THE INFLUENCE OF FOOD SOURCE ON THE BEHAVIOURAL ECOLOGY OF BROWN HYAENAS _HYAENA BRUNNEA_ IN THE NAMIB DESERT.

by

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ABSTRACT

On the central Namib Desert coast, in the vicinity of the town of Lüderitz, radio-collared hyaenas were found to be living almost exclusively off seal pups. The maintenance of an excessively large territory containing an abundant and highly concentrated food source appears to be the result of an evolutionary lag in a changing environment, in which inland food sources have recently become unproductive. When the behavioural ecology of these animals is compared with that of brown hyaenas in other areas, the species can be seen to exhibit substantial flexibility. This makes the brown hyaena well adapted to meet the demands of unusual, hostile and rapidly changing environments.

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1. INTRODUCTION

MOTIVATION

Our knowledge of the Carnivora resulting from recent studies, has culminated in a vast amount of descriptive information pertaining to the basic biology of most species becoming available. Behavioural aspects in both wild and captive animals have usually been well covered and in some species the behavioural ecology has received attention. The situation now exists in some families and even species where inter- and intraspecific variations in social behaviour are becoming apparent. Macdonald (1978,1979) has indicated that, with sufficient information on intraspecific variations in behaviour and the selective pressures causing them, we will be able to define the limits of flexibility of the social systems of different species. Comparison of these limits could aid in the elucidation of unexplained differences in carnivore social systems.

An example of this approach is found in Harris (1982) in which the author found urban badgers (Meles meles) to be exhibiting specific behavioural and social adaptations which led him to conclude that the badgers' social organisation, foraging behaviour and patterns of habitat utilisation may be more variable than had been previously indicated.

Apart from defining differences in behaviour between or within species, we can fruitfully relate these differences to ecological aspects and even attempt to explain the selective research. Moreover, the areas in its behavioural ecology which are most productive to these ends are its feeding ecology, social organisation and its interactions with other species.

The prime objective of the present study was to establish the extent to which food availability, quality and distribution influenced social organisation and space utilisation in the brown hyaena and to establish and quantify the effects of interspecific interaction on the brown hyaena's temporal and spatial activity patterns. Having fulfilled these primary objectives, the broader aims of the project were to elucidate the functional and adaptive value of the strategies employed by brown hyaenas in particular, and the Carnivora in general. This will be attempted by comparing present results with those from studies undertaken on brown hyaenas in different environments and to a lesser extent with the results of studies on other carnivore species in both similar and different habitats to that in the proposed study.

THE STUDY AREA (refer Fig.1)

The study area is on the southern South West African/Namibian coast, around the town of Lüderitz (26°39'S, 15°09'E). Lüderitz has a population of approximately 3500, all of whom are involved in industry and commerce in the town itself or are unemployed. The town is situated in an enclave in Diamond Area No. 1 which is a highly restricted zone running along the coast and approximately 100 km inland. As a result

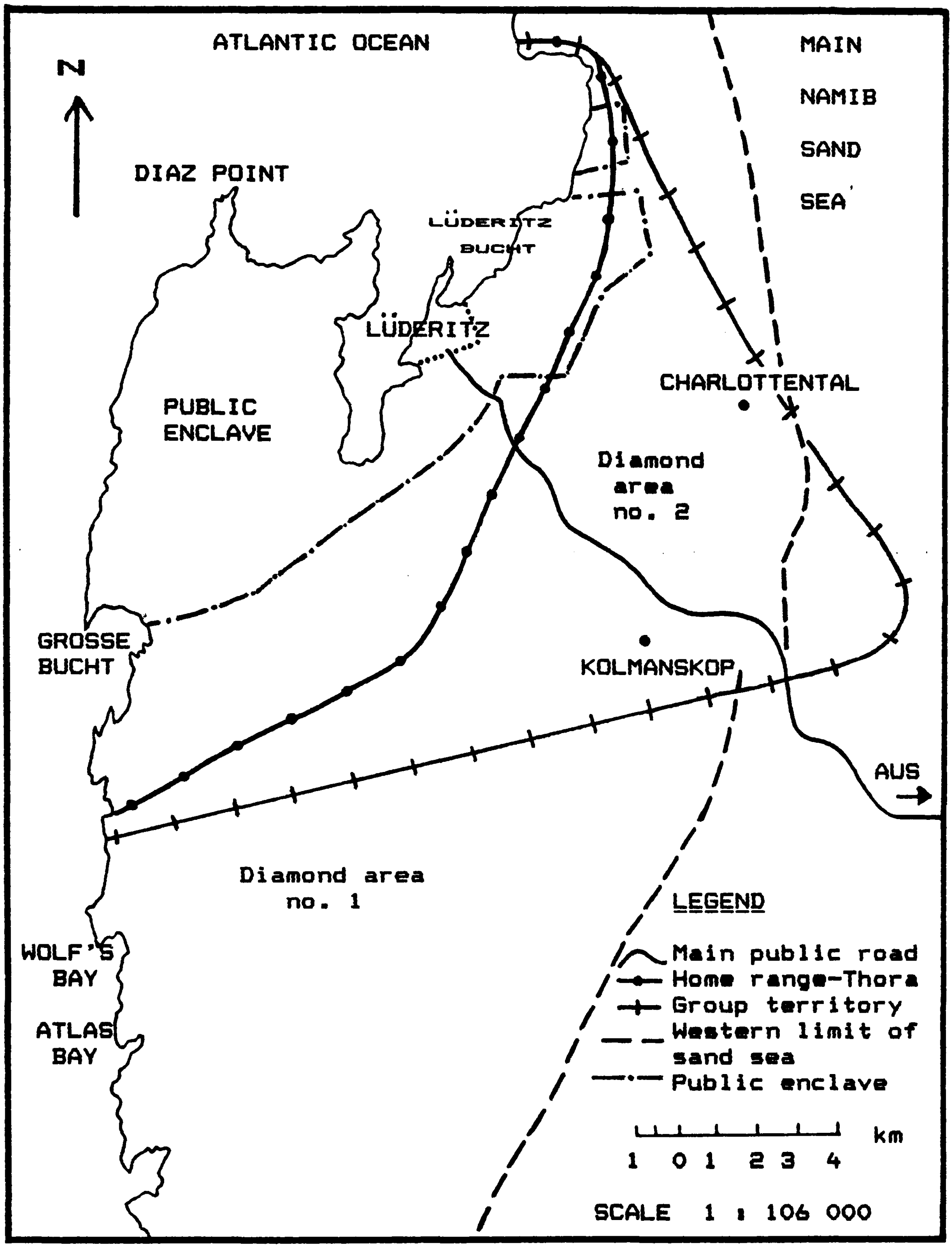


FIGURE 1. MAP OF THE STUDY AREA SHOWING THE GROUP'S TERRITORY AND THORA'S HOME RANGE.

of the presence of surface diamonds, access to the area, which covers 35000 km^2, is restricted by Consolidated Diamond Mines. The area is uninhabited at present, but remnants of earlier mining activities exist in the form of ruined, abandoned towns and machinery (Fig.1).

The enclave in which the town is situated is approximately 70 km^2 in extent and access to this area in unrestricted. This space is used for recreation by the townsfolk and tourists and is traversed by a number of roads. Large tracts of land are used to dry kelp and seaweed on a commercial scale, and this industry, which is extremely labour-intensive, creates some diurnal disturbance in the area. Human activity in the Diamond Area is virtually non- existant with the exception of an annual seal culling operation at Wolf's Bay and Atlas Bay, approximately 30 km to the south of Lüderitz. This lasts 5-8 weeks per annum and, apart from local disturbance at the colonies, disturbance is limited to an increase in traffic on the otherwise extremely quiet roads in the area.

The area has been classified as being extremely dry (Lancaster, Lancaster & Seely, 1984), with an average annual rainfall of under 100 mm (Besler, 1972), and as such forms part of the Namib desert. The cold Benguela current is often considered to be an important factor in the development and maintenance of desert conditions in this region (e.g. Van Zinderen Bakker, 1975; Tankard & Rogers, 1978). Ward, Seely & Lancaster (1983) propose that the desert pre-dates the full development of the Benguela current and its associated upwelling, whilst the current has subsequently accentuated desertic conditions and contributed to the unique character of the present desert ecosystem. The current affects temperatures on the west coast profoundly (Jury, 1985) and causes the occurrence of frequent sub-zero temperatures. The upwelling has a cause-and-effect relationship with the inshore wind field, especially in summer (Kamstra, 1985). The combination of these low temperatures and very high wind speeds on the coast means that animals living here are experiencing extremely cold environmental conditions (Skinner, Van Aarde & Van Jaarsveld, 1984).

Vegetation is very sparse, and, where present, consists of extremely hardy grass species or succulent xerophytes which occur mainly in sheltered drainage channels. To the north and east of Lüderitz the shifting sands of the Namib begin; the main Namib sand sea stretches north as far as Swakopmund and is approximately 160 km wide. The sands are almost entirely unvegetated and have been blown into dunes which reach heights of hundreds of metres in places. South and west of Lüderitz the topography consists of wide gravel plains and parallel rocky ridges which are highly metamorphosed sediments of the Bogenfels Formation and form part of the Archeaen Basement Complex (Mountain, 1968). The coastline is generally highly convoluted and rocky, but the larger bays often have long sandy beaches at their heads. Large flocks of seabirds (eg. flamingos (_Phoenicopterus_ spp) and cormorants (_Phalacrocorax_ spp) are found along the coast but the density and diversity of mammals in the study area is very low. The springbok (*Antidorcas marsupialis*) population was estimated to consist of 6-8 animals and although single gemsbok (*Oryx gazella*) were occasionally seen, they were not resident in the area.

Brown hyaenas (*Hyaena brunnea*), black-backed jackals (*Canis mesomelas*) and feral dogs (*Canis familiaris*) were found in the area in low numbers and although there were no marine mammals resident in the study area itself, Cape fur seals (*Arctocephalus pusillus*) frequently came ashore from two large colonies to the south. No evidence was found to suggest the presence of any other mammal species in the area but it is very likely that some rodent species and a species of hare (*Lepus* spp) occur here.

MATERIALS AND METHODS

Specific materials and methods were dealt with in the subsequent relevant chapters. The general materials and methods used in this study are relatively simple. They had previously been tested and used extensively in the vicinity of the study area and to a limited extent in the study area itself by Skinner & Van Aarde (pers. comm.).

Hyaenas from the group frequenting Lüderitz were captured by means of a baited drop-door trap constructed of 2mm steel diamond mesh (side 200mm). The trap was set in the vicinity of Lüderitz at well-frequented spots such as access routes, drinking points or foraging sites like the municipal refuse dump. Cow and sheep heads, entrails, foetuses, lungs and hooves as well as seal pups were most frequently used as bait, but pigs' intestines, fish and pieces of gemsbok carcass were also used. The bait was sometimes dragged for a distance of up to 3 km in order to lay a scent trail to the trap, and a blood trail was occasionally laid for the same purpose.

Once trapped, the animals were anaesthetised by means of a hand-administered intra-muscular injection of ketamine hydrochloride (Ketalar, Parke Davis Laboratories (Pty) Ltd., Isando) and xylazine hydrochloride (Rompun, Bayer Pharmaceuticals (S A) (Pty) Ltd., Johannesburg). Whilst under anaesthesia, the animals' breathing was regularly monitored; in one case respiration had to be stimulated using an intramuscular injection of doxapram hydrochloride (Dopram, A.H.Robins, Div., Keatings Pharmaceuticals Ltd., Johannesburg.). The animals were weighed and measured where possible, and photographs were taken of their teeth in order to aid in age classification following Mills (1982d). They were then fitted with collars containing LM SB2 radio transmitters supplied by AVM Instrument Co., Dublin, California. Once fully recovered, the hyaenas were released and followed by means of the use of vehicle-mounted, omni-directional and directional antennae connected to an LA 12 receiver from the above supplier.

The hyaena to be followed on a given night was located before sunset if possible, and observations commenced at 18h30 or as soon after this time as possible. After dark, details were observed with the aid of a spotlight and a pair of 8 x 30 binoculars. The animal was observed for as long as possible during the night and observations ceased at 07h30. Field observations were recorded on a tape recorder for subsequent transcription.

RESULTS AND DISCUSSION

a) Trapping success (Table 1)

Traps were set for 130 trap-nights between 17 May 1984 and 25 September 1984. Over this period 13 brown hyaenas, seven dogs and one black-backed jackal were caught. Of the 13 hyaenas trapped, there were five different individuals -yielding a success rate of one hyaena per 10 trap-nights and one previously untrapped hyaena per 26 trap-nights. The latter figure is similar to that reported by Mills (1977) in the southern Kalahari but the former is lower. This may be as a result of the animals' frequent interaction with humans in one way or another since these encounters almost invariably lead to the hyaena being intimidated, severely frightened, shocked, injured or killed. Under these circumstances one would expect the trauma of being trapped to result in a lower re-capture rate than in the southern Kalahari where human-hyaena interactions are extremely rare.

Gemsbok bait accounted for 54% of the successes, whilst the other bait types accounted for the remainder in almost equal

TABLE 1. TRAPPING SUCCESS OVER 130 TRAP-NIGHTS.

SPECIES TRAPPED	INDIVIDUAL	AGE CLASS	TOTAL TIMES TRAPPED	BAIT TYPE	BAIT AGE
H. brunnea	BUBBLES	2b	5	GEMSBOK	FRESH
H. brunnea	BUBBLES	2b	5	GEMSBOK	FRESH
H. brunnea	BUBBLES	2b	5	GEMSBOK	OLD
H. brunnea	BUBBLES	2b	5	SHEEP	FRESH
H. brunnea	BUBBLES	2b	5	COW	OLD
H. brunnea	YORICK	1	3	GEMSBOK	FRESH
H. brunnea	YORICK	1	3	GEMSBOK	FRESH
H. brunnea	YORICK	1	3	PIG	OLD
H. brunnea	FLOPPY EAR	5	2	GEMSBOK	FRESH
H. brunnea	FLOPPY EAR	5	2	FISH/COW	FRESH
H. brunnea	THORA	4	1	COW	FRESH
H. brunnea	MARGY	1	1	GEMSBOK	OLD
H. brunnea	un I.D.	-	-	PIG	FRESH
Canis mesomelas	-	-	1	GEMSBOK	OLD
Canis familiaris	-	-	7	VARIOUS	-

proportions, with the exception of seal carcasses which did not result in a single successful trapping. The relatively strong odour of the "wild" gemsbok bait, when compared to the other bait types may account for the high success rate when using this bait in the Namib. Mills (1977) found that the type of meat used as bait was unimportant.

Fresh bait, i.e. bait which was one or two nights old, accounted for 69% of the trappings, whilst dragging the bait or laying an ox-blood trail to the trap did not result in a successful trapping on the eight occasions that this was done. The fact that fresh bait was more effective in trapping hyaenas is in agreement with the findings of Mills (1977), and the stronger odour of the fresher bait may well be the reason for this.

"Trap-happy" and "trap-shy" individuals appeared to exist: one individual, Bubbles, was trapped five times and was chased from the trap site on two other occasions when she might have been trapped again, whilst other hyaenas in the area could not be trapped at all. It appeared that all individuals encountered the trap with similar frequency and thus the animals' readiness to enter the trap seemed to vary greatly from one individual to another.

On three occasions hyaenas escaped with the bait without springing the trap. It appeared that this was the same individual in each case and that it had learned to shear through the heavy nylon rope attached to the bait without pulling out the release pin holding up the drop-door.

A second trap, constructed of a metal frame covered by steel wire (2mm) diamond mesh (700mm x 700mm) was unable to contain the captive hyaena which bit a hole in the side and escaped.

b) Immobilisation and Collaring

The immobilisation injection proved very difficult to administer by hand in certain cases. These cases involved animals which were aggressive or extremely highly strung.The necessity of having the animal's rump or shoulder close to the edge to the trap for long enough to administer the injection made the whole process rather drawn out, tiring and traumatic for the hyaena in particular and for all involved in general. It is recommemded that some restraining device is used to keep the animal in position during injection or that a dart gun is used when an animal is seen to be highly stressed by its captive situation.

The above problem was aggravated by the fact that the recommended Ketalar dosage of 10 mg/kg and 0,5 Rompun mg/kg (Van Aarde, pers. comm.; Mills 1977) proved inadequate for immobilising the hyaenas. Doses of up to three times the recommended dose had to be given to the more highly stressed individuals before they became tractable and thereafter boosters were required at frequent intervals to maintain sedation. One possible explanation for the high dosage required was that the drugs used may have been subjected to adverse storage conditions, such as heat, prior to their being used on this project. Weight and measurement records for the individuals immobilised are incomplete as a result of the difficulties mentioned above; they also resulted in the animals' taking longer to habituate to human presence once released.

Of the five different hyaenas caught, two were successfully collared. The first was Bubbles, a pre-reproductive adult female of estimated age 3-4 years i.e. Age class 2b following Mills (1982d) and weight 43,0 kg. The second was a mature female, Thora, of estimated age 6-8 years (Age class 4) and weight 49,5 kg. She was the mother of three newborn cubs. Two of the others caught were very young, i.e. Age class 1, and of estimated age 13-15 months. One was fitted with a collar which left enough room for growth because it was anticipated that it might prove impossible to remove it. The cub got rid of the collar, therefore the second cub was not collared.One very old individual (Age class 5) was trapped. The animal was in extremely poor condition and its neck was hairless and completely covered with abscesses and sores which were in an advanced stage of sepsis; applying a collar would have been inhumane. It was injected with long-acting penicillin (Lentrax, May and Baker Ltd., Dagenham England) and released.

The use of Mills' (1982d) method of age determination in this particular study may result in an underestimation of the animals' true age since the method relies on tooth eruption and wear. Tooth eruption may be influenced by the effect of diet on growth and development and attrition is dependent on diet. In the Kalahari, bones are an important component of the brown hyaena's diet (Mills & Mills, 1978), whilst in the present study the animals were found to be feeding almost exclusively on seal pups. Only rarely were old bones eaten, and the bones of the seal pups which were eaten would have been relatively soft. This diet would result in a slower rate of attrition than was the case in the Kalahari, hyaena ages would thus be underestimated. More rapid toothwear in the Kalahari in the case of lions (Panthera leo) was attributed to the inadvertant ingestion of sand during feeding by Smuts, Anderson & Austin (1978) and Mills (1982) speculates that this factor may also play a part in the tooth wear of the Kalahari brown hyaenas. The hyaenas around Luderitz would only have been susceptible to ingesting sand when feeding on the beaches i.e. when eating carcasses at the place of location. Less than 50% of the food consumed was eaten in this way.

c) Radio Tracking and Observation (Table 2)

The hyaena Bubbles was located on 42 nights between 3 June 1984 and 21 August 1984, and observed for a total of 283,3 h. Her temperament was such that it was possible to follow her at a distance of approximately 80 m from the moment of her release. During the course of the study she began to ignore the vehicle even when it was as close as 5-10 m. Once located, Bubbles could be followed for an average of 6,75 h per night, but was unable to be located on 14 nights. The

TABLE.2 LOCATION AND OBSERVATION OF THE TWO ANIMALS CONTRIBUTING THE BULK OF THE DATA.

