.e. } 4,51$ ($n = 24$) ($d = 3,018$; $f = 21$; $p < 0,01$).

From the fourth month the mother and other group members begin to

bring food to the den. The food is usually carried right to the hole and left as far down the hole as the adult can reach. If the cubs are out of the den when an animal arrives with food, they run over to the carrier which will then drop the food. The cubs next pick up the food and carry it into the den themselves. The food is mostly consumed underground and often it was noticeable how the cubs took turns inside a den when I knew there was food there. The food remains are eventually brought out of the den.

As the cubs grow older they begin to spend more time out of the den, emerging at sunset even though no large brown hyaenas are at the den. They do not venture far from the den and if they should be frightened by anything, even by an approaching brown hyaena, they immediately run back into the den.

By four months of age the cubs are able to secrete a black substance when pasting.

Cubs: 10 - 15 months old

The visits to the den by the mother become increasingly rare as the cubs grow older. At dens with cubs 10 - 15 months old, the mother only visited the den on 16 (35 per cent) of 46 nights of observations. This is significantly fewer visits than in the 4 - 9 month period ($\chi^2 = 20,95$; $df = 1$; $p < 0,001$). Consequently the contribution of milk to the diet of the cubs becomes less important. I do not know when the cubs are weaned. I twice saw cubs of approximately one year old suckling for 66 and 34 min respectively, and the immobilised mother of 11-month old cubs was still found to be lactating. On the other hand I once observed a female to snap at her 10-month old cub which tried unsuccessfully to suckle.

When the cubs are approximately 10 months old they may spend the day away from the den. One of them may move off a short distance from the den in the morning and spend the day under a bush. In the evening it returns to the den, but not necessarily by the shortest route. The distances moved in the mornings from the den, and particularly the distances travelled in the evenings on the return journeys, gradually increase and the cubs begin to find some food on these trips. They may also forage during the day, at least in winter (Mills 1977).

By the time that the cubs are a year old, these foraging trips are quite extensive and the cubs may move more than 20 km before returning to the den. They may even spend a whole day and night away from the den, although they usually return each night. These foraging trips are mostly done alone, although occasionally the cubs might move together. They were never observed to accompany their mother or any other adults for any distance.

At the Kaspersdraai den the mother of the cubs died when they were approximately one year old. This was a den where the mother was the only animal seen to bring food, and I did not find any evidence of food being brought to the den after she had died. The cubs, however, managed to find enough food for themselves and lived at the den for another six weeks before abandoning it at an earlier stage than usual. I do not know what happened to them thereafter.

By the time that the cubs are 15 months old they are almost certainly weaned. They have their full permanent dentition and are able to secrete both black and white pastes. They are now classed as subadults. By this time their mother may have had another litter.

Subadults: 16 - 30 months old

If there is a den in the territory, i.e. if the mother has another litter of cubs, or if another female in the group has cubs, the subadults spend much time at the den and will sometimes go into the den if it is large enough.

Although I never saw a subadult attempt to suckle, they do feed on food that has been brought to the den, sometimes robbing an adult as it arrives with food. Once, for example, a two-year old female was at the den of her mother's seven-month old cubs, when the mother approached carrying a steenbok carcass. When the adult was about 50 m away her daughter ran over to her. The mother tried to run past the daughter, which then ran after her, and dropped the carcass as she reached the den. The daughter picked it up and ran off with it. The mother, who had put up little opposition, then sniffed around the den for a few seconds before she moved off.

On another occasion the same adult female arrived at her den in which she had four five-month old cubs. She was carrying a bat-eared fox. Her daughter's 15-month old son was at the den, grabbed the bat-eared fox from her and ran off with it. After a few minutes, however, he returned with the carcass and the adult female snapped at him. He then dropped the fox into the hole, moved over to the female, presented to her and then moved off.

Towards the end of their subadulthood brown hyaenas start to carry food back to the den for cubs. Three individuals were first observed to bring food to the den when they were 22, 24 and 27 months old respectively. There appears to be a transition period for subadults between carrying food to the den and taking food that other adults have brought to the den. The example concerning the bat-eared fox cited above illustrates this.

Communal denning

In the southern Kalahari brown hyaenas normally raise only one litter of cubs at a den. Of 11 dens where I was able to document the number of cubs, two (18 per cent) had two litters of cubs in them. These were at the Kwang dens in 1977 and 1980 when a female (0/2) and her eldest daughter (12/0) had cubs in the same den. The older female's cubs were six and eight months older than her daughter's cubs in 1977 and 1980 respectively.

Owens and Owens (1979 a) report that female brown hyaenas suckle other cubs besides their own. This was also observed in the present study at the 1977 Kwang den, although the females showed a clear preference for their own cubs. Of 13 occasions where a cub attempted to suckle from a female that was not its own mother, it was only successful, in that it was able to drink for more than 1 min, three (23 per cent) times. Twice the daughter allowed one of her mother's cubs to suckle for 22 and 6 min, and once the mother allowed one of her daughter's cubs to suckle for 52 min.

Feeding of cubs

Adult and large subadult brown hyaenas regularly carry food back to the den for the cubs. The type of food carried to the den is fairly specialised, consisting mainly of small or medium-sized mammal remains (Mills and Mills 1978).

The mean distance that food was observed to be carried to a den was $6,4 \text{ km} \pm \text{s.e. } 0,64$ ($n = 27$). The most spectacular feat was when a brown hyaena carried the remains of a domestic cow calf, which weighed

approximately 7,5 kg, a distance of 15 km to a den.

Normally only a carcass with meat left on it will be carried back to the den. A springbok carcass which has been picked clean by vultures and jackals and which only comprises of bones and skin, therefore, will usually not be taken to the den. Similarly, if several brown hyaenas feed from a carcass with some meat on it, nothing will be left to take to the den.

Between December 1974 and August 1978 I observed 39 cases where a brown hyaena from the Kwang group found food which I judged to be suitable to be taken to the den, according to the above criteria. In two (5 per cent) of these instances other brown hyaenas (one in one case and two in the other) were also at the carcass, but these were both untouched springbok carcasses and thus provided much food. A hyaena carried all or part of the food to the den in 25 (64 per cent) of the cases; in 10 (40 per cent) without eating anything first and in the remaining 15 (60 per cent) after eating part of the food first. There was therefore a definite tendency for the hyaenas to take at least some of this food to the den rather than to eat it all themselves.

Of the cases cited above, males were involved 16 (41 per cent) times and females were involved 23 (59 per cent) times (Table 22). The males carried food back to the den nine times and the females 16 times ($\chi^2 = 1,42$; $df = 1$; $p > 0,05$). Observations at other dens during the present study also revealed males bringing food to the den. At the Cubitje Quap den the same male was seen to bring food to the den three times, and at the Rooikop den another male was seen to bring food once. No systematic observations were made at the Kwang den in 1980, but when I gave a springhare to a known male (0/33) he ate part of it and carried the rest to the den. These observations are contrary to what has been recorded by Owens and Owens (1979 a) in the central Kalahari, who only observed females

Table 22: Number of times that known brown hyaenas of the Kwang group in the southern Kalahari carried food to cubs; December 1974 - August 1978.

ANIMAL	SEX	NUMBER OF SUITABLE CARCASSES FOUND	NUMBER OF CARCASSES CARRIED TO THE DEN	PERCENTAGE OF CARCASSES CARRIED TO THE DEN
0/2	Female	20	14*	70
12/0	Female	3	2	66
3/0	Male	4	1*	25
3/3	Male	7	3	43
0/12	Male	4	4	100
4/2	Male	1	1	100
Total		39	25	64

* These two individuals each once carried part of a large carcass to a den. These observations have not been included as such food was not regarded as normally being suitable for cubs.

bringing food to the den.

The few data from the Kwang group suggest that all members of a brown hyaena social group contribute to the feeding of the cubs (Table 22). The fact that these brown hyaenas were more likely to carry a suitable carcass to the den than to eat it all themselves, and the distances over which they sometimes carried the food, suggest that this behaviour does at times entail a significant energy cost to the carriers of the food.

It is, therefore, important to know the degree of genetic relatedness (r) between the members of the group; in other words the probability that a gene in one animal is a replica of a gene in the other, by virtue of descent from a shared ancestor (Bertram 1976). Assuming that each litter of cubs born into the Kwang group was fathered by different and unrelated males, an approximate value for r has been calculated for all but two of the members of the Kwang group during the study (Table 23). From these data the average degree of relatedness between the males which were observed to carry food to dens and the cubs at the dens is calculated as 0,2. The old male (3/0) who was the only adult male in the group from December 1974 until August 1976, is unlikely to be the father of any of the cubs born into the group (see earlier), although he may have been some relation of the original female (0/2). He was twice observed carrying food to the den. The relationship between the male which joined the Kwang group in June 1980 (0/33), and the cubs that he was observed feeding, was also unknown, but again it is unlikely that he was their father.

The presence of related helpers at dens has been recorded in several other carnivore species; in dwarf mongooses Helogale parvula (Rood 1978), African wild dogs (Frame, Malcolm, Frame and Van Lawick 1979), red foxes Vulpes vulpes (Macdonald 1979 b), black-backed jackals (Moehlman 1979)

Table 23: The approximate degrees of genetic relatedness (r) between the members of the Kwang brown hyaena group in the southern Kalahari; December 1974 - August 1978. Grouped animals belong to the same litter.

YEAR OF BIRTH	?	1974		1975		1976			1977			1978	
SEX	F	M	F	M	F	M	F	F	M	M	M	M	F
ANIMAL	0/2	3/3	12/0	0/12	0/13	4/2	14/0	34/0	0/14	4/0	0/4	2/0	1/0
0/2	-	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{2}$	$\frac{1}{2}$
3/3	-	-	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$
12/0	-	-	-	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{4}$
0/12	-	-	-	-	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{4}$	$\frac{1}{4}$
0/13	-	-	-	-	-	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{4}$	$\frac{1}{4}$
4/2	-	-	-	-	-	-	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{4}$	$\frac{1}{4}$
14/0	-	-	-	-	-	-	-	$\frac{1}{2}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{4}$	$\frac{1}{4}$
34/0	-	-	-	-	-	-	-	-	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{4}$	$\frac{1}{4}$
0/14	-	-	-	-	-	-	-	-	-	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{8}$	$\frac{1}{8}$
4/0	-	-	-	-	-	-	-	-	-	-	$\frac{1}{2}$	$\frac{1}{8}$	$\frac{1}{8}$
0/4	-	-	-	-	-	-	-	-	-	-	-	$\frac{1}{8}$	$\frac{1}{8}$
2/0	-	-	-	-	-	-	-	-	-	-	-	-	$\frac{1}{2}$
1/0	-	-	-	-	-	-	-	-	-	-	-	-	-

and European badgers (Kruuk pers. comm.).

It has been shown that in black-backed jackals, helpers improve survival rates (Moehlman 1979, 1981 and Montgomerie 1981). Not enough data are available for the brown hyaena to be sure if the same holds true for this species. At the 1977 Kwang den six cubs survived when there were two helpers, whereas at five dens where there were less than two helpers, never more than three cubs survived. However, at the 1978 Kwang den where there were three helpers, only two out of a litter of four cubs survived. Whether this was exceptional or not is unknown. For example, the cubs which died may have done so as a result of an unrelated phenomenon such as the contraction of a disease. Clearly more observations are needed at dens where there are several helpers in order to gauge the value of these non-breeding males.

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1981.

CHAPTER 5 : COMMUNICATION AND BASIC SOCIAL BEHAVIOUR PATTERNS'

INTRODUCTION

"Communication is said to occur when an animal, the actor, does something which appears to be the result of selection to influence the sense organs of another animal, the reactor, so that the reactor's behaviour changes to the advantage of the actor" (Dawkins and Krebs 1978: 283). Communication can be achieved through visual, tactile, vocal and olfactory means. Different species rely on these various forms of communication to varying degrees, depending largely on the habitats that they live in and their socio-ecology. The brown hyaena employs olfactory and visual communication to a larger degree than it does vocal communication, with tactile communication being of little importance.

In this chapter the communication system and basic social behaviour patterns of the brown hyaena are described and the functional significance of the more important aspects of communication are speculated on.

From the central Kalahari, Owens and Owens (1978, 1979 b) have described some of the behaviour patterns discussed in this chapter. Where possible, therefore, I will use the same descriptive terms as they have used, as well as make comparisons between the results of these two studies.

VISUAL COMMUNICATION

Basic postures

Communication through attitudes and postures in the brown hyaena is conveyed by pilo-erection along the neck and back, by the position of the tail, the ears, the head and the lips, and by leg positions and movements. Two basic postures at either end of a continuum display either a tendency to attack: the hair raised - stand erect posture; or a tendency to flee: the hair raised - body low posture.

The hair raised - stand erect posture

The most striking aspect of this posture which is illustrated in Figs 44 a and b, is the erection of the long hairs along the back and neck. In addition the tail is elevated, often curled over the back, the anal pouch extruded and the animal stands erect with its mouth closed and ears cocked (Fig. 44). The head is sometimes held up (Fig. 44 a) and sometimes lowered (Fig. 44 b). The posture is often accompanied by the hoot and by scratching the ground with the forefeet. If a hyaena moves whilst holding this posture it does so slowly with a stiff-legged gait.

This posture is typically displayed by a feeding hyaena at the approach of another one. Usually it has the apparent effect of deterring the approacher (Table 24). Of the 53 occasions that this posture was exhibited by a feeding brown hyaena (possessor) at the approach of another one, the possessor kept the food in 43 cases (81 per cent) and lost it in 10 (19 per cent) ($\chi^2 = 20,55$; $df = 1$; $p < 0,001$). It is also seen prior to or after neck-biting, when it is performed by the winner.

Table 24: Occurrence of the hair raised - stand erect posture exhibited by a feeding brown hyaena (possessor) towards another one which is approaching it (approacher) in the southern Kalahari; December 1974 - August 1978.

RESPONSE	NUMBER OF TIMES OBSERVED	PER CENT OF OBSERVATIONS
Approacher retreats or does not come nearer	30	56,6
Approacher takes over the food	9	17,0
Approacher joins possessor on food	8	15,1
Possessor picks up food and carries it off	4	7,5
Approacher attacks possessor	1	1,9
Possessor attacks approacher	1	1,9
Total	53	100,0

The hair raised - body low posture

Here again the hairs along the back and neck are normally raised, but the body is held low and the ears are flattened backwards. The tail is usually tucked in, but it may sometimes be raised over the back, with the anal pouch extruded. The posture is accompanied by growling and in extreme cases by yelling.

This posture is exhibited by the loser during neck-biting (Fig. 45), and in other situations such as when a brown hyaena is being mobbed by spotted hyaenas, or when a brown hyaena in a trap is being approached by a person on foot. In this last mentioned case defaecation also occurs.

Basic behaviour patterns

Neck-biting

The most extreme form of aggression observed between brown hyaenas is fighting involving biting at the neck. This has been referred to as neck-biting by Owens and Owens (1978).

During the present study I observed 16 neck-biting interactions, lasting from a few seconds to several minutes. In all of them there was a clear difference between the winner and the loser, with the winner maintaining an erect posture with its ears cocked, and the loser tending to crouch with its tail tucked in and its ears flattened backwards (Fig. 45). The winner grabs the loser on the side of the neck just below the ear and shakes it or pulls it around, while the loser yells and growls. If the loser is unable to shake itself free, it is eventually pulled down, or voluntarily drops onto its stomach, with the winner standing

over it. This occurred in seven (44 per cent) of the observations. Keeping in these positions the two hyaenas would pitch their heads from side to side, parrying and thrusting at each other with open mouths, but without making contact, the loser growling and yelling continuously. After a few minutes the loser would stand up and move away slowly, the winner watching it go and in at least four cases pawing the ground with alternate forefeet. In five (31 per cent) of the neck-biting interactions the winner then chased the loser away.

Muzzle-wrestling

The behaviour pattern referred to as muzzle-wrestling by Owens and Owens (1978) has similarities to the neck-biting described above.

A muzzle-wrestling bout is often initiated by a hyaena raising a front paw at another and "pawing" at it. At other times one animal will suddenly run up to another and "attack" it by attempting to bite it around the head or neck. A third way in which muzzle-wrestling might commence is when two hyaenas are indulging in mutual grooming which then develops into mutual biting. The duration of the muzzle-wrestling bouts is highly variable and they last from a few minutes to over an hour.

The participants (usually two, although sometimes more, brown hyaenas) stand face to face and attempt to bite each other on the jowls or the side of the neck (Fig. 46), particularly at a white spot at the base of the ear. Sometimes they drop onto their carpals when clashing. They continually and rapidly pitch their heads from side to side as they parry and thrust at each other. If one manages to grab the other, it shakes it for a few seconds before releasing the grip, or it may sometimes walk with the victim, pulling it along for a short distance.

Alternatively, it pulls its victim downwards, at which the wrestle may continue with one standing over the other, or with both lying face to face kicking and biting at each other. During the activity the contestants often soft growl and make a panting noise.

In between clashes the animals may chase each other. The area over which these chases occur varies with the size of the hyaenas taking part. When small cubs are involved, the area covers just the immediate vicinity of the den, whereas with subadults and adults chases may be over 1 km in extent. The chases are slow and the chased animal eventually stops, often at a tree or bush, and the wrestling continues. During these chases the chaser sometimes bites at the other's back legs. At other times the participants may lie down close to each other and groom themselves between clashes, chew on some bones or indulge in other unconnected activities.

When two brown hyaenas of different ages, e.g. an adult and subadult, muzzle-wrestle, the larger animal is usually, although not always, the one that manages to grab and drag the other one around. Younger animals, however, are more inclined to initiate muzzle-wrestling and readily come back for more.

Muzzle-wrestling may take place anywhere in the territory. The den is a particularly favoured area, as is a large carcass around which several hyaenas have collected. I once saw two brown hyaenas muzzle-wrestle in a rain pool.

Muzzle-wrestling has certain elements in common with neck-biting. In both, the contestants try to bite each other on the side of the face or neck and to pull each other downwards, and the clashes are sometimes intermingled with chasing. There are, however, some important differences which in most cases clearly differentiate these two activities. In neck-biting there are clear differences between the winner and the loser,

both in the posture that they adopt and in the vocalisations that they emit. These are not nearly so marked in muzzle-wrestling which is never accompanied by yelling. Also, neck-biting bouts terminate with the loser moving off quickly, sometimes being chased away by the winner, whereas after muzzle-wrestling the contestants remain together or drift away slowly. Neck-biting is a far more aggressive behaviour pattern than muzzle-wrestling is, although, as will be discussed in Chapter 6, muzzle-wrestling may grade into neck-biting.

Food acquisition

Food acquisition (Owens and Owens 1978) occurs on those few occasions that a brown hyaena attempts to join another which is feeding on a small carcass; it was observed seven times. The approacher moves in rapidly with its body held low, hair slightly raised and ears flattened out sideways, uttering a harsh whine. There is an element of aggression shown by the holder of the posture and it may snap at the possessor of the food.

Greeting

When brown hyaenas from the same group greet they sniff each other around the head and face (Fig. 47), along the neck and body and/or at the anus (Fig. 48). The most involved type of greeting ceremony is characterised by anal sniffing which is normally preceded by one of the animals presenting its hind region to the other.

Before presenting the presenter cuts in front of the presentee with its head held low, its ears flattened out sideways, its lips drawn back

into a "grin" and often uttering the harsh whine. The presenter then stops in front of the presentee, drops onto its carpals so that its hind region is elevated and its tail curled over its back, and extrudes its anal pouch. The presentee sniffs at the anal pouch for a few seconds (Fig. 48 b), before the presenter stands up. The presenter may then move forward so that the two animals are standing head to tail, at which the presentee will lift its tail and be briefly sniffed at by the presenter.

In some greeting ceremonies there was a clear difference in the behaviour of the two hyaenas, with one animal presenting to the other. In other cases, however, both participants showed an inclination to present and in still others neither participant presented (Table 40).

Discussion

Of the six basic postures and behaviour patterns outlined above, only greeting has no elements of aggression. Certain attitudes, such as standing erect with the ears cocked, clearly display a high degree of aggression and a tendency to attack, whereas others such as keeping low with the tail tucked in and the ears flattened backwards, display a tendency to flee.

Pilo-erection, the most conspicuous visual display of the brown hyaena, occurs in a variety of circumstances and at different intensities. Rieger (1978) illustrated differences in pilo-erection in captive striped hyaenas Hyaena hyaena depending on the "mood" of the animal, but I am unable to show this with brown hyaenas. Pilo-erection, in conjunction with various other postures does, however, give these signals a composite nature and thus a wider meaning.

The posture adopted by an animal prior to presenting during the

greeting ceremony and the accompanying vocalisation, are almost identical to those adopted by cubs when wanting to suckle. Compare, for example, the position of the ears of the younger animals in Figs. 41 and 48 a. Such infantile-derived postures may be selective in that they cause a parental response rather than one which would be directed at a rival (Ewer 1973). It is likely, therefore, that this greeting ceremony is derived from the begging behaviour of cubs. This, coupled with the fact that the presenter exposes a vulnerable area of its body to the teeth of a conspecific, suggests that one function of the greeting ceremony might be appeasement. This has also been postulated by Kruuk (1972) to be a function of the greeting ceremony in spotted hyaenas.

TACTILE COMMUNICATION

Fourty two incidents of social grooming between pairs of brown hyaenas were observed; in 39 cases (93 per cent) one hyaena groomed the other and in 3 cases (7 per cent) the hyaenas mutually groomed each other. The grooming was directed at the neck in 30 cases (71 per cent), the back in 11 cases (26 per cent) and at the side of the body once (2 per cent). In 27 (64 per cent) of the observations the animal being groomed lay with its neck presented to the groomer and its eyes closed. On three (11 per cent) of these occasions the groomee soft whined. In the remaining 15 (36 per cent) observations of social grooming the animals sat or stood next to each other. Thirty (71 per cent) of the grooming bouts lasted less than 1 min, seven (17 per cent) lasted from 1 - 5 min and five (12 per cent) lasted more than 5 min.

This form of communication, although relatively unimportant for brown hyaenas, may serve to reinforce the social bonds within the group

and may also have a sanitary function, as most grooming is directed at areas that the groomer cannot reach itself. Social grooming was occasionally observed by Rieger (1978) in captive striped hyaenas, and is also rather a rare occurrence in spotted hyaenas (Kruuk 1972 and personal observations).

Excluded from the above discussion are those numerous cases when a mother was observed to groom cubs under approximately six months of age. Such grooming entails vigorous licking (sometimes the licked cub will fall over) and is orientated at the anus and underparts. The function of this behaviour is most likely purely a sanitary one.

VOCALISATIONS

Definition of terms

The terminology used in describing the physical properties of the brown hyaena sounds analysed here, follows that of Davis (1964), Bondesen and Davis (1966) and Struhsaker (1975):-

PITCH: The subjective interpretation of frequency, but also dependent upon the intensity of the sound.

STACCATO: An abrupt, sharply detached sound showing rhythm.

TONAL SOUND: Sound having energy clearly separated into relatively narrow frequency bands when analysed with the wide band filter.

FUNDAMENTAL FREQUENCY: The lowest frequency in tonal sound.

OVERTONE: A component of tonal sound having a frequency higher than the fundamental.

NONTONAL SOUND: Sound that has energy that is continuously spread over a relatively wide frequency range at the same instant.

UPPER FREQUENCY: The highest frequency of a particular unit.

NOISE: Sound without definite organisation of frequencies.

UNIT: The basic element of a sound, distinguished as a continuous tracking on the spectrogram.

BOUT: A cluster of one or more units separated from other similar clusters by a time interval approximately twice or more than that between units within a bout.

DURATION: Length of a unit in seconds.

The vocal repertoire

As pointed out in Chapter 1, the analyses of the vocalisations in the present study are rudimentary and of a general nature. Four categories of vocalisations were identified for the brown hyaena; the whine, the yell, the growl and the hoot. In two of the categories, the whine and the growl, it was possible to subdivide the vocalisations further.

Whine

Harsh whine: The harsh whine is a high pitched, loud sound, often with a staccato element (the younger the animal the higher the pitch). With cubs it may last for several minutes with short breaks, but usually it only lasts a few seconds.

Some of the units are tonal, others are non-tonal, but all are characterised by a considerable amount of noise. Most of the energy lies between 0,4 and 3 kHz with the upper frequency sometimes rising to above

8 kHz. The duration of a unit varies between 0,06 and 0,75 s. A bout lasts several seconds. Figure 49 is a sonogram from the harsh whine of an adult female.

As mentioned earlier, the harsh whine is made by cubs whilst following their mother prior to being suckled (Fig. 41). It is also uttered by cubs and subadults prior to greeting, when approaching animals of an older age-class than themselves, and also sometimes by adults when approaching other adults.

Brown hyaenas sometimes give short duration, harsh whine-like calls when squabbling over food. This is uttered by a younger animal when trying to get food from an older one, but also by an adult during the food acquisition behaviour pattern.

Soft whine: The soft whine sounds similar to the harsh whine and is on the same continuum, but it is of a lower pitch. It has a tonal sound component with the fundamental frequency around 0,6 kHz and an overtone around 1,0 kHz. The duration of the tonal unit is 0,9 s and a bout lasts several seconds. Superimposed on the tonal unit are non-tonal units. These are up to 1,6 kHz and 0,06 s duration and are reminiscent of harsh whine units (Fig. 50).

This vocalisation was heard to be made four times by cubs; three times when a large cub was lying and being groomed by a subadult or adult and once when a large cub was elaborately sniffing an adult along the neck and back as the adult was lying.

A vocalisation lying between the harsh whine and the soft whine was twice heard to be made by a subadult female which was being aggressively dealt with by an older female.