INDIVIDUAL	DATES	TOTAL HOURS OBSERVED	TOTAL DISTANCE FOLLOWED (KM)	MEAN TIME /TRACKING SESSION (HRS)	MEAN DIS. / TRACKING SESSION	NO. NIGHTS LOCATED	NO.NIGHTS UNLOCATED
BUBBLES	3JUNE '84 - 21AUG '84	283,3	477,0	6,75	11,4	42	14
THORA	22AUG '84 - 26SEP '84	323,3	306,0	10,8	10,2	30	0

main cause of premature termination of a tracking session was the inability of the vehicle to traverse the rugged terrain in the study area, and the subsequent loss of contact with the hyaena.

Thora was located on 30 nights between 22 August 1984 and 26 September 1984, and observed for 323,3 h. Habituation of this female proved much more difficult and she remained much less tolerant of the vehicle throughout the study. This may have been because she was inherently nervous of humans or that she had very young cubs. Thora could always be located at the start of a night's observation and contact was maintained for an average of 10,8 h per tracking session.

The telemetry equipment functioned without fault and had a range of between 100 m and 2800 m, depending on the positions of the receiver and transmitter and the intervening terrain.

Bubbles could usually be located by driving in the vicinity of her known resting sites or in the core area of her home range. If she could not be located before sunset, one's best chance of subsequent location was to attempt to predict her movement using experience from the previous few nights; if this proved unsuccessful, it was unlikely that she would be located. Thora was almost invariably at the den at which her cubs had been left. If she was not there at sunset, she would always arrive within the next couple of hours.

As found by Mills (1977), the spotlight and vehicle, if used with discretion, had no noticeable effect on the hyaenas' behaviour. An exception to this was when the animals were in the environs of Lüderitz. They clearly became less tolerant of the vehicle's presence as one approached the town, and when one tried to follow them in the town itself they often ran from the vehicle or the light. The use of a red filter did little to alleviate this problem and it became more acute if contact with the animals was lost for a period whilst they were in or near the town. This behaviour, which almost certainly influenced the results to some extent, is a consequence of persecution of hyaenas by the population of the town.

2. SPACE USE

INTRODUCTION

A resource should only cause competition when it is limited to some extent. As a corollary to that statement then: the more limited a resource is, the more intense will be the competition for that resource between individuals or species. Brown (1964) for example, has argued that competition for limited resources is essential for the evolution of territoriality.

A resource, such as free oxygen in a natural system, is effectively unlimited, and thus no special behaviour patterns are associated with the utilisation of this resource. Other resources, such as food, mates, water or nesting/shelter sites, are often in shorter supply and, depending on the demand for them by one or more species, specific behavioural patterns have developed in connection with their utilisation. By the same token, a resource which is of such relatively poor quality that it cannot be effectively utilised by a species will have little effect on the species' behaviour, whilst one of extremely high relative quality may elicit special behaviours for its utilisation, providing that a higher quality of resource is of greater value to the species and that it is not over-abundant.

We would also expect the dispersion of a resource to affect the territorial behaviour of a species to a lesser or greater extent: an area containing widely scattered resources will have less value than one containing highly clumped resources, since the more scattered resources will need greater expenditure of energy for their utilisation. This energy expense must be offset against the actual value of the resources. In this case then,the area can be seen as the resource, and the question of distribution again becomes one of quality.

The important fundamental point, is that the actual characteristics of the resource are not directly responsible for significantly influencing animals' behaviour; potential or existing competition for these resources is the major driving force in creating highly developed behaviour patterns. The characteristics or qualities of the resources only affect behaviour through their influence on the provision of opportunities for competition i.e. on the "competition potential".

"Territoriality is now generally regarded as a form of more or less direct competition for critical resources in short supply" (Kaufman, 1983). In many cases food is just such a resource, and here I will consider the effects of food availability, quality and distribution on the behavioural patterns of various species. A number of researchers have drawn attention to the importance of food in moulding the social behaviour and space utilisation of various mammalian species. Mills (1982a) has found that the territory size of the brown hyaenas in the southern Kalahari is affected by the distribution of food, whilst group size depends on the quality of the food in the territory. Kruuk & Parish (1982) conclude that the distribution of food is the main factor affecting territory size in the European badger. Harrison (1983) found that green monkeys (*Cercopithecus sabaeus*) did not maintain fixed territories but responded in a flexible manner to variable competition for food which was governed by the seasons.

The golden jackal (*Canis aureus*) has a highly flexible social system under dependent on conditions of food availability and dispersion (Macdonald, 1979) as has the spotted hyaena (*Crocuta crocuta*) (Kruuk, 1972, 1975). Macdonald (1983) has reviewed the ecology of carnivore social behaviour and concluded that food "patch dispersal influences territory size whereas patch quality independently influences group size."

With a decrease in the availability of food, aggression is found to mount in wolves and foxes, with a resultant expulsion of lower-ranking individuals from the territory or group. It would presumably follow that a degradation of food quality would have a similar effect. Apart from the effects of food on group and territory size however, there is doubtless extensive flexibility in carnivore social behaviour in response to a number of other variables (Macdonald, 1983). Gittleman & Harvey (1982), in reviewing relationships between home-range size, metabolic needs and ecology of various species in the order Carnivora, found that home-range size increased with metabolic needs, irrespective of taxonomic status. These authors implicate energy intake as the major determinant of home-range size and also stress that intraspecific variation in feeding patterns may also play a very large rôle in this respect.

MATERIALS AND METHODS

Data on the hyaenas' movements was obtained by direct observation from the vehicle. The animals were located and followed using radio telemetry, and their direction of travel ascertained by using a compass, the sun, moon, stars and various landmarks. Distances were recorded from the vehicle's odometer and allowance was made for differences in the hyaenas' and the vehicle's paths of travel where necessary. Landmarks such as cliffs, beaches, coves, significant rocky outcrops, roads and other man-made features were also recorded when the hyaenas passed them. The hyaenas' nightly movements were then plotted onto an aerial photograph of scale 1:52 800 using 500 m x 500 m grid blocks on transparent overlays. Direction and distance data were used as the prime means of plotting movements, and minor corrections were then made according to landmark data. A thorough knowledge of the area resulted in very accurate plotting, since the rocky and unvegetated nature of the terrain enabled easy recognition of landmarks on the aerial photograph.

Territorial boundaries and individual home ranges were delineated by the smallest convex polygon method and size was calculated using the ¼ km^2 grid blocks referred to above. The quality of the territory in terms of defence was estimated by calculating defendability (Mitani & Rodman, 1979). The calculation requires two factors, (1) the animal's night range and (2) the size of the home range. The average night range was obtained by converting the actual distance the animal was observed to have moved to a distance/ hour and assuming that movement continued for 13h. The individuals' home ranges were used in the calculations since individual variation in terms of defendability was expected to be significant.

By noting the position of occurrence of various observations and plotting them on a map as previously described, the importance of specific areas with regard to different activities could be seen and a differential space use pattern could be recognised. Examples of these activities are foraging, feeding, caching, scentmarking, resting and denning.

Two estimates were made of the intensity of the use of space occupied by the hyaenas, the first used the distance moved and the second the time spent in each grid block throughout the territory by each individual. They were then analysed separately using the DISSPLA programme (Integrated Software Systems Corporation, San Diego, California.) DISSPLA produces a contoured map with a three-dimensional effect by plotting frequencies per block (i.e. distance moved, or time spent in this case) on the third (vertical) axis. Peaks on the map represent high values i.e. highly utilised space in the territory. The direction from which the map is viewed (N W) and the area which it covers is shown in Fig. 2.

Certain specific areas were favoured by the hyaenas for particular activities, e.g. feeding, foraging, denning, patrolling, interaction with conspecifics and resting. With the exception of the last, these special uses of space are dealt with later in their appropriate chapters. Lying-up localities are shown later in this chapter on a map (Fig. 9).

RESULTS

a) Territory Size and Shape

The home ranges of the two individuals followed, (Thora and Bubbles) are shown in Fig. 1. The entire home range of Thora can be seen to fall within that of Bubbles. Behavioural patterns (discussed in greater detail in Chapter 5) indicate that the boundaries of Bubbles' home range coincide with the territorial boundaries of the group and that this animal's home range and the group's territory are thus congruent. Thora's home range was 107km^2 whilst that of Bubbles was almost exactly double the size, with an area of 220km^2 .

b) Distance Followed Per Night

The shortest distance which Bubbles was observed to have

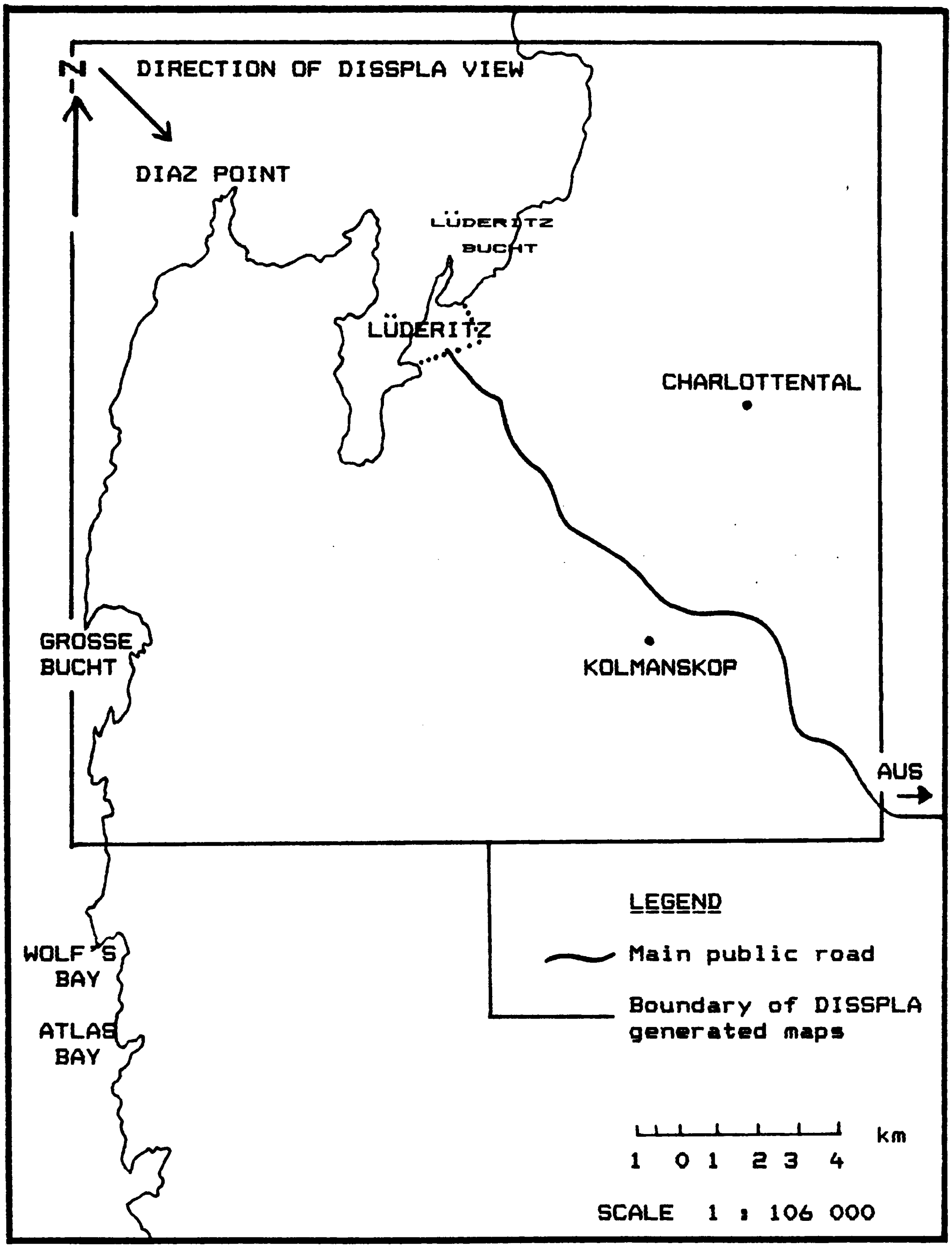


FIGURE 2. MAP OF THE STUDY AREA SHOWING THE AREA COVERED IN THE DISSPLA MAPS AND, THEIR DIRECTION OF VIEW.

moved in a full night (i.e. 13 h period) was 2,0km and the greatest distance was 42,0km. Thora, however, stayed at the den all night on occasions, effectively moving less than 100m in its vicinity, whilst the greatest distance which she was observed to cover in a full night was 34,0km. As indicated in Table 2, the mean distance followed per tracking session was 11,4km for Bubbles and 10,2km for Thora.

c) Defendability of the Territory (Mitani & Rodman, 1979)

Defendability (D) = d/c

where d = average night range

and c = 4.home range/π

i) Bubbles

Total observed distance covered: 477km

Total hours observed : 283,3 h

Total nights observed : 42 nights

Extrapolating to 13h nights : 42 x 13 = 546h

Total h obs./Total possible h = 283,3/546 = 0,51886

Total distance obs./0,51886 = 919,3km (in 42 x 13h nights)

919,3/43 = 21,9km/night = average night range.

D = d/c

where d = 21,9

and c = 4.220/π

D = 21,9/280,1 = 0,0782

ii) <u>Thora</u>

Total observed distance covered: 306km

Total hours observed : 323,3h

Total nights observed : 30 nights

Extrapolating to 13h nights : 30 x 13 = 390h

Total h obs./Total h possible = 323,3/390 = 0,8290

Total distance obs./o,8290 = 369,1km (in 30 x 13h nights)

369,1/30 = 12,3km/night = average night range

D = d/c

where d = 12,3

and c = 4.220/π (note that group home range used because individual home range is not defended)

D = 12,3/280,1 = 0,0439

d) Intensity of Space Use

As reflected by distance moved

The results generated by the DISSPLA program are shown for Bubbles in Fig.3, for Thora in Fig.4 and for the sum of both individuals in Fig.5. The coastline is shown on all the figures. Figure 1 is a map showing major features in the study area and Fig.2 (which includes some co-ordinates) helps to orientate the DISSPLA- generated figures. The vertical scale in these figures represents the total observed distance moved by the animal in each grid block during the study. A peak in the figure thus indicates a large distance having been moved by the hyaena in a particular block. As such, the figures illustrate greater intensity of use of certain localities within the territory, with intensity being measured in terms of distance moved by the animals.

As reflected by time spent

Figures 6, 7, and 8 have also been generated by the DISSPLA program, but in these cases, the criterion for measuring intensity of use is the amount of time which the animal was observed to spend in each grid block during the study. This parameter is represented on the vertical scale. The coastline is again indicated on each figure.

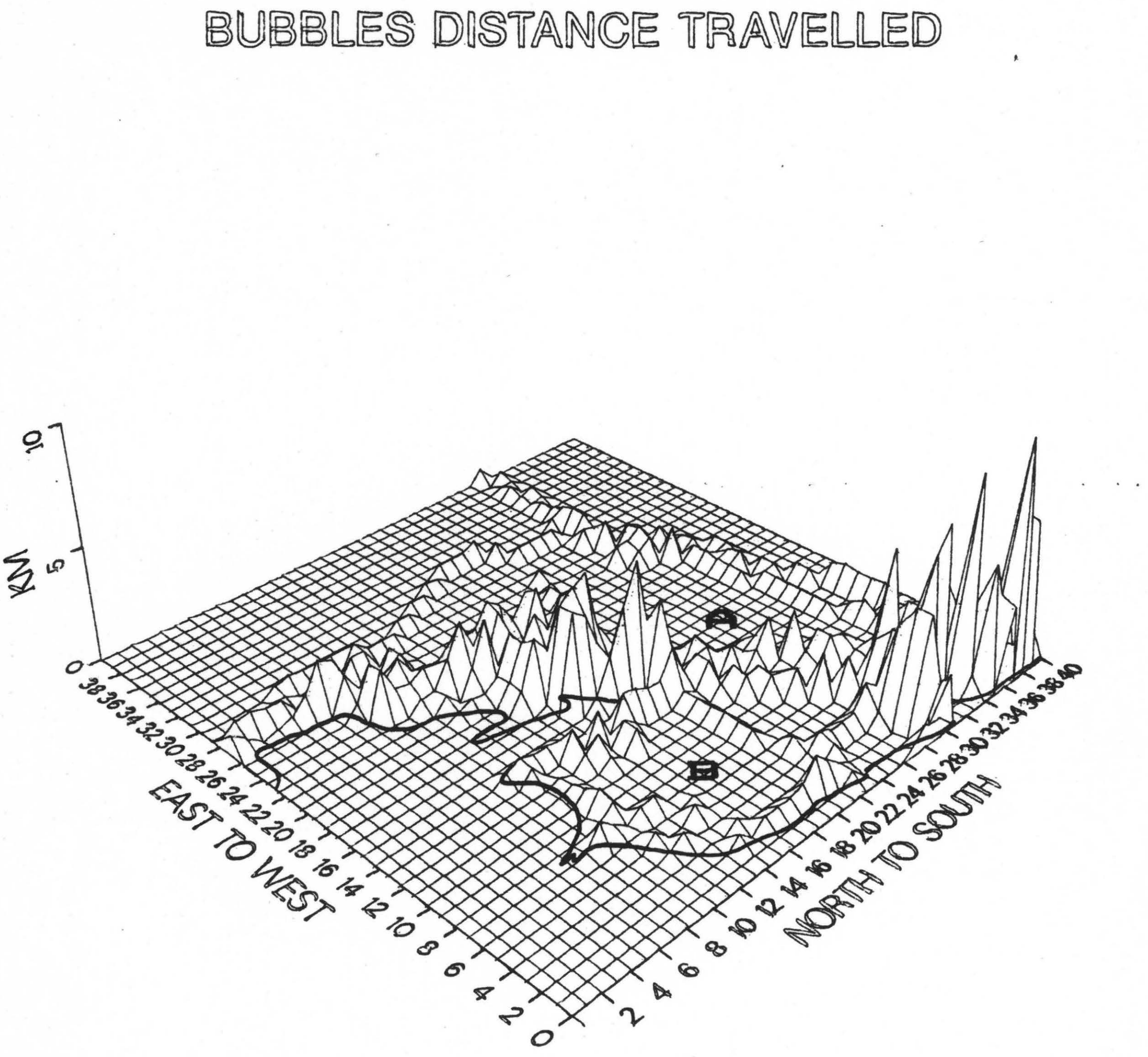


FIGURE 3. THREE-DIMENSIONAL, DISSPLA-GENERATED MAP OF BUBBLES' SPACE USE, BASED ON DISTANCE TRAVELLED BY HER IN EACH GRID BLOCK.

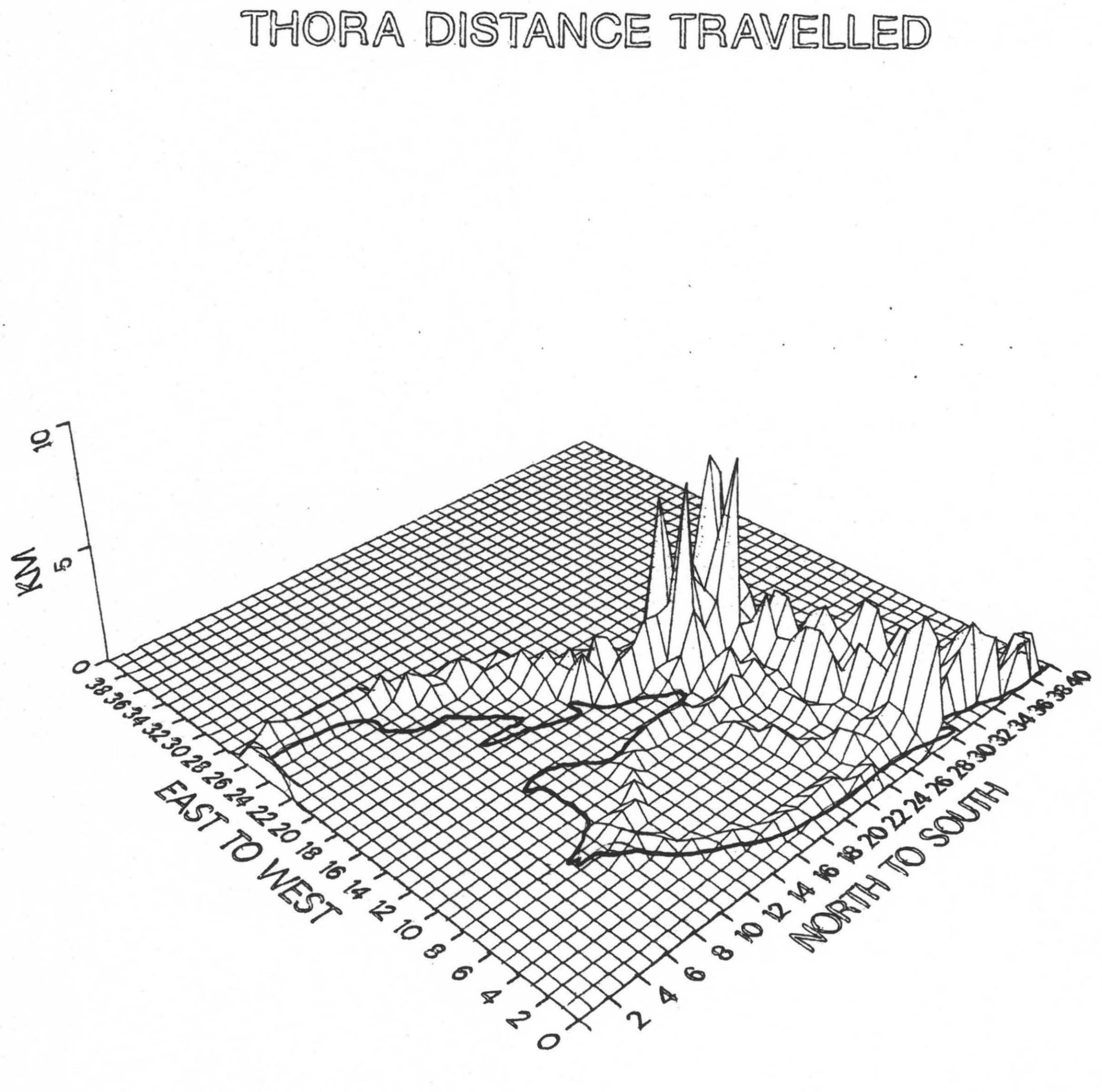


FIGURE 4. THREE-DIMENSIONAL, DISSPLA-GENERATED MAP OF THORA'S SPACE USE, BASED ON DISTANCE TRAVELLED BY HER IN EACH GRID BLOCK.

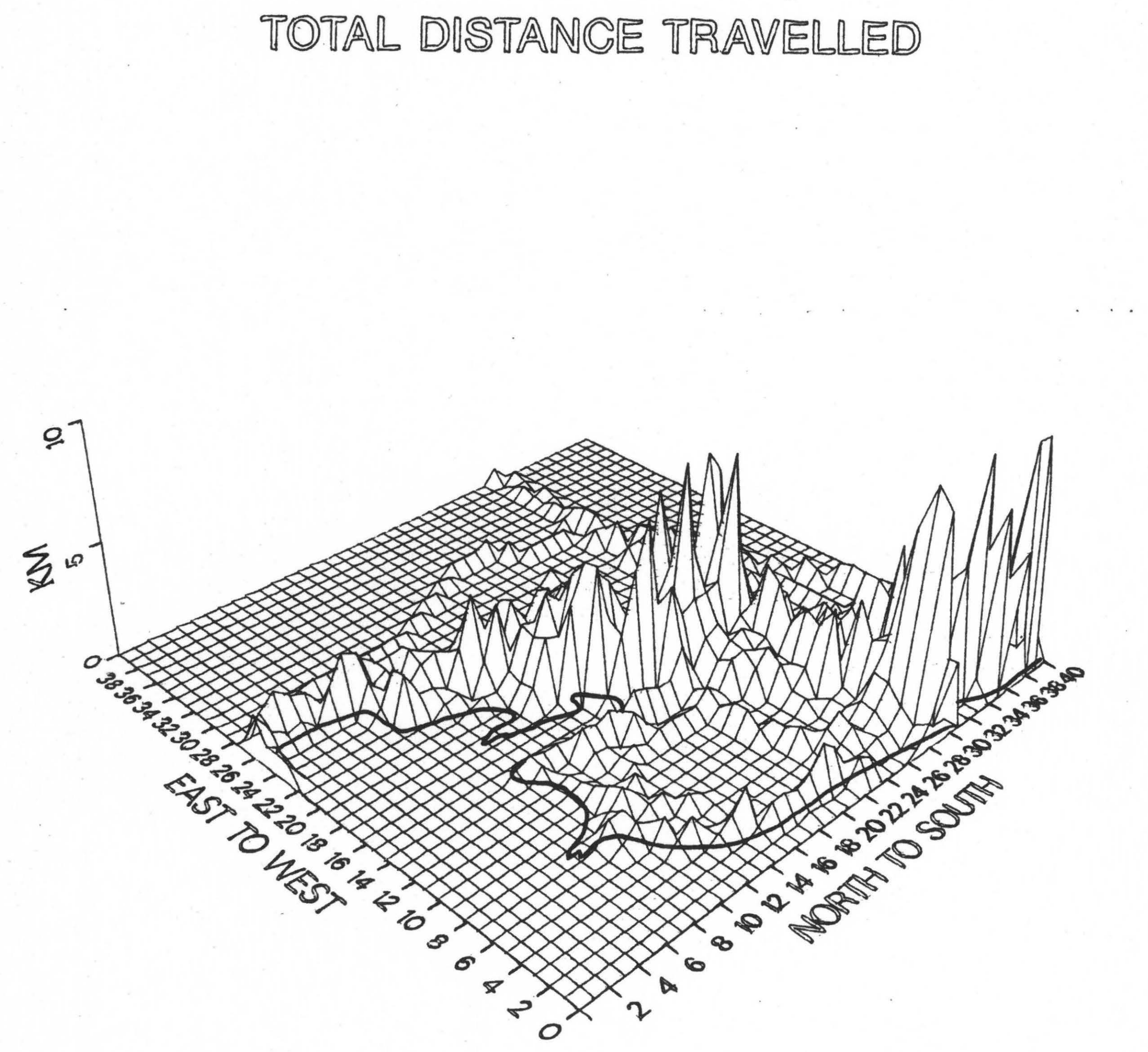


FIGURE 5. THREE-DIMENSIONAL, DISSPLA-GENERATED MAP OF BUBBLES' AND THORA'S SPACE USE, BASED ON DISTANCE TRAVELLED BY THEM IN EACH GRID-BLOCK.

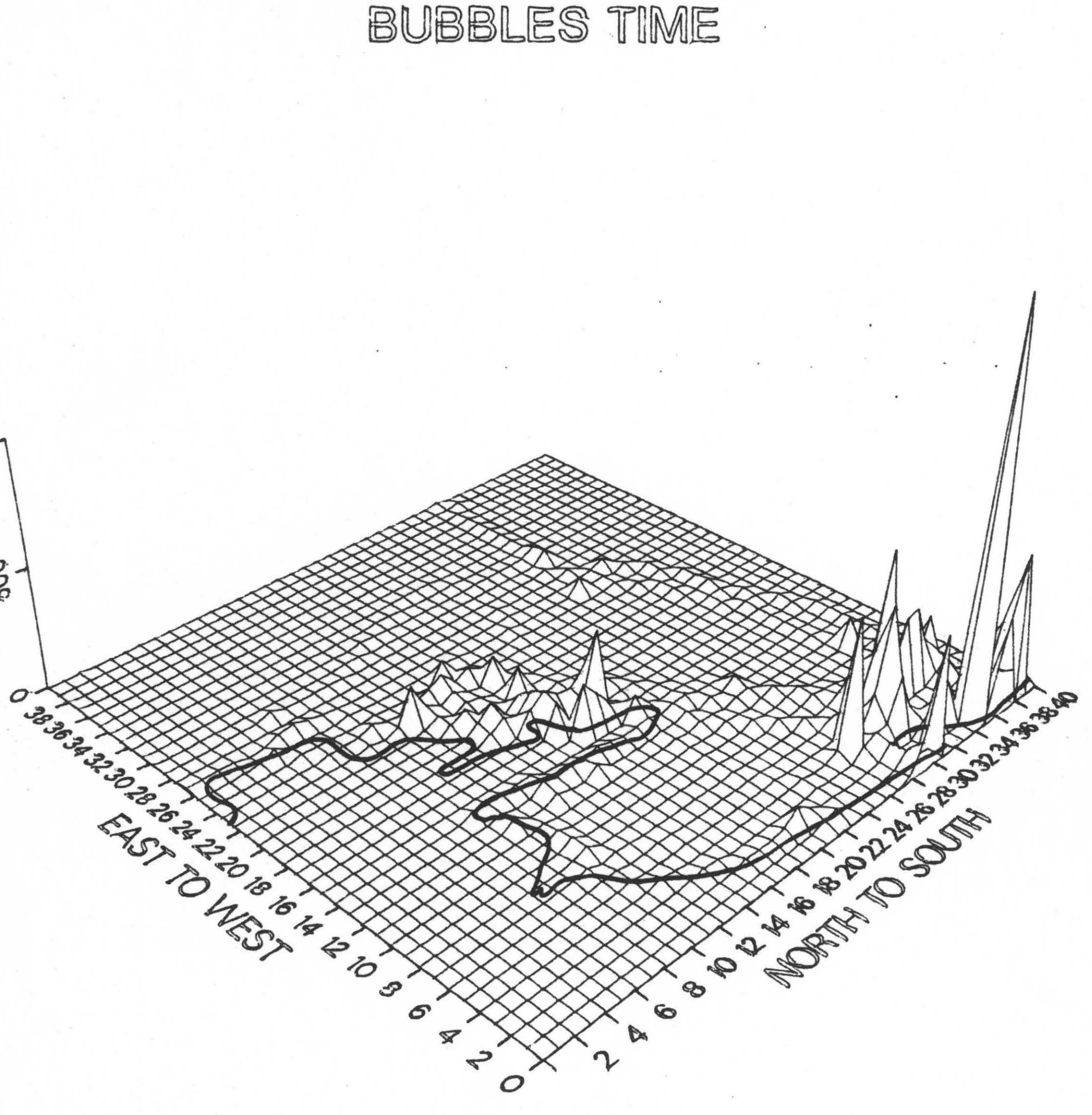


FIGURE 6. THREE-DIMENSIONAL, DISSPLA-GENERATED MAP OF BUBBLES' SPACE USE, BASED ON TIME SPENT BY HER IN EACH GRID BLOCK.

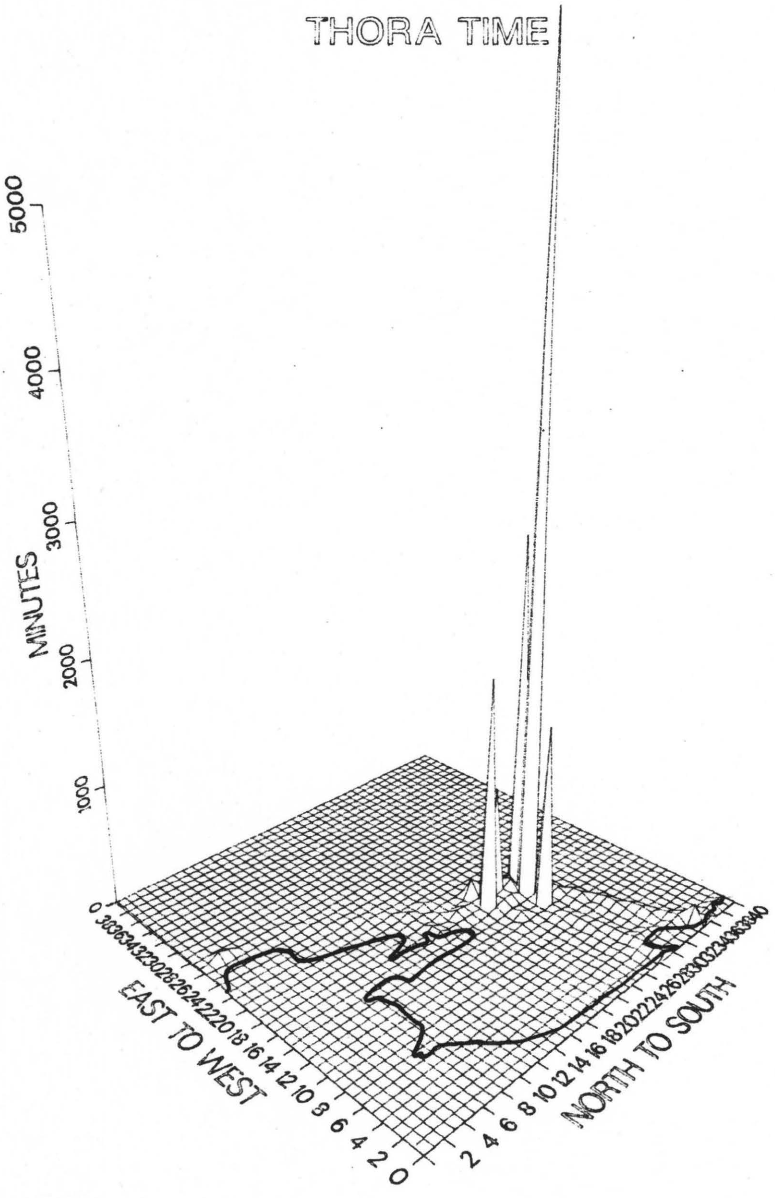


FIGURE 7. THREE-DIMENSIONAL, DISSPLA-GENERATED MAP OF THORA'S SPACE USE, BASED ON TIME SPENT BY HER IN EACH GRID-BLOCK.

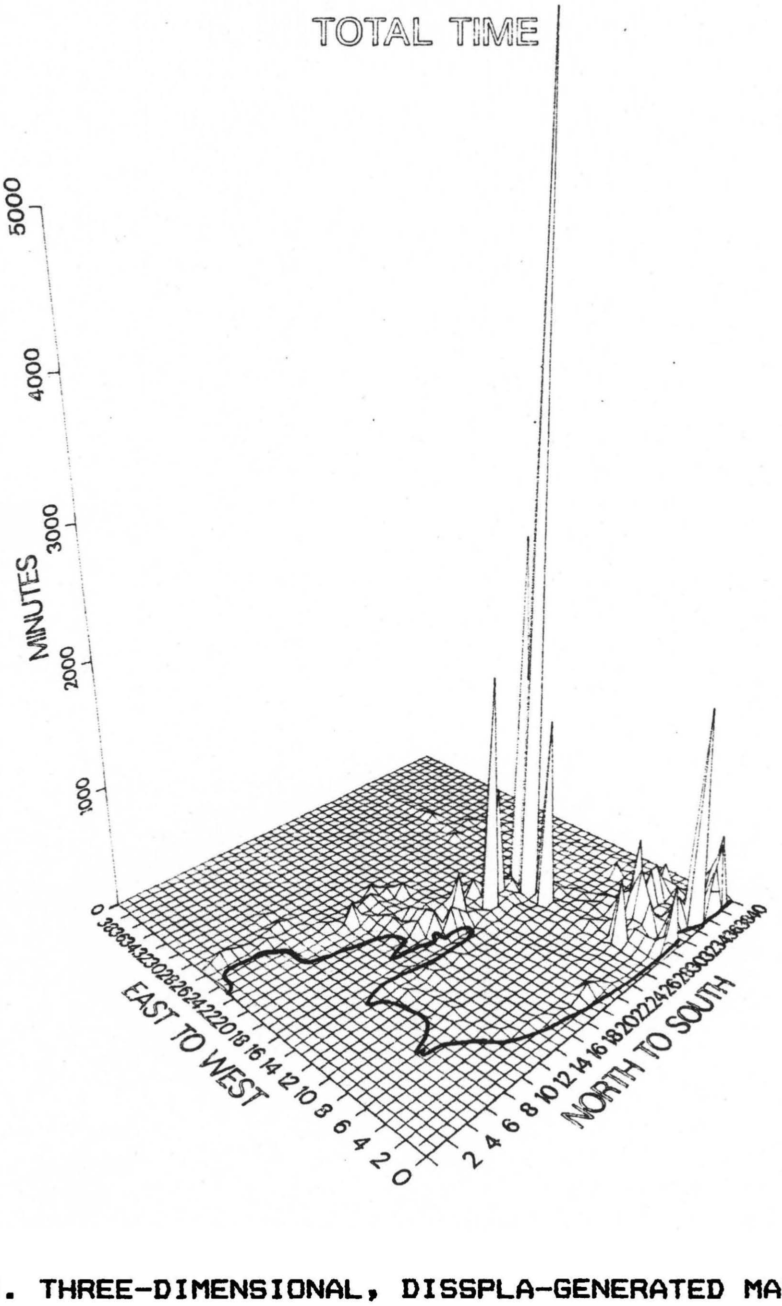


FIGURE 8. THREE-DIMENSIONAL, DISSPLA-GENERATED MAP OF BUBBLES' AND THORA'S SPACE USE, BASED ON TIME SPENT BY THEM IN EACH GRID-BLOCK.

e) Lying-up Localities

Figure 9 is a map of the study area showing maternity dens, overday refuges and resting sites. The dens which are described as being used are those which Thora was observed to utilise as a refuge for her cubs during the course of the study. Unused dens were caves, which could be identified as having been used for the purpose by hyaenas in the past by the fact that there were signs of excavation, there were invariably latrines nearby and there were large concentrations of bones and other unpalatable material such as skin or hair around the entrances to the caves.