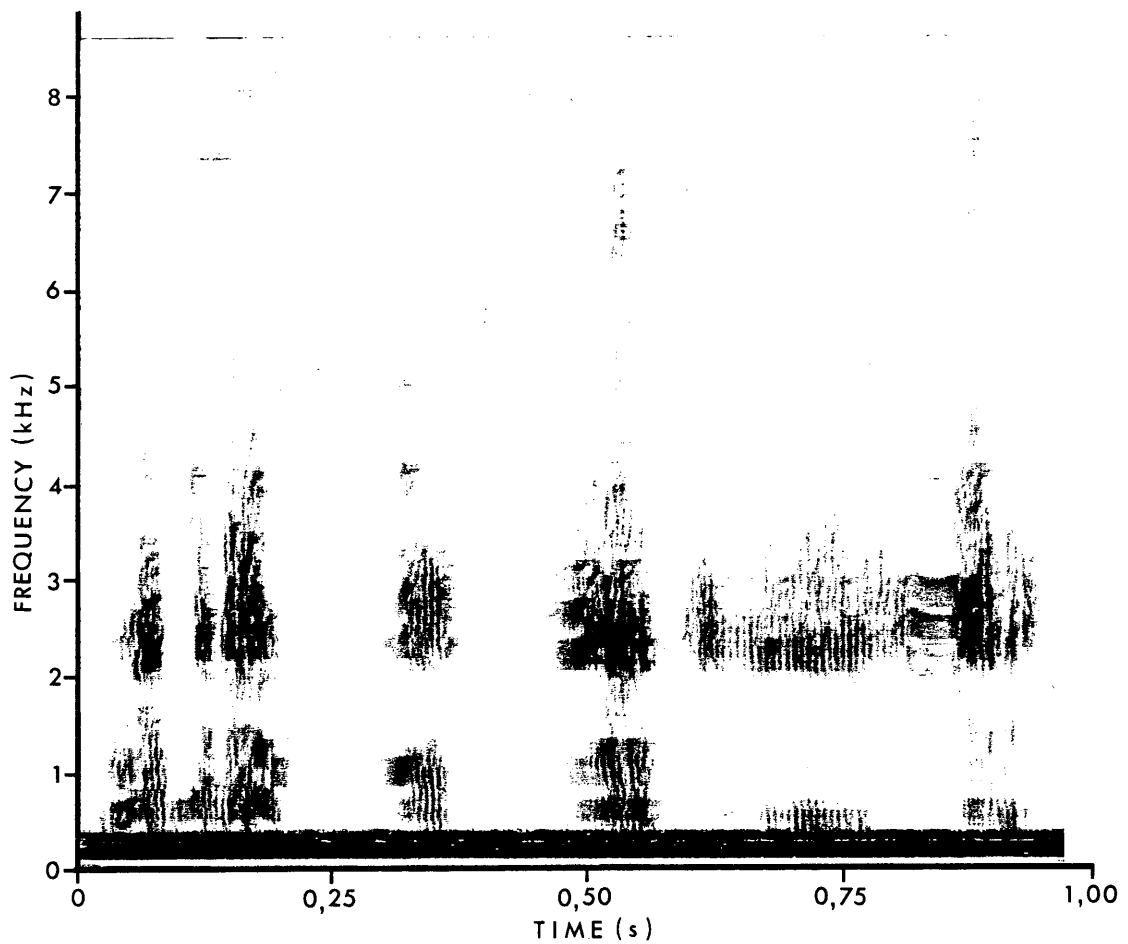


Figure 49: Sonogram of the harsh whine of an adult female brown hyaena in the southern Kalahari; March 1976. The recording is marred by background noise between 0,08 - 0,4 kHz.

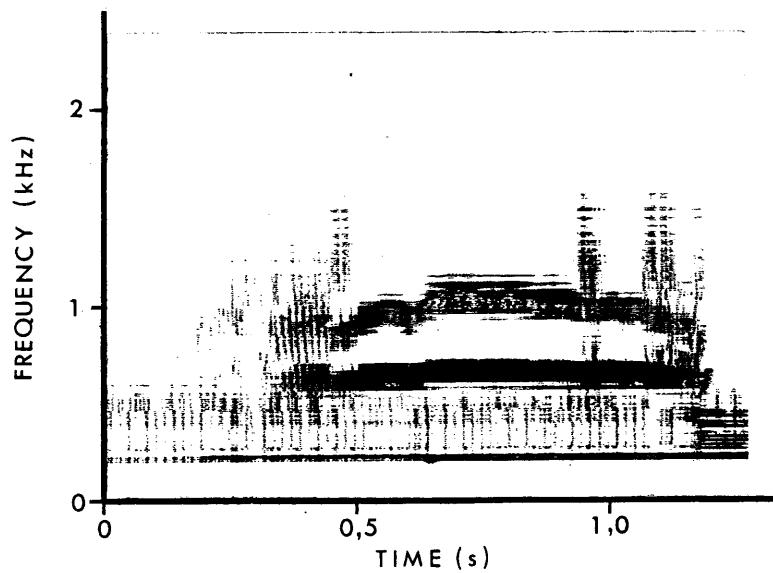


Figure 50: Sonogram of a soft whine of a large brown hyaena cub in the southern Kalahari; May 1978.

Yell

The yell is the loudest sound made by brown hyaenas. It is varying in pitch, starting at a low pitch then working into a crescendo, and can be heard by a human from over 1 km away.

The units are tonal with considerable variation in the energy distribution, with fundamental frequencies varying from around 0,6 - 1,4 kHz. Most of the energy lies under 2,2 kHz. The overtones typically rise and fall at frequencies up to 4 kHz. The number of overtones in each unit vary from 2 - 7. The duration of a unit varies from 0,1 - 0,7 s (Fig. 51).

The yell is most often heard during neck-biting. It is made by the losing animal and is accompanied by the loud growl. It was also made three times (11 per cent) by a brown hyaena when being attacked by a larger carnivore. The loud growl and the yell often grade into each other and it is sometimes difficult to say where one ends and the other begins.

Twice during aggressive encounters over food between large cubs, a vocalisation was uttered which sounded like a combination of the harsh whine and the yell. I was, however, unable to see any details of these interactions. Once during an aggressive encounter between an adult female and an unknown large cub, the cub growled and yelled, although here too the yell had a strong harsh whine connotation to it.

Growl

Four growls were recognised.

Loud growl: The loud growl is a non-tonal, staccato sound with the

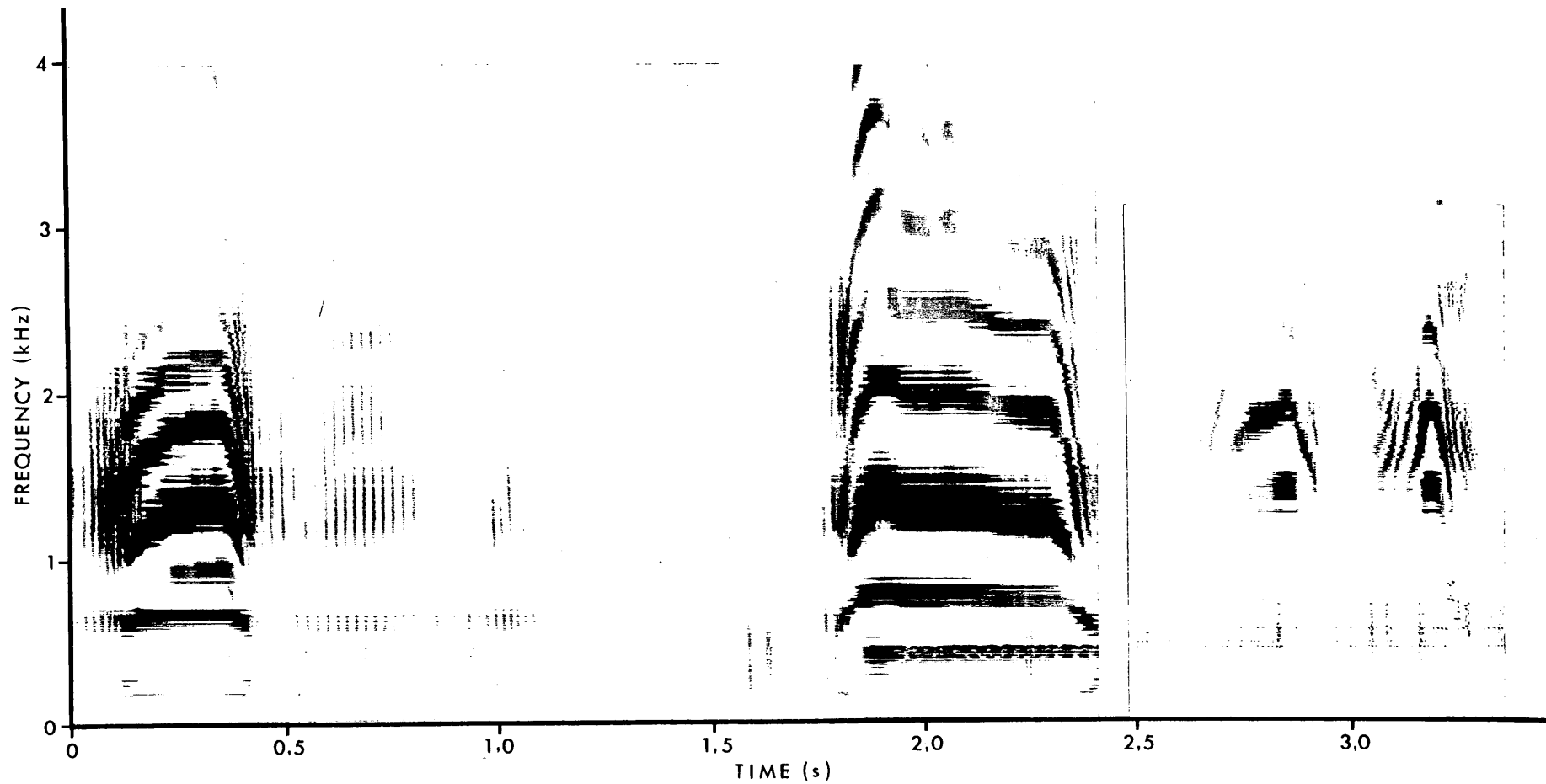


Figure 51: Sonograms of the yell of an adult female brown hyaena in the southern Kalahari; September 1977.

energy widespread between 0,2 and 3,5 kHz. In the example shown in Fig. 52 a, most of the energy is concentrated between 2,0 and 2,5 kHz.

This vocalisation is most often uttered together with the yell. At other times when the hyaena is obviously frightened, such as when being approached in a trap, or when being harassed by spotted hyaenas, it growls, but less frequently yells. Once during a mating sequence as the male attempted to mount the female, one of the hyaenas growled a little, but I was unable to discern which one did so.

Short deep growl: This vocalisation (Fig 52 b) is a low frequency, non-tonal sound with most of the energy between 0,04 and 0,6 kHz, although some reaches 2,3 kHz. The duration of a unit is 0,4 - 0,65 s.

Once when a brown hyaena came face to face with a lioness, the hyaena gave a short deep growl and ran off with its hair raised. Another time a lioness chased a brown hyaena and the hyaena growled in a similar manner when the lioness almost caught up with it. On another occasion as a brown hyaena and a cheetah clashed, a short growl was heard to be made by the hyaena. The other times (16) that this vocalisation was heard was during certain encounters with spotted hyaenas. These were when the brown hyaena stood its ground with its hair raised when being approached by spotted hyaenas. Twice the growl had elements of the hoot and once it had elements of the harsh whine in it.

The short, deep growl appears to be an interspecific vocalisation. It is mainly used in situations where the hyaena stands its ground and is seen as signifying defensive threat.

Soft growl: The soft growl, sometimes accompanied by a panting noise, is occasionally made by cubs and subadults when muzzle-wrestling. I was never sure if one or both of the participants growled. It is a

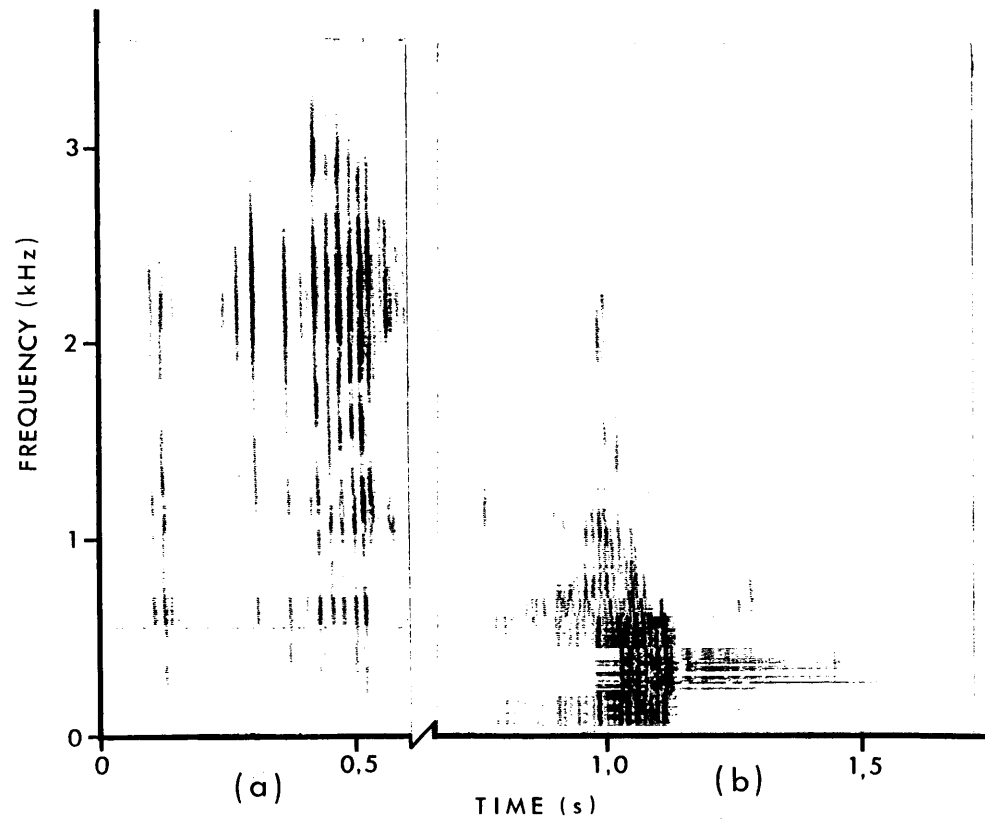


Figure 52: Sonograms of two growls of brown hyaenas in the southern Kalahari; (a) A loud growl of an adult female; September 1977. (b) A short deep growl of a subadult male; February 1978.

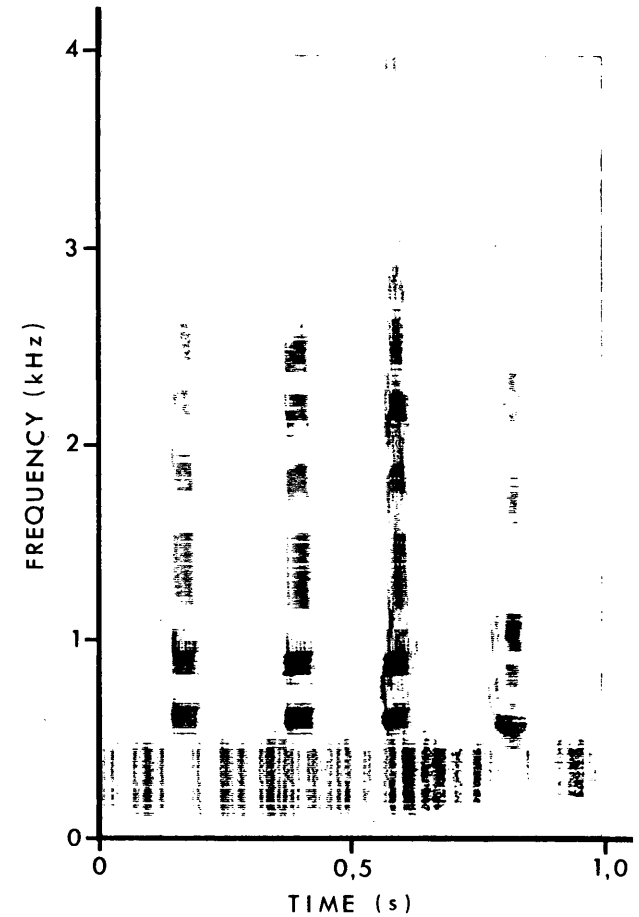


Figure 53: Sonogram of the hoot of an adult male brown hyaena in the southern Kalahari; January 1978. The recording is marred by background noise between 0,1 - 0,5 kHz.

deep-throated growl for such young animals. It was heard to be made by cubs as young as four months old, and, except for the loudness, is similar to the loud growl.

Very soft growl: No recordings were made of this vocalisation which was only heard twice. It is an extremely soft, growl-like sound only just audible to the human ear from a distance of 3 m, and lasts a few seconds. Both times it was made by an adult male with its head down in a den. When an adult comes to a den and the cubs are inside it, the adult often puts its head into the den for a few seconds before the cubs emerge. It is likely that when the adults do this they are calling to the cubs by growling very softly.

Hoot

This vocalisation is a soft sound. The units are tonal with the fundamental frequency around 0,6 kHz. Overtones are developed at 0,9, 1,4, 1,8, 2,2 and 2,5 kHz. The upper frequency reaches 4 kHz. The duration of the units is constant at 0,05 s, except that sometimes the last unit is prolonged, and the time between each unit is 0,17 s (Fig. 53). A bout typically consists of 5 units.

This vocalisation was heard 22 times and was invariably accompanied by the hair raised - stand erect posture. Eleven times (50 per cent) it was made by an animal towards another which approached it whilst feeding on a carcass. On one of these occasions, when a subadult hooted at an adult, there was a harsh whine element in the hoot. On eight (36 per cent) occasions one animal hooted when two or more hyaenas were feeding on a carcass and, in one of these cases, the hooter then attacked the other and they clashed briefly. Twice (9 per cent) an animal hooted at another

and then attacked it as it came to a carcass. The final observation was of a subadult hooting at another during muzzle-wrestling.

As the hoot is accompanied by the hair raised - stand erect posture and may lead to attack, this vocalisation has an aggressive function communicating a tendency to attack.

Discussion

Although the vocal repertoire of the brown hyaena is small, its graded nature leads to a greater scope of vocal communication than a system of discrete vocalisations would. All the vocalisations are, however, short distance vocalisations.

Graded vocal systems such as that of the brown hyaena, are difficult to categorise because the categories are linked by intermediates, both within and between categories. Even two vocalisations such as the loud growl and the yell, which, at their extremes, are obviously different both aurally and sonographically, may sometimes grade into each other. It is, therefore, not surprising that my analysis of the brown hyaena's vocal repertoire does not agree with that of Owens and Owens (1978). They list five vocalisations, although they do not provide any sonograms. These five vocalisations appear to fit into three of my categories: What they call the squeal or whine and squeak are apparently analagous to what I call the whine, what they call the growl or grunt is analagous to what I call the growl, and their yell and scream categories are analagous to what I call the yell. They did not record a vocalisation equivalent to the hoot.

SCENT MARKING

Pasting

The deposition onto grass stalks of two distinct, strong-smelling substances (Fig. 54) produced in the anal scent pouch (Fig. 55) is the most common form of scent marking in the brown hyaena and is known as pasting. The pasting behaviour of the brown hyaena has been described in detail by Mills et al. (1980). The following account is taken largely from this paper.

Pasting behaviour and the structure of the anal scent pouch

During pasting a brown hyaena bends a grass stalk forward by walking over it, often lifting a foreleg and turning slightly as it does so. The hyaena continues to move forward until the base of the grass comes to lie between its hindlegs and the stalk runs forward under its belly. Then the hyaena, with its tail curved up over its back and its hindlegs slightly bent, extrudes its anal pouch (Fig. 55).

The anal pouch, which lies between the rectum and the base of the tail, consists of two distinct regions. The large central area, which is normally covered by an accumulation of white secretion, has a distinct, deep groove running vertically. Lying, one to each side of the central area, and separated from it by non-secretory epithelium, are two circular areas which produce the black secretion (Figs. 55 and 57).

Having extruded its pouch, the brown hyaena now feels for the grass stalk, sometimes for several seconds, and eventually succeeds in

positioning it in the groove running down the white central area. The hyaena then moves forward, pulling the anal pouch along the grass stalk and at the same time retracting the pouch. The first effect of this action is to smear a thick, creamy blob of white paste on to the grass stem. Then, as the pouch continues to retract, the non-secretory portions of the pouch and the black secretory areas, collapse in turn on to the stem. In this way a thin smear of the black secretion is deposited some distance above the blob of white paste. The dimensions of these paste marks are given in Table 25.

Brown hyaenas usually paste on to clean grass stems but under certain circumstances (see below) they will paste on top of existing pastes (Fig. 55). The freshly deposited secretions have a strong odour, the white being different from the black. The smell of the white paste can still be detected by the human nose 30 days after deposition. By this stage it has turned black. The smell of the black paste is not as long-lasting as that of the white paste.

Histologically, the central area of the pouch which produces the white paste is composed of numerous, enlarged sebaceous glands (Fig. 57). This tissue, and the white paste produced by it, are rich in lipid (Table 26).

In contrast the circular areas responsible for producing the black secretion consist almost entirely of apocrine, sudoriferous tissue (Fig. 57). The black colour of the paste is due to accumulations of lipofuscin, a common metabolite of apocrine tissue (Table 26). In contrast to the white paste the black material contains little lipid.

The dispersion pattern of pastings within the territory

The dispersion patterns of pasting sites in the Kwang group's

Table 25: The dimensions of 50 brown hyaena pastings from the southern Kalahari.

DIMENSION	MEAN (mm)	STANDARD ERROR
Length of black secretion	11,9	0,5
Distance between black and white secretions	12,4	0,5
Length of white secretion	12,7	0,1
Height of grass above the ground, to bottom of white secretion	687,2	21,9

Note: The mean shoulder height of 20 adult brown hyaenas is 787,0 mm \pm s.e. 81,0.

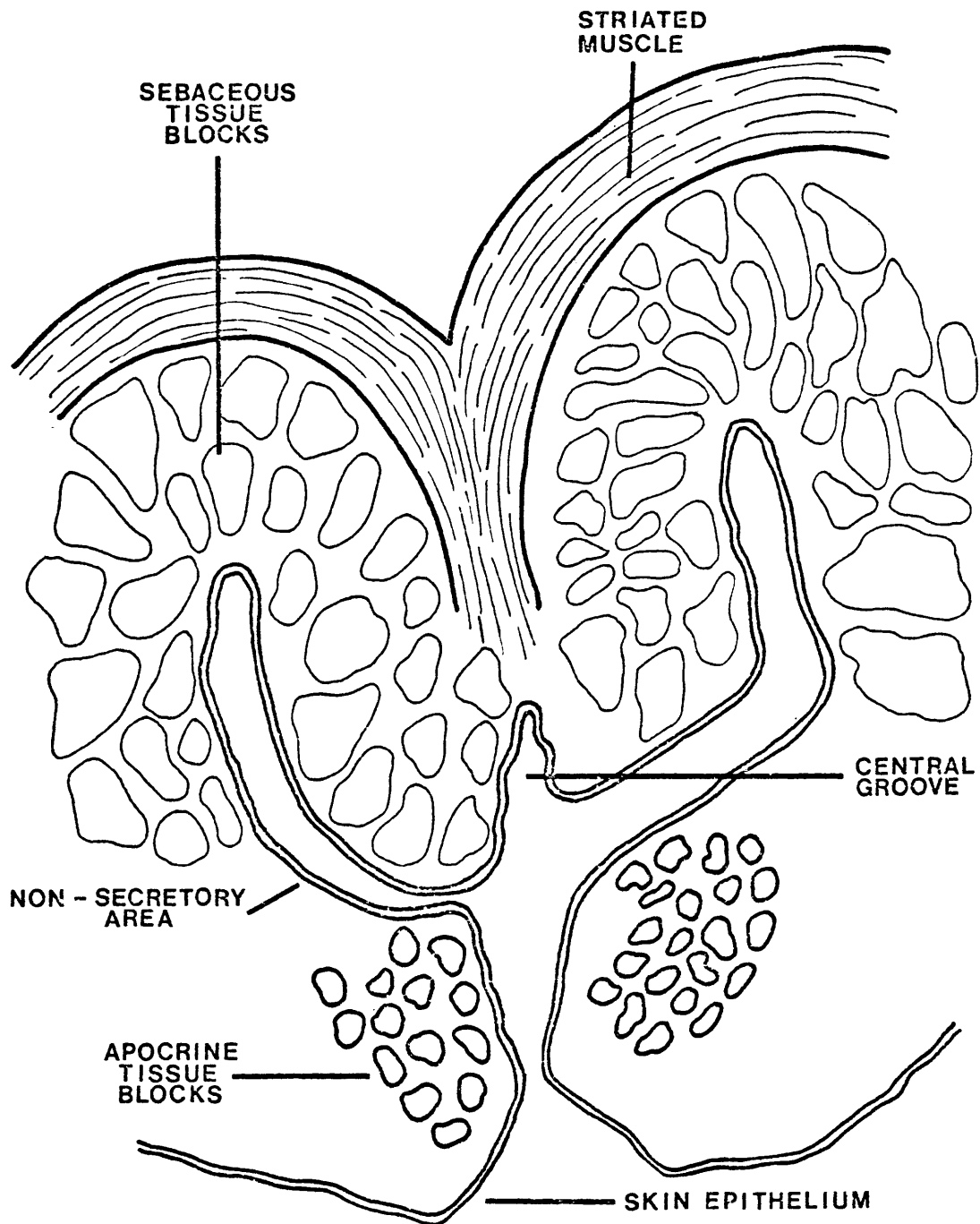


Figure 57: Drawing of a horizontal section through the centre of the retracted anal scent pouch of a brown hyaena. The central sebaceous area with its central groove, and the two lateral apocrine areas can be clearly seen. The complex musculature terminating near the central groove consists of voluntary muscle blocks and functions to retract the pouch.

Table 26: The histochemical reaction of tissues from the brown hyaena anal pouch from the southern Kalahari; 1978. (From Mills, Gorman and Mills 1980).

SUBSTANCE	REACTION (Pearse 1968)	SECTION	SEBACEOUS GLAND	APOCRINE GLAND
Free lipids	Oil Red	Frozen	+++	+
Polysaccharides	Periodic acid/Schiff	Paraffin	+	+++
Free aldehydes	Schiff	Paraffin	-	±
Acid muco- polysaccharides	Toluidine Blue	Paraffin	-	++
	Alcian Blue	Paraffin	-	++
	Methylation/Alcian Blue	Paraffin	-	-
Lipo-fuscin	Nile Blue & Schmorls Methods	Paraffin	-	+++
Iron	Perle's Method	Paraffin	-	+++ (pigment)

- No reaction.

+ to +++ Increasingly strong reaction.

territory were documented in 1976 and in 1977 - 1978 when following certain members of this group (Table 27). These dispersion patterns are illustrated in Figs. 58 and 59, which show the positions of all the pastings (and latrines) observed to be deposited by adult hyaenas in the Kwang group in 1976 and 1977 - 1978 respectively. The figures show that the pastings are scattered throughout the territory, but not uniformly so. Assuming that a brown hyaena moves on average 32 km per night (Mills 1978 b) and pastes on average 2,6 times per km (Table 27), the five adult brown hyaenas in the Kwang group deposited 151 840 pastings in their territory during the 12 months of observations in 1977 - 1978.

The pasting data were further analysed by means of three-dimensional SYMVU maps (Figs. 60 and 61). The third vertical dimension in these maps reflects the density of pasting points. The SYMVU maps show clearly that the highest densities of pastings are to be found near the centre of the territory with a progressive decrease in density towards the borders. To test the difference in density between border and interior statistically, those squares on the periphery of the territory were designated border squares and the others internal squares as explained in Chapter 1 (Figs. 8, 58 and 59). The mean density of pastings was significantly lower in border squares than in interior ones both in 1976 and 1977 - 1978 (Table 28).

The difference in the density of pastings between border and internal squares is due to the fact that the number of pastings deposited in a square is related to the distance travelled in that square by the hyaenas (Fig. 62). The greater the distance the more pastings are deposited. Since brown hyaenas use the interior of their territory more than the periphery (Table 29), it follows that most pastings will be deposited in the interior squares.

Table 27: Distances for which the members of the Kwang brown hyaena group in the southern Kalahari were followed from January - July 1976 and from July 1977 - August 1978, during which the number of pastings were recorded.

PERIOD	INDIVIDUAL	SEX	DISTANCE (km) FOLLOWED	NUMBER OF PASTINGS DEPOSITED	PASTINGS PER km
1976	0/2	Female	767	1 760	2,3
1976	3/0	Male	353	1 218	3,5
1977 - 1978	0/2	Female	154	296	1,9
1977 - 1978	3/0	Male	28	56	2,0
1977 - 1978	12/0	Female	188	578	3,1
1977 - 1978	3/3	Male	341	908	2,7
1977 - 1978	0/12	Male	116	328	2,8
Total			1 947	5 144	-
Mean			-	-	2,6

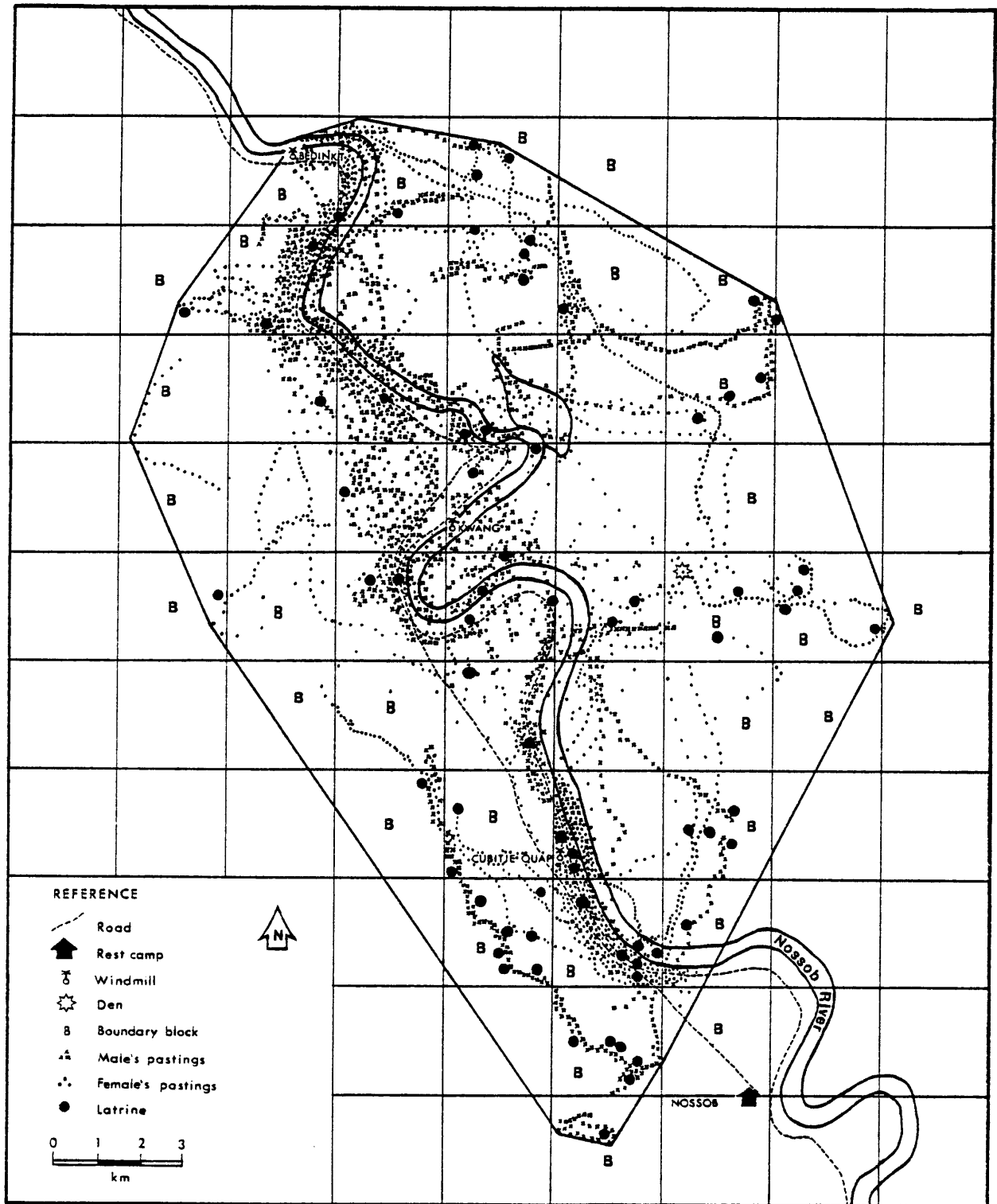


Figure 58: A map of the locations at which two members of the Kwang brown hyaena group in the southern Kalahari were seen to paste and visit latrines; January - July 1976.

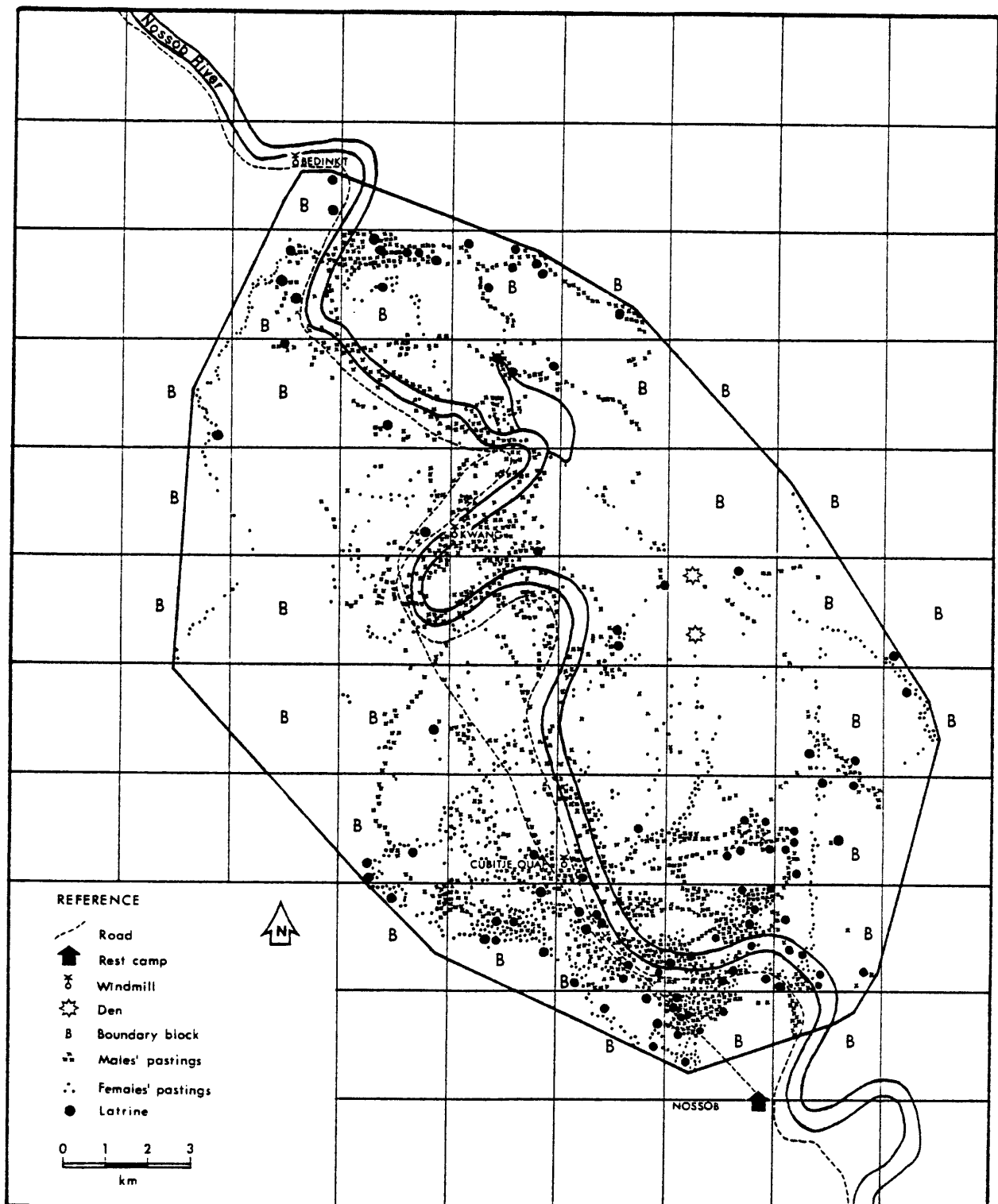


Figure 59: A map of the locations at which five members of the Kwang brown hyaena group in the southern Kalahari were seen to paste and visit latrines; July 1977 - August 1978.

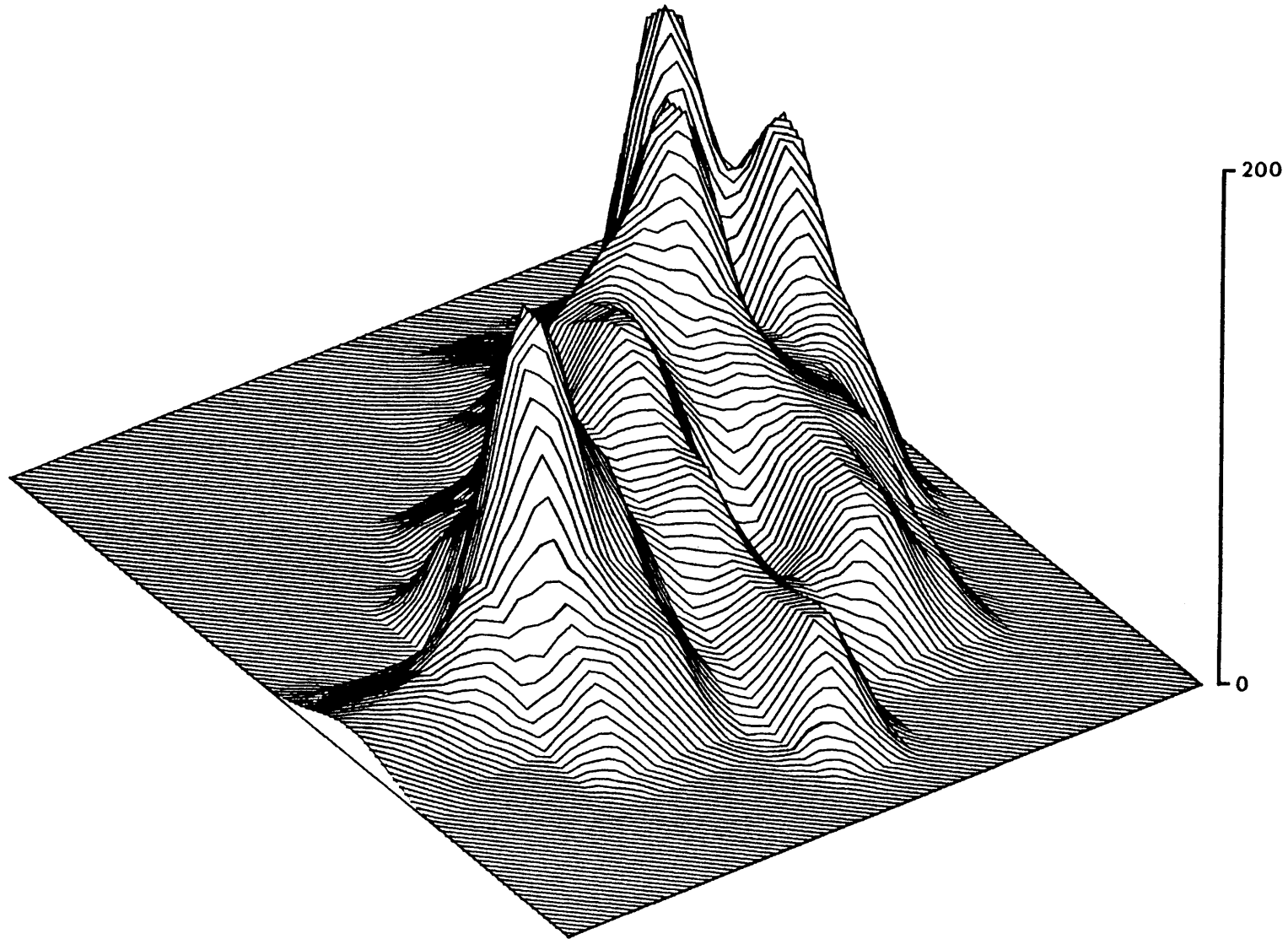


Figure 60: A three-dimensional map, generated by SYMVU, of the density of pastings in the territory of the Kwang group of brown hyaenas in the southern Kalahari; January - July 1976. The scale represents the number of pastings per 2,5 x 2,5 km square. The area covered by the map and the orientation are as in Fig. 9.

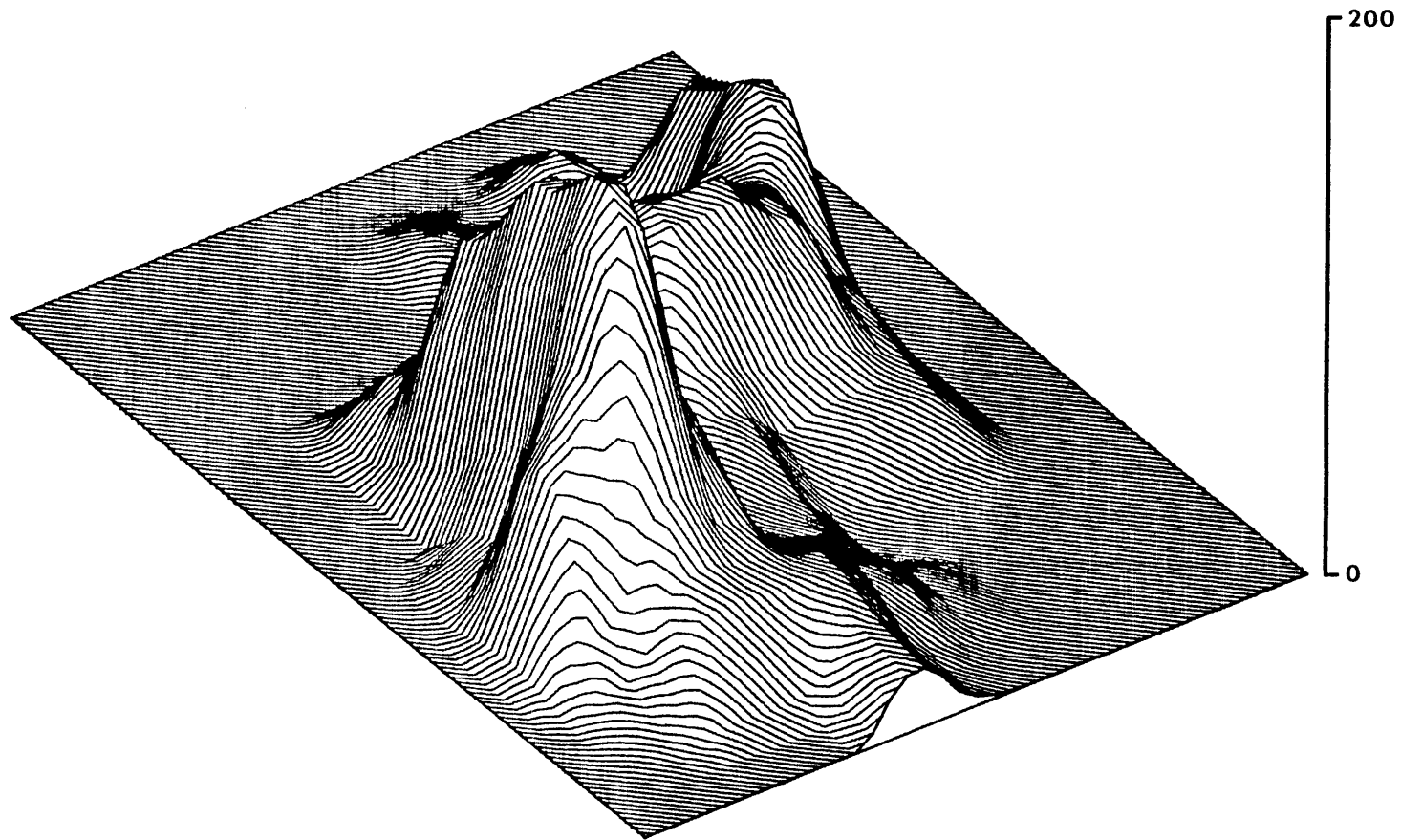


Figure 61: A three-dimensional map, generated by SYMVU, of the density of pastings in the territory of the Kwang group of brown hyaenas in the southern Kalahari; July 1977 - August 1978. The scale represents the number of pastings per 2,5 x 2,5 km square. The area covered by the map and the orientation are as in Fig. 9.

Table 28: The mean number of pastings deposited by brown hyaenas of the Kwang group in the southern Kalahari in internal and border squares of their territories; January - July 1976, July 1977 - August 1978.

YEAR	MEAN NUMBER OF PASTES PER SQUARE		t	p
	Border squares	Internal squares		
1976	57,7	90,0	4,18	$p < 0,001$
1977 - 1978	42,0	67,0	1,91	$p < 0,05$

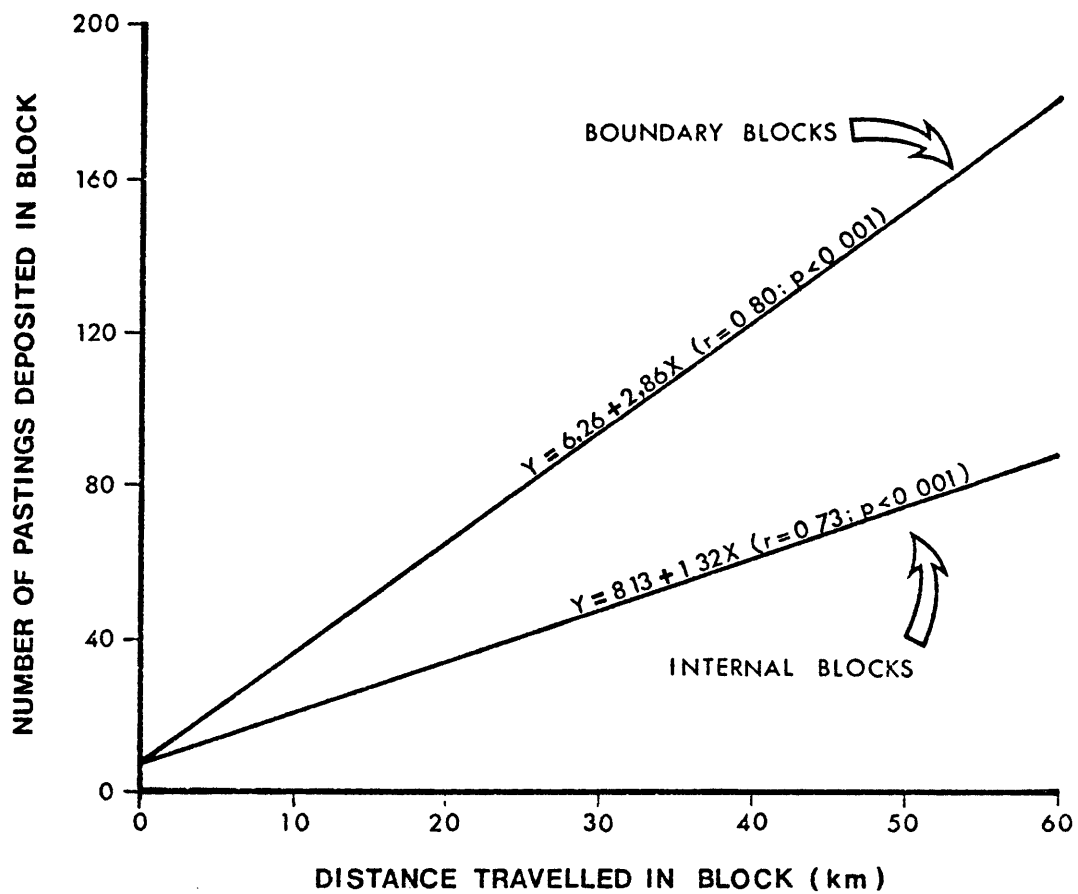


Figure 62: The relationship between the distance moved by brown hyaenas in the southern Kalahari in a particular 2,5 x 2,5 km square and the number of pastings deposited in it; January - July 1976, July 1977 - August 1978. (Data taken from Mills, Gorman and Mills 1980).

Table 29: The observed total distances brown hyaenas of the Kwang group in the southern Kalahari were observed to travel in border and internal squares of their territories, and the expected distances they would have travelled had they used these different parts of their territories in proportion to their occurrence; January 1976 - August 1978.

YEAR	DISTANCE (km) TRAVELLED		χ^2	p
	Border squares	Internal squares		
1976				
Observed	374	743	193,55	<0,001
Expected	701	415		
	62,8 per cent of area	37,2 per cent of area		
1977 - 1978				
Observed	256	546	148,98	<0,001
Expected	499	303		
	62,2 per cent of area	37,8 per cent of area		

The rate of pasting

The difference in slope between the two regression lines relating the number of pastings deposited to the distances travelled in border and internal squares (Fig. 62) indicates that brown hyaenas paste at a higher frequency when they are in border squares than when in internal ones. By combining the data for all study animals it is possible to show statistically that the frequency of pasting, expressed as pastings per km travelled, was significantly higher for border squares than for internal ones in both 1976 and 1977 - 1978 (Table 30).

As mentioned in Chapter 3 three brown hyaenas were observed to make excursions into areas judged to be outside the group territory. During these excursions the rate of pasting dropped markedly to 0,4 pastings per km (Table 17).

The reaction of brown hyaenas to pastings that they encounter

Sometimes, before pasting, a brown hyaena will sniff and lick at a grass stem. At other times it will sniff and lick the stem and then not paste on it, although it may then paste close by. In all cases where it could be discerned, grass stems that were sniffed in this way already had a pasting on them. The response of a brown hyaena to a pasting investigated in this way depends upon where in the territory the pasting is encountered. Of 88 pastings sniffed at in border squares a hyaena pasted on top of the pasting or close by (within approximately 5 m) 65 times (74 per cent). Of 87 pastings encountered in internal squares, however, a hyaena reacted by pasting 26 times (30 per cent) ($\chi^2 = 34,31$; $df = 1$; $p < 0,001$).

A pasting encountered in a border square has a higher chance of

Table 30: The overall pasting frequencies of brown hyaenas of the Kwang group in the southern Kalahari in border and internal squares; January - July 1976, July 1977 - August 1978.

YEAR	MEAN PASTING FREQUENCY (PASTINGS PER km)		MANN-WHITNEY U TEST (ONE-TAILED)		
	Border squares	Internal squares	U	z	p
1976	4,54	2,46	335	-3,50	<0,0002
1977 - 1978	4,37	2,16	796	-5,57	<0,00003

Table 31: The reaction of brown hyaenas in the southern Kalahari to pastings from their own group and from foreign groups; 1978.

RESPONSE	NUMBER OF OCCASIONS		p*
	Pasting from own group	Pasting from foreign group	
Approached within 1 m but did not sniff or paste	6	0	0,018
Approached within 1 m and then sniffed and/or pasted	6	11	

* Fisher exact probability test (two-tailed).

having been left by a brown hyaena from another social group than does one found in an internal square. This may account for the difference in response of the hyaenas; they may be more likely to paste on top of foreign pastes than on to those deposited by animals from their own group. The few data available on the response of hyaenas to pastings of known origin support this possibility.

On 23 occasions, all in internal squares, brown hyaenas from the Kwang group were observed to come upon a fresh pasting whose author I knew. In nine of these cases I had taken a pasted grass from another territory and had placed it in the Kwang group's territory. On the other 14 occasions I had seen one hyaena paste and later another individual come up to the pasting. Twelve of the total of 23 cases involved pastings made by members of the Kwang group and 11 were made by animals from other groups. From these few data there are clear indications that brown hyaenas can distinguish between pastings belonging to their own group and those deposited by foreigners (Table 31). Brown hyaenas are more likely to investigate closely, and paste on top of, the pastings left by hyaenas from other groups than they are to the pastings made by members of their own group.