The status of the various resting places is indicated in the key to Fig. 9. The data presented is not quantitive in terms of time spent at these sites, and where sites were used more than once this are not indicated. The purpose of Fig. 9 is to show the spatial rather than temporal significance of resting.

Figure 10, a pie chart, shows the amount of time spent resting by Bubbles in the various physiographic zones. Note that Thora never rested anywhere except in the vicinity of one of her dens and that on all occasions (n = 14) that Bubbles' overday refuge was locatable it was in the southern sub-coastal zone. The zones were defined as follows:

coastal - below or less than 100m above the high-water mark
inland - more than 1000m from the high water mark
southern - south of Grosse Bucht (see Fig. 1).

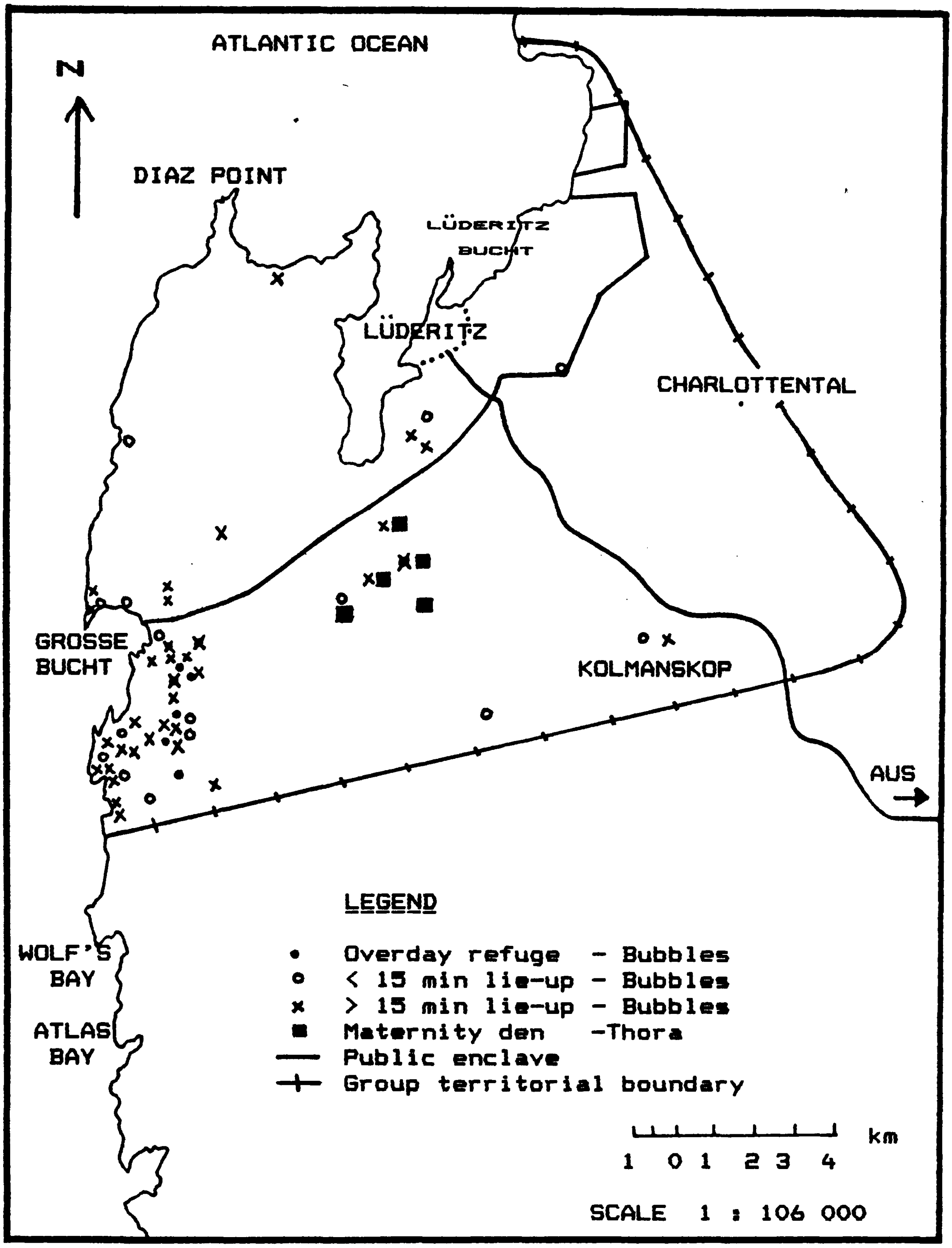


FIGURE 9. MAP OF RESTING SITES AND DENS

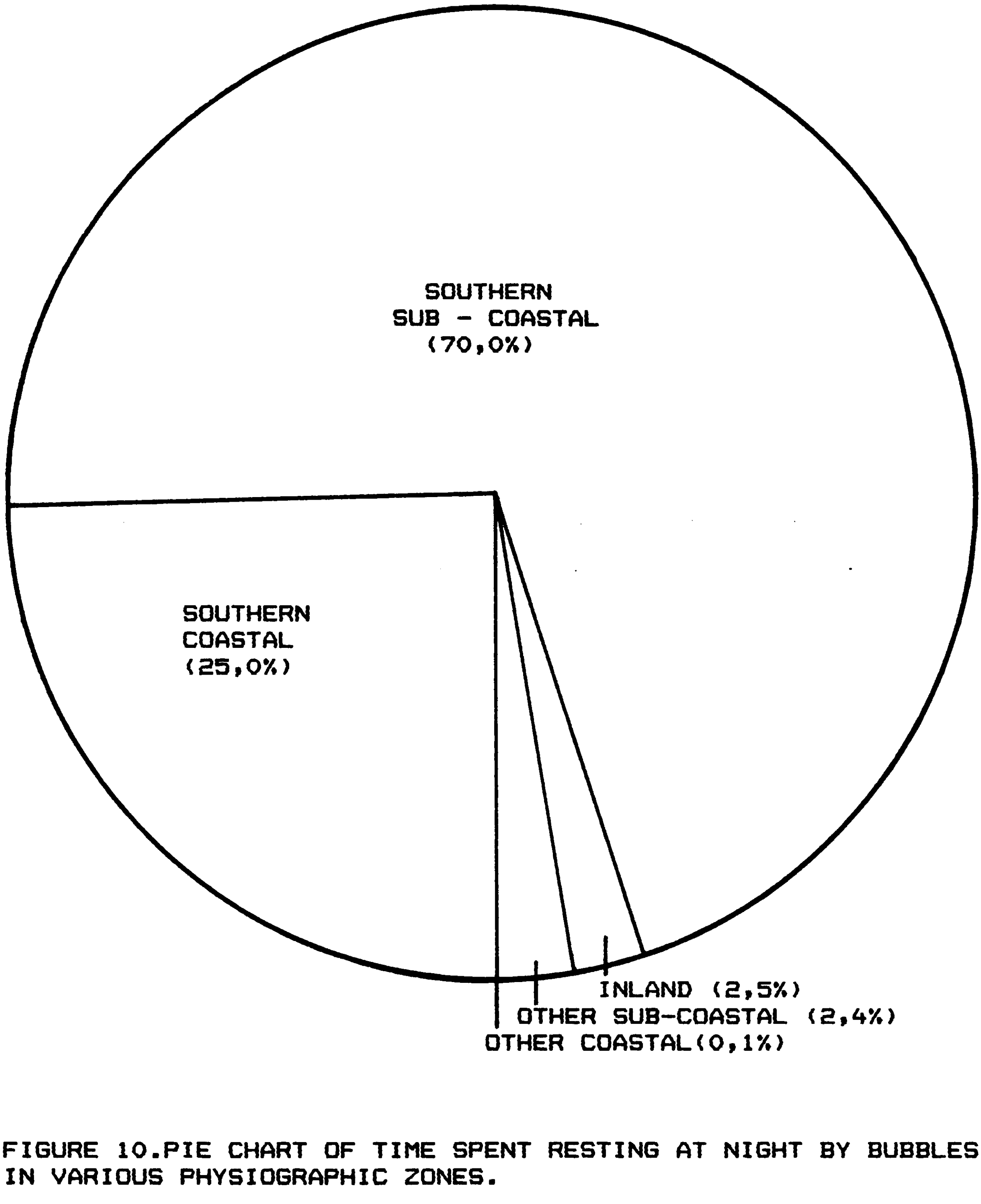


FIGURE 10.PIE CHART OF TIME SPENT RESTING AT NIGHT BY BUBBLES IN VARIOUS PHYSIOGRAPHIC ZONES.

DISCUSSION

Territory Size

Mills (1981, 1982a, 1983a) states that hyaena group home ranges in the southern Kalahari can be regarded as territories, since their land tenure system meets with the criteria generally laid down for a territorial system, and Owens & Owens (1978, 1979b) agree that brown hyaena clans do defend territories. Individual brown hyaenas, however, do not defend a given portion of their home range and are therefore not territorial (Owens & Owens, 1978). As indicated in Fig. 1, the home range of Thora lies entirely within that of Bubbles, resulting in a complete overlap of the two animals' ranges. Mills (1981) does not differentiate between the home ranges in a given group, whilst Owens & Owens (1978) state that individual hyaenas have home ranges to which they generally adhere in their movements, but that there is a great overlap between members of the group. These authors found an average dry season home range (maximum during year) of 40km^2. The home ranges of Bubbles and Thora respectively were 220km^2 and 107km^2.and the average home range was thus 163,5km^2. Other members of the group were frequently encountered around the extremeties of Bubbles' (220km^2) home range. In these cases, the animals' behaviour was identical to that of Bubbles when she visited her home range extremes i.e. the animals were clearly patrolling a route, following a clear track, walking very fast and scentmarking frequently (Chapter 5).

This leads me to conclude that Bubbles' home range is congruent with the group's territory, and that Thora's contracted range was a result of the special pressures acting upon her in her rôle as a mother with young cubs to suckle. Owens & Owens (1978) also noted that the range scope of a female with small cubs was considerably reduced because she generally visited her den twice during a night. This fact has lowered the average individual home range and means that it is probably even greater than four times as large as the average found by the Owenses in the central Kalahari.

The group territory size of 220km^{2} is much smaller than the mean of 330km^{2} obtained by Mills (1981, 1984); it is however larger than the 170km^{2} reported by Owens & Owens (1979b). Gittleman & Harvey (1982) relate carnivore home range size to metabolic needs and ecology, using a home range size of 132,5km^{2} for Hyaena brunnea in their calculations. Chapter 4 deals fully with foraging behaviour and the location of food within the territory: a few facts of relevance to this discussion do, however, need to be mentioned at this stage.

Seventy eight percent of all food items found by the hyaenas were located on the coast within 100m of the sea. These were mostly unscavenged or almost uneaten seal pup carcasses, whereas the items found away from the coast were either small scraps remaining in places where the hyaenas had already finished eating carcasses, or human refuse; the proportion of the mass of food eaten which was found in this area was therefore greater than 78%. Ninety one percent of all food items were located within 1km of the coast, and, of these, 57% came from a 3,5km section of the coast on the southern boundary of the territory. Moreover, the high masses of most items from this particular area would make these proportions even higher if they were based on mass. Since we are looking at the importance of specific areas in terms of food provision, these figures do not include items which were brought to Thora at her inland dens by group members, as it was not possible to ascertain the source of these food items. The figures clearly demonstrate the overriding importance of the coastal strip, and particularly that of a very small section of this strip, with regard to the provision of food. Figure 11 shows the location of this "food-rich" area in relationship to the hyaenas' territory. The shape and vast size of the territory seem to be unrelated to the food source.

Mills (1981) has argued that the smallest possible territory size will be selected for because of the costs involved in maintaining large territories. In the Namib this does not appear to hold true. Possible hypotheses which may explain the maintenance of this apparently excessively large territory are:

i) The animals are using the food-poor portion of the territory for some other important activity such as be shelter from the human activity during the day, when the hyaenas are resting or as prime denning sites which may exist in the food-poor portion.

ii) Some nutritive resource, unavailable near the food source, may exist in the interior e.g. alternative food sources of higher quality and greater security from interspecific interaction, fruits, important mineral supplies or water.

iii) Territorial boundaries may be kept as far from the food source as possible, in order to prevent discovery of the resource by neighbouring clans; this would lead to a decrease in the potential for competition. The shape of the territory, when viewed in the light of intruder pressure and population density of neighbouring areas, may elucidate this aspect. Areas with higher densities and intruder pressures should be more difficult to defend and this should result in an encroachment of those boundaries towards the food source. The defendability of the territory has been calculated following Mitani & Rodman (1979), in order to ascertain whether the territory is capable of being actively maintained by the hyaenas.

iv) As a result of the amount and quality of food available and the ease with which it can be utilised, the hyaenas may have enough time and energy at their disposal to maintain a "super-territory", i.e. one larger than necessary, in order to decrease the fitness of other hyaenas and thus increase their own relative fitness (Verner, 1977).

v) The behaviour may be innate and carried over from a time when food supply fluctuated greatly. The hyaenas' inclusive fitness would then be increased by maintaining a territory large enough for the group in the leanest times. This may be more economical than expanding and contracting the territory constantly in response to food supply.

vi) The behaviour may be learned from previous generations of adults who had access to an alternate resource or resources which no longer exist in the present-day unproductive area.

During the course of the study, no important use of the food-poor portion of the territory was identified, which would have supported hypothesis i. Although the denning and resting sites were away from Lüderitz and other human activity, Fig. 9 indicates quite clearly that the inland extent of the territory was not a result of the interior being used for shelter. Bubbles tended to lie up in the southern coastal region and Thora at the dens in the central area, directly south of Lüderitz.

Hypothesis ii has no foundation: on one occasion only was an old piece of cattle-hide (a very poor quality food item) found near Kolmanskop in the interior. No fruit or usable minerals existed in the area, and when the animals drank, it was from man-made sources such as pipe-leaks, in the immediate vicinity of Lüderitz.

There is insufficient data on intruder pressure and on populations, in order that gene flow does not spread the inhibitory trait between the populations. The extent to which the hyaenas in the study area are isolated is not clear, but if (as one would expect), the mating system here is similar to that in the southern Kalahari described by Mills (1982b), then a large amount of gene flow would be expected.

ii) Low dispersal throughout the life history should favour the existance of inhibitory traits. As above, one would expect a reasonable dispersal rate in this species.

iii) Behavioural inhibition is of less importance than inhibition by physiological means (such as secretion of a toxin) since the animal is physically limited in the number of others that it can inhibit. The hyaenas appear to use both here; i.e. scentmarking would allow the animals to inhibit others without actually physically encountering them. They thus have the opportunity to inhibit a greater number of competitve conspecifics.

iv) The cost of inhibiting should be low and the value of the contested resource high, but more important is the fact that the defended resource is of very little apparent value, and thus its loss to competitors has no real significance, i.e. the value of the inhibition to the inhibitor in this case would appear extremely low.

To summarise then: although certain of the conditions which favour inhibition are met, the majority appear to be absent in this case, resulting in the rejection of hypothesis iv. Some doubt has also been cast on Verner's (1977) principles by Rothstein (1979).

Kaufman (1983) maintains that a territory might be maintained even when all resources are super-abundant (which appears to be the case here) because it will be useful if resources become scarce and that this is more likley if the territory, once given up, is difficult or expensive to regain. Wagtails (Motacilla alba) have been shown to adopt this strategy by Davies (1976). Fluctuating resources are required for this hypothesis to be relevant. This does not appear to be the case under present conditions in the study area, but the fact that there is one populated town in the area, and three others which have been deserted, does mean that in the last fifty to one hundred years food supply within this particular area may, in fact, have fluctuated in a dramatic fashion, as did the human population. The possiblity even exists that the study group may well have been able to scavenge so much food from the mining towns of Kolmanskop and Charlottental during their hey-dey that the inclusion of the highly productive south-western coastal strip into their territory may not have been essential to their survival, as is the case today; in the past the group to the south of the Lüderitz group may well have controlled the entire output from the seal colony in their territory. Thus, if the hyaenas' present behaviour patterns are as a result of the previously productive food patches which are now defunct, one sees from Fig. 1 that the wide patch dispersal of the past is resulting in a large territory being maintained - a conclusion which is, in fact, in agreement with the findings of Mills (1982a) and Macdonald (1983), i.e. that patch dispersal influences territory size.

Thus, although naturally occurring food supplies appear to be stable at present (and to have been so in the recent past), food supplies in the territory have almost certainly declined rapidly with the exodus of much of the human population. Continuing to maintain what was a food-rich sector of the area on the off-chance that it will become productive again would seem to be an advantageous strategy for the hyaenas to adopt. One must also bear in mind that the hyaenas may not be as flexible in the short term as we imagine. The cultural transmission of information, such as territorial boundaries, is a highly evolved and certainly deep-seated mechanism, which would probably be unable to react quickly to changes (and as discussed earlier, it also should not do so, in order to be most effective in the long term). I would thus postulate that a combination of hypotheses v and vi are correct in explaining the existence of this very large, rather unproductive territory. In all of these discussions, however, the cost-benefit relationship is of great import. Territoriality is selected for when the individuals' resulting increased access to resources outweighs the accompanying expenditure of time and energy and the increased risk of injury and predation (Kaufman, 1983). Davies (1978) states that for territoriality to be of net benefit, the following inequality must hold: $A + B < C + D$, where A = Basic cost of living

B = Added cost of being territorial

C = Yield to individual if not territorial

D = Extra yield gained by territorial defence of resources

If we examine the Lüderitz hyaenas in terms of this equation, we see that A seems to be extremely low and that C is very high, as a result of the large, concentrated and predictable food source (Chapter 4); thus the inequality will still hold even if we have a relatively high value of B and a low D value. This is actually the case, since maintaining the territory is a very expensive exercise and the yield in direct terms is negligible (although the long term yield may be substantial, as discussed earlier).

How are territories maintained? Clearly, maintenance of a territory requires that an individual encounter the perimeter of its range sufficiently frequently to monitor potential intruders (Hamilton, Buskirk & Buskirk, 1976; Smith, 1977) and thus a longer perimeter (i.e. a larger territory) would require greater effort in its effective maintenance. Intuitively one expects a vulnerable territory to be more "expensive" to maintain than a less vulnerable one. A vulnerable territory would be one in which all boundaries are susceptible to intrusion from outside, and the opposite would apply. From Fig. 1 we can see that almost half of the territorial boundary consists of coastline. This part of the boundary is obviously absolutely secure in terms of intrusion by other hyaenas and it thus requires extremely infrequent patrolling i.e. the "territorial perimeter" is effectively halved. the costs of maintaining this specific territory (even though it is very large) are probably considerably less than would be the case in an equal-sized territory which is subject to intrusion from all directions.