Chemical analysis of the pastings

GLC analyses were performed on fresh uncontaminated pastings. In all 11 white pastes, five from one male brown hyaena (3/3) and six from another (0/12), and 15 black pastes, eight from the first male and seven from the other, were examined. Typical chromatograms for the white and black pastes are shown in Figs. 63 and 64 respectively. The chemical composition of each is clearly complex and the two are distinctly different; work is continuing on identifying the major chemical

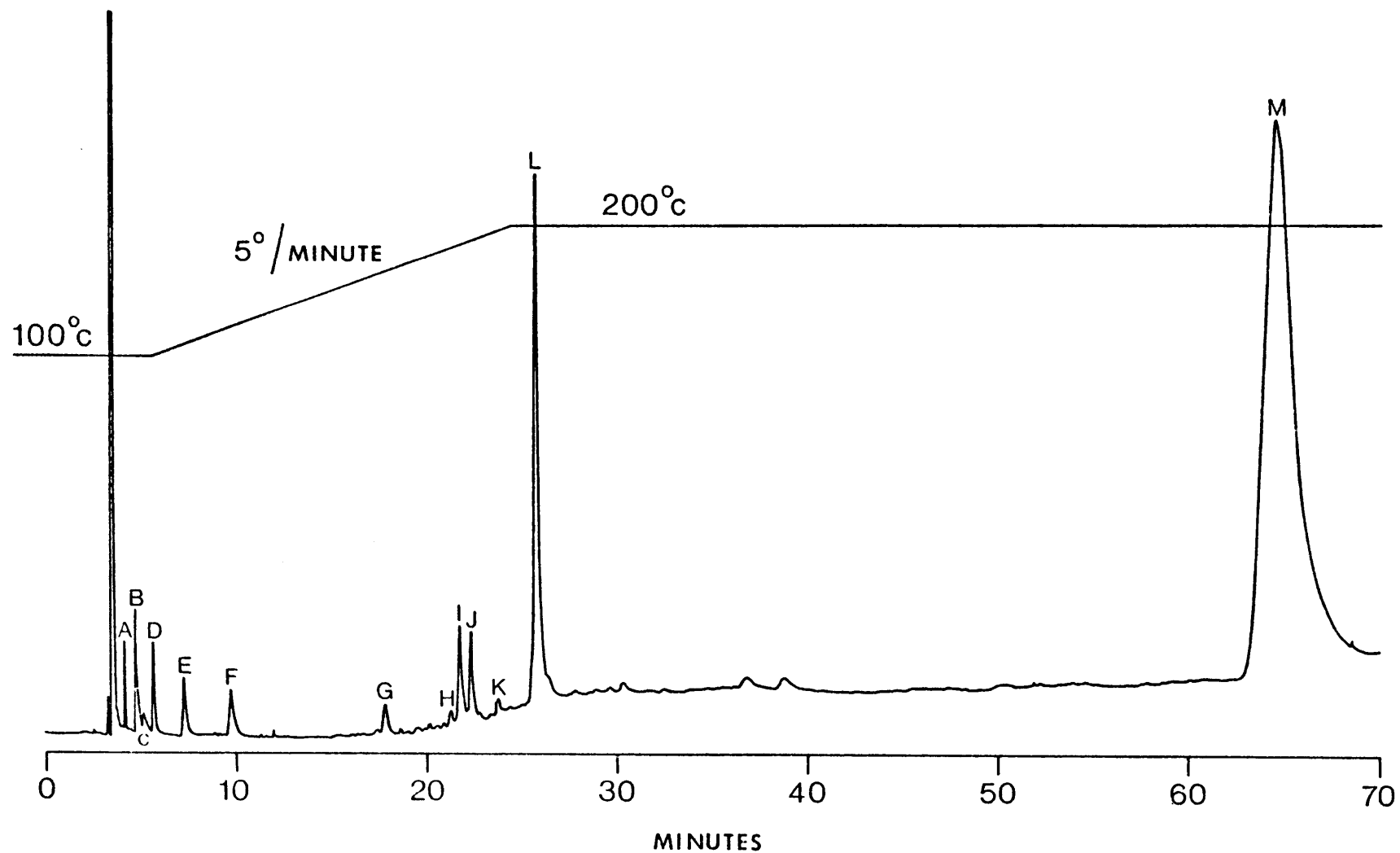


Figure 63: A typical gas-liquid chromatograph of the white paste from a male brown hyaena in the southern Kalahari. The temperature programme used in the analysis is shown on the figure. The letters indicate the peaks used in the analysis of individual differences.

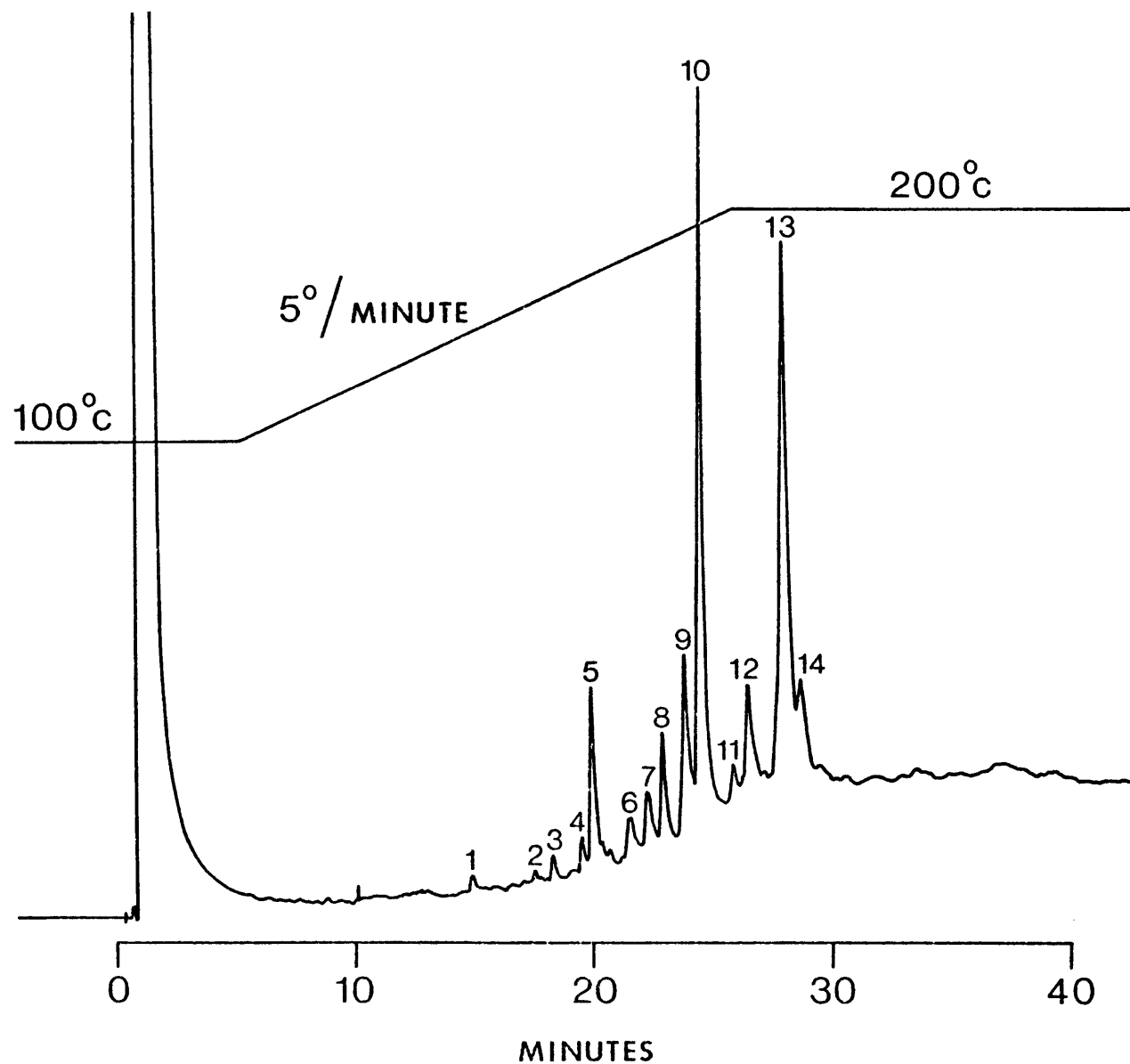


Figure 64: A typical gas-liquid chromatograph of the black paste from a male brown hyaena in the southern Kalahari. The temperature programme used in the analysis is shown on the figure. The letters indicate the peaks used in the analysis of individual differences.

constituents.

The aim here, however, is to demonstrate differences in the secretions of different individuals which could be used by brown hyaenas to identify the author of the pasting. Such differences are unlikely to be based on different animals having unique chemicals in their pastes, but are more likely to be based on differences in the relative concentrations of the constituents of a complex chemical mixture (Gorman 1976).

To detect possible differences in the relative concentrations of the compounds making up the black and white pastes, the areas under selected peaks of the relevant chromatograms have been expressed as percentages of the total area under all of those peaks. Then for each individual animal the mean percentage for each peak, together with its standard deviation have been calculated, using the data from the different pastes analysed (Figs. 65 and 66). Such an analysis reveals clear differences between the two males examined. For example, in the case of the white paste, peaks C and K are relatively major components for 0/12 but minor ones for 3/3. Again peaks A and B are relatively large in 3/3's paste but small in 0/12's (Fig. 65). Equally clear differences between the two hyaenas can be seen in the black paste (Fig. 66). Furthermore the small standard deviations in Figs. 65 and 66 suggest that the pastes deposited by an individual are similar to each other, at least over the 72 h periods during which the samples were collected.

Latrines

Description

Brown hyaenas will defaecate anywhere in their territory, frequently

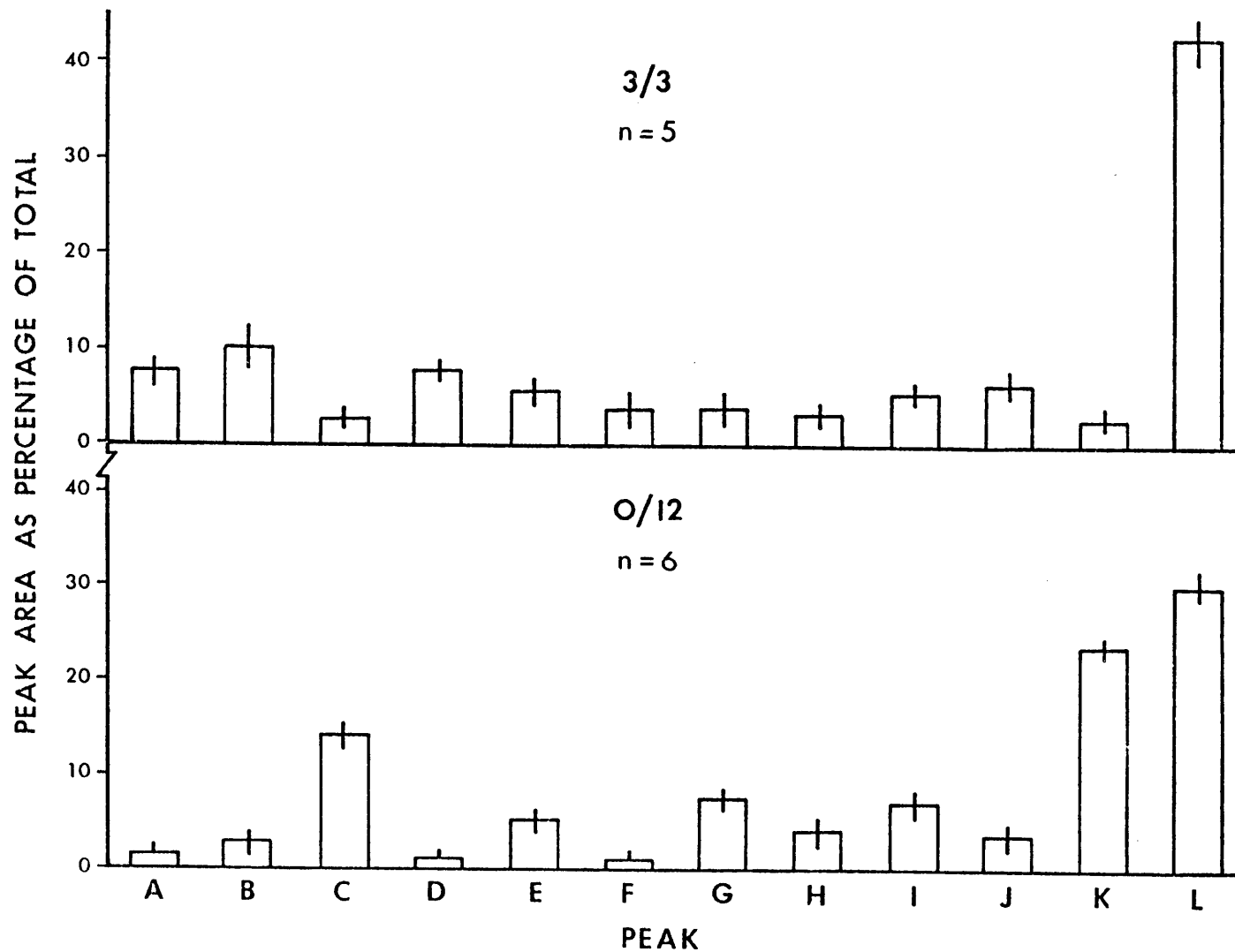


Figure 65: Individual differences in the white pastes of two male brown hyaenas (3/3 and 0/12) from the southern Kalahari. The number of samples analysed is given by n and the histograms represent the mean area of each peak measured as a per cent of the total area of all the peaks. The vertical lines represent the mean \pm one standard deviation. The pastes of each individual were collected over a 72 h period.

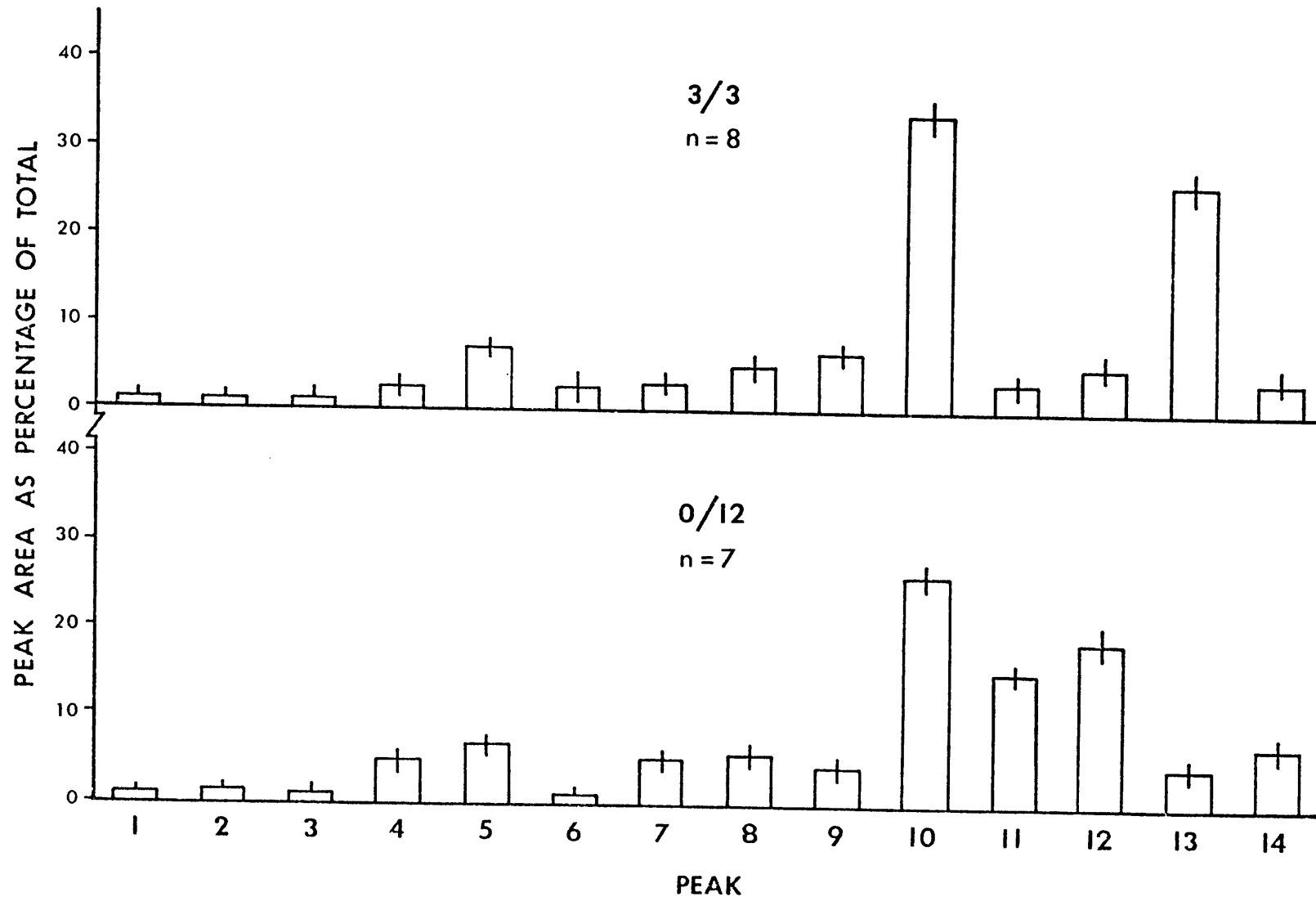


Figure 66: Individual differences in the black pastes of two male brown hyaenas (3/3 and 0/12) from the southern Kalahari. The number of samples analysed is given by n and the histograms represent the mean area of each peak measured as a per cent of the total area of all the peaks. The vertical lines represent the mean \pm one standard deviation. The pastes of each individual were collected over a 72 h period.

on getting up after a rest. At other times, however, defaecation is carried out at specific places where there are accumulations (usually 5 - 10, but on rare occasions up to 50) of faeces. These are called latrines (Fig. 56). Defaecation carried out at latrines is often accompanied by other scent marking behaviour. Typically a brown hyaena will come to a latrine and spend several minutes sniffing at the faeces (sometimes even pawing at it) and at grass stalks. Then it will defaecate, scratch the ground alternatively with its forefeet and paste before continuing on its way. Unlike with spotted hyaenas (Kruuk 1972) no smell could be detected from the areas scratched by brown hyaenas.

Although large concentrations of cubs' faeces accumulate around dens, I do not regard these as latrines as adults rarely defaecate at them and, when they do, they do not exhibit any other scent marking behaviour.

Table 32 records the locations of the latrines found during the present study. The majority were situated next to a tree or bush, 117 (66 per cent) of which were Boscia albitrunca trees (Fig. 56). At 34 randomly selected latrines at Boscia albitrunca trees the orientation of the faeces was noted using a compass. Twenty four (71 per cent) of the latrines were situated on the south side of the tree, seven (21 per cent) on the west side, three (9 per cent) on the east side and none (0 per cent) on the north side. Thus there is a significant tendency for faeces to be situated on the south side of a tree ($\chi^2 = 40,59$; $df = 3$; $p < 0,001$). Why this should be so is not readily apparent. Perhaps it is advantageous to the hyaenas to have the faeces concentrated at one fixed point rather than scattered around the tree, so that unnecessary time is not wasted in searching for the faeces.

Bearder and Randall (1978) found that the specific site of a latrine was important to spotted hyaenas. If they moved the faeces from a latrine, even a distance as short as 20 m, the hyaenas continued to defaecate

Table 32: Location of brown hyaena latrines in the southern Kalahari;
1972 - 1978.

LOCATION	NUMBER OF LATRINES	PER CENT OF LATRINES
Tree or bush	178	75,1
Side of road	36	15,2
Remains of large ungulate	12	5,1
Dried out pool in river-bed	5	2,1
No obvious land mark	6	2,5
Total	237	100,0

at the original site and not at the new one. The same holds true for brown hyaenas. I moved all of the approximately 50 scats from a latrine next to a tree, to an equally prominent tree 40 m away and covered the original area with a thick layer of sand. Two weeks later the original area had once again been used as a latrine and I could find no traces of fresh faeces or scratchings in the sand at the new site. Four months later the original latrine was still in use and there was still no sign that the experimental latrine had been used.

The dispersion pattern of latrines within the territory

The dispersion patterns of latrines in the Kwang group's territory were documented in 1976 and 1977 - 1978 in the same way as the dispersion pattern of pastings were. Figures 58 and 59 show the positions of all latrines which were observed to be used by the brown hyaenas followed during these time periods. Again it is clear that the latrines are scattered throughout the territory, but not uniformly so.

The three-dimensional SYMVU plots of the distribution of latrines, where the third vertical dimension reflects their density, are shown in Figs. 67 and 68. Here it can be seen that the highest densities of latrines are mainly around the boundaries of the territories. This is particularly clear in the 1977 - 1978 data. The mean density of latrines was higher in border squares than interior ones both in 1976 and in 1977 - 1978, although this difference was only significant in 1977 - 1978 (Table 33). This difference in mean density of latrines is not due to the fact that the number of latrines found in a square was dependent on the distance travelled by the hyaenas in that square, as I have shown in Table 29 that the hyaenas used the interior of their territory more than the periphery. Rather it would appear to be a result of actual

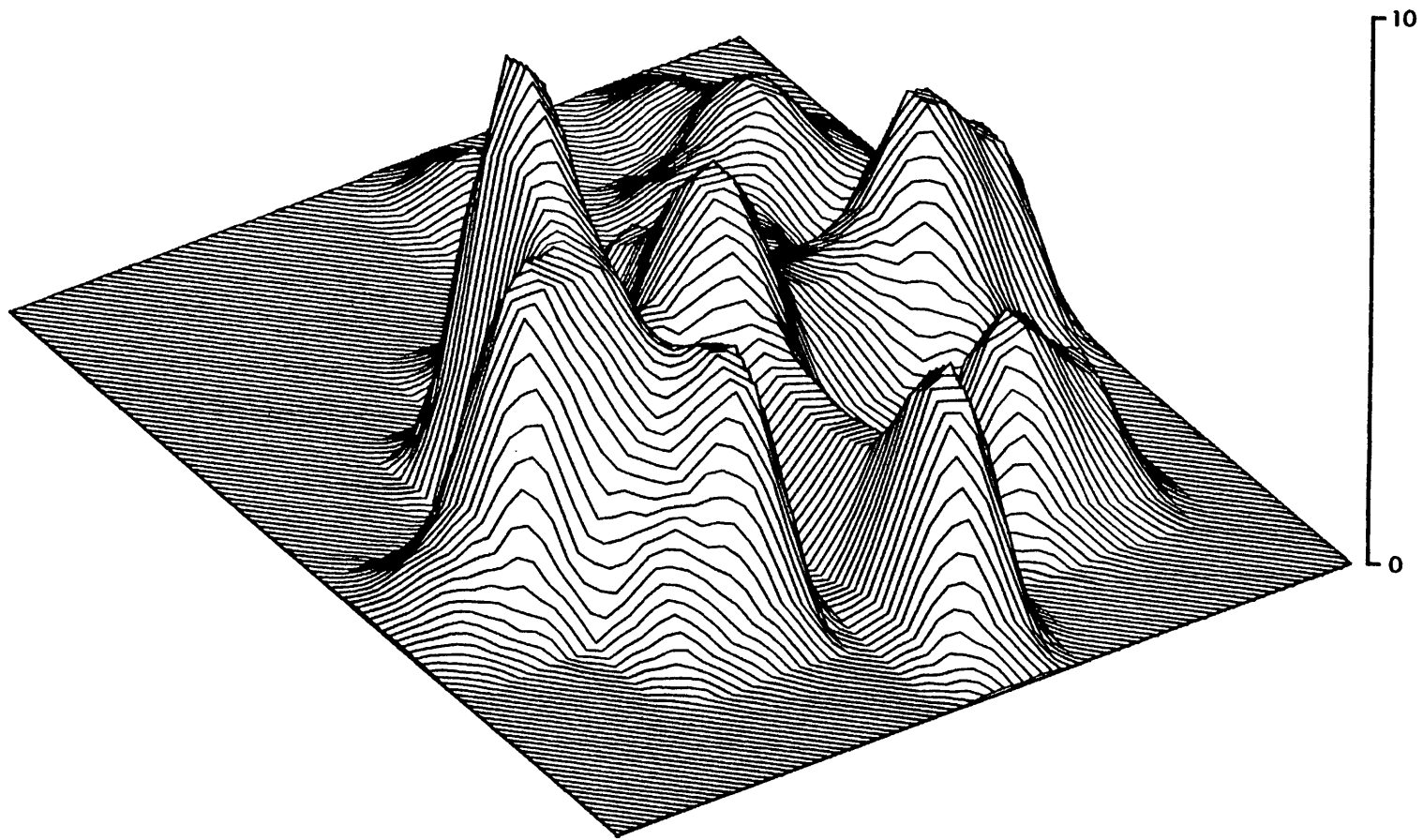


Figure 67: A three-dimensional map, generated by SYMVU, of the density of latrines in the territory of the Kwang group of brown hyaenas in the southern Kalahari; January - July 1976. The scale represents the number of latrines per 2,5 x 2,5 km square. The area covered by the map and the orientation are as in Fig. 9.

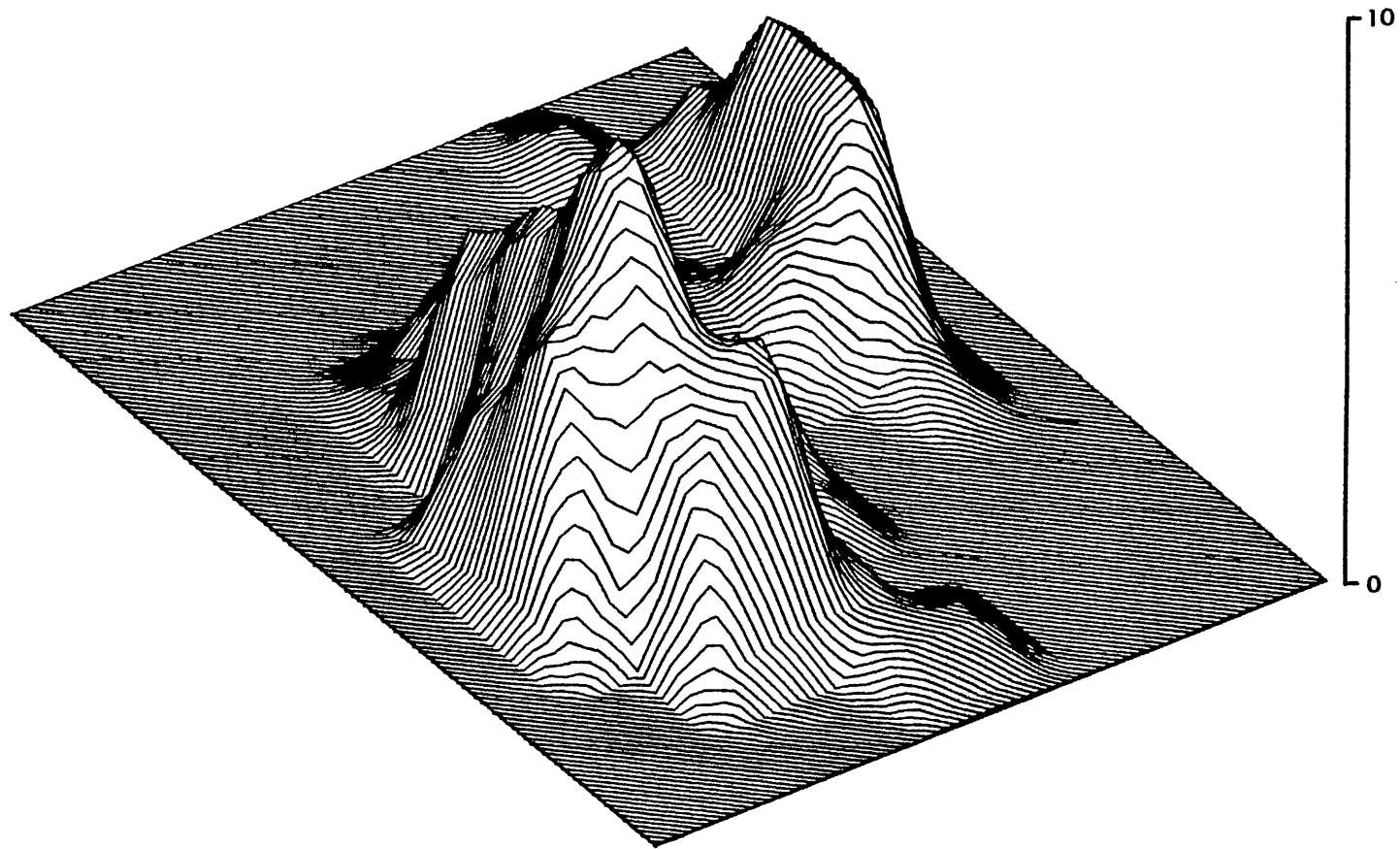


Figure 68: A three-dimensional map, generated by SYMVU, of the density of latrines in the territory of the Kwang group of brown hyaenas in the southern Kalahari; July 1977 - August 1978. The scale represents the number of latrines per 2,5 x 2,5 km square. The area covered by the map and the orientation are as in Fig. 9.

Table 33: The mean number of latrines used by brown hyaenas of the Kwang group in the southern Kalahari, in border and internal squares; January - July 1976, July 1977 - August 1978.

YEAR	MEAN NUMBER OF LATRINES PER SQUARE		t	p
	Border squares	Internal squares		
1976	1,8	1,5	0,33	> 0,05
1977 - 1978	2,8	1,1	3,53	< 0,001

Table 34: The overall frequency of latrine visits by brown hyaenas of the Kwang group in the southern Kalahari; January - July 1976, July 1977 - August 1978.

YEAR	LATRINES VISITED PER km FOLLOWED		MANN-WHITNEY U TEST (ONE-TAILED)		
	Border squares	Internal squares	U	z	p
1976	0,14	0,04	131,5	- 2,38	0,0087
1977 - 1978	0,33	0,09	503,0	3,44	< 0,0003

differences in the density of latrines in border and internal squares.

Frequency of visits to latrines

Not only are there more latrines in border squares than internal ones, but by combining the data for all hyaenas followed in 1976 and 1977 - 1978 it can be shown statistically that the frequency of latrine visits, expressed as latrines visited per km travelled, was significantly higher for border squares than for internal ones in both time periods (Table 34).

Figure 69 records the number of visits by brown hyaenas to specific latrines in the Kwang group's territory between 1975 and 1978. One hundred and fifty (94 per cent) of these visits were by Kwang group members, but nine (6 per cent) were by five individuals from other groups. The high number of single visits to latrines observed suggests two things. Firstly, that the total number of latrines found is only a proportion of the actual number of latrines in the territory. As mentioned in Chapter 1, however, I believe that the observed movements accurately represent the true movements of the hyaenas of the Kwang group and, therefore, the relative distribution of latrines is correctly represented in the data.

Secondly, it suggests that many of the latrines were short-term latrines. Observations on some specific latrines bear this out. They were regularly used over a short period after which they were unused. Such temporary latrines might be near a large carcass which would attract several hyaenas for a few nights, after which the hyaenas ceased to return regularly to the area and to use those specific latrines. Other latrines were more permanent. One, for example, was discovered in August 1972 and was still in use in July 1980. Bearder and Randall (1978) record similar

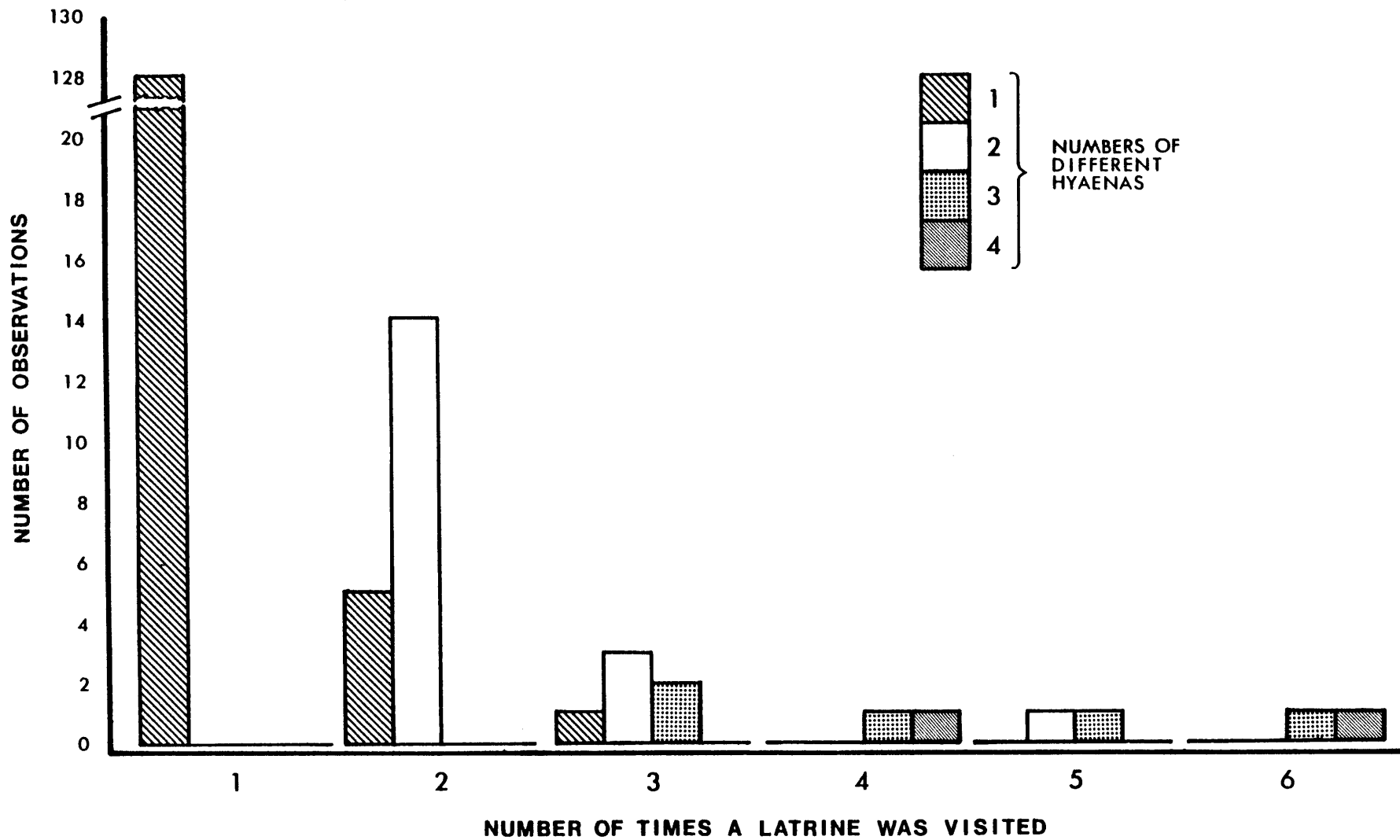


Figure 69: Number of visits to specific latrines by brown hyaenas in the southern Kalahari and number of different hyaenas visiting the latrines; December 1974 - August 1978.

temporary and long-term latrines for spotted hyaenas. Although I do not have any quantitative data, the position of the latrine in the territory did not appear to have an effect on its lifetime.

Discussion

Brown hyaenas in the southern Kalahari paste throughout their territory but mostly in the central, heavily utilised areas (Figs. 60 and 61). However, when they are moving near the border of their territory they increase their rate of pasting (Table 30). In this way the whole territory becomes saturated with the smell of the resident animals.

Apart from pastings, numerous latrines are scattered throughout a brown hyaena territory. These, however, tend to be more concentrated around borders (Figs. 67 and 68), and brown hyaenas moving near the border of their territories visit latrines at a higher frequency than they do when in the interior (Table 33).

The biological function of scent marking in carnivores is little understood (Kleiman 1966, Ewer 1973, Gorman 1980 and Macdonald 1980). In the brown hyaena scent marking could fulfill at least two functions. Firstly it could be used to convey information within the social group. Brown hyaenas nearly always forage alone and often feed on items that suffice one animal only. It is therefore important for them to know which hyaenas are in the territory, and where they are foraging or have foraged in the recent past. By scent marking the individuals can reinforce their presence in their territory without having to repeatedly come into contact with other group members and so waste foraging time. Also, they can avoid foraging in areas which are likely to be unproductive. The series of pastings left by brown hyaenas may fulfill such a role.

As the black paste loses its smell relatively quickly, it may transmit information on the length of time that has elapsed since a hyaena passed that way. A similar hypothesis for scent marking helping animals to avoid unproductive foraging areas has been proposed by Henry (1977) in the red fox. Here urine marking is seen to be used as a signal showing that, although there might be a food odour at a particular place, the food has been eaten.

In addition to this intra-group function scent marking may also serve to pass information between social groups. Saturation of the territory with scent by brown hyaenas could function to ward off intruders i.e. to show that the territory is occupied, and thus to save time and energy in fighting. This information is possibly transmitted both by faeces and by the long-lasting white paste.

Kruuk (1972) has shown that pasting and its component anal bulging are sometimes aggressively motivated in spotted hyaenas and speculated that "anal bulging has the function of a 'scent display' indicating the likelihood to attack" (Kruuk 1972: 223). Ralls (1971) also suggested that marking and aggression may be closely related. Anal bulging is also associated with aggression in the brown hyaena and therefore appears to function in a similar manner. Furthermore, scratching with the forefeet in the sand is closely associated with scent marking. Although it is unknown if brown hyaenas secrete any substance through interdigital glands when scratching, this behaviour frequently occurs in conjunction with defaecation at latrines. It is also often seen in aggressive interactions. It is possible, therefore, that pasting and defaecating in the brown hyaena have evolved from aggressive displays and thus would be likely to be involved in territorial marking.

Both of the possible functions of scent marking outlined above demand that brown hyaenas can distinguish between the scent marks of

different individuals. In other words that the smells left by a hyaena contain at least information on the identity of its author. This has been found to be the case with the small Indian mongoose Herpestes auropunctatus (Gorman 1976). Both behavioural and chemical evidence for individual smells in the pastings of brown hyaenas have been presented, although it is unknown if this applies to faeces. The different reactions of hyaenas to pastes deposited by fellow group members and those deposited by others, indicates clearly that pastes can be told apart. The differences in the chemical profiles of pastes from different individuals provide a chemical basis for such behavioural discrimination. Sniffing at the anal pouch during greeting, moreover, provides the means whereby brown hyaenas can remain familiar with the smells of different individuals.

CHAPTER 6 : SOCIAL INTERACTIONS

INTRODUCTION

Having described the communication system and basic social behaviour patterns of the brown hyaena in the previous chapter, I will now analyse the contexts in which some of them occur and which animals take part in them.

Social interactions are of two basic kinds. There are those that occur between animals of the same social group; intra-group interactions, and those that occur between members of a group and animals not of that group. These latter interactions are either between animals from neighbouring groups, or between animals of which at least one does not belong to any group. As I was often not sure to which of these categories strange animals belonged, I have lumped the interactions between group members and other brown hyaenas into one section.

INTERACTIONS BETWEEN HYAENAS NOT BELONGING TO THE SAME GROUP

Interactions, other than sexual, between members of known groups and animals of known sex which were not members of the same group, are analysed in Table 35. Each interaction between two animals was placed into one of five categories:-

1. Greeting: When two animals perform the greeting ceremony.
2. Ignoring: Where the two animals displayed no obvious attention towards each other. Typical examples of this behaviour would be when

two animals fed together on the same carcass showing no more aggression towards each other than would be shown by hyaenas from the same group; or when two animals passed each other at a distance of not more than 50 m without displaying or changing direction.

3. Avoidance: Where one or both of the animals, on seeing the other, stopped and looked off in that direction, turned around and moved off in the opposite direction.
4. Aggression: Where one or both of the animals displayed aggressive tendencies, identified by pilo-erection accompanied by scratching the ground with the forefeet.
5. Neck-biting: Where two animals resorted to physical combat.

The first two interactions are regarded as non-agonistic, the last three as agonistic (Wilson 1975).

In only 10 cases (Table 35) did I know that the two animals that met were from neighbouring groups, and here there were clear differences in behaviour depending on whether or not the two were of the same sex. Animals of the same sex always acted agonistically towards each other (six observations), whereas animals of opposite sex were never agonistic towards each other (four observations) (Fisher exact probability test $p = 0,005$; one-tailed).

Of the interactions where the origin of one of the contestants was unknown, females always behaved agonistically towards females, males behaved agonistically towards some outside males and not towards others, and animals of opposite sex were normally not agonistic towards each other (Table 35). Only twice were two males which were known to be from different groups observed to meet; once they fought and once one of them avoided contact with the other. This rather scanty evidence suggests that males from neighbouring groups behave agonistically towards each other. If this were true, perhaps the non-agonistic interactions observed

Table 35: Interactions between brown hyaenas from known groups and others of unknown origin in the southern Kalahari where the sex of both participants was known; April 1972 - December 1980.

PARTICIPANTS	SEXES INVOLVED	TYPE OF INTERACTION						
		Agonsitic				Non-agonistic		
		Neck-biting	Aggression	Avoidance	Total	Ignore	Greet	Total
Both participants from different groups	Male : male	1	0	1	2	0	0	0
	Female : female	2	1	1	4	0	0	0
	Female : male	0	0	0	0	3	1	4
Origin of one of the participants unknown	Male : male	0	1	1	2	4	1	5
	Female : female	1	2	0	3	0	0	0
	Female : male	1	4	0	5	14	3	17
Total		5	8	3	16	21	5	26

between group-living males and strange males, were when the group-living males met up with nomadic males. Certainly in all the cases where I believed the strange male to be a nomad this was so.

Once when a nomadic male was feeding on a carcass with two adult males and two adult females from the Kwang group, a second strange hyaena approached the carcass. The nomadic male immediately ran over to the newcomer and attacked it, and was joined by one of the Kwang males. After 1 min the attackers left the newcomer which ran off, bleeding slightly from one ear.

Although animals of opposite sex were mostly non-agonistic towards each other irrespective of their origins, there was occasionally some antagonism between group-living females and strange males. Once an unmarked male ran up to a group-living female who was feeding on a wildebeest carcass, and grabbed and shook her briefly by the side of the neck, the female flattening her ears and yelling. The two animals then parted and started feeding. After a few minutes the male again attacked the female at which she moved away from the carcass.

On another occasion a strange male approached a group-living female which was lying down. The female flattened her ears and curled her tail over her back. The male stopped 5 m away and raised his hair. After a few seconds the male turned around and moved away.

Neck-biting

In Table 36 I have analysed the 16 observed neck-biting bouts. The expected frequencies of each aspect analysed in the table were calculated as follows:-

1. Origin of contestants: From the number of interactions observed between

- members of the same group (236) and the number observed between a member of a known group and an animal not from that group (79).
2. Sex of contestants: Assuming that males and females are equally represented in the population.
 3. Relationship between location of fight and food: From the number of interactions observed between group members and animals not from that group at food (58) and the number away from food (21).
 4. Position of contestants in their territories: From the percentage of the total distance that animals were followed in their territories in boundary blocks (35 per cent), and the percentage of the total distance that they were followed in internal blocks (65 per cent).

From Table 36 it can be seen that in all neck-biting bouts where the contestants were of known origin, they were never from the same group. Both males and females fought equally (assuming that the chances of identifying males and females were the same), but, as I pointed out earlier, rarely with each other. There was no significant difference in the number of fights which took place at food as opposed to those that took place away from food, but significantly more took place in boundary blocks than in internal blocks.

On two occasions I followed the defeated animal after a fight and in both instances it immediately moved away from the area in which the fight had taken place. On six other occasions when I stayed in the vicinity of the fight, the defeated animal was not seen again that night. Only once in the seven cases that I observed the winner's subsequent behaviour after a fight did it immediately leave the vicinity, and in this case the hyaena carried food back to its den. Thus there was a clear tendency for the loser of a fight to retreat from the area and for the winner to stay in the area (Fisher exact probability test $p = 0,0002$; two-tailed).

Table 36: Analysis of aspects of neck-biting bouts between brown hyaenas in the southern Kalahari; 1972 - 1980.

ASPECT ANALYSED	OBSERVED NUMBER OF OBSERVATIONS	EXPECTED NUMBER OF OBSERVATIONS*	χ^2	p
<u>Origin of contestants</u>				
Members of the same group	0	10,5	42,00	<0,001
From different groups	14	3,5		
Origin of both unknown	2			
<u>Sex of contestants</u>				
Male	8	10,5	1,19	>0,05
Female	13	10,5		
Unknown	11			
<u>Relationship between location of fight and food</u>				
At food	9	11,7	2,32	>0,05
Away from food	7	4,3		
<u>Position of contestants in their territories</u>				
In boundary blocks	11	6,2	5,67	<0,02
In internal blocks	7	11,8		
Unknown	14			

* See text.

In all but one of the neck-biting interactions which I observed, the impression gained was that the two animals only became aware of each other's presence when they were within visual contact of each other. The brown hyaena's sense of smell is so acute, however, that scent almost certainly plays a role as well, but only once was this obvious. A female brown hyaena was eating a springbok lamb. After 30 min she carried the remains of the lamb off for 0,9 km and stored it under a bush. She then proceeded to move slowly with her hair raised, sniffing the ground most of the time, until, after moving 600 m, she encountered another brown hyaena. She immediately attacked it and they fought for 2 min with the former hyaena clearly the winner. The fight ended with the stranger being chased for at least 50 m. The original hyaena then returned to the springbok lamb and carried it back to her den.

In all the fights observed it was clear from the onset which contestant would be the winner. It was as if the outcome had been decided before the fight began. This does not appear to be related to where in the territory the fight took place, as there was no significant difference in the likelihood of a hyaena winning a fight when it was in an internal block as opposed to when it was in a boundary block (Fisher exact probability test $p = 0,4169$; one-tailed).

It is noteworthy how rarely brown hyaenas do fight with each other. The 16 neck-biting bouts which I observed took place in 2 500 h of observations. One reason for this is that members from different groups rarely meet up with each other. As I was more likely to encounter a strange hyaena in the Kwang territory when I was alone than when I was following one of its members (Table 37), it is possible that brown hyaenas purposefully avoid meeting up with strangers, something which could be accomplished through scent marking. Even when they do meet up with potential rivals, moreover, brown hyaenas do not often resort to physical

Table 37: The number of brown hyaenas from the Kwang group and the number of strange brown hyaenas seen, when driving around at night in the Kwang group's territory in the southern Kalahari, either when following hyaenas, or when alone during 1978.

OBSERVATION	FOLLOWING A HYAENA (462 km)	NOT FOLLOWING A HYAENA (2 491 km)	χ^2	p
Number of Kwang group members seen excluding the one being followed	49	35	7,59	<0,01
Number of hyaenas seen not from the Kwang group	1	10		

combat. Of the 14 agonistic encounters analysed in Table 35, for example, only five (36 per cent) resulted in neck-biting.

In the southern Kalahari, therefore, neck-biting is predominantly a behaviour displayed between members of different groups, the main function appearing to be that of territorial defence. This is in sharp contrast to the observations of Owens and Owens (1979 b) who maintain that, in the central Kalahari, neck-biting is carried out between members of the same group as an expression of dominance. They noticed no effort by the loser of a fight to leave the area after the fight and sometimes after neck-biting the two contestants would even feed side by side with no further interactions.

INTERACTIONS BETWEEN HYAENAS OF THE SAME GROUP

At food

Although brown hyaenas mostly feed alone, in areas where large carcasses are relatively common, several hyaenas will sometimes collect around the carcass of a large ungulate (Fig. 13). This was particularly common in the Kwang area during the 1977 - 1978 observation period.

The most striking feature of brown hyaenas feeding on the remains of large carcasses is the way in which usually only one hyaena feeds at a time. Typically a hyaena will break a piece off a carcass as quickly as possible and carry it away (Fig. 70) for consumption away from the carcass, or to be stored (Mills 1978 b). Any other brown hyaenas in the vicinity of the carcass will often wait around for the carcass to be

vacated before coming to feed. If more than one hyaena do feed from a carcass simultaneously, low intensity aggression will be displayed in the form of pilo-erection, growling and hooting, and they may tug the carcass in different directions (Fig. 71).

In Table 38 I have examined the outcomes of dyadic interactions over food between animals of different ages and sexes, to see if animals from any group consistently gained access to food at the expense of any other. Only large carcasses (e.g. blue wildebeest), where there was no meat left, or smaller carcasses (e.g. springbok) with or without meat on them, i.e. only carcasses where food was considered to be at least partially limited, have been included in the analysis.

It was usually impossible to tell why a hyaena left a carcass when another arrived. In only 10 (19 per cent) of the observations was it a result of aggression by the arriving hyaena. Sometimes the leaver may have been satiated, but in most cases it is unlikely that it reached that point just as a new animal arrived. I have reasoned therefore, that if one sex or age group of hyaenas scored significantly higher in the analysis than another, then that group could be considered to have priority to food over the other. Table 38 shows, however, that no age or sex group of animals has a clear priority at carcasses.

Muzzle-wrestling

Muzzle-wrestling is a behaviour pattern which is predominantly carried out between members of the same group. Of 97 muzzle-wrestling bouts observed, only one occurred between animals that were not from the same group. This was when a subadult male from the Kwang group was observed to muzzle-wrestle with a strange adult male.

Table 38: An analysis of the outcome of interactions at food between different sex and age groups of brown hyaenas of the Kwang group in the southern Kalahari; December 1974 - August 1978. The analysis considers which of the two hyaenas fed during an interaction. If, for example, a hyaena was feeding and another approached but then moved away and lay down, the interaction was considered to have ended and the possessor received a score. If the approacher later stood up and came back to the carcass and the two fed together, both animals would receive a score. Then, if the original possessor soon moved away, the new possessor would receive another score.

AGE AND/OR SEX OF POSSESSOR OF CARCASS	AGE AND/OR SEX OF ANIMAL ARRIVING AT CARCASS	POSSESSOR'S SCORE	ARRIVER'S SCORE	χ^2	p
Adult or subadult Cub	Cub Adult or subadult	7 5	2 2	-	0,4154*
Adult Subadult	Subadult Adult	10 16	10 9	1,56	>0,05
Adult or subadult male Adult or subadult female	Adult or subadult female Adult or subadult male	10 19	12 10	2,95	>0,05
Adult or subadult male	Adult or subadult male	16	13	0,31	>0,05
Adult or subadult female	Adult or subadult female	8	8	0,00	>0,05
Total		88	69	2,29	>0,05

* Fisher exact probability test.

Table 39 shows the frequencies with which animals from different age groups were observed muzzle-wrestling with animals from the same or other age groups. The data show that not all age groups partake in muzzle-wrestling equally ($\chi^2 = 39,00$; $df = 5$; $p < 0,001$). Taking into account the relative times spent observing animals from different age groups, it is clear from Table 39 that subadults are involved in muzzle-wrestling more often than would be expected and that, although adults rarely muzzle-wrestle with each other, they often do so with subadults.

Subadults take much trouble in initiating muzzle-wrestling with adults, but the adults do not always readily respond. Once, for example, a subadult male was observed to follow an adult male for 6,1 km, during which time the subadult ran up to the male on six occasions and tried to initiate muzzle-wrestling. Each time the adult rebuffed the subadult lightly by snarling at him. On the seventh attempt they stopped at a dead tree and muzzle-wrestled for 1 min before parting.

On two (2 per cent) occasions muzzle-wrestling between members of the Kwang group developed into what appeared to be a more seriously aggressive encounter than muzzle-wrestling normally appeared to be. These occurred between the eldest daughter (12/0) of the original adult female (0/2) and two subadult females (0/13 and 14/0), which were younger offspring of the original adult female. On another occasion an adult female of the Seven Pans group was observed to harrass an unknown, but obviously not fully grown animal, in an even more aggressive manner. In all these interactions the younger animals displayed some of the characteristics of the losing animal in the aggressive neck-biting interactions which are uncharacteristic of normal muzzle-wrestling; they flattened their ears backwards, opened their mouths and made little attempt to retaliate. Furthermore they uttered various whine-related sounds, which are more characteristic of interactions in which one

Table 39: Analysis of muzzle-wrestling bouts observed between brown hyaenas of different ages from the Kwang group in the southern Kalahari; December 1974 - August 1978. A bout is defined as a sequence of muzzle-wrestling during which the participants do not move out of sight of each other or engage in some other activity.

AGE GROUPS	NUMBER OF HYAENA HOURS OBSERVATIONS	NUMBER OF MUZZLE- WRESTLING BOUNTS OBSERVED	MUZZLE- WRESTLING BOUNTS PER HYAENA HOUR	EXPECTED NUMBER OF MUZZLE- WRESTLING BOUNTS
Cub - cub	330	33	0,10	28,4
Cub - subadult	157	22	0,14	13,5
Cub - adult	316	11	0,03	27,2
Subadult - subadult	31	6	0,19	2,7
Subadult - adult	140	23	0,16	12,1
Adult - adult	152	2	0,01	13,1
Total	1 126	97	-	97,0

animal accepts the superior social status of another - for example, as a cub begging from an adult - rather than of muzzle-wrestling where the participants are more equal.

A second type of interaction, which was different from normal muzzle-wrestling, was observed twice between an adult male and an adult female from the Botswana group. In the first instance, having first been attracted to the scene by a brown hyaena yelling, I found the two animals running off slowly, stopping approximately every 50 m, usually at a tree or bush, and wrestling briefly. Approximately 1 km after I found them they stopped at a bush, and for 35 min they intermittently tossed their heads from side to side with their mouths open a few centimetres apart, without ever biting each other. The male growled and yelled most of the time and gave the impression of a losing animal in a neck-biting bout, with the female standing over him. In between bouts they would lie still for approximately 30 s, or the male would move off a few metres before turning back. Then they would start again. Several times the male, with blood around his mouth, would cut in front of the female, "grinning", with his ears flattened out sideways. In the end the male walked off slowly and the female watched him intently. Then after sniffing the ground for several seconds where they had been, she too moved off in the opposite direction.

Seven months later I again encountered these two animals behaving in a similar manner. I was again attracted to the scene by the yelling and growling and found them tussling at a dead tree. Then the male circled the tree and came up to the female, resting his chin on her back as she stood with her head held down. After a few minutes they moved off together, with the female alternatively running and walking approximately 30 m ahead of the male, and stopping repeatedly to look back at the male. After they had moved approximately 1 km I lost them.

It is difficult to interpret this behaviour. There were aspects of neck-biting, such as the growling and yelling of the "loser", of muzzle-wrestling, such as the chasing and stopping at a tree or bush to wrestle, and also of mating behaviour, such as the laying of the chin by the male on the back of the female. The events leading up to and following on these interactions were unknown. It may be akin to the equally strange "female baiting" behaviour of the spotted hyaena (Kruuk 1972), although with the brown hyaenas it was the male that was "baited".