In summary: the large unproductive territory is maintained as a result of the "behavioural inertia" associated with cultural transmission between generations ie an evolutionary lag exists in this changing environment. It may also be an advantageous strategy in the light of long term fluctuations in food supply within the territory, and , finally, the great abundance of food allows the hyaenas the "luxury" of going to great expense in territory maintenance whilst enjoying very little immediate benefit therefrom.

Territory Shape

From Fig. 11 it can be seen that the territory shape is not linear and parallel to the coast (and the coastal town of Lüderitz) as one would expect, with these being the almost exclusive sources of food for the hyaenas. The effect of the inclusion of the ghost town of Kolmanskop into the territory can be clearly seen when comparing the home ranges of Thora and Bubbles. Thora never embarked on territorial patrols into the interior but utilised the coast in order to obtain food. Even under these conditions, one sees that the geometry of the coastline results in a reasonably large home range for Thora i.e. by moving between the food-rich area in the south-west (south of Grosse Bucht) and Lüderitz, and by moving

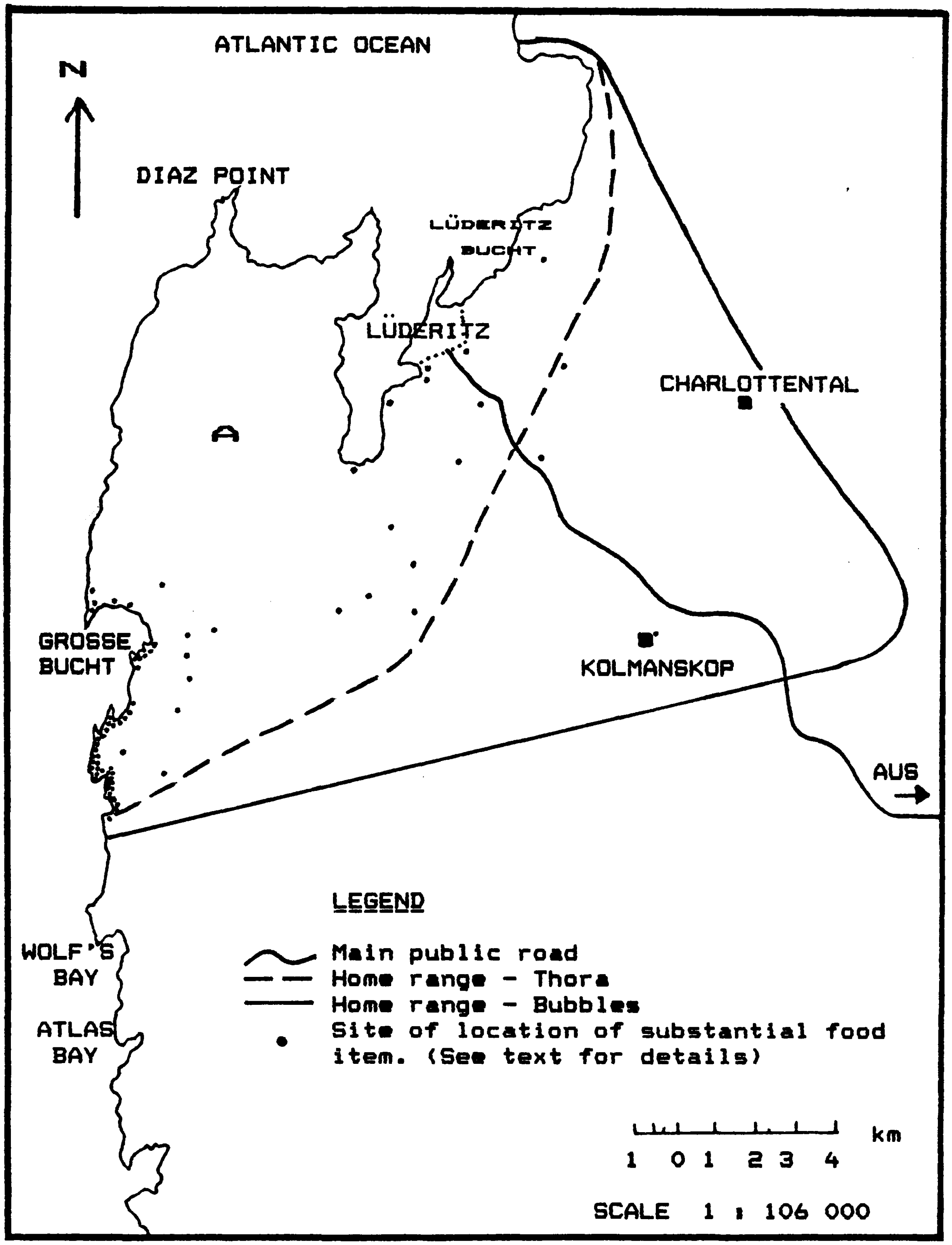


FIGURE 11. MAP OF FOOD LOCATION SITES FOR BUBBLES AND THORA

along the coast, the large peninsula marked A is included in her range although she visited this area very infrequently (Figs. 4 and 7). The same applies to Bubbles, but in her case the inclusion of Kolmanskop results not only in a doubling in range size, but also in a vast, although infrequently used, inland area being included in her range (Figs. 3 and 6).

Distance followed per night

The mean distance for which the individual hyaenas were followed per night, is, in itself, not a very significant statistic, because the mean length of the tracking sessions varied substantially between the two hyaenas viz. 6,75 h for Bubbles and 10,8 h for Thora. The reasons for this are given in Chapter 1. Of greater significance are the maximum and minimum distances travelled. The minimum distance travelled by Bubbles was on an occasion when she had eaten well the previous night and then located a seal carcass early in the evening, with the rest of the night then being spent resting in the same vicinity. Her maximum distance travelled was whilst patrolling the inland boundaries of the territory. Such a patrol is characterised by rapid, directional walking and frequent scent-marking and the following of well-established paths. In Thora's case, she spent a number of full nights with her cubs at the dens and was supplied with food by other group members. The maximum distance she travelled in a night was shorter than that of Bubbles, and was a coastal patrol culminating in a foraging session in the south.

Defendability of the Territory

Mitani & Rodman (1978) argue that territoriality will evolve only when resources are limited and defendable. Their measure of defendability is the frequency with which an animal can encounter the boundaries of its territory, given its normal day range and the size of the home range. This index has been calculated for Thora and Bubbles with values of 0,0439 and 0,0782 being generated respectively. Note that, for Thora, the group home range has been used since this is the actively defended unit and not the individual home range. This calculated value is the ratio of the observed nightly path length, to an area equal to the diameter of a circle with area equal to the home range of the animal. The condition that the home range does not deviate extremely from circular shape is fulfilled in this case. The value of D indicates the number of times which the animal would possibly encounter the diameter of the range in a night. Thus, Thora would encounter the boundary approximately every 23 days, and Bubbles every 13 days. Mitani & Rodman (1978) found that, for primates, species with an index of one or greater were territorial, whilst those with an index of less than one were not territorial. There were exceptions to the former but not to the latter generalisation. The figures obtained for the brown hyaenas are quite clearly very much lower than one, and, using the criteria applied to primates, they would be extremely inefficient in defending their home range. Before drawing any such conclusion, let us examine some of the possible causes of this extremely low D value for a species that is known to be territorial (Owens & Owens, 1978; Mills,1981).

First, Mitani & Rodman (1978) are dealing either with groups which move as units or with single individuals which maintain territories of their own. In the case of the hyaenas, there are a number of animals patrolling and maintaining the territory and thus the sum of the D values for the entire group should be used when calculating the defendability of the territory by the group. A minimum estimate for the study group size is five adults and four subadults (Chapter 5). Assuming that the subadults are entirely ineffective in defending the territory (an assumption that is almost certainly not true), and that the other three adults apart from Bubbles and Thora are as active in maintenance as Bubbles is, and that the same would apply to Thora when not lactating or suckling, we can calculate a total D value of : 5 x 0,0782 = 0,391. As pointed out earlier, at least half of the perimeter is effectively defended as a result of its coastal nature; this means that, for Bubbles, the circle diameter d is halved and the D-value is doubled. The D-value for the group now becomes 0,782. This low D-value may be attributed to the fact that :

i) The subadults have been ignored for the purposes of the calculations, but do in fact contribute to defence to some extent by their presence.

ii) The group size estimation is a minimum; one more adult in the group would increase the D-value to 0,938.

iii) Mitani and Rodman point out that food dispersion affects defendability through its effect on range size, by affecting the ranging patterns of animals. Their calculation of D assumes uniform and random movement over the home range. In the case of the hyaenas, the average night range may be relatively small as a result of a concentrated food source. On certain nights, however, they will not forage, but spend the entire period patrolling the perimeter. My argument is that although this behaviour may be less frequent, the boundary is extremely intensively defended on these occasions i.e. the question becomes one of quality - D indicates the number of times the animal would encounter the boundary in a night, assuming random movement throughout the territory; it does not take into account the length or quality of that encounter. This means that an intensive 13 h patrol along the entire perimeter every eleven days may be a more effective form of defence than a single brief encounter with the boundary, lasting only a few minutes once a night.

iv) We have established that the hyaenas may have a low index of defendability. D, in itself however, is not sensitive to intruder pressure - an important variable when considering defendability, since a low intruder pressure would require a low index of defendability in order to allow a territory to be successfully maintained. The effect of the coastline has already been mentioned in this respect, but the same principle would apply to a great deal of the inland perimeter as well. The interior is extremely inhospitable (particularly the sand-sea on the north-eastern side of the territory) and it is unlikely that this area is inhabited by hyaenas. Thus the need to defend all but the northern and south-western extremities of the territory may be very small indeed (Fig. 1). In fact, as can be seen in Figs. 5 and 8, the hyaenas did maintain a very strong presence in these areas (particularly in the south-west, where intruder pressure appeared to be greatest) and would almost certainly have been encountering the these crucial portions of the perimeter much more than once a night.

v) D relies entirely on the animals' physical presence as a deterrent. The brown hyaenas regularly scentmark their territories and the longlasting effect of these "sign posts" may alleviate the need for the hyaenas to be physically present (reflected by lower D-value) in order to deter potential intruders from entering the territory.

Intensity of Space Use

Mills (1981) and Mills & Mills (1982) found that the extent to which a brown hyaena will frequent a given area is affected by the distribution of food within its home range. Figure 3 shows two major centres of activity for Bubbles : the one in the centre of the map around co-ordinates 20.20 and the other in the south-western corner. The south-western centre is by far the most highly utilised area in the territory, with the "peaks" in this area being substantially higher than anywhere else. Bubbles' intense use of this area can be attributed to the fact that she obtained her food almost exclusively from this area (Chapter 4), that intruder pressure appeared to be greatest here (Chapter 5) and that the area may therefore have required more intense defence. Bubbles' major lying-up and refuge sites were in this area (Fig. 9) and a maternity den, which was utilised by three large cubs during part of the study, existed here. Thus, food, refuge, sociality and defense (in order of importance) resulted in this area being much used.

The central well-used area is around Lüderitz but its attraction is difficult to explain. As a food source the town has limited importance, but there are a number of fresh water sources in its vicinity. The importance of this water to the hyaenas is debatable and is discussed in detail in Chapter 4. Probable reasons for the hyaenas' intense activity around Lüderitz may be related to their curiosity towards and interaction with man and man-made objects (which is apparently very strong), and their attraction to unusual (although small) dietary items which they obtain from around the town.

Another readily apparent feature in Fig. 3 is the well-used corridor from the N.E. corner to the S.W. This corridor links the two activity centres and continues through to the north-eastern coastal boundary. Note that this high-use strip follows the general trend of the coast if one ignores the unproductive peninsula with Diaz Point at the apex. Apart from this corridor, it is apparent that the entire coast is used by Bubbles, and the "ridge" well inland represents the well-patrolled territorial boundary which encompasses the deserted town of Kolmanskop. Two large, sterile and unused inland areas (marked A and B) are apparent in Fig. 3. The implications of this largely unused area being maintained by the hyaenas has been discussed earlier in this chapter.

Figure 6 shows Bubbles' space use (based on time in specific areas). The pattern is very similar to that in Fig. 3, but the high use of the Lüderitz and S.W. coastal areas is accentuated (the importance of the latter in particular is apparent). Relating Figs. 3 and 6 gives an idea of speed (distance/time) of movement in the different areas e.g. the territorial boundary and the corridor between the S.W. and Lüderitz are both relatively "flat" in Fig. 6 when compared with Fig. 10; this indicates reasonably frequent but rapid movement through these areas, and is understandable when viewed in the light of the sterility of these areas.

Figure 4 shows Thora's space use in terms of the distance which she travelled. The three dimensional plot here indicates a similar trend to that of Bubbles, with the exception of the inland perimeter patrol around Kolmanskop. Note, again, the importance of the so-called "corridor", and that the prime activity centre is approximately 6km south west of Lüderitz. This is the area in which Thora established her maternity dens and where her three young cubs remained. The unused area, B, also applies to Thora, and the south-west food-rich area can be seen to be much less used by this individual than was the case with Bubbles. This stems from the fact that she was largely supplied with food by the other group members and was thus relieved of her foraging task. Figure 7 shows the very large amount of time spent by Thora at her maternity dens. The fact that these peaks were not so prominent in Fig. 4 indicates that she was largely inactive in these areas (see Chapter 3).

Figures 5 and 8 show total space use by both individuals. Again, the importance of the strip from the N.E. to the S.W. can be seen, and high use of the area around Lüderitz, Thora's dens and the S.W. coast is apparent.

Lying-up Localities

The southern coastal and sub-coastal areas were of prime importance in providing Bubbles with lying-up sites (Fig. 9) The high concentration of sites in the sub-coastal zone was related to the terrain in this area; steep cliffs and broken, rocky high edges make passage here difficult and ensure minimal disturbance to the hyaenas. Other group-members were frequently seen in this area at dawn and dusk, suggesting that it was a popular over-day refuge for them as well. The area is within the prohibited Diamond Area and human activity here was thus minimal.

Mills (1977) found that brown hyaenas in the southern

Kalahari had no fixed resting sites, and spent the day in suitably concealed places anywhere in the home range. This author does, however, also state that some general areas "such as an area near a potential food source", are more often selected for resting than others. Kruuk (1976), found similar resting behaviour in the striped hyaena (Hyaena hyaena) which was also independant of resting sites and had a very large home range. It appears that, although the principle described by these two authors holds in the Lüderitz area,the predictable and concentrated food source resulted in a specific area (and specific spots within this area) being very much more frequently utilised, as occurred to a limited extent in the Mills' (1977) study. Van.Aarde (pers. comm.) reports that, in the group to the south of the Lüderitz study group, the hyaenas almost invariably returned to the same site to spend the day; these animals were an exceptional case since the seal colony itself was located within the boundaries of their territory.

The hyaenas tended to rest (day or night) close to the food source (the coast), but, as can be seen from Fig. 10, the vast majority of the time spent resting at night was away from the coast itself. I would attribute this phenomenon to the fact that there was a great deal more activity (human, hyaena, jackal and feral dogs) on the coast itself, and thus disturbance here is more likely. The effects of these species on the hyaenas is described in Chapter 5. Figure 10 shows that 95% of Bubbles' nocturnal resting took place in the south-western corner of the territory. The fact that this is where the food was located seems to have been related to this phenomenon, since the hyaenas would frequently either eat a seal carcass close to the place where it was found and then spend a large amount of time intermittently eating the carcass and sleeping, or, more frequently, they would cache the carcass in the sub-coastal zone, with similar behaviour to that described above then taking place at the cache site (Chapter 4). Another reason for the extremely high percentage of resting in this zone is that, as described earlier, it was favoured as an overday refuge. There were occasions when the hyaenas only started moving well after sunset (i.e. observations had commenced) or lay up well before sunrise for the day, and these two periods accounted for a large proportion of the resting time (Chapter 3).

The reason for the exclusive use by Bubbles of only two general areas for resting is that when she was elsewhere in the territory, she was either foraging (i.e. on the coast), or she was travelling between two points (e.g. along the "corridor" described earlier) or on a territorial patrol. The sense of purpose which appeared to prevail when involved in these pursuits appeared to override any inclination to rest. In Thora's case, the same reason appeared to apply, in that rapid directional walking between major sites (i.e. between den and either food or water) characterised her movement pattern; Thora was never seen to rest except in the vicinity of the den. Denning behaviour is discussed in detail in Chapter 5, but it is worth mentioning here that Thora spent much more time at the den in use at the time (almost all of it resting) than has been reported by other workers. Food abundance in the territory is once again implicated.

3. ACTIVITY PATTERNS

INTRODUCTION

Activity patterns, and particularly variations in these patterns, can be explained in terms of ecological variables pertaining to a given species. Also, it is possible to predict certain variations in activity patterns once such variables have been elucidated. Long-term changes or shifts in these patterns can often be related to seasonal changes (e.g. Mills, 1977; Harris, 1982). In a species such as the brown hyaena, where various time-consuming activities such as competing for mates and nest-building are either absent or temporally insignificant and where food is generally available in concentrated high quality packages, food and foraging play a very important rôle in determining the animals' activity patterns. Long-term seasonal changes in activity could not be monitored as a result of the relatively short duration of the study, but nocturnal activity patterns of the hyaenas can be fruitfully related to the specific feeding regime (with its attendant behavioural effects) which exists in the study area. These can also be compared to activity patterns in conspecifics and other species elsewhere. Weather may have profound effects on behaviour patterns, as was found in captive striped hyaenas (Rieger & Weihe, 1975). This aspect was beyond the scope of the present project, and, although it is given some attention in the discussion, data were insufficient to draw any firm conclusions.

MATERIALS AND METHODS

From the data collected on the two radio-collared hyaenas it was possible to calculate their activity budget in terms of seven types of activity. These were :

Foraging - actively searching for food; this could be recognised by the hyaena's behaviour of slow, semi-directional walking in areas which were known to be productive e.g. coast and Lüderitz vicinity. This activity was also characterised by frequent sniffing on the ground and in the air, as described by Mills (1977).

Walking

Caching - defined as an activity where the animal is moving a food item from its place of location to an alternate site for possible later consumption.

Interacting with conspecifics

Eating

Resting - all occasions on which the animal lay down (including to suckle), excluding situations where the animal was actively interacting with another hyaena, sand-bathing or eating.

Other - interacting with other species, digging, sand-bathing, drinking and playing with an inanimate object.

Moving babies - in the case of Thora only. This activity was defined as when she was carrying a baby from one den to another, returning to collect one of the others or leading one or more of the babies between dens.

These data, presented in Figs. 12, 13 and 14, reflect the hyaenas' activity over the 13 h observation period as described in Chapter 1. If an animal was left sleeping before sunrise, and was found in the same spot the following evening at the start of the next observation period, it was assumed that the animal had remained inactive until the end of the 13 h period in question. If it had moved, the assumption was not made, and only the direct observations were recorded.Of the 12 occasions on which a hyaena was left sleeping before sunrise, it was found to have moved on returning the following evening on only two occasions.

From the data it was also possible to construct a nocturnal activity pattern for each individual by calculating the percentage of each hour over the 13 h period (or part thereof) that the animal was observed to be inactive."Active" was as described earlier i.e. all activities except resting. The assumption with regard to early termination of an observation period when leaving a hyaena sleeping also applied in this case.

At the start of an evening, it was often apparent that the hyaena had decided on a given plan for the rest of the night. Although the plan was flexible to a certain extent, depending on the events during the course of the night, the hyaena generally kept to the behaviour which it had started with earlier in the evening. Thus, the possible night plans which a hyaena could embark on could be classified according to the individual.

For Bubbles, they were : i) Walk to the S.W. coastal "food source", locate a seal carcass and eat/rest at the carcass for the remainder of the night.

ii) Patrol/forage along the "unproductive" coastline south of Lüderitz.

iii) Walk to Lüderitz and spend the night foraging and exploring in its vicinity, with a possible movement up the coastline to the north of Lüderitz.

iv) Territorial patrol to the interior via Kolmanskop and the coastline to the north of Lüderitz.

v) Remain relatively inactive in her refuge area; often with a cached seal carcass, or interacting with another hyaena.

For Thora, these were : i) Remain at the den, with a possible walk to a water source to drink.

ii) Walk to the S.W. "food source", eat on a seal carcass before carrying it back to den.

iii) Coastal forage/patrol to the north or south of Lüderitz.

In order to ascertain whether a night plan was influenced by the activities of a previous night i.e. if these activities were ordered or sequential, each individual's nocturnal activities were classified as indicated above. Because the animals' hunger state was suspected as having a large influence on their activity, meals were noted. These were subjectively categorised into substantial (50% or more of a seal pup) and small (< 50% of a seal pup).Food items which took < 10 min to consume were not included in this analysis. These categories proved to be adequate in that there were only two cases where the meal was a borderline case; normally unscavenged or very well scavenged seal carcasses were located. Food items other than seal pups were classified according to their estimated mass, and there were very few items which took < 10 min to consume, apart from extremely small, unidentifiable, insignificant scraps which were picked up whilst the animal was on the move.

Further simplification of the major activities into eating, walking and resting allows a clearer picture of the effect of food on the animals' mobility to be obtained. In this case, if a major walk (longer than 6km) to a food source, and a major walk following a meal took place on the same night, they would be classified as two separate activities. This was particularly applicable in the case of Thora, who would have to walk approximately 11km to the food source in the S.W. before locating a food item.

In order to ascertain whether these three activities were in any way linked, i.e. whether their order represented a Markov chain, the probabalistic sequences in Tables 3 and 4 were analysed through the use of transition matrices which were then compared to random models and statistically tested for significance using the chi-square test. This procedure has been outlined by Lehner (1979).

The times at which the hyaena under observation first entered Lüderitz on a given night, were extracted from the field notes. Times at which other hyaenas were sighted in Lüderitz were also noted, in order to elucidate any trends or patterns in their temporal use of the urban area. An animal was recorded as having entered the town if it came within 30m of a fenced property or currently-used building within the boundaries of the urban area.

RESULTS

a) Activity Breakdown

The proportion of time spent on the various activities (detailed in the previous section of this chapter) out of the total time of observation is shown on the pie charts in Figs. 12 and 13. This breakdown is based upon 283,3 h of observation between 18h30 and 07h30 for Bubbles, and 323,3 h of observation over the same period for Thora. Fig. 14 shows a combined pie chart of the activity breakdown of Bubbles and Thora, calculated from totals for the two animals and not from average percentages. The total observation time on which this chart is based is 606,6 h.

b) Nocturnal Activity Patterns

Graphs of the observed activity patterns for Bubbles, Thora

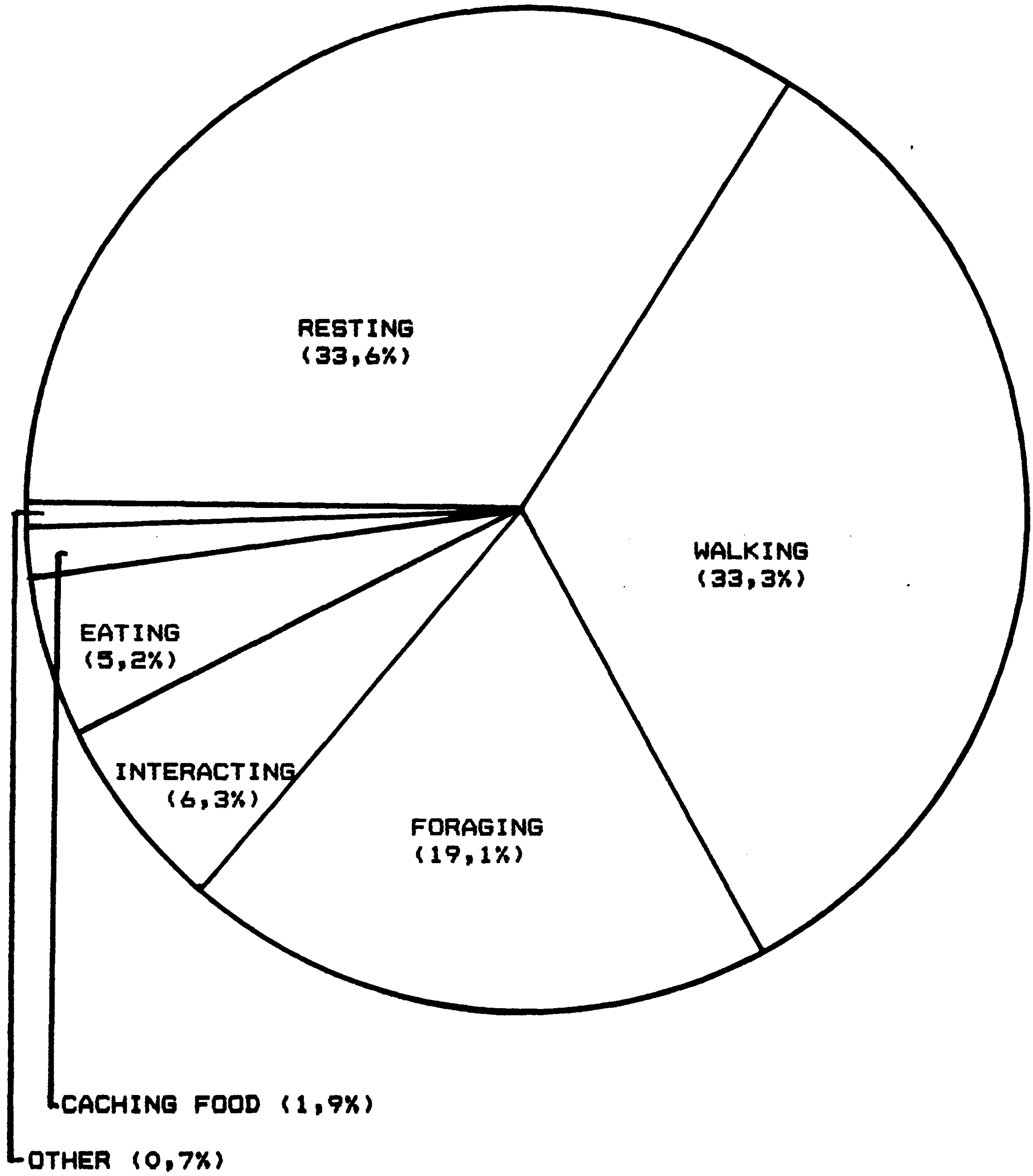


FIGURE 12. PIE CHART OF BUBBLES' NOCTURNAL (18h30 - 07h30) ACTIVITY BREAKDOWN.

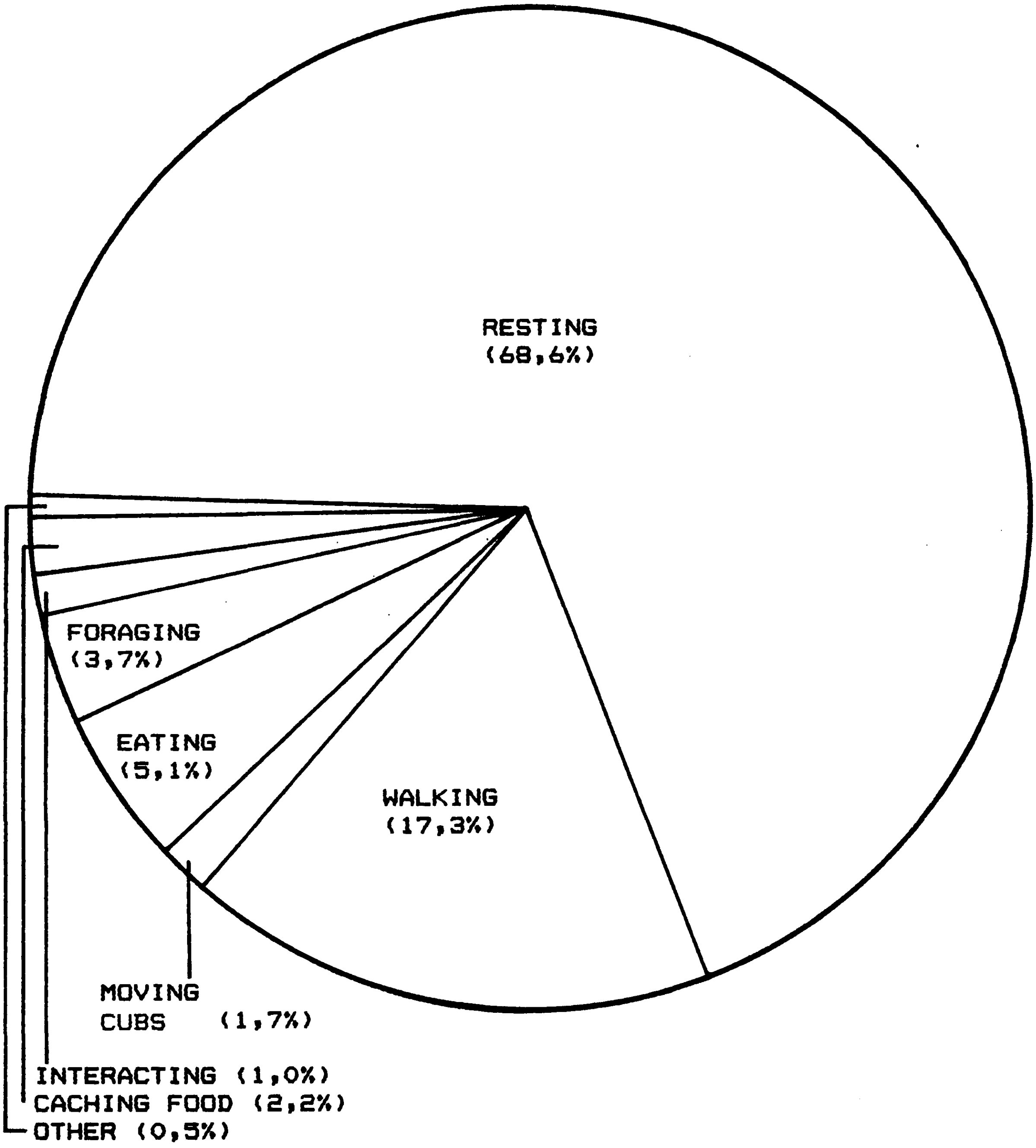


FIGURE 13. PIE CHART OF THORA'S NOCTURNAL (18h30 - 97h30) ACTIVITY BREAKDOWN.

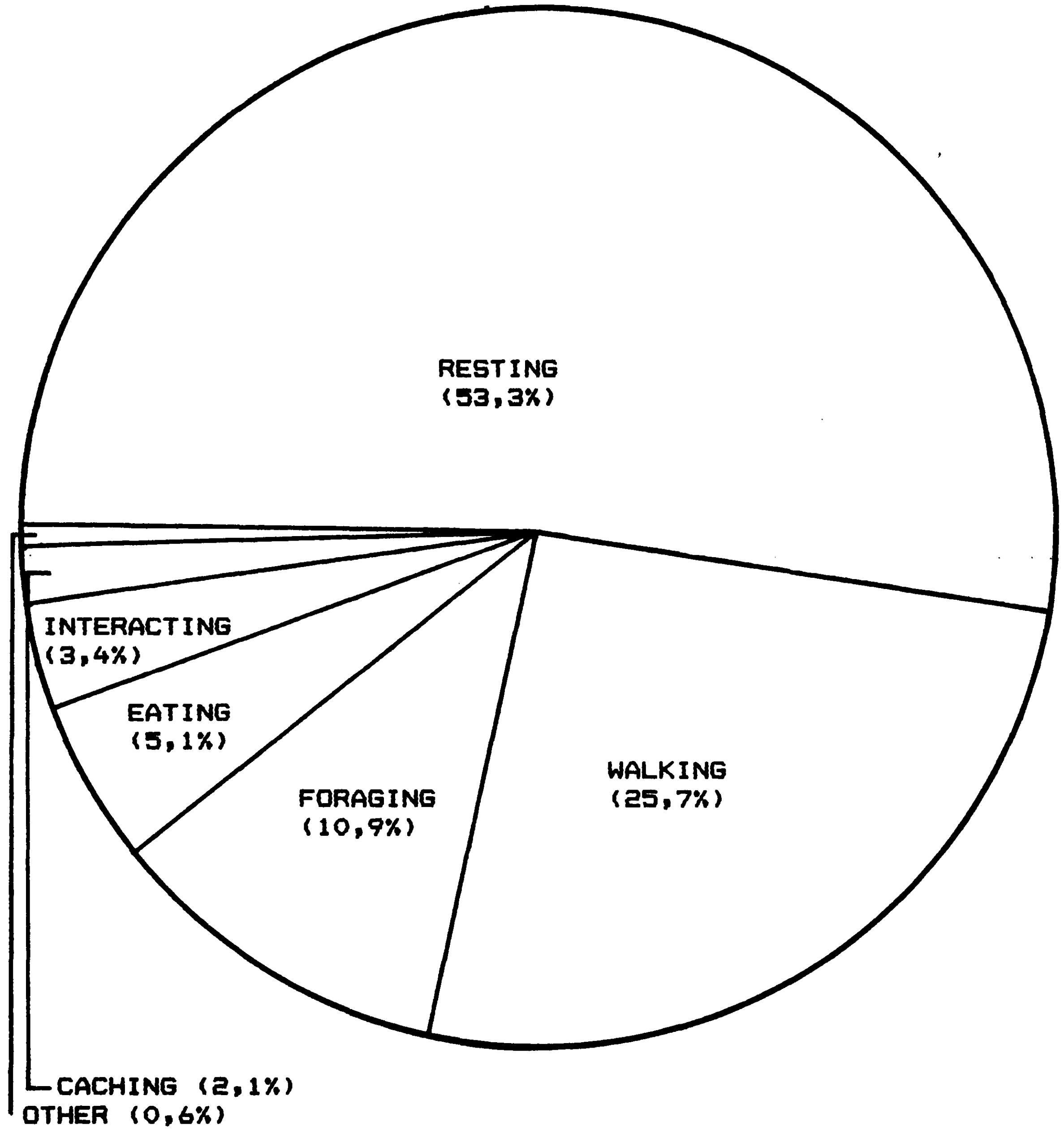


FIGURE 14. PIE CHART OF COMBINED NOCTURNAL (18h30 - 07h30) ACTIVITY BREAKDOWN FOR BUBBLES AND THORA.

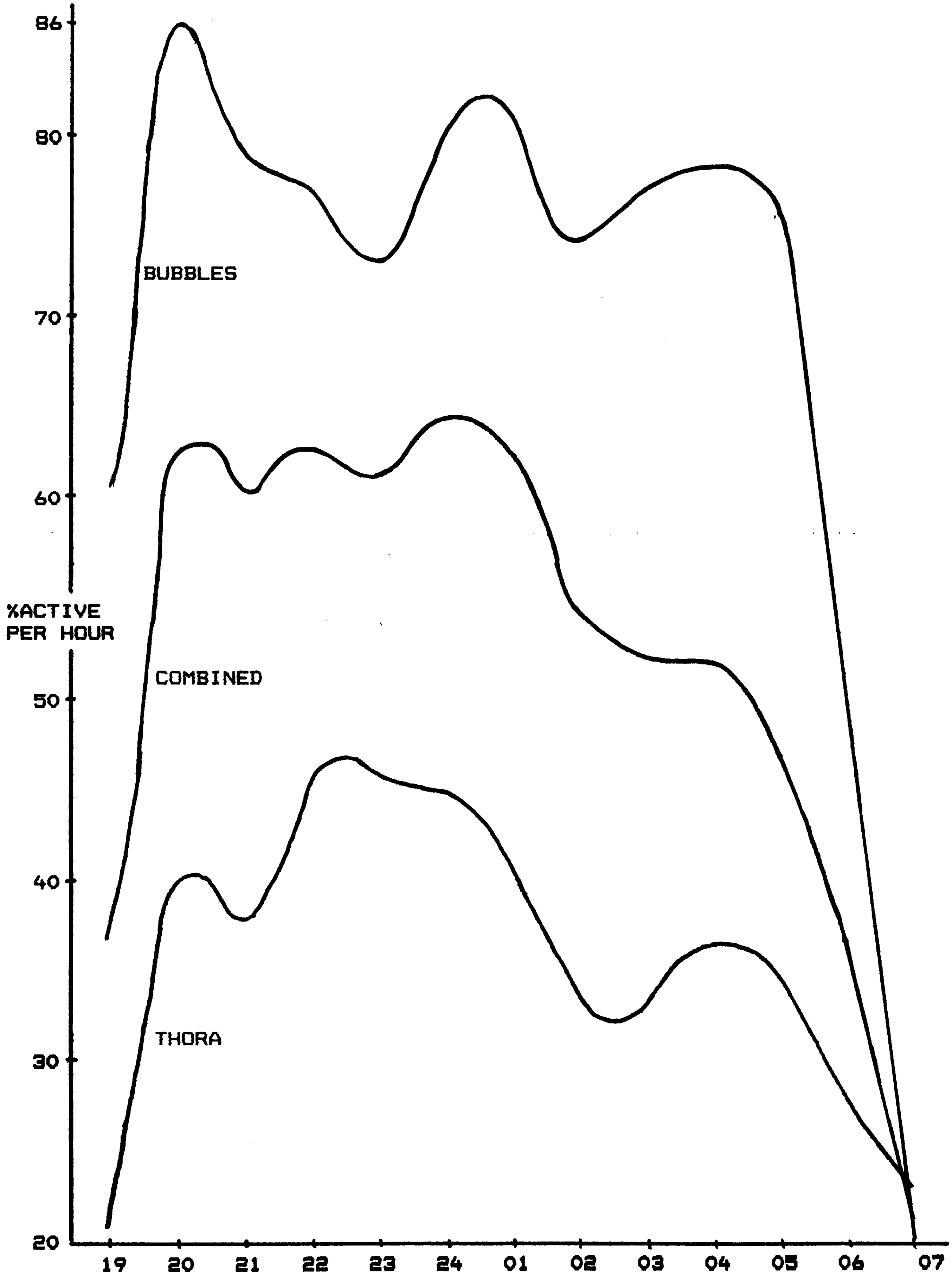


FIGURE 15. GRAPHS OF NOCTURNAL ACTIVITY PATTERNS FOR BUBBLES, THORA AND FOR THE TWO ANIMALS COMBINED.

and total percentages of the two between 18h30 and 07h30 are presented in Fig. 15. The vertical axis represents the percentage of each hour for which the animal was observed to be active; each hour of the thirteen hour observation period is represented on the horizontal axis. The data are based on the same total observation period as in a).

c) Patterns in Night Plans

Bubbles' categorised activities are shown in sequence in Appendix A. The digits indicate appropriate plans according to the text; a dash indicates no observation on that night or an incomplete observation i.e. where an animal may have embarked on a different plan after being left or lost; M indicates a substantial meal and m, a small meal (see earlier for details). The same applies to Thora, whose data are also presented in Appendix A.Tables 3 and 4 show ordered plan sequences for Bubbles and Thora respectively. These represent simplifications of appendix A and were constructed by placing nocturnal activities into the categories : walking, eating and resting.Using Lehner's (1979) procedure, described earlier, the relationship between the three activities was not found to be significant in either case (chi-squared = 3,445; d.f. = 4). Using the same method, no relationship was found between "feeding nights" and "walking nights".

d) Temporal Utilisation of Lüderitz by the Hyaenas

Figure 16 is a bar graph, showing the times of first entry to

TABLE 3. SIMPLIFIED ACTIVITY SEQUENCE FOR BUBBLES.
TABLE 4. SIMPLIFIED ACTIVITY SEQUENCE FOR THORA.