Greeting

Greeting through anal sniffing is another predominantly intra-group behaviour (Table 35). In Table 40 I have recorded the frequencies with which animals from different age groups presented to members of other age groups during the greeting ceremonies. Although I did not quantify the numerous observations of cubs greeting with subadults and adults, I never saw a subadult or adult presenting to a cub. Similarly adults were never observed presenting to subadults. When cubs and subadults greeted with larger animals, they would several times cut in front of and present to the larger animal (Fig. 48), then circle around behind it before cutting in front and presenting to it again.

The few observations that I have of subadults greeting with each other suggest that they normally present mutually or not at all (Table 40). When adults meet, one will present to the other in approximately half the cases and mutual or no presenting occurs in the other half (Table 40). Whether an animal will be presented to, or whether mutual or no presenting will occur in a greeting ceremony between adults, does

Table 40: Number of occasions that brown hyaenas of different age groups presented to each other during greeting ceremonies in the southern Kalahari; December 1974 - August 1980.

AGE GROUPS GREETING	NUMBER OF OCCASIONS	PER CENT
<u>Cub greeting adult or subadult</u>		
Cub presents	Numerous	-
Adult or subadult presents	0	0
Mutual or no presentation	0	0
<u>Subadult greeting adult</u>		
Subadult presents	39	98
Adult presents	0	0
Mutual or no presentation	1	2
<u>Subadult greeting subadult</u>		
One of the pair presents	1	25
Mutual or no presentation	3	75
<u>Adult greeting adult</u>		
One of the pair presents	14	58
Mutual or no presentation	10	42

not appear to be sex-linked (Fisher exact probability test $p = 0,8534$; two-tailed). Neither was there any obvious tendency for one individual to be presented to, or to present more frequently than the others, although the data were too few to test this statistically.

Allogrooming

In Table 41 I have analysed the frequency with which different age groups were involved in allogrooming. As with muzzle-wrestling, not all age groups partake in allogrooming equally ($\chi^2 = 16,92$; $df = 5$; $p < 0,01$). Taking into account the relative times spent observing animals from different age groups, it is clear from Table 41 that subadults and adults are more likely to groom each other than any other combination of animals are, with adults being observed to groom subadults seven times and subadults being observed to groom adults seven times. All the other combinations of age groups tested were involved in grooming activities in approximately the same proportions as would be expected.

apparently usually located by chance or sometimes by scent, or, in the case of wild fruits, the hyaenas may learn where large patches are situated in their territories. Insects are either snapped up as they are flushed by a foraging hyaena or, in the case of termites, the hyaenas might hear them generating a noise (Mills 1978 b). In none of these cases, therefore, is it likely that group foraging would significantly increase the efficiency of finding food. Furthermore, the small size of many of the food items means that they often provide a meal for one hyaena only. Thus group foraging might lead to competition between group members.

Although the success rate in hunting small animals might be enhanced if more than one hyaena co-operated in hunting, the small size of the prey again makes it unlikely that more than one hyaena could satisfactorily feed off the carcass. In the one observation made of two brown hyaenas co-operating to catch a springhare, the hyaena that actually caught the prey did not allow the other to eat any of it (Mills 1978 b).

By foraging alone brown hyaenas forego any chance of being able to overcome large prey species, as other group-living large carnivores such as spotted hyaenas (Kruuk 1972), wolves (Mech 1970), African wild dogs (Estes and Goddard 1967 and Kruuk and Turner 1967) and lions (Schaller 1972) do. Some of the physical features of the brown hyaena, such as the extremely weakly developed back legs and the long, shaggy coat, apparently make it difficult for them to run fast for long distances. They are unable to run as fast and seem to lack the stamina of the spotted hyaena (personal observations). This probably prevents them from catching up with all but the most unfit of ungulates. It is likely, therefore, that the formation of hunting packs by brown hyaenas would not substantially augment the acquisition of food.

However, even though brown hyaenas do not openly co-operate during foraging, there are other ways in which group living could increase their

foraging efficiency. Solitary foraging by group-living brown hyaenas might increase the efficiency in finding food for the cubs, which are normally brought small or medium-sized carcasses, as, if more than one hyaena should find such a carcass it is unlikely that anything would be left for the cubs. Furthermore, by foraging in different parts of the territory simultaneously, several adults have a better chance of finding a suitable carcass for the cubs than they would if they foraged together.

Being in a group at a carcass may enable a carnivore to defend its food better against other competitors (Bertram 1978 and Lamprecht 1978). This does not hold true for brown hyaenas. Several brown hyaenas are unable to keep even a single spotted hyaena or lion away from a carcass, mainly because, even when several brown hyaenas are simultaneously at a carcass, they do not co-operate in defending the food. Black-backed jackals too, are undeterred by the presence of several brown hyaenas feeding at a carcass (Fig. 13).

Group members could communicate to each other the whereabouts of food sources. This has been suggested by Ward and Zahavi (1973) to be the case in some bird species. It is difficult to test this for the brown hyaena and I observed nothing obvious in this respect. However, a brown hyaena could, for example, follow the scent trail of another which had just come from a good food source, with neither of these pieces of information being apparent to an observer. Members of the group continuously make contact with each other at their dens and at other points in their territories and it may be that during these meetings some information on the whereabouts of food is passed on.

Clearly brown hyaenas do not live in groups in order to co-operate in foraging, at least not in the southern Kalahari. Even though some benefits in foraging efficiency might accrue to group-living brown hyaenas, these are unlikely to be the main selective pressures causing

group living.

Factors regulating territory size and group size

If brown hyaenas do not live in groups in order to co-operate in foraging, then it is possible that the dispersion pattern of their food influences their social organisation. Bradbury and Vehrencamp (1976 a and b) have constructed a model for the determination of what they call the social dispersion of organisms, based on their studies of emballonurid bats. Social dispersion is the simultaneous comparison of group size and territory size and these, Bradbury and Vehrencamp suggest, are limited by components of the food distribution. "Territory size is determined by the average distance between successively available food sites, the number of such sites needed per year, and the average size of these sites. Maximal group size is then determined as a result of this territory size minimisation and equals average richness of currently used food patches" (Bradbury and Vehrencamp 1976 b: 383).

Studies of the European badger by Kruuk and Parish (In press) have shown that territory size of these group-living, but solitary foraging carnivores, is determined by the distances between patches of their most common food, the earthworm Lumbricus terrestris. The size of the badger groups inhabiting the territories is a function of the quality of the food patches, which is reflected in the biomass of earthworms per patch. Is there any evidence that brown hyaena territory and group sizes are determined in a similar way?

Territory size

In Fig. 72 I have schematically represented the way in which food

might be distributed in three hypothetical brown hyaena territories. I have assumed that the number of food sites or patches in each territory represents the minimum number of sites needed per year to ensure enough food in the territory, taking into account the influences of seasonality and other factors on the distribution of food.

Territory A represents a territory comprising mainly river habitat. In this territory much of the food is distributed along the river-bed, which is in effect one extremely large food site, with a few smaller sites in the dunes. Such a territory will have a large average size of food sites and, because of the fact that one of them is so large, the average distance between successively available food sites will be small.

Territories B and C represent two territories which comprise mainly dunes habitat. In territory B there are numerous small food sites, which are close together. In territory C there are fewer food sites, some of which are quite large (perhaps a small piece of river habitat and a few large pans). Although the average size of the food sites in territory C are slightly larger than those in territory B, they are on average twice as far apart. Territory C is much larger than territory B, which in turn is slightly larger than territory A.

Such a dispersion of food sites may explain the large observed differences in territory sizes. Territory A may represent the way in which food was dispersed in the Kwang 2 territory (249 km^2), Territory B the way in which it was dispersed in the Kaspersdraai territory (276 km^2) and territory C the way in which it was dispersed in the Seven Pans territory (481 km^2).

If food dispersion does affect territory size in the way I have suggested, it would be expected that animals living in smaller territories would have to travel shorter distances between successive food items than animals living in larger territories would. This does in fact seem to be

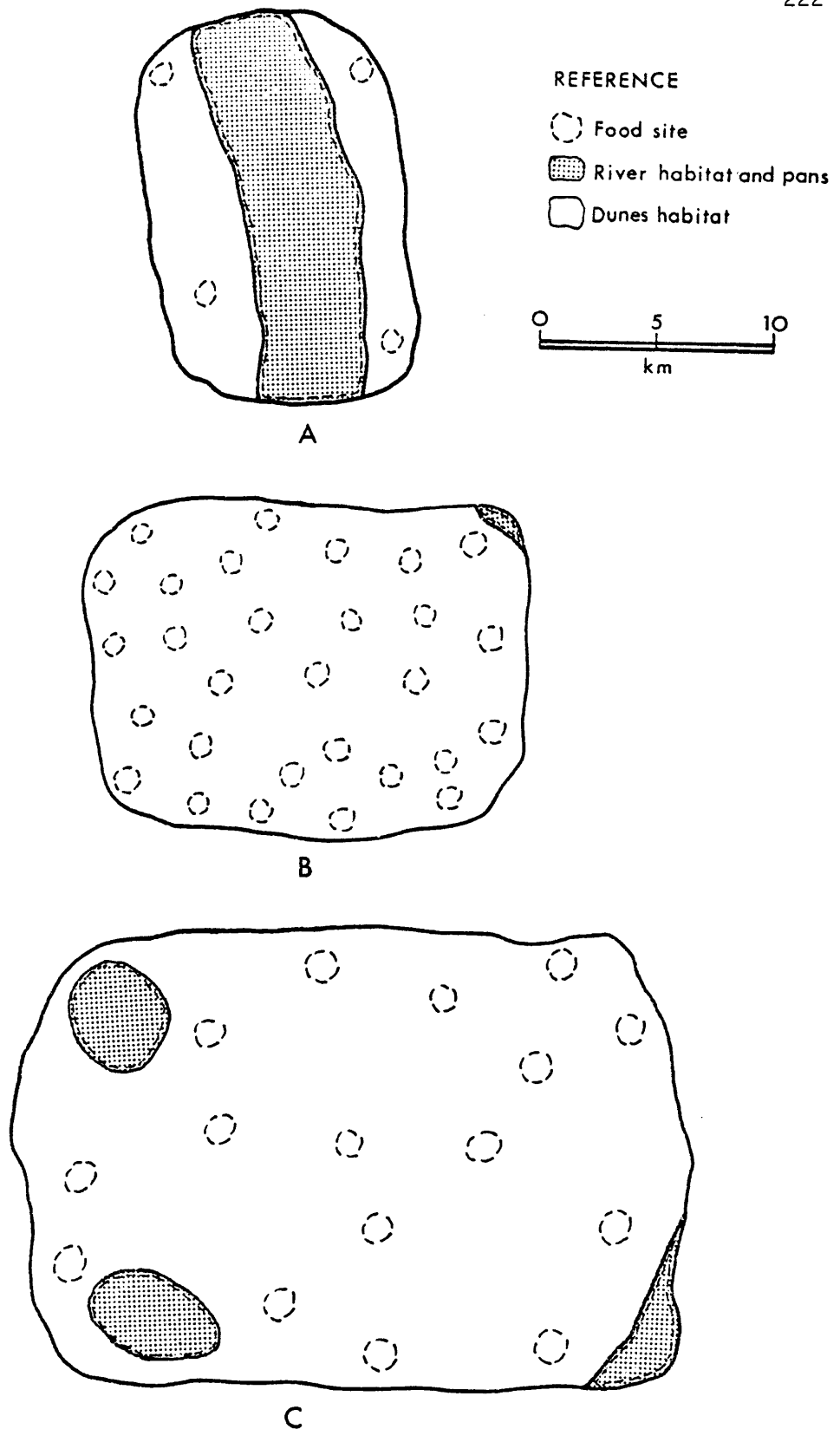


Figure 72: Schematic representation of the distribution of food sites in three hypothetical brown hyaena territories.

the case, as the observed average distances travelled between mammal food items was significantly correlated with territory size. This is possibly because, either the distances between food sites were smaller in the small territories, or some of the food sites were so large that several successive food items could be found in one food site without the hyaena having to travel to another site.

River habitat with its generally higher year round biomass of vertebrates than the dunes, is potentially a food site which could fulfill all a brown hyaena's nutritional needs, yet no brown hyaenas inhabited territories which comprised exclusively river habitat.

The main reason why brown hyaenas should include a proportion of dunes habitat in their territories is that wild fruits, particularly the tsama and gemsbok cucumber, grow almost exclusively in the dunes and these often provide an easily obtainable and abundant, albeit widely scattered, source of food. When tsamas occur they do so in large patches which are irregularly and widely scattered in the dunes. Gemsbok cucumbers also grow in large patches and tend to grow in the same areas each year. For hyaenas to take advantage of this food when it is available, therefore, they must include a large enough portion of dunes habitat in their territories.

Furthermore some small animals, notably steenbok and korhaans, are far more abundant in the dunes than in river habitat, and these too are important food items, being particularly suitable for cubs.

An exclusive river habitat territory, moreover, would become so stretched out and the distance from the den to much of the territory would become so great, that it might impose heavy burdens on the females and other group members when taking food to the cubs. A stage would probably be reached when the territory would become uneconomical in terms of energy balance. Furthermore, as pointed out by Kruuk (1978 b), the ratio of border

to surface area of a greatly elongated territory would make it more difficult to defend.

Two factors unrelated to food dispersion also apparently select for brown hyaenas to include dunes habitat in their territories. Their breeding dens are nearly always situated in the dunes, probably so that they are removed from the river-bed which is the main centre of activity for other large carnivores. In addition, brown hyaenas rarely lie up for the day in river habitat. In summer particularly, the shade provided by the common tree in the dunes, Boscia albitrunca, particularly those chosen as resting sites by brown hyaenas which have large branches close to the ground, are probably important in helping the hyaenas to keep cool (Mills 1977). Although the air temperature under trees in river habitat, such as Acacia reficiens, may be slightly cooler than that under Boscia albitrunca trees (Bothma pers. comm.), the cover provided by the low Boscia albitrunca trees is far superior to that provided by the long-stemmed river habitat trees. Concealment, therefore, may also be important to brown hyaenas.

Another factor not directly related to food dispersion which may affect territory size is the local density of spotted hyaenas. I have shown that those areas well frequented by spotted hyaenas tend to be avoided by brown hyaenas. Where such an area occurs in a brown hyaena's territory, those brown hyaenas might have to increase their territory size, as their accessibility to the food sites in the high spotted hyaena density area would be limited.

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Group size

The only component of food dispersion which could be significantly correlated with group size was the average annual number of blue wildebeest, the most numerous large ungulate, along the 40 km strip of river-bed in the Kwang territory. A large ungulate carcass such as that of a blue wildebeest can be considered in a similar light to a rich food source in that it provides food for several brown hyaenas at any one time. A smaller carcass, such as that of a springbok, usually only provides a meal for one brown hyaena. There was good evidence that in those years of high average numbers of blue wildebeest and other large ungulates in the Kwang area, more large ungulate carcasses became available to the brown hyaenas than in other years. Patch richness here, therefore, is a product of the size of the carcasses which were available to the brown hyaenas and is correlated with group size. The total biomass of ungulates in the territory could not be shown to be significantly correlated with group size.

The number of brown hyaenas living in any of the hypothetical territories in Fig. 72 appears to depend on the richness of the food sites. If the main food item along the river-bed in territory A is springbok carcasses, the main food items in territory B pieces of bone and tsamas, and the main food items in territory C gemsbok carcasses, there will be x hyaenas in territory A, y in territory B and z in territory C, where $z > x > y$. The biomass of ungulates living in territory A, however, may be greater than that in territory C.

This relationship between group size and the number of large ungulates in a territory could be disrupted by a number of factors. For example, a large number of spotted hyaenas in the brown hyaena territory would deprive the brown hyaenas of much of this rich food source, or the absence of lions

or non-violent mortality agents would decrease the number of carcasses. It is important that the large ungulates become available to the brown hyaenas through some agent as brown hyaenas are unable to catch the large ungulates themselves.

Conclusions

Although more data from more groups and more detailed measurements of food dispersion, particularly in the dunes, are needed, the data collected during the present study strongly suggest that both territory size and group size of brown hyaenas are affected primarily by the way in which their food supply is distributed. The factors affecting group and territory size of brown hyaenas, moreover, are similar to those affecting these variables in emballonurid bats (Bradbury and Vehrencamp 1976 a and b) and the European badger (Kruuk and Parish In press). In badgers, however, group size is correlated with the total biomass of earthworms in the territory. In brown hyaenas the biomass of ungulates in the territory does not appear to influence group size. It is the size of the carcasses, in this case blue wildebeest, that are available which is important.

The observations of Owens and Owens (1978) in the central Kalahari suggest that similar factors to those in the southern Kalahari affect brown hyaena social organisation there. Large ungulate carcasses, including such large animals as giraffe Giraffa camelopardalis, were available to the brown hyaenas along a fossil river-bed and spotted hyaenas were rare. Brown hyaenas were found to occur in relatively large groups in this area.

REPRODUCTIVE STRATEGIES

An unusual mating system was observed in the brown hyaena in the present study. Mating was done by nomadic males which occasionally passed through the mixed-sex group territories of their conspecifics. No comparable system has been found in any other carnivore species.

Bradbury and Vehrencamp (1977) maintain that the mating structure of a species occurs within the bounds set by the female dispersion of that species. In this section I discuss the options which are open to individual brown hyaenas of either sex to maximise their inclusive fitness (Hamilton 1964) or, as Dawkins (1976) puts it, to pass on to the next generation as many of their genes as possible, and then speculate on the selective pressures which might have brought this unusual mating system into being.

Options open to individuals

Females

Brown hyaena cubs spend approximately 15 months in the den. A female brown hyaena, therefore, needs to inhabit an area which contains a suitable denning site, surrounded by a foraging area which can fulfill the energy requirements of her and her cubs. For reasons that I shall go into later, the area should be kept as small as practicable. Defence of the area by the female would help to ensure an adequate food supply.

If there should happen to be enough food in the area to support more than one brown hyaena and her latest litter of cubs, the female might be able to enhance her inclusive fitness by allowing one or more of her

daughters to stay in the area and breed. The females co-operate in raising the cubs by sharing the same dens and by occasionally suckling each others cubs. It might also be advantageous to allow some males, which help in the feeding of cubs, to stay. These additional animals could also assist in territorial defence.

The advantages and disadvantages to females in staying in or leaving their natal territories are listed in Table 42. It would seem that in most cases females would do best to remain with their natal group if possible. Nomadic females are unlikely to be able to successfully raise cubs and the chances of finding a vacated territory in a seemingly saturated and undisturbed population, such as exists in the Kalahari Gemsbok and Gemsbok National Parks, are probably few.

Males

Male brown hyaenas are faced with two reproductive options; they can either be breeders or they can be non-breeders. In addition they can either stay with their natal group or they can leave it to become nomads. In Table 43 I have listed the possible advantages and disadvantages to males of staying or leaving when adopting either of these reproductive options. It would seem that if a male exercises the option to breed he should be nomadic, whereas if he exercises the option not to breed he would do better to stay with his natal group.

Some males may vary their options depending on the prevailing conditions. Three males of the Kwang group, for example, stayed in their natal territory for 15, 11 and 7 months respectively after reaching subadulthood and then disappeared, perhaps to take up a nomadic existence. I know that at least one of them did not die, as I saw him 13 months later 20 km from the southern boundary of his natal territory. Another male

Table 42: Possible advantages and disadvantages to female brown hyaenas in the southern Kalahari in staying with or leaving their natal group.

ADVANTAGES		DISADVANTAGES	
In staying with natal group	In leaving natal group	In staying with natal group	In leaving natal group
Can breed and have advantage of having kin to help raise cubs	May find a vacated territory and become the primary breeder	May have to take second or lower place to older females in breeding rate	May be unable to find a vacated territory and therefore may never be able to breed
Can remain in a known area which may enhance foraging efficiency	May find a territory in better habitat and be able to raise more cubs	Will have to compete with other group members for food which may be in short supply	May be forced to live in poorer habitat

Table 43: Possible advantages and disadvantages to male brown hyaenas in the southern Kalahari when exercising either of their possible reproductive options.

BREEDER				NON-BREEDER			
Stay with natal group		Leave natal group		Stay with natal group		Leave natal group	
Advantages	Disadvantages	Advantages	Disadvantages	Advantages	Disadvantages	Advantages	Disadvantages
Can remain in a known area which may enhance foraging efficiency	Few or no mating opportunities	Best opportunities for mating	Will have to leave a well known area and forage in unknown areas	Can help raise cubs of closely related females, possibly enhancing reproductive fitness by kin selection	Will have to compete with other group members for food which might be in short supply	May find better areas to forage in	Will have to leave a well known area and forage in unknown areas
Can wait for a better time to leave group	Will have to compete with other group members for food which may be in short supply	May find better areas to forage in		Can remain in a known area which may enhance foraging efficiency			

joined a group that he was not born into and was once observed carrying food to cubs from that group. It is possible that he was the father of some of the cubs he was observed feeding, but based on the present knowledge of the mating system of the brown hyaena it seems unlikely. It is not, therefore, clear how he could enhance his reproductive fitness by this behaviour.

At first glance it would appear that the best option for all males to follow would be to become nomadic breeders. This strategy does not entail any demands on the males to expend their energy in helping to raise their offspring. Once a male has mated with a female he can move on to search for the next receptive female. The females and the group-living males will see to the welfare of his cubs.

It is not, however, as clear cut as this. The number of successful matings that a nomadic male achieves in his life time are probably few; there are long and erratic intervals between births, some copulations are unsuccessful and it is possible for more than one male to mate with a female during an oestrus period. In addition nomadic males do not have the possible advantage of living in a well defined area and thus the opportunity of becoming familiar with the best foraging areas.

Group-living males on the other hand have numerous opportunities to feed cubs to which they are related. The important evolutionary question is whether this helping benefits the helpers (Emlen 1978). Do the non-reproductive males increase their inclusive fitness through kin selection? The rather scanty evidence from the present study suggests that brown hyaena helpers may, at least under some conditions, contribute significantly to cub survival and therefore to their own inclusive fitness.

In addition to the possible kin selection benefits accruing to group-living males, they live in and defend a comparatively small area which they can become well acquainted with. This may lead to greater foraging

efficiency. Given the problems facing nomadic males, therefore, remaining with a group may be as productive a strategy as being a nomadic male.

Selective pressures acting on the mating system of the brown hyaena

Kleiman (1977) suggests that monogamy in mammals occurs when a female requires help in raising a litter, but where the habitat does not allow more than one female to breed simultaneously within the same home range. As in some areas of the southern Kalahari females can raise their cubs alone (Kaspersdraai territory), and in others more than one female can breed simultaneously (Kwang territory), the conditions for monogamy do not appear to occur widely in the southern Kalahari.

If nomadic males rarely achieve a successful mating, why has a system not evolved where a dominant male emerges in a group who has exclusive mating rights with the females in the group? Such a male could be expected to achieve more matings than a nomadic male would. The most likely explanation is that the territories are large and the group members are widely scattered for most of the time. The male, therefore, would be unable to ensure that the females did not mate with other males, unless he was with them for their entire oestrous period. Females in oestrus, however, are alone for much of the time, and it is difficult to see how the male would be able to prevent other males from mating with the females. Furthermore, the long, erratic intervals between successful matings, means that males might have to spend long periods in a territory without having any successful mating opportunities, and the danger for the male would exist that he would be dislodged by another male before the next successful mating. Polygyny through dominance or territoriality, therefore, would not seem to be a particularly rewarding strategy for male brown hyaenas.

Although the main selective pressures acting on the mating system of the brown hyaena are almost certainly ecological, a successful mating system would have to be one in which excessive inbreeding was prevented. Because of the close genetic relationships that exist between the members of the small brown hyaena groups, this danger exists, but does not occur. Zimen (1976) reported that among captive wolves litter mates failed to show sexual interest in each other. According to Maynard Smith (1978) there is no evidence that animals can recognise their relatives by their genotypes, yet the severity of inbreeding depression seems to have favoured outcrossing. As a device to avoid inbreeding, Maynard Smith (1978) maintains that it is sufficient that an animal should recognise those individuals with which it was raised and should refrain from mating with them. This may be the mechanism which prevents group-living brown hyaena males from mating with the females from their group.

THE MECHANISMS INVOLVED IN GROUP AND TERRITORY SIZE REGULATION AND MAINTENANCE

Group size regulation and maintenance

Of the four mechanisms which can regulate group size, the number of subadults which emigrated from the group was found to be the most important. Natality appeared to be less important, as enough cubs reached maturity to increase group size but did not always stay, and immigration and mortality were found to be least important.

As far as natality is concerned the rate at which cubs are born into

a group is governed mostly by differences in the time intervals between litters, less so by the number of breeding females in the group, which in the present study was never more than two, and litter size. It would appear that differences in the time intervals between litters was due either to a failure to conceive, or to bring gestation to a successful end, rather than to a failure to come into oestrus, as four of six observed copulation bouts were unsuccessful.

There are advantages and disadvantages to subadults in staying in or leaving their natal group (Tables 42 and 43). I have suggested that some options may be better than others, but the consequences of the option that an individual follows will depend on the particular circumstances prevailing in each case.

A relationship has been shown between the number of large food items in a territory and group size. It is possible, therefore, that the number of large carcasses in a territory is an important factor in subadult recruitment. Zimen (1976) recorded that curtailment of food caused by, amongst other things, a reduction in prey size and an increase in pack size, resulted in more aggressive behaviour amongst a pack of captive wolves. He suggested that this may lead to low ranking adults or juveniles leaving the pack either through active ejection or voluntarily. A similar mechanism may operate amongst the members of a brown hyaena group, but I have little supportive data. The heaviest subadult emigration in the Kwang group occurred between July 1979 and January 1980, a period during which I made no detailed observations.

It is possible that subadult females were expelled from the group. The younger female of the Kwang group was observed to be aggressive to two of her younger half-sisters, both of which subsequently disappeared from the group. Neither of these interactions took place over food and it is impossible to say if or how food availability was implicated in these

interactions. The older female of the Kwang group was never observed to behave aggressively towards her daughters. There may have been more incentive for the daughter to get rid of these females than for the older female. Being the younger female and perhaps a less successful breeder, additional females in the group may have further decreased her own chances of raising cubs. On the other hand, as half-sister, the younger female was not as closely related to the females that she was aggressive to as was their mother. Bertram (1973) reported that there is evidence for female lions only driving individuals out of a pride which were not their own offspring.

Muzzle-wrestling is an intra-group behaviour pattern which is predominantly performed by subadults. It may be that this behaviour has more than one function:-

1. When muzzle-wrestling with adults, subadults may be attempting to integrate themselves into the group. Subadults were always the ones to initiate muzzle-wrestling bouts with adults, sometimes going to great lengths to get the adults to react. The fact that muzzle-wrestling between an adult and a subadult twice escalated into a more aggressive interaction, further suggests that this behaviour is associated with subadult recruitment.
2. When subadults muzzle-wrestle with each other, they may be competing for a place in the group. Muzzle-wrestling bouts between subadults often appeared to be more aggressive than those between subadults and adults or cubs, but these data could not be quantified.
3. It is tempting to label muzzle-wrestling, particularly when cubs are involved, as social play, a concept which has caused a great deal of debate by Ewer (1973), Bekoff (1972, 1974 and 1976), Fagen (1974) and Wilson (1975), to mention only a few. Without experimentation and detailed behavioural observations, however, little can be gained from

further speculation on this topic.