TABLE 3

W	W	—	—	—	R	E
E	W	—	E	E	—	—
—	—	E	—	E	E	W
W	W	R	E	—	W	—
—	W	E	E	R	E	W
W	E	W	—	W	—	E
E	W	R	W	—	—	—
—	W	—	—	—	—	—
W	W	W	E	—	—	—
—	—	E	W	—	E	E
W	W	E	—	—	E	R
E	W	—	W	E		

TABLE 4

E	E	E	E	E	W	E
W	—	—	E	E	W	R
E	E	—	—	W	E	—
W	E	—	W	E	R	W
R	W	E	W	E	W	R
E	W	E	W	W		

W - WALK
E - EAT
R - REST

See text for details

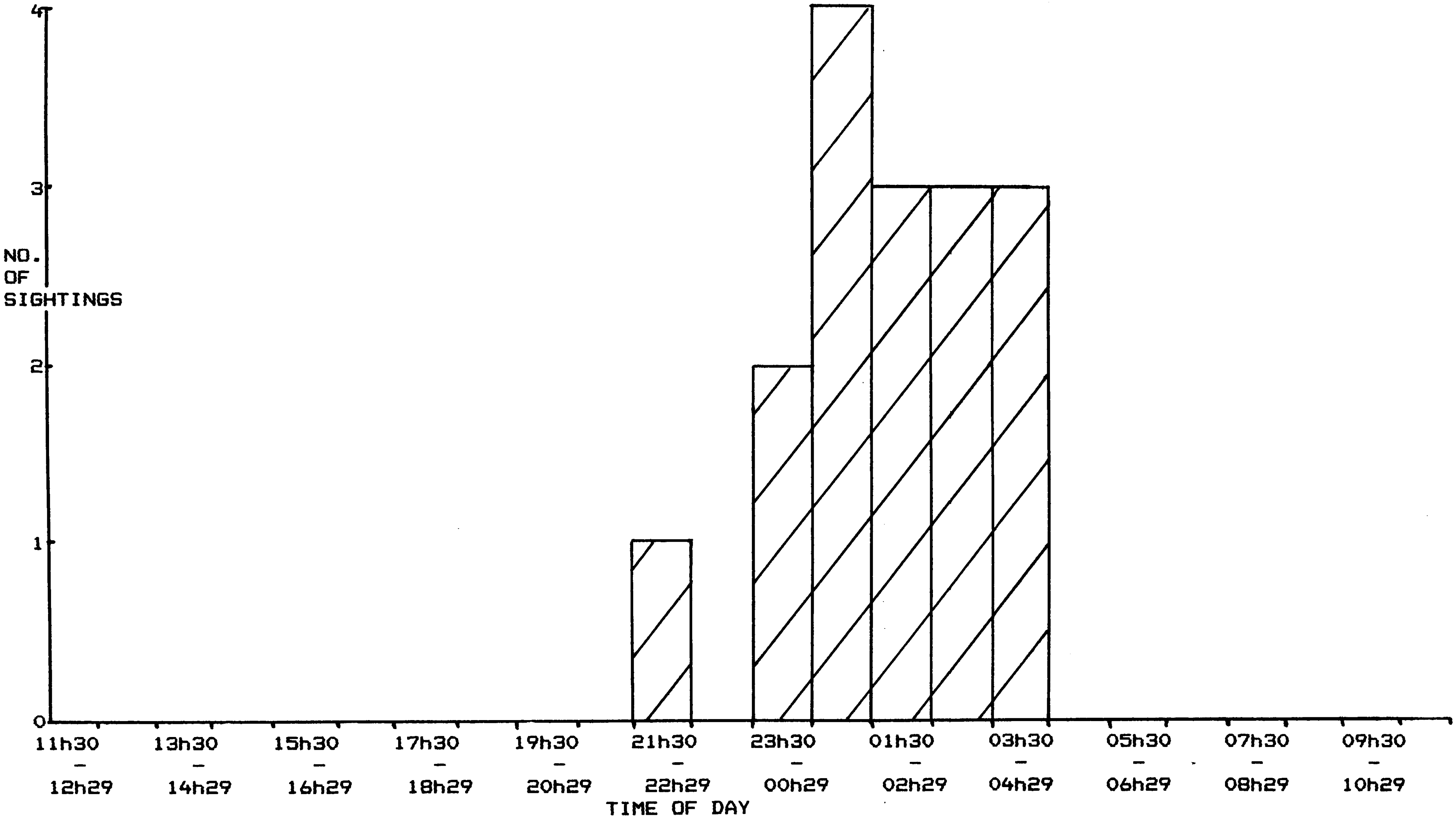


FIGURE 16. BAR GRAPH SHOWING TEMPORAL DISTRIBUTION OF HYAENA SIGHTINGS IN LUDERITZ

Lüderitz by the hyaena under observation, and the times at which other hyaenas were observed in the town. Bubbles was observed to enter town on 10 occasions, and lay up outside the town before entering on three occasions (for 62 min, 43 min and 14 min). Thora was never observed to enter Lüderitz, and other hyaenas were observed in the town on six occasions.

DISCUSSION

The activity budgets shown in Figs. 12 and 13 can be fruitfully compared and related to broader aspects pertaining to the individuals to which they refer. The most prominent difference in the two charts is the relatively large amount of time which Thora spent resting. This resting time is at the expense of time spent walking and foraging : these two activities are much less prominent than is the case with Bubbles. This can be explained by the fact that Thora was provided with food at the maternity den by other group members. The pressure on her to forage for her own food was thus largely alleviated. Thora may also have been more skilled and experienced at foraging than Bubbles, as a result of her greater age, and located food faster and much more efficiently than Bubbles (see Chapter 4). As a possible result of her increased responsibility in caring for her cubs, Thora did not undertake the long territorial patrols which accounted for a large proportion of Bubbles' "walking time". All of Thora's "resting time" was spent at or near a maternity den, and thus the importance of these sites to her was very great. This aspect is clearly illustrated in Fig.17.

Bubbles spent more time interacting with other hyaenas than did Thora (Thora's associations with her cubs were not included); this is a result of the fact that Thora reacted very aggressively towards other group members whilst at her den. Interactions, although relatively frequent, were very short, whilst Bubbles encountered other group members less frequently but when she did so the encounters were of relatively long duration.

The other activities' proportions were fairly similar for the two hyaenas, and it is interesting to note that eating accounted for almost exactly the same proportion of both hyaenas' time, suggesting that this aspect may be a constant in a given environment. Thora would have been expending a great deal of acquired energy in suckling her cubs, but saving energy by resting for most of the time, whilst long border patrols and much walking would have been energy-expensive for Bubbles but she would not have had to cope with the energy-drain imposed by lactation.

The value of combining the data obtained on the two animals (Fig. 14) is questionable since the sample size is very small and the variation between the two has been shown to be relatively great. The data obtained on Bubbles are probably more representative of the group as a whole than is this combined breakdown, since Thora's situation was unusual, short-lived and affected her behaviour profoundly.

Mills (1977) breaks down the brown hyaenas' activity in the southern Kalahari into only four categories. Walking is omitted as a category since this activity is regarded as foraging in the Kalahari. He also analyses the behaviour over the full 24 h period, and not over a part thereof, as was the case in the Lüderitz study. In order to compare the proportion of time for which the hyaenas were active, in these two areas, we can assume, by extrapolating the curves in Fig. 15, that Bubbles was inactive for approximately 95% of the remaining 11 h a day, and Thora for 97%. These values yield figures of 62,7% being spent inactive for Bubbles and 81,7% for Thora. The figure for Bubbles is slightly higher than that of 57,4% obtained by Mills in the Kalahari, and is perhaps lower than expected in the light of the food supply in the Namib. The inactive period for Thora is understandably high in comparison to the figure obtained in the Kalahari. A figure of 2,8% was obtained for the proportion of time spent eating over the 24 h period; this is lower than the figure of 4,2% obtained by Mills, and may be a result of the fact that seal pups eaten in the Namib are higher quality food items than the vertebrate remains which the Kalahari hyaenas rely on for food.

The fact that the Kalahari hyaenas spent 37,6% of their time foraging, as opposed to 10,3% for Bubbles and 2,0% for Thora, emanates from the predictable and concentrated nature of the food source in the Namib.

Aschoff's (1966) bigeminus or two peak activity pattern in the 24 h period has been reported in spotted (Crocuta crocuta) and striped (Hyaena hyaena) hyaenas in East Africa (Kruuk 1972, 1976) and in brown hyaenas in the central Kalahari (Owens & Owens, 1978). Mills (1977) did not find this pattern in the southern Kalahari. In the Namib,,no clear pattern is evident (Fig. 15) although both Thora and Bubbles do appear to exhibit three activity peaks rather than two. For both there were definitely more active and less active periods during the 13 h observation period between 18h30 and 07h30, although these did not coincide for the two individuals as can be seen from the plot of their combined activity. There does however appear to be an increase in activity between 03h00 and 06h00 for both animals.

If the amount of foraging which an animal must do influences the activity pattern in the way suggested by Mills (1977), i.e. the necessity to forage a great deal "fills" the trough between two activity peaks and hides the bigeminus pattern, then we would expect the pattern to be extremely clearly defined in the Namib where the animals forage comparatively little (Figs. 12 and 13). This is not the case, however, and it appears that, as with space use, these animals' active use of time is not directly related to food availability. Earlier it was pointed out that Bubbles' inactive time is less than expected when compared to Mills' data and when food availability is taken into account. She appears to be using the time placed at her disposal (through not having to forage much) on other activities, the most notable being walking i.e. patrolling or moving between Lüderitz and the food-rich south-west.

The probabalistic sequences constructed by categorising overall nights's activity (Appendix A/Tables 3 and 4) for Bubbles and Thora, were found to yield very little relationship between successive nights' activities. Once again, the fact that food is abundant, predictable and easily obtained, means that the animals' behaviour does not appear to be greatly affected by the need to eat and to forage. If food was in short supply, one would expect the hyaenas to devote a night to walking (thereby forfeiting the opportunity to eat) only after eating well on the previous night : a clear relationship between the two activities would thus be apparent. However, in this case, the animals could afford to go without food without previously having eaten well - a secure food supply allowing them greater behavioural flexibility and diminishing the relationship between, and dependance on feeding and foraging.

A pattern which is far more rigid than the above, was the time at which the hyaenas entered and used Lüderitz. Figure 16 clearly shows the importance of the five hours between 23h30 and 04h30 in this respect. The one sighting between 21h30 and 22h30 was of an inexperienced subadult, which was scared by a car after having spent only a very brief period in the town. The most likely reason for this pattern is that the animals were using Lüderitz when the likelihood of interacting with people was lowest. Without having quantitative data to substantiate this hypothesis, it was clearly apparent that human activity in the town had ceased almost entirely by 23h30, and recommenced at approximately 05h00 (by which time the hyaenas had moved out of the vicinity).

The hyaenas' activity patterns did not appear to be profoundly affected by weather conditions. they were observed to be active in very heavy fog, light rain, dust storms and high winds. Weather conditions in the study area were clearly extremely locally variable, as a result of the cold Benguela sea current. The collection of meteorological data from static stations would thus have been meaningless unless a very large number of stations were set up, in order to continually monitor the conditions to which the hyaena under observation was exposed. A mobile station was not feasible. The combination of frequent strong winds and cold temperatures makes the climate on the Namib coast particularly hostile. Hill's cooling factor has been calculated for this area by Skinner _et al._ (1984). This factor expresses the cooling power of the air, and, when its value is calculated as being greater than 20, it is regarded as being extremely cold (Lamb, 1977). Skinner _et al._ (1984) calculated Hill's cooling factor on the Namib coast as 27. The hyaenas' long hair and piloerective ability may contribute to their being able to inhabit this hostile region.Their specific physical and physiological adaptations to this environment have yet to be studied.

4. DIET AND FORAGING BEHAVIOUR

INTRODUCTION

Optimal foraging theory rests on one fundamental cornerstone : as long as a predator is able to improve its survival or reproductive success by hunting more efficiently, natural selection will tend to maximise efficiency in predation. The way in which actively foraging animals can increase their efficiency, is by making the best possible choice with regard to which type of food, and what type of search path to use in hunting for prey (Krebs, 1978). The best decision will be the one which enables the animal to maximise its energy intake per unit time spent in acquiring this energy, and these decisions will obviously vary intraspecifically depending on the environment in which the individual is living.

In the southern Kalahari, brown hyaenas are predominantly scavengers of vertebrate remains, but also supplement their diets with wild fruits, insects, birds' eggs and, very occasionally, by killing a small animal (Mills, 1977; Mills & Mills, 1978). In the central Kalahari, the dietary items were found to be very similar (Owens & Owens, 1978), but with some notable differences. In this area, hyaenas actively hunt much more of their prey, and their diet consists of fewer insects and reptiles. Hyaenas are very opportunistic, and take advantage of any available food resource. This fact is well emphasized when one considers the very wide range of dietary items which have been described by various workers, and which have been adequately reviewed by Mills (1977).

Hyaenas on the Namib coast should require very specific behaviour patterns, in order to forage optimally in this particular environment. Although little data exist from direct observations on the hyaenas' feeding ecology in this area, there have been reports on bone accumulations at brown hyaena dens (Skinner & Van Aarde, in press), stomach contents (Shortridge, 1934; Roberts, 1954 & Stuart & Shaughnessy,1984) and scat analyses (Skinner & Van Aarde, 1981; Siegfried,1984; Stuart & Shaughnessy, 1984).

All the above workers are in agreement that the Cape fur seal (Arctocephalus pusillus) forms the major part of the hyaenas' diet. Findings on the proportions of rodents and birds in the diet are more variable, but this may be as a result of local variation in species composition between the sampling sites.

MATERIALS AND METHODS

No special materials or methods were used in this section of the study. Data were obtained by direct observation, and are presented in maps, charts and tables. The three-dimensional plots of the number of food items per block, and per kilometer travelled per grid block, were produced by the DISSPLA program. In analysing the extent to which the hyaenas cached food, only the large food items which they encountered were considered. A large food item was defined as being one which was equivalent or superior in mass or quality to a scavenged seal pup carcass, i.e. a carcass which was over 50% intact. On this basis, the only potentially "cachable" food items were, in fact, seal carcasses. Only carcasses of this size and quality were considered, since the smallest food item seen to be cached was of approximately this size. A carcass was taken as haveing been cached if it was either moved > 200 m, or if it was obviously moved to a place where the likelihood of it still being there at a later hour or date was increased. Examples of this case are where the carcass was moved above the high-water mark, ensuring that it would not be washed away by the incoming tide, and where the carcass was moved a short distance from the sea and concealed in a bush, hole or under a rock. This reduced the chance of it being found by other hyaenas or jackals foraging close to the water's edge.

The animals' diet was analysed and classified from the direct observation data. The importance of the different food categories was measured according to the time which the animal spent eating each food item. The food items were classified as follows:

1. Unscavenged carcass. Carcass found at the water's edge and normally very fresh.
2. Scavenged carcass. Partially eaten by another animal but 50% or more of original mass; normally 1 or 2 days old.
3. Old/well scavenged carcass. Carcasses which had very little meat left on them, or which were still relatively intact but very old; were largely unable to be utilised by the hyaenas.

4. Seal kill. Only two cases fit into the "seal kill" category : there may have been a number of cases when a pup was killed by the hyaena but was placed in the "unscavenged carcass" category as a result of the hyaena being obscured at the moment of location of the seal.