Allogrooming is another behaviour pattern which has given rise to much speculation (Wilson 1975). It probably has a sanitary function in the brown hyaena, as animals mainly groom areas of the groomee which it cannot reach itself, but it may also have a social significance. It is also a behaviour pattern in which subadults are much involved, mainly either grooming or being groomed by the adults, and again this behaviour may be related to subadult recruitment.

Clearly the important question of subadult emigration and recruitment requires further study. The role played by the food supply and the way in which social behaviour is implicated, as well as the eventual fate of the emigrants, would be worthwhile avenues of investigation.

When two brown hyaenas meet and perform the greeting ceremony, younger animals invariably present to older animals. If the participants are of the same age, one of the pair may present, or mutual or no presenting will occur. No consistencies in presenting or being presented to could be found for any individuals or sexes. I have suggested that the posture adopted by an animal prior to presenting in the greeting ceremony and the accompanying vocalisation, make one of the functions of the greeting ceremony appeasement. I have further suggested that, by sniffing at the anal pouch, the animals remain familiar with the smell of fellow group members so that they can recognise each other's pastings, and that these are important intra-group signals. The greeting ceremony, therefore, is probably important in the maintenance of group cohesion.

Owens and Owens (1978 and 1979 b) maintain that amongst brown hyaena groups in the central Kalahari, a well defined hierarchy exists which is maintained through neck-biting and other social interactions, and that dominant animals have priority at carcasses. I found little evidence for a dominance hierarchy amongst brown hyaenas in the southern Kalahari.

Neck-biting was never observed to take place between members of the same group and no members of a group consistently gained access to carcasses. The only behaviour suggestive of dominance was that younger animals presented to older ones during the greeting ceremony. This apparent difference in social structure between brown hyaenas living in two different areas may reflect differences in densities of hyaenas in the two areas, the central Kalahari population being a high density one.

Dominance is frequently associated with mating rights and access to food (Schaller 1972, Wilson 1975 and Halliday 1978). As group-living male brown hyaenas in the southern Kalahari were unknown to be involved in mating, and all adult females in a group appear to be able to breed, albeit for some perhaps not quite as regularly as others, and because so much of their feeding is done alone, there do not appear to be strong selective pressures on these hyaenas to form a rigid dominance hierarchy.

Territory size regulation and maintenance

I have argued that the minimum territory size must be one which holds enough food sites to maintain a brown hyaena for a year. The richer these food sites are the larger the group inhabiting the territory will be. But why do brown hyaenas in poor habitats not increase their group size by increasing the size of their territories?

There are several reasons which suggest that small territories are advantageous:-

1. The distances which animals have to move from the den and particularly to carry food back to the den will be smaller. This will lessen the energy burden on the animals. It might also lessen the chances of them being robbed of any food that they may be carrying.

2. A smaller territory will be easier to defend.
3. The animals inhabiting a small territory will be more easily able to learn the best places to forage in, both in the long-term and the short-term.

It may be, therefore, that the main selection pressure is for the smallest possible territory size.

I have shown that territorial boundaries and sizes may change from year to year. This suggests that there are strong pressures on the inhabitants of the territories to defend them. Territorial defence is carried out in two ways; indirectly by scent marking and directly through active defence.

It is striking how rarely members of different groups meet up with each other. Although this might be expected in a species with such a low population density, there is evidence of active avoidance. I was more likely to find a brown hyaena from another group in a neighbouring territory, when I was driving around in that territory on my own, than I was when following a hyaena from the resident territory. In areas of overlap in territory, therefore, it seems as if temporal spacing occurs. I have suggested earlier how this may be accomplished by scent marking.

No matter how effective scent marking might be in maintaining the territorial system and in keeping potential rivals apart, members from different groups do meet occasionally. The outcomes of these meetings vary depending on the sexes of the animals concerned. Animals of the same sex are agonistic towards each other, whereas animals of opposite sex usually ignore each other. Why this should be so is not readily apparent, but it does appear to be a phenomenon found in several carnivore species including lions (Schaller 1972), black-backed jackals (Moehlman 1979) and badgers (Kruuk pers. comm.).

The form of the agonistic encounters varies. Two animals may actively avoid contact, they may display mutual aggression, or they may resort to outright combat by neck-biting. The factors which dictate the form that an encounter will take are unknown. Neck-biting is just as likely to occur away from food as at food, and males and females are equally likely to neck-bite. More neck-biting occurs around boundaries, but this is to be expected as this is where neighbours are most likely to meet each other. The past history of encounters between the two animals, as well as their present motivational state and the stakes involved, are probably important considerations here (Dawkins and Krebs 1978).

When neck-biting does occur there is always a clear-cut difference between the winner and the loser. The loser, however, often does not retreat immediately, but continues the unequal struggle. As potentially severe injuries can result from these neck-biting encounters, there must be an advantage to the loser in not retreating. One possibility is that the loser is showing that it is prepared to fight back, even though it is defeated. This may put it in a better position the next time that the two hyaenas meet; today's winner may not be so ready to attack next time.

Group-living males apparently accept the presence of nomadic males in their territories, but not males from neighbouring groups. I even observed a group-living male join a nomadic male in attacking a third, unknown individual. This implies that group-living males can readily differentiate between nomadic males and their neighbours.

That group-living males can differentiate between other group-living males and nomads is possibly explained by the fact that they learn to recognise their neighbours over time, through repeated meetings. Any male that a group-living male does not recognise, therefore, can be assumed to be a nomad. How nomads recognise other nomads from group-living males is more difficult to explain. It may in fact be that nomadic males

have a distinguishing characteristic that readily identifies them from other males. A subtle difference in postures or a distinctive nomadic male smell are two possibilities. This poses yet one more question in this most intriguing, but still imperfectly understood, social system.

EVOLUTIONARY TRENDS IN HYAENID BEHAVIOUR

The family Hyaenidae comprises three genera with four species. The three genera in the family, Hyaena, Crocuta and Proteles, represent three grades, each with its characteristic lifestyle, which can be modified within certain limits according to the prevailing ecological conditions (Kruuk 1972, 1975, Macdonald 1978 and Mills 1978 a). In this section I will discuss some of these differences in life style between the members of these grades and attempt to explain why they should occur. Because of the state of our present knowledge, much of the discussion will be confined to the brown hyaena and spotted hyaena.

Communication

Perhaps the most striking difference in the communication systems of the four members of the Hyaenidae is found in their vocalisations. The spotted hyaena is far more vocal than any other member of the family. In Table 44 I have attempted a classification and comparison of the vocalisations of the four species. The classification is largely subjective and the data, especially for striped hyaenas and aardwolves Proteles cristatus, are rudimentary. This analysis, therefore, is by no means complete and requires more observations and spectrographic analyses.

Table 44: A comparison of the vocalisations of the Hyaenidae. Data for the spotted hyaena are taken from Kruuk (1972) and Mills (in prep.), for the brown hyaena from the present study, for the striped hyaena from Kruuk (1976 a) and for the aardwolf from Smithers (1971) and Kingdon (1977).

TYPE OF CALL	HYAENID			
	Spotted hyaena	Brown hyaena	Striped hyaena	Aardwolf
Whoop	+	-	-	-
Fast whoop	+	-	-	-
Groan	+	-	-	-
Low	+	-	+	-
Giggle	+	-	+	-
Yell	+	+	+	+
Loud growl	+	+	+	+
Short deep growl	-	+	-	-
Soft growl or grunt	+	+	-	+
Very soft growl	-	+	-	-
Short grunt laugh	+	-	-	-
Loud grunt laugh or hoot	+	+	-	-
Harsh whine	+	+	+	-
Soft squeal or soft whine	+	+	-	-
Bark	-	-	-	+
Total	12	8	5	4

+ Present

- Absent or not recorded

Nevertheless it is clear that the repertoire of the spotted hyaena is the largest of the four species.

In addition to their larger vocal repertoire, spotted hyaenas are much noisier than any of the other species. Even where the species have equivalent calls the spotted hyaena's calls tend to be louder than those of any of the others (Kruuk 1976 a and personal observations). The whoop, which is the loudest call of all, is only found in the spotted hyaena. Furthermore, the frequency with which these different calls and particularly the louder ones are made, is highest in the spotted hyaena.

Pasting is found in all the Hyaenidae (Kruuk 1972, 1976 a, Kruuk and Sands 1972, Rieger 1977 and this study). It seems, however, that the brown hyaena secretes the most complex substances, as none of the others secrete two distinct pastes. Brown hyaenas paste at a far higher frequency than spotted hyaenas do. In the southern Kalahari the mean pasting frequency for brown hyaenas was 2,6 per km ($n = 1\ 947$ km), whereas the mean for spotted hyaenas was 0,1 per km ($n = 1\ 959$ km) (Mills in prep.). Spotted hyaenas mainly paste in areas where spotted hyaenas from other social groups are likely to pass, for example, on territorial boundaries (Kruuk 1972), and pasting mainly has an intra-group function. Brown hyaenas and probably striped hyaenas too, paste throughout their ranges and in these two species pasting has both inter- and intra-group functions. Aardwolves appear to paste mainly around territory boundaries, sometimes at a rate of approximately one pasting per min (Kruuk and Sands 1972), so pasting in this species may have an intra-group function.

The use of latrines is found to a greater or lesser extent in all four species (Kruuk 1972, Kruuk and Sands 1972, Macdonald 1978 and this study), and, except in the aardwolf (Kruuk and Sands 1972), latrines appear to have a scent marking function.

In the context of visual communication pilo-erection is a conspicuous posture in brown and striped hyaenas as well as in the aardwolf. Although spotted hyaenas erect the short hairs on their necks during aggression, it is not nearly so striking as in the other three species. On the other hand the dark tail of the spotted hyaena contrasts markedly with its light coloured body, thus enhancing the signaling value of the tail. Both brown and striped hyaenas do not have contrastingly coloured tails, although the aardwolf does.

It is worthwhile speculating why some of these differences in communication systems have evolved in these closely related species. Spotted hyaenas are the most social of the Hyaenidae, living in well organised groups called clans throughout their distribution range (Kruuk 1972, Bearder 1977, Whateley and Brooks 1978, Tilson, Von Blottnitz and Henschel 1980 and Mills in prep.). The members of a clan continually change their foraging group sizes from one to several, depending on what type of food they are exploiting. They also communally defend their territories from other spotted hyaenas and often interact in groups with their major competitors, notably lions (Kruuk 1972). It is, therefore, often important for spotted hyaenas to know where the other members of the clan are at any one time so that they can, if needs be, rapidly come together. They have therefore evolved a long range whoop call, one of the functions of which is to help accomplish this (Mills in prep.). They have also evolved a number of other vocalisations such as the fast whoop, the low and the giggle which are important in communal antagonistic situations (Kruuk 1972).

The other three species in the Hyaenidae are solitary foragers, normally feed off small food items and do not partake in group attacks (Bothma 1971 b, Smithers 1971, Kruuk and Sands 1972, Kruuk 1976 a, Skinner 1976, Cooper and Skinner 1978, Macdonald 1978, Owens and Owens

1978, Bothma and Nel 1980 and this study). Therefore they do not need to know where the other members of the social group are at any one time and do not have any long range vocalisations. Nor have they the need for a complex repertoire of group orientated vocalisations.

As I have mentioned, however, it is important for brown hyaenas, and probably for striped hyaenas too, to know where other members of the species have foraged in the recent past, so as not to waste energy by foraging in areas which are likely to be unproductive, and to keep up to date with the composition of the group. This may account for the fact that pasting only has an intra-group function in spotted hyaenas, whereas it has both inter- and intra-group functions in brown hyaenas. This is borne out by the higher pasting frequency of the brown hyaena, the apparently more complex chemicals produced by it, as well as the different ways in which the pastings of the brown hyaena and the spotted hyaena are distributed. Pasting in the aardwolf may not be necessary for intra-group communication because of the small size of their territories (Kruuk and Sands 1972).

The fact that aardwolf latrines do not have a scent marking function has been suggested by Kruuk and Sands (1972) to be related to the fact that their faeces have a strong termite smell. As termites are the aardwolf's main food source, it is possible that, by depositing their faeces at regular sites and by covering them, the aardwolves prevent themselves from becoming confused whilst foraging.

The increased signalling efficiency of the spotted hyaena's tail is a further manifestation of its more social way of life, when compared with the brown hyaena and the striped hyaena. The aardwolf's conspicuous tail is an apparent anomaly, but not enough is known about the aardwolf to explain this.

Further manifestations of the more highly evolved social system of

the spotted hyaena can be found in its complex greeting ceremony and associated modifications of the sexual organs, and in the expression of such behaviour patterns as social sniffing and communal scent marking (Kruuk 1972). Greeting ceremonies in the brown and striped hyaena are more simple and no complex morphological structures have evolved to accomplish this. Furthermore, communal social behaviour activities are non-existent.

The fact that pilo-erection is so well developed in the three less social members of the Hyaenidae is at first glance inconsistent with the above arguments and needs explaining. It is perhaps significant that this posture, which at least under certain conditions, makes the animal performing it appear to be larger, is so well developed in the solitary, smaller and least aggressive members of the family. When a brown hyaena stands its ground against a spotted hyaena, it raises its hair and utters the short deep growl, which to me was the fiercest sounding vocalisation I heard a brown hyaena make. It is tempting to conclude that the brown hyaena is attempting to make itself appear as large and fierce as possible. The fact that this behaviour often appears to deter the spotted hyaenas is perhaps testimony to its successfulness.

Alternatively, spotted hyaenas often feed on fresh carcasses and because of their manner of killing and eating (Kruuk 1972 and Mills in prep.) often get themselves covered with blood. Long hair would obviously be a disadvantage in such cases. Shorter hair may, therefore, have evolved in spotted hyaenas as an adaptation to feeding.

Denning behaviour

The denning behaviour of the brown hyaena is similar to that of the

striped hyaena (Kruuk 1976 a, Skinner and Ilani 1979 and this study). The major differences between the denning behaviour of these two species and that of the spotted hyaena are that spotted hyaenas do not carry food back to their cubs, and spotted hyaenas invariably den communally (Deane 1962, Kruuk 1972 and Mills in prep.). The single observation over a $3\frac{1}{2}$ -year period by Hill (1980) of a spotted hyaena carrying a dead domestic sheep back to a den in Amboseli National Park, Kenya, cannot be taken as unequivocal evidence of a spotted hyaena providing food for cubs. The circumstances surrounding the incident may have been atypical, for example, the spotted hyaena may have been disturbed by man and, therefore, behaved unusually.

Because brown hyaenas and striped hyaenas are solitary foragers and often feed off small food items, an individual which finds a suitable food item for cubs can usually carry it back to the den as there are no other hyaenas competing with it for the food. At the den there are normally few cubs and competition for the food is spread amongst cubs of equal age.

The social feeding behaviour of spotted hyaenas, where several individuals often feed off a large food item at the same time, and where competition is expressed in the speed of eating (Kruuk 1972), makes it important for each individual to eat as much as it can as quickly as possible. Mostly, therefore, there is nothing left to be taken back to cubs except perhaps for skin and bones, which the cubs would have difficulty in eating. Even if there was enough food left over, in some areas such as the Serengeti and the southern Kalahari, the large distances from the dens that the hyaenas are often forced to move in order to find food (Kruuk 1972 and Mills in prep.), make it difficult for them to carry back large amounts of food to the den. Furthermore, at the dens which typically have several litters of cubs of different ages, the larger cubs

would get most of the food.

Spotted hyaena cubs therefore rely on their mother's milk to a greater extent than do brown hyaena cubs (Kruuk 1972 and this study). Spotted hyaena litters almost always comprise one or two cubs only (Matthews 1939, Deane 1962, Kruuk 1972 and Mills in prep.), whereas brown hyaena litters are larger ($\bar{X} = 2,9$). It is possible that smaller litter size in the spotted hyaena has evolved as a result of the heavy dependence of the young on milk. By providing additional food, brown (and striped hyaenas) can probably raise larger litters.

Brown hyaenas in the southern Kalahari only rarely den communally. The only communal dens found during the present study were during times of abundant food. The two communal dens referred to by Owens and Owens (1979 a) in the central Kalahari were also in rather atypical circumstances for this region, i.e. along a fossil river-bed where there were exceptionally high densities of ungulates due to good rains (Owens and Owens 1978). It would be interesting to know if the brown hyaenas in the dune areas of the central Kalahari, where food is probably less abundant, den communally.

Conclusions

From the above discussion it is clear that a wide range of behavioural adaptations to feeding ecology have evolved in the Hyaenidae. At the same time there are many similarities in basic behaviour patterns. Pasting onto grass stalks, for example, is common to all Hyaenidae and many of the vocalisations of hyaenids are similar. Kruuk (1976 a) describes how spotted hyaenas and striped hyaenas react to some of the other species' signals as if they were conspecific; they paste on each other's pastings

and they show a clear mutual attraction. A similar state of affairs exists between brown hyaenas and spotted hyaenas and I once observed an interaction between an aardwolf and two spotted hyaenas where mutual attraction was obvious. It would seem, therefore, that on certain behavioural levels the three genera of the Hyaenidae are less well isolated than they are on others such as diet and foraging behaviour.

CHAPTER 8 : MANAGEMENT CONSIDERATIONS

INTRODUCTION

All indigenous animals are resources of inherent interest and value to man and we have a moral obligation to conserve them. This moral obligation, however, must be balanced with many practical considerations which, in the case of carnivores, are more complex than with most other animals (Kruuk 1976 b).

In areas such as national parks and game reserves some of the points to consider in the management of the brown hyaena are the influence of other large carnivores on the brown hyaena population, whether the area is large enough to conserve a viable population, and what to do about the overflow of surplus animals into adjacent agricultural areas where they may pose a threat to domestic livestock. Outside conservation areas the protection of domestic livestock and the "deeply ingrained tendency in man to kill the killer" (Kruuk 1976 b: 2) must be considered.

In this chapter I discuss some aspects of brown hyaena management, firstly in the southern Kalahari, then in other areas.

IN THE KALAHARI GEMSBOK AND GEMSBOK NATIONAL PARKS

Because of their rareness and because they are large carnivores, brown hyaenas are one of the species sought after by tourists visiting the Kalahari Gemsbok National Park. Apart from their ecological role, therefore, they have an added importance as far as management is concerned.

The brown hyaena population in the Kalahari Gemsbok and Gemsbok National Parks is obviously viable because of the large area of suitable habitat. An important variable which favours the brown hyaena in the southern Kalahari is the low density of other large carnivores, particularly spotted hyaenas, which, because of their relative scarcity in the area, are obviously not as well adapted to this harsh environment as are brown hyaenas.

Spotted hyaenas pose a threat to brown hyaenas through direct predation and through competition for food. However, in the southern Kalahari the influence of spotted hyaenas on the brown hyaena population is small, because of the low density of spotted hyaenas. In areas of high spotted hyaena density they may well have a detrimental effect on the brown hyaena population. Several other studies on closely related sympatric carnivores have also suggested that the smaller species tend to be more common in areas not well frequented by the larger one. In the Namib desert brown hyaenas are reported to be found mainly along the coast, whereas spotted hyaenas range further inland (Skinner and Van Aarde In press). Schaller (1967) and Seidensticker (1976) found that leopards tend to avoid high density tiger Panthera tigris areas. Kruuk (1976 a) recorded that striped hyaenas are more common in low productivity habitat areas which tend to be avoided by spotted hyaenas, and in Minnesota, U.S.A. Berg and Chessness (1978) found no coyotes in an area adjacent to one containing wolves.

Lions are obviously important agents in providing food for brown hyaenas. At the same time lions pose a threat to brown hyaenas, as has been shown in the section on mortality. The southern Kalahari has a low lion density in comparison with many other conservation areas in Africa (Mills et al. 1978), and the food that they provide for brown hyaenas probably outweighs the effect of predation. Should the lion density

increase significantly in the southern Kalahari more food would become available to brown hyaenas, but the number of fatal brown hyaena encounters with lions might increase to the point where the effect of predation outweighs that of the provision of food.

Certain aspects of the brown hyaena's behaviour seem to be poor adaptations to withstanding competition from other large carnivores. Brown hyaena cubs spend long periods foraging on their own. This may make them especially vulnerable to predation by carnivores such as lions, leopards and spotted hyaenas as the young brown hyaenas lack experience and are comparatively slow-moving. Also the fact that brown hyaenas carry food, sometimes strong smelling carcasses, for long distances back to their cubs, invites interception by other carnivores as does the presence of these carcasses at the den. Twice during my study spotted hyaenas were observed at brown hyaena dens; once consuming a carcass which had earlier been brought to the den by an adult brown hyaena and once attacking one of the cubs which managed to escape, apparently unharmed.

Judging by the speed and extent to which the size of the Kwang group and its territory fluctuated during the present study, the southern Kalahari brown hyaena population has the potential to fluctuate appreciably and rapidly, depending on the way in which the prevailing ecological conditions affect the food supply. Changes in the number of ungulates becoming available to brown hyaenas appears to be the most important factor causing these population fluctuations. Ungulate numbers, however, are difficult to manipulate and control in this arid region where rainfall is the most important ungulate population regulating factor, both in the short-term (Bothma 1972 and Bothma and Mills 1977) and in the long-term (Mills in prep.). Notwithstanding, the provision of artificial water along the river-beds does appear to have had a positive effect on blue wildebeest numbers in these areas (Eloff 1966 and Mills and Retief 1981) and therefore

probably on brown hyaena numbers as well. Additional provision of artificial water along the river-beds could further increase blue wildebeest and brown hyaena numbers, but this must be carefully weighed against other factors, such as the possibility of excessive grazing pressure by blue wildebeest along the river-bed and the possibility of lion and spotted hyaena numbers increasing to that point where they start having a negative effect on brown hyaena numbers.

The management of the two National Parks in the southern Kalahari as a single ecological unit is most important both for the continued maintenance of the viable brown hyaena population and for many of the other species in the area. As many of the brown hyaenas use the Nossob river-bed, i.e. the boundary between the two National Parks, to forage in and regularly cross from one side to the other, it stands to reason that any barrier to this freedom of movement would be detrimental to the population. Not only would it directly affect all the brown hyaena groups which live along the Nossob river-bed, but it would also affect the amount of gene flow through the population by limiting the number of nomadic males and cutting down the options open to dispersing subadults.

The western and south-western boundaries of the two National Parks are already fenced off from the neighbouring farming areas. While this fence is necessary to stop carnivores from moving onto farms, it has decreased the areas open to non group-living brown hyaenas and is indirectly an important cause of mortality in the population. Although this apparently only affects the population moderately at present, any further large scale restriction on the movements of the brown hyaena might well have a more severe impact on the population.

Finally, any ecological splitting of the two National Parks would severely affect the brown hyaena's food supply. Many of the ungulates live in and around the Nossob river-bed and regularly move in and out from

one side to the other on both a daily and a seasonal basis. Without this freedom of movement it might be impossible to maintain these ungulate populations.

The foraging behaviour of the brown hyaena precludes any chance of it ever having a detrimental effect on any prey population. Likewise no competing carnivore is believed to be severely hard pressed through interspecific competition with the brown hyaena.

As the southern Kalahari is prime brown hyaena habitat, is it worthwhile translocating "problem animals" from other areas to the Kalahari Gemsbok National Park? The fact that many brown hyaenas are killed along the western and south-western boundaries of the Park suggests that there is already competition for space amongst the resident brown hyaenas. This, coupled with the potential danger of mixing gene pools (Greig 1979), are reasons for avoiding translocations into the area.

Because of their nocturnal habits brown hyaenas are rarely seen by tourists. The present study has shown that brown hyaenas, particularly cubs, are quickly habituated to vehicles. As brown hyaenas often den in the same area over many years, locating a den with the help of a tracker is relatively easy to accomplish. Tourists could then be given the opportunity to observe and photograph the hyaenas at sunrise and sunset. The chief difficulty in implementing such a scheme would be the necessity of providing a suitable vehicle and guide for reaching the den.

IN OTHER AREAS

Besides the southern Kalahari, viable brown hyaena populations which enjoy at least partial protection are known to exist in the Central

Kalahari Game Reserve, Botswana (Owens and Owens 1978), the coastal regions of the southern Namib desert (Shaughnessy pers. comm. and Skinner and Van Aarde In press) and probably Kaokoland (Viljoen 1980) and the Etosha National Park in South West Africa/Namibia (Von Richter 1974), as well as perhaps in southern Angola (Huntley 1974).

An area which is large and has a low density of spotted hyaenas, would appear to be required for the successful maintenance of a viable brown hyaena population. No other conservation area within the brown hyaena's distribution range appears to exist at present which fulfills these two demands adequately.

The introduction and maintenance of brown hyaenas in smaller game reserves is a complex question. In the first place the area would have to be adequately fenced, which is expensive, and it would also have to provide enough food for the hyaenas. On the other hand, if tourists could observe these animals, for example, feeding at night at bait stations, this could add much to the attraction of the reserve and could be used for educational purposes too.

Outside conservation areas, good habitat for brown hyaenas exists on agricultural land. There is an adequate supply of food both from wild and domestic animals and spotted hyaenas and other large carnivores are usually absent. Viable populations of brown hyaenas exist in many of these areas, particularly in the Transvaal (Skinner 1976).

There are, however, important practical questions which need to be solved before rational management of brown hyaenas can be achieved in agricultural areas. It is of prime importance to establish the magnitude

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

of loss of domestic livestock to brown hyaena predation and to find economically efficient control methods with the emphasis on non-lethal or selective lethal methods (Sterner and Shumake 1978 and Wade 1978). In addition research into the best management practices which farmers should adopt to protect their livestock, for example, the effect of synchronising calving and increasing vigilance at night during the calving season, and to obtain the optimum ecological benefit from brown hyaenas on their farms, for example, how to deal with carcasses of stock that have died from disease, should be carried out. Certain areas of South Africa have been defined as suitable only for extensive cattle production (Anon 1965). It is there that a major research effort should be aimed as it is in such areas that the chances of effective damage-control are best.

Once a sound management plan has been drawn up, the support of the people living in the relevant areas is essential if the plan is to be successively implemented, a point emphasised by Mech (1977) and Macdonald and Boitani (1979) when discussing wolf management. This will entail an efficient and extensive education campaign which will be of benefit to the local human inhabitants of the area.

Predator control generally seeks to decrease predator populations, but it is the damage, not necessarily the pests, that must decrease. "It may be that by reducing the number of pests, damage will also be decreased. There are many other ways to reduce damage, however, than by increasing mortality" (Giles 1978: 106).

CONCLUSIONS

The brown hyaena is listed as vulnerable in the I.U.C.N. Red Data

Book. Because of its nocturnal and secretive behaviour it is difficult to establish its exact status. Undoubtedly its numbers have been reduced in many parts of its former range in recent years, particularly in those areas where small domestic livestock are farmed. There are, however, several large conservation areas in ideal brown hyaena habitat, e.g. the southern and central Kalahari and the Namib desert coast, which harbour viable brown hyaena populations. Furthermore the species has shown that it is well able to adapt to many of man's activities, particularly in parts of the Transvaal (Skinner pers. comm.). As long as the large conservation areas are maintained in their present state and a rational approach to the management of brown hyaenas in other areas exists, the future survival of the brown hyaena can be viewed with optimism.

J.D. Skinner. Mammal Research Institute, University of Pretoria, Pretoria, 0001. November 1981.

CHAPTER 9 : CONCLUSIONS

The present study has shown that the brown hyaena population in the southern Kalahari is strongly affected by its feeding ecology and that, as has been found in many other species (see Chapter 1), a close relationship exists in the brown hyaena between social behaviour and organisation, and diet and distribution of the food supply.

Of the nine basic questions posed in Chapter 1, the most difficult ones to answer have been those of how the food supply is distributed and how the social system is maintained through behaviour.

Although the distribution of the food supply was reasonably documented in river habitat, it was not so well documented in the dunes. The dispersion pattern of food in the dunes is probably the key to understanding why there were such large differences between the sizes of territories in the dunes.

Important questions about the social system which need to be better answered include:-

1. How do non-breeding males enhance their reproductive fitness - do they, by helping to feed cubs, contribute significantly to cub survival?
2. What factors determine whether an individual will stay with or leave its natal group, as well as whether an outsider will join a group?
3. What happens to those hyaenas, particularly females, which do leave their natal groups?

SUMMARY

The main aim of the present study was to investigate the relationship between the social organisation and behaviour, and the diet and distribution of the food supply of the brown hyaena Hyaena brunnea, as a contribution to its conservation.

The study was done in the adjacent Kalahari Gemsbok and Gemsbok National Parks in the arid southern Kalahari. Two main habitats are recognised; the river-beds and environs, and the dune areas.

Most observations were made from a vehicle, either by following radio-collared individuals, or by making observations at carcasses and dens, and to a lesser extent by tracking spoor. Caught brown hyaenas were individually marked and aged on the basis of tooth eruption and wear. All observed movements of brown hyaenas, as well as the pasting points and latrines of hyaenas from two territories, were plotted on a 1:10 000 map. Territory boundaries were delineated by the smallest convex polygon method and the size of each was measured with a planimeter. Data from three territories were further analysed with SYMAP and SYMVU computer programmes. Histological analyses of two anal scent pouches and GLC analyses of the pastings from two brown hyaenas were performed. Tape recordings of certain vocalisations were subjected to sonographic analysis. Food availability was measured by daytime counts of large and medium-sized ungulates, night counts and spoor counts of small animals and random strip counts of wild fruits.

Mammal remains are the brown hyaena's most important food, with wild fruits an important secondary food. During the study large and medium-sized mammal numbers, as well as those of wild fruits, fluctuated markedly in the study area. The years 1977 - 1980 were particularly good years for brown hyaenas in the study area, mainly because of the large number of blue wildebeest Connochaetes taurinus carcasses which were available.

Although solitary foragers, brown hyaenas in the southern Kalahari were found to live in small groups of mixed sex and age, in which the majority of individuals were related to one another. The size of an intensively studied group was significantly correlated with the mean number of blue wildebeest in that territory each year, from 1975 to 1980. Subadult recruitment and emigration were the most important variables in brown hyaena group size regulation. In addition to group-living and dispersing subadult brown hyaenas, 8 per cent of the population consisted of nomadic adult males.

Group territories varied in size between 235 - 480 km². No correlation between group size and territory size was found. Territory size was positively correlated with the mean distance travelled by the hyaenas from that territory between finding successive mammal food items. The foraging patterns of brown hyaenas from different territories varied, depending on the distribution of the food in the territory. A high local density of spotted hyaenas Crocuta crocuta apparently affected brown hyaena density, either through necessitating an increase in territory size or a reduction in group size. The brown hyaena density in the southern Kalahari was calculated as 1,8 hyaenas per 100 km².

Mating was only observed between nomadic males and group-living females and consisted of numerous, short duration mountings. Oestrus lasts several days and the male and female are not together for the entire period.

The cubs are at least partially dependent on a den for 15 months. For the first three months of their lives the cubs' only source of nutrition is their mother's milk. After this age their diet is supplimented with food that is carried back to the den by the other group members. From approximately 10 months of age the cubs begin to forage to an ever increasing extent for themselves. Mostly only one litter of cubs is

raised at a den, but at two dens (18 per cent) two litters were simultaneously raised. Both males and females contribute equally in the amount of food that they carry back to the den and, although not conclusive, there was the suggestion that helpers contribute to cub survival.

The brown hyaena employs olfactory and visual communication to a larger degree than it does vocal communication, while tactile communication is of little importance. Pasting and defaecation at latrines are the two most common forms of scent marking in the brown hyaena. Scent marking is seen as having both inter- and intra-group functions.

All interactions between brown hyaenas of the same sex from different groups were agonistic, whereas interactions between animals of opposite sex and different groups were usually not. The most extreme form of agonistic behaviour is neck-biting which functions in territorial defence.

Within the group no individual, or sex or age group of animals, could be shown to have priority at carcasses. Subadults were more often involved in muzzle-wrestling than adults and cubs were. Occasionally muzzle-wrestling escalated into an apparently more aggressive behaviour than it normally appeared to be, and may be related to subadult eviction.

The dispersion pattern of the brown hyaena's food strongly influences its social organisation; the way in which the food is distributed influencing territory size, which for several reasons should be kept as small as practicable, the "quality" of the food influencing group size. The selective pressures moulding the unusual mating system are also seen to be mainly ecological, occurring within the bounds set by the dispersion pattern of females. The factors involved in group size regulation, i.e. subadult recruitment and emigration are little understood. Females it seems, would usually do best in terms of gene survival to stay with their natal group if possible, whereas males can spread their genes, either by

becoming nomadic breeders, or by remaining with their natal group as kin selective helpers.

Amongst the Hyaenidae the three genera represent three grades, each with its characteristic life style. Differences in communication patterns and denning behaviour between the genera are described and discussed in terms of the ecological pressures acting on the members of each genus.

Conditions in the southern Kalahari are considered to be ideal for the maintenance of a viable brown hyaena population. No specific management practices need be adopted in this area at present. The Central Kalahari Game Reserve and Namib desert also harbour viable protected brown hyaena populations. In most other conservation areas, however, the habitat does not seem to be suitable for brown hyaenas. It is suggested that the main conservation-orientated research effort for this species should be directed towards selective agricultural areas unsuitable for small stock.

OPSOMMING

Die doel van die huidige ondersoek was om die verwantskap tussen sosiale organisasie en gedrag, en die dieet en verspreiding van voedselbronne van die bruinhiëna Hyaena brunnea, as 'n bydrae tot die bewaring van dié species, na te volg.

Die studie is in die aangrensende Kalahari Gemsbok en Gemsbok Nasionale Parke in die droë suidelike Kalahari uitgevoer. Twee tipe habitatte, wetende die rivierbeddings en omgewing, en die duingebiede is onderskei.

Meeste waarnemings is vanuit 'n voertuig gemaak, of deur diere toegerus met radio-nekbande na te volg, of deur waarnemings by karkasse en nesgate te maak, en tot 'n mindere mate deur spoorsny. Gevangde hiënas is individueel gemerk en ouderdomme is op basis van tanderupsie en slytasie bepaal. Alle waargenome bewegings van bruinhiënas, sowel as 'pastingspunte' en latrines van hiënas van twee territoriums is op 'n 1:10 000 kaart aangeteken. Territoriale grense is afgebaken deur die kleinste konvekse veelhoek metode en die grote van elke territorium is met behulp van 'n planimeter bepaal. Inligting van drie territoriums is verder deur die gebruik van SYMAP en SYMVU rekenaarprogramme geanaliseer. Die anale ruiksakke van twee diere is histologies ondersoek en GKV-ontledings van afskeidings van twee hiënas is uitgevoer. Bandopnames van sekere klanke van bruinhiënas is sonografies ontleed. Voedselbeskikbaarheid is deur dagtellings van groot en medium-grote wildeboksoorte, deur nagtelike en spoor tellings van kleiner diersoorte, en deur ewekansige lyntellings van wilde vrugte, bepaal.

Soogdieroorblyfsels is die mees belangrikste voedsel van bruinhiënas, terwyl wilde vrugte dien as 'n sekondêre voedselbron. Gedurende die studietydperk het die getalle van groot en medium-grote soogdiersoorte,

sowel as die hoeveelheid wilde vrugte, opvallend gefluktueer. Die jare 1977 - 1980 was veral goeie jare vir bruinhiënas in die studiegebied, hoofsaaklik as gevolg van die beskikbaarheid van groot hoeveelhede blouwildebees Connochaetes taurinus karkasse.

Alhoewel alleenlopend wanneer kos gesoek word is vasgestel dat bruinhiënas in die suidelike Kalahari in klein groepe van beide geslagte en verskillende ouderdomme bly. Meeste van die individue in 'n groep is aanmekaar verwant. Vir 'n groep wat intensief nagevolg is is gevind dat groepgrote betekenisvol gekorreleer is met die gemiddelde aantal blouwildebeeste wat in daardie territorium gedurende elke jaar vanaf 1975 tot 1980 voorgekom het.

Die aanwas van onvolwassenes en emigrasie was die mees belangrike veranderlikes in die regulering van die groete van 'n groep. Aanvullend tot groeplewende en verspreidende onvolwasse bruinhiënas het 8 persent van die bevolking bestaan uit nomadiese mannetjies.

Groepterritoriums het in oppervlakte vanaf 235 tot 480 km² gevarieer. Geen verwantskap het tussen groepgrote en territoriumgrote bestaan nie. 'n Positiewe verwantskap het tussen territoriumgrote en die gemiddelde afstand wat deur hiënas in 'n spesifieke territorium tussen soogdiervoedsel-items wat gevind is, beweeg word. Die bewegingspatrone van bruinhiënas van verskillende territoriums wanneer kos gesoek word varieer en was afhanklik van die verspreiding van voedsel in die territorium. 'n Hoë lokale digtheid van gevlekte hiënas Crocuta crocuta het skynbaar 'n affek op die digtheid van bruinhiënas gehad, of deur 'n toename in territorium-grote of 'n afname in groepgrote. Die digtheid van bruinhiënas in die suidelike Kalahari is bereken op 1,8 hiënas per 100 km².

Paring is slegs tussen nomadiese mannetjies en groeplewende wyfies waargeneem en het bestaan uit 'n groot aantal, kortdurende besteigings.

Estrus het 'n aantal dae geduur en mannetjies en wyfies was nie vir die totale tydperk bymekaar nie.

Die welpies is gedeeltelike afhanklik van 'n nesgat vir die eerste 15 maande. Gedurende die eerste drie maande na geboorte is moedersmelk die enigste voedselbron. Daarna word die dieet van welpies aangevul deur voedsel wat na die nesgat gedra word deur lede van die groep. Vanaf 'n ouderdom van 10 maande begin welpies teen 'n toenemende tempo kos soek vir hulle self. Gewoonlik word net een werpsel per nesgat grootgemaak maar in die geval van twee nesgate (18 persent) is twee werpsels gelyktydig grootgemaak. Mannetjies en wyfies dra 'n gelyke hoeveelheid by tot die voorsiening van kos aan die nesgat en alhoewel nie definitief waargeneem nie, was daar 'n aanduiding dat helpers 'n bydrae maak tot die oorlewing van welpies.

Bruinhiënas kommunikeer hoofsaaklik olfaktories en visueel terwyl taktiese kommunikasie van geringe belang is. 'Pasting' en mis by latrines is die twee mees algemene vorm van reukmerking by die bruinhiëna. Reukmerking word beskou om 'n inter- sowel as intragroep funksie te hê.

Alle interaksies tussen hiënas van dieselfde geslag van verskillende groepe was agonisties, terwyl interaksies tussen diere van verskillende geslagte van verskillende groepe nie agonisties was nie. Nekbytery wat gebruik word in territoriale verdediging is die mees uiterste vorm van agonistiese gedrag.

Binne 'n groep kry geen individue, of geslag, of ouderdomsklas van diere voorkeur by karkasse. Onvolwasse diere was meer dikwels betrokke by stoeiery as volwassenes en welpies. Soms het 'n gestoeiery oorgegaan tot 'n skynbare meer ernstige aggressiewe gedrag. Laasgenoemde hou waarskynlik verband met die uitsetting van onvolwasse diere.

Die verspreidingspatroon van die voedsel van bruinhiënas het 'n

belangrike invloed op sosiale organisasie; die wyse waarop voedsel versprei is beïnvloed territoriumgrote, wat vir verskeie redes so klein en prakties as moontlik gehou moet word, die "kwaliteit" van voedsel beïnvloed groepgrote. Seleksiedruk verantwoordelik vir die ongewone paringsstelsel word beskou om hoofsaaklik ekologies te wees en vind plaas binne die perke gestel deur die verspreidingspatroon van wyfies. Die faktore betrokke in die regulering van groepgrote, bv. die aanwas van onvolwasse diere en emigrasie word nog nie ten volle verstaan nie. Dit wil voorkom asof wyfies gewoonlik die beste sal doen, in terme van die oorlewing van genetiese materiaal, deur te bly by die groep waarin hul gebore is, terwyl mannetjies hul gene kan versprei deur nomadiese telers te word, of te bly by die groep en 'n bydrae te maak tot die oorlewing van naasbestaendes.

Tussen die Hyaenidae verteenwoordig die drie genera drie verskillende grade wat elk gekenmerk word deur verskillende lewenspatrone. Verskille in die patroon van kommunikasie en gedrag by nesgate tussen die genera word in terme van ekologiese druk op lede van die genera beskryf en bespreek.

Toestande in die suidelike Kalahari word beskou as ideaal vir die voortbestaan van 'n lewenskragtige bruinhiëna bevolking. Geen bestuurspraktyke hoef tans aangeneem te word in die gebied nie. Die sentrale Kalahari Wildreservaat en Namib woestyn dien ook as vestings vir lewenskragtige bruinhiëna bevolkings. In meeste ander bewaringsgebiede is die habitat egter nie geskik vir bruinhiënas nie. Dit word voorgestel dat bewaringsgeoriënteerde navorsing vir die spesies tot geselektierde landboukundige gebiede wat nie geskik is vir kleinvee gerig word.

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Results and discussion

I have calculated the mean mass of 13 brown hyaenas less than 24 h old which were born in captivity as $693,2 \text{ g} \pm \text{s.e. } 17,58$ (Schultz 1966, Lang 1958 and Anderson In litt.). At four weeks the mean mass of eight of these animals was $1,94 \text{ kg} \pm \text{s.e. } 0,082$, at eight weeks the mean mass of four was $3,49 \text{ kg} \pm \text{s.e. } 0,134$, and at 10 weeks the mean mass of three was $4,78 \text{ kg} \pm \text{s.e. } 0,116$.

The youngest brown hyaena that I weighed was approximately eight months old and weighed 19,9 kg. Two litter mates of approximately 10 months old weighed 24,9 kg and 29,9 kg respectively. Brown hyaenas are full-grown at approximately 30 months of age, although parameters such as ear length, tail length and hind foot length, show little variation after 10 months of age (Fig. A 1).

The mean mass of 11 adult male brown hyaenas that I weighed was $40,2 \text{ kg} \pm \text{s.e. } 0,90$ (Range: 35,0 - 43,3 kg). The mean mass of eight non-pregnant adult females was $37,7 \text{ kg} \pm \text{s.e. } 1,12$ (Range: 28,0 - 47,5 kg). The mean mass of an animal was used in the above calculations if it was weighed more than once. Contrary to the findings of Skinner (1976), there was no significant difference between the mass of males and females ($t = 1,77$; $df = 17$; $p > 0,05$).

There was a large amount of variation in the mass of different adults of the same sex. The amount of variation between the two sexes as shown by the coefficient of variation, which for males was 7,4 per cent and for females was 8,9 per cent, was, however, similar. Although variables such as inherited characteristics and the number of good meals eaten in the recent past obviously play a role here, Fig. A 1 suggests that this phenomenon might also be related to age. Although sample sizes are small, age-class 5 animals were found to be significantly lighter

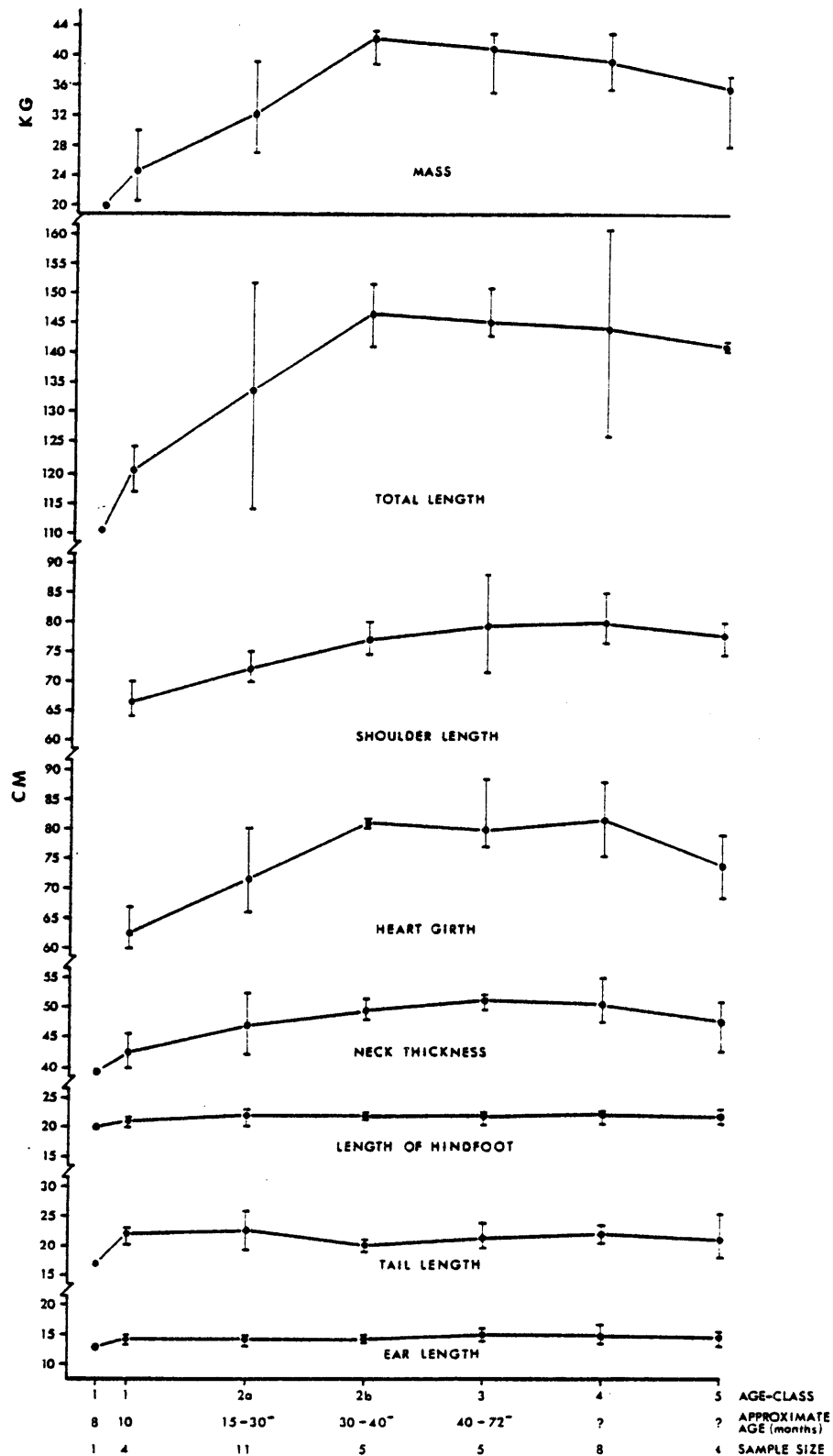


Figure A 1: Mass and linear body measurements of brown hyaenas of different ages from the southern Kalahari; June 1972 - August 1979. The mean and range for each parameter in each age-class are shown.

than adults from the other age-classes combined ($t = 2,97$; $df = 18$; $p < 0,01$). One possible reason for this discrepancy in mass with age could be the fact that older animals, with their worn teeth, have more difficulty in consuming bones that younger ones do, and thus do not have access to as wide a range of food.

Brown hyaenas from most other areas are similar in mass to those from the southern Kalahari. From the southern and northern Transvaal, Skinner (1976) gives the mean mass of five males as $43,9 \text{ kg} \pm \text{s.e. } 2,4$ (Range: $38,0 - 47,5 \text{ kg}$) and that of three females as $40,9 \text{ kg} \pm \text{s.e. } 2,5$ (Range $37,0 - 43,1 \text{ kg}$). I have calculated the mean mass of 10 brown hyaenas collected from various parts of southern Africa, the northern Cape (Liversidge pers. comm.), the Orange Free State (Lynch In litt.), Zimbabwe (Smithers and Wilson 1978) and Botswana (Smithers 1971) as $41,0 \text{ kg} \pm \text{s.e. } 1,2$ (Range: $36,3 - 46,3 \text{ kg}$). A female brown hyaena from Bedford in the eastern Cape, however, is reputed to have weighed $67,6 \text{ kg}$ (Swanepoel In litt.) and Roberts (1951) gives the mass of two unsexed brown hyaenas from the eastern Transvaal lowveld as $72,6 \text{ kg}$ and $59,9 \text{ kg}$.

Various combinations of body measurements and their logarithmic equivalents were tested on a computer in order to obtain the best correlation between a set of linear measurements and body mass. The highest correlation coefficient ($r = 0,919$; $p < 0,001$) was obtained when

R. Liversidge. Alexander McGregor Museum, P.O. Box 316, Kimberley, 8300. August 1973.

C.D. Lynch. National Museum, P.O. Box 266, Bloemfontein, 9300. 23 April 1974.

P. Swanepoel. Kaffrarian Museum, King Williams Town, 5600. 14 February 1973.

body mass was plotted against neck thickness x heart girth (Retief pers. comm.) (Fig. A 2).

P.F. Retief. Department of Research and Information, National Parks Board, P. Bag X402, Skukuza, 1350. November 1980.

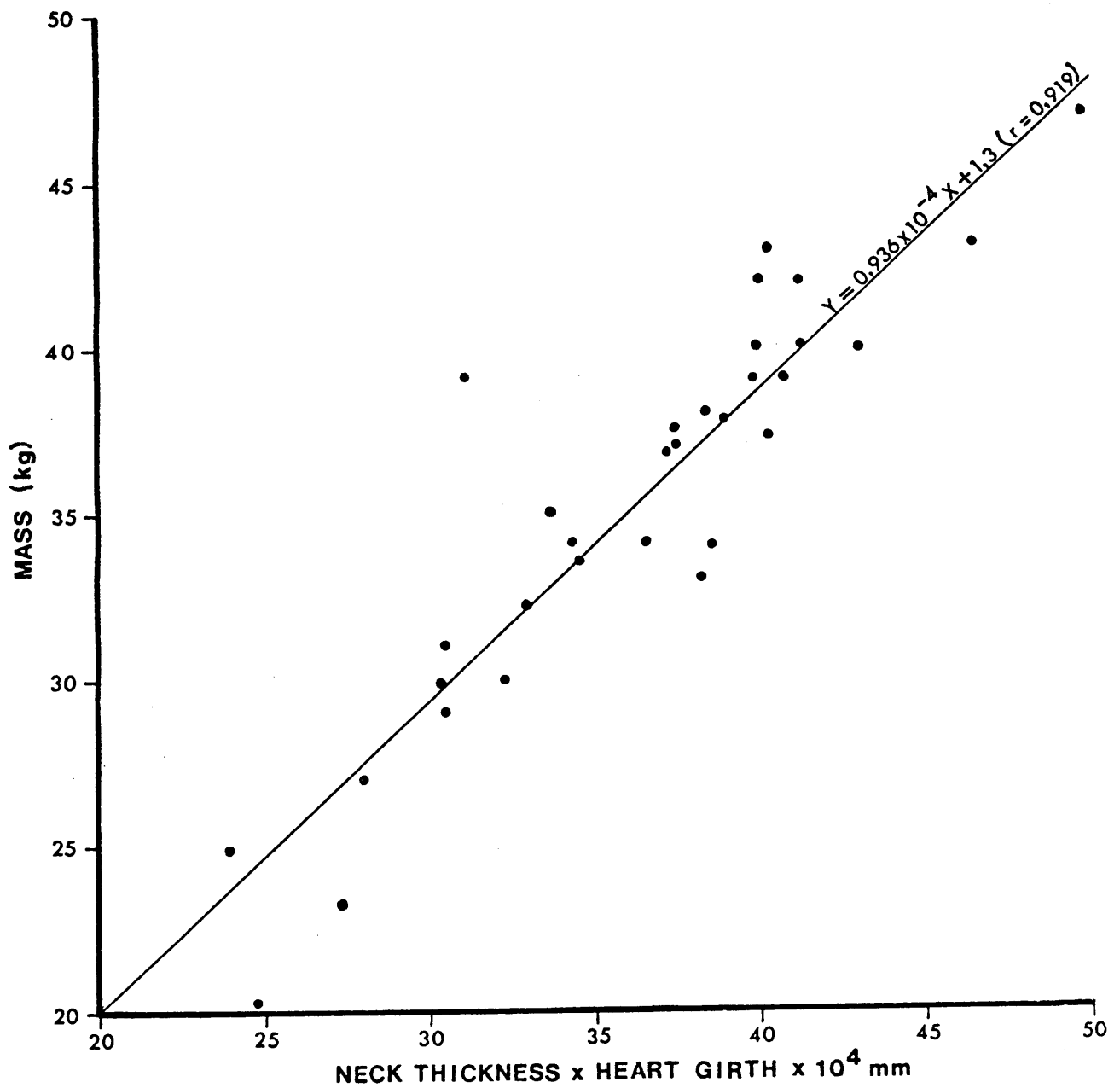


Figure A 2: The relationship between mass and neck thickness x heart girth of brown hyaenas from the southern Kalahari; June 1972 - August 1979.