5. Other. Domestic animal bones, e.g. cow, goat, sheep and gemsbok bones; dog and gemsbok skull.

RESULTS

a) Food Location/Feeding Sites

These are indicated on the three-dimensional map in Fig. 17, whilst the same data are shown as a function of the distance moved by the hyaenas in each grid block in the three-dimensional grid map in Fig. 18. Note that these sites are only for food items which took two minutes or more to eat, i.e. location sites of very small items are not indicated on the maps.

b) Foraging Behaviour

The hyaenas foraged mainly on the coast within 80m of the water, and to a limited extent in the vicinity of Lüderitz. They appeared to use their sense of smell quite extensively in order to locate their prey, and would frequently stand with nose held high, sniffing the wind before proceeding upwind to a food item. When foraging, their behaviour was as described by Mills (1977) and Owens & Owens (1978). The

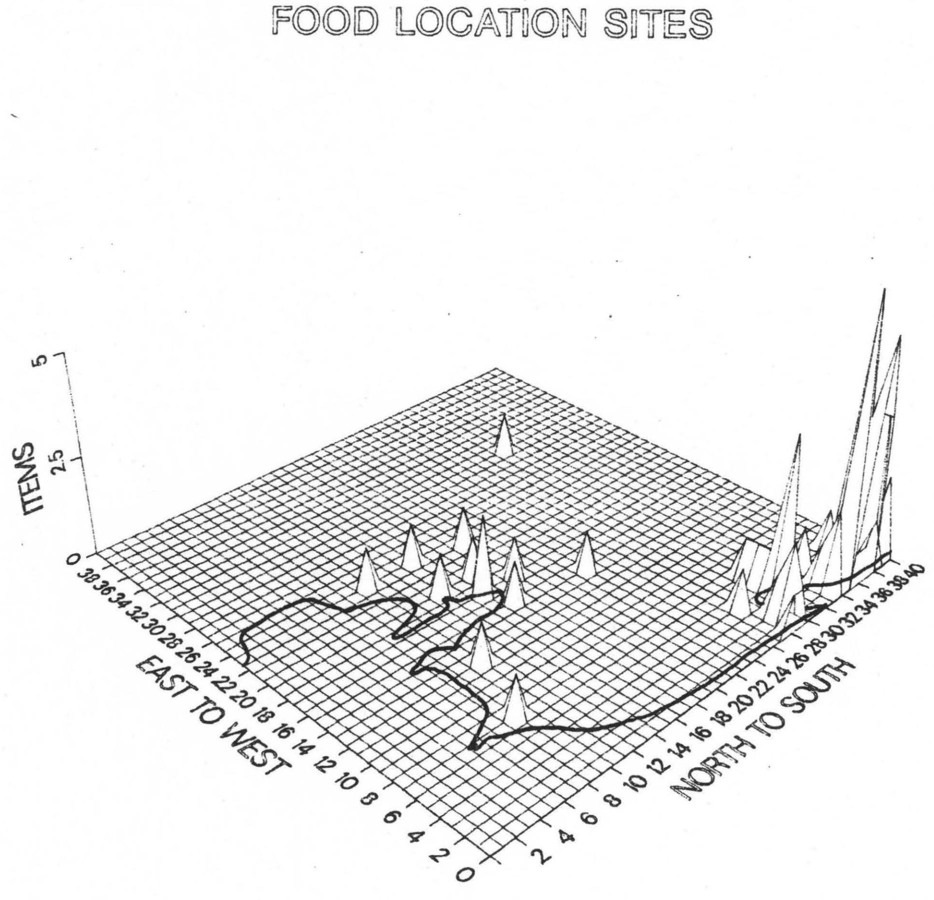


FIGURE 17. THREE-DIMENSIONAL, DISSPLA-GENERATED MAP SHOWING THE DISTRIBUTION OF LARGE FOOD ITEMS FOUND BY BUBBLES AND THORA.

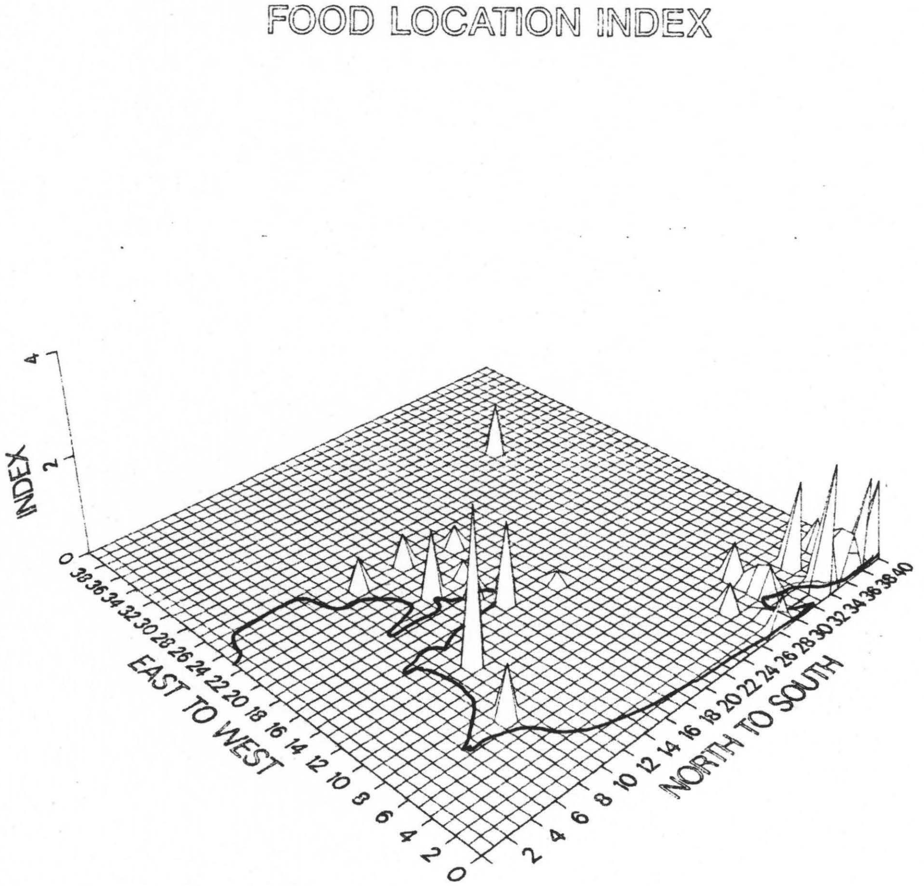


FIGURE 18. THREE-DIMENSIONAL, DISSPLA-GENERATED MAP SHOWING DISTRIBUTION OF LARGE FOOD ITEMS FOUND BY BUBBLES AND THORA AS A FUNCTION OF DISTANCE TRAVELLED BY THEM IN EACH GRID-BLOCK.

hyaenas were also able to smell seal pups in the sea at distances of up to about 300 m ; they would often wait on the shore for the waves to bring in a carcass which they had smelt floating out at sea. In places such as sandy beaches or lagoons, where it was possible to wade relatively safely, the hyaenas were observed to go into the water (or surf) up to their necks, in order to secure a food item or cross to an island. At times they certainly had to swim short distances, but did not appear to be very strong swimmers or to spend time in the water if this could be avoided. The hyaenas would dash around in short, fast bursts after getting out of the water; this was presumeably in order to dry off and to warm themselves up. The low temperature of the water along this coast is probably the major deterrent which keeps the hyaenas' aquatic activities to a minimum. On the east coast , with its warmer currents, brown hyaenas may have spent considerable periods in the sea when they still occurred in this area. Atwell (1985) reports one such occurrence in the Transkei in 1923.

When away from the sea, where it was quieter, the hyaenas would often listen, for potential danger in the form of human activity or in order to locate potential prey, such as dogs or birds. Although there was no direct observation of a dog being killed by a hyaena, on one occasion Bubbles almost certainly killed a small dog. After stopping to listen to some barking, she approached very slowly, with head held forward, in a definite stalk. She used an embankment as cover and then dashed to the source of the barking. The actual contact was not seen, but she was observed thirty seconds later with a small dog carcass in her mouth. The dog carcass was very fresh, but the possibility does exist that the hyaena did not in fact kill it, since dog carcasses are often left lying around in the vicinity of the town. (Residents of Lüderitz report brown hyaenas as having killed dogs in the town in the past).

Each hyaena was observed to kill a seal pup once only. These pups were encountered close to the sea and, being relatively immobile on land (and possibly exhausted or sick), they were very easy prey for the hyaenas. Both were encountered by chance and the hyaenas were only aware of their presence when they were almost on top of the seals. A pounce and a single bite at the back of the skull were all that were required to immobilise the prey.

Large flocks of flamingoes (Phoenicopterus ruber) occur along the coast, and Bubbles made one attempt to catch these birds. This attempt consisted of a one to two hundred metre dash through the six-inch deep water of the lagoon. One of the birds, slightly slow in taking off, was caught and died almost instantly after being bitten in the neck.

It was Bubbles, that, coming across a large unidentifiable gecko, pawed it briefly and then bit it two or three times. It appeared to be foul-tasting or to secrete some sort of noxious substance, because the hyaena subsequently grimaced, sneezed and repeatedly pawed her mouth. The gecko was left uneaten. A small snake which Bubbles encountered was given a wide berth by the hyaena.

c) Diet

The frequency with which various food items were eaten by the hyaenas is shown in Table 5 for Bubbles and Table 6 for Thora. The total time which the animal spent in eating each food category, as well as the mean time per item in each class, are also shown in the tables. The standard deviation shown is for the mean time per item, and the range is the range of times per item in the category indicated. Figures 19 and 21 give a clearer representation of the proportional frequency of occurrence of various food items in the diets of Bubbles and Thora respectively. Figures 20 and 22 show the proportion of time spent eating various dietary items, in the cases of Bubbles and Thora respectively.

d) Provisioning at the Den

Thora was supplied with various food items by other group members at the maternity dens. She was provided with 14 unscavenged seal pup carcasses and one gemsbok skull; these represent a total of 634 min of eating, or 62% of the total time spent eating by Thora. Thora located five seal pups herself, whilst the origin of a further three unscavenged seal pups was unknown. By extrapolation, one can reasonably assume that two of the latter were supplied by other group members; this assumption increases the percentage (by time)

TABLE 5. THE COMPONENTS OF BUBBLES' DIET AND THE TIME SHE SPENT EATING EACH.

CATEGORY	SEAL KILL	UNSCAVENGED SEAL CARCASS	SCAVENGED SEAL CARCASS	OLD/WELL SCAVENGED SEAL CARCASS	UNIDENTIFIED SCRAP	BIRD	FISH	HUMAN REFUSE	CANIS FAMILIARIS	OTHER
FREQUENCY	1 + 1	13 + 21	15	13 + 6	28 + 5	2	1	11 + 3	3 + 1	16 + 2
TOTAL TIME (MIN)	24,0	356,0	222,0	122,0	16,0	16,0	2,0	9,0	32,0	58,5
MEAN TIME (MIN)	24,0	27,4	14,8	9,4	0,8	8,0	2,0	1,6	10,7	3,5
RANGE	-	5,0-76,0	1,0-33,0	2,0-23,0	0,5-3,0	1,0-15,0	-	0,5-3,0	2,0-25,0	0,5-24,0
STD. DEVIATION	-	20,6	8,7	8,2	0,6	9,9	-	0,8	12,5	6,6

TABLE 6. THE COMPONENTS OF THORA'S DIET AND THE TIME SHE SPENT EATING EACH.

CATEGORY	SEAL KILL	UNSCAVENGED SEAL CARCASS	OLD/WELL SCAVENGED SEAL CARCASS	UNIDENTIFIED SCRAP	OTHER
FREQUENCY	1	21	6	5	2
TOTAL TIME (MIN)	30,0	936,0	31,0	4,0	20,0
MEAN TIME (MIN)	30,0	44,6	5,2	0,7	10,0
RANGE	-	23,0 - 127,0	1,0 - 13,0	0,5 - 1,0	-
STD. DEVIATION	-	21,9	4,5	0,3	-

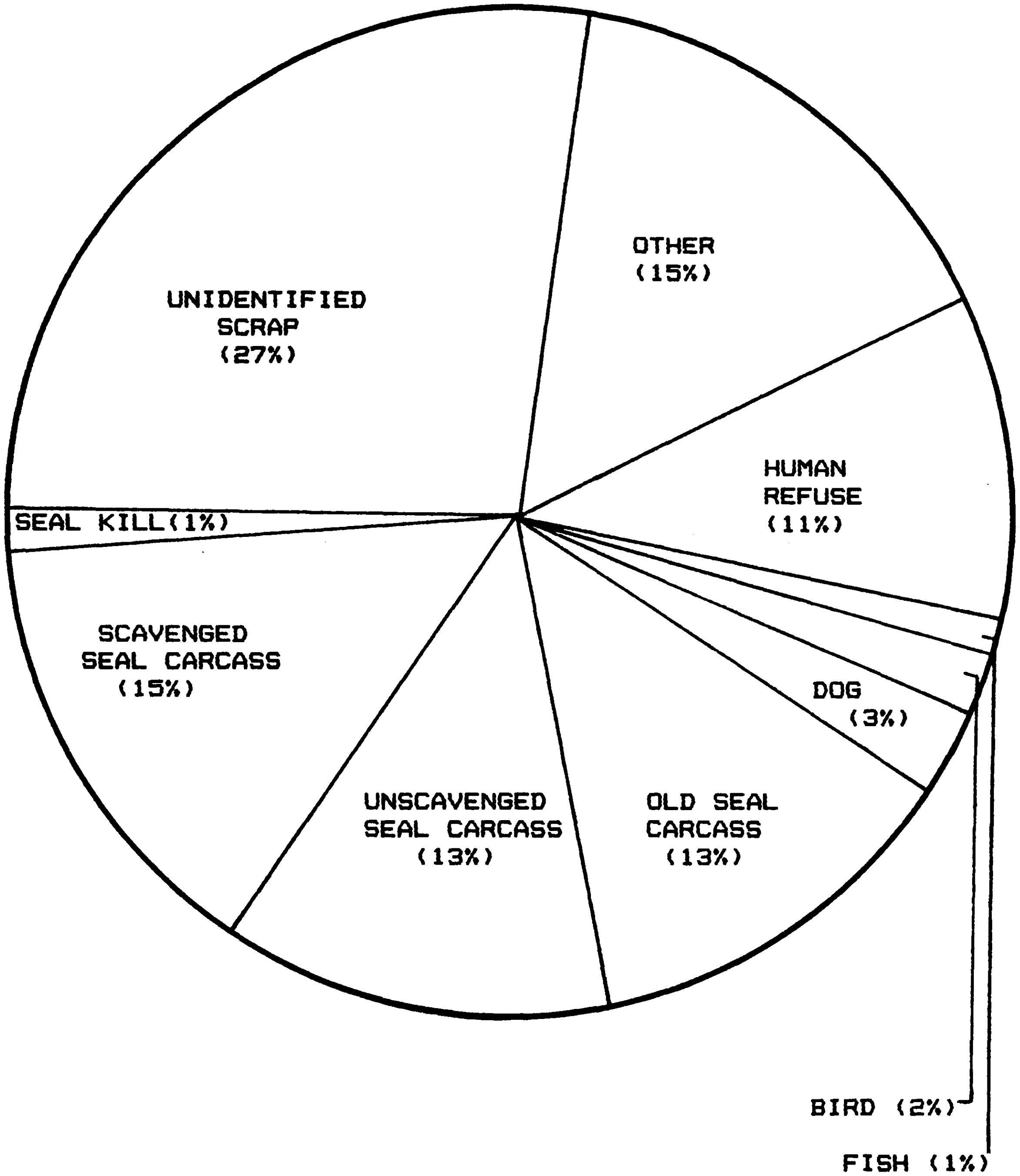


FIGURE 19. PIE CHART OF FREQUENCY OF OCCURRENCE OF VARIOUS FOOD ITEMS IN BUBBLES' DIET.

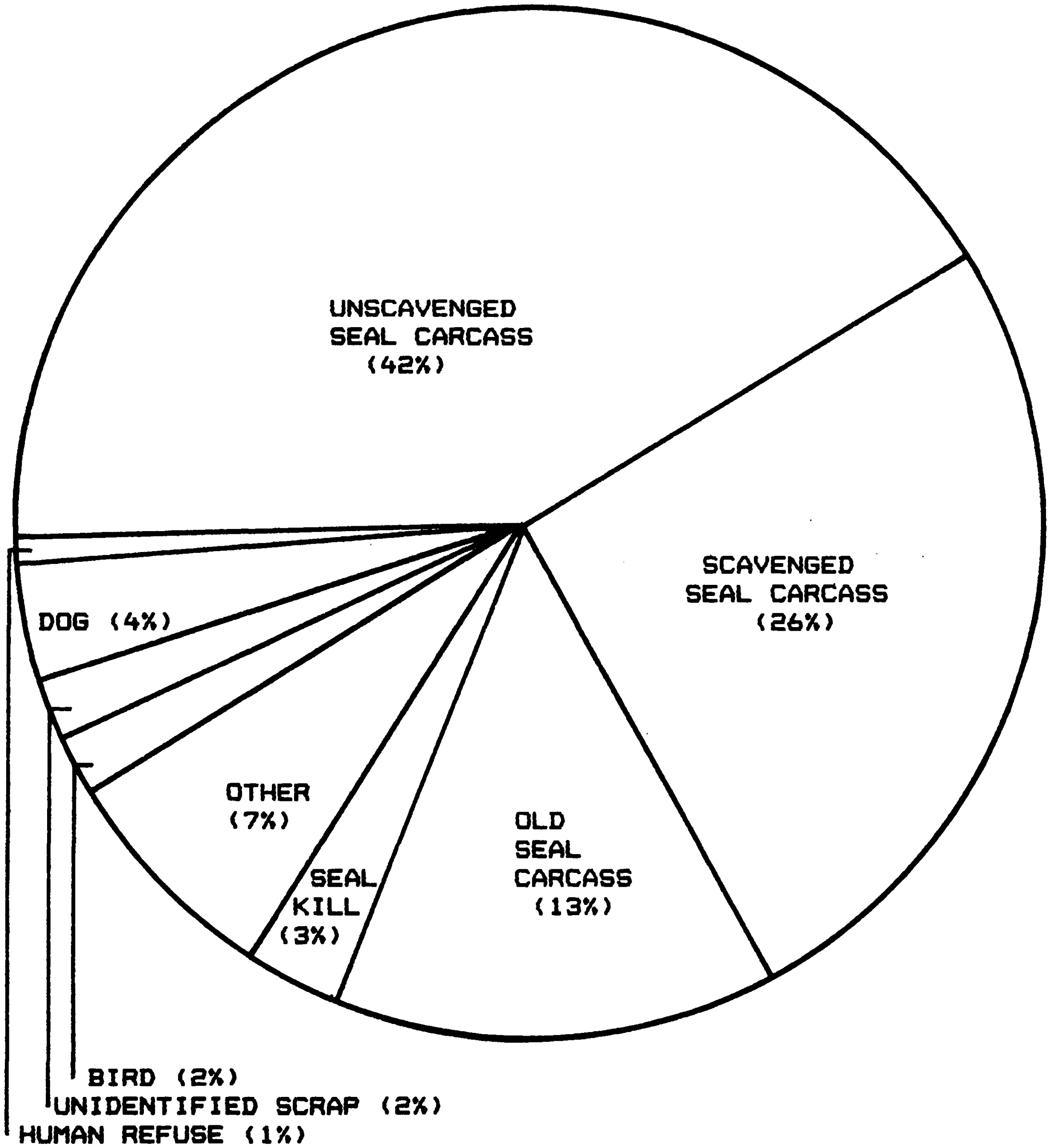


FIGURE 20. PIE CHART OF TIME SPENT EATING VARIOUS DIETARY ITEMS - BUBBLES.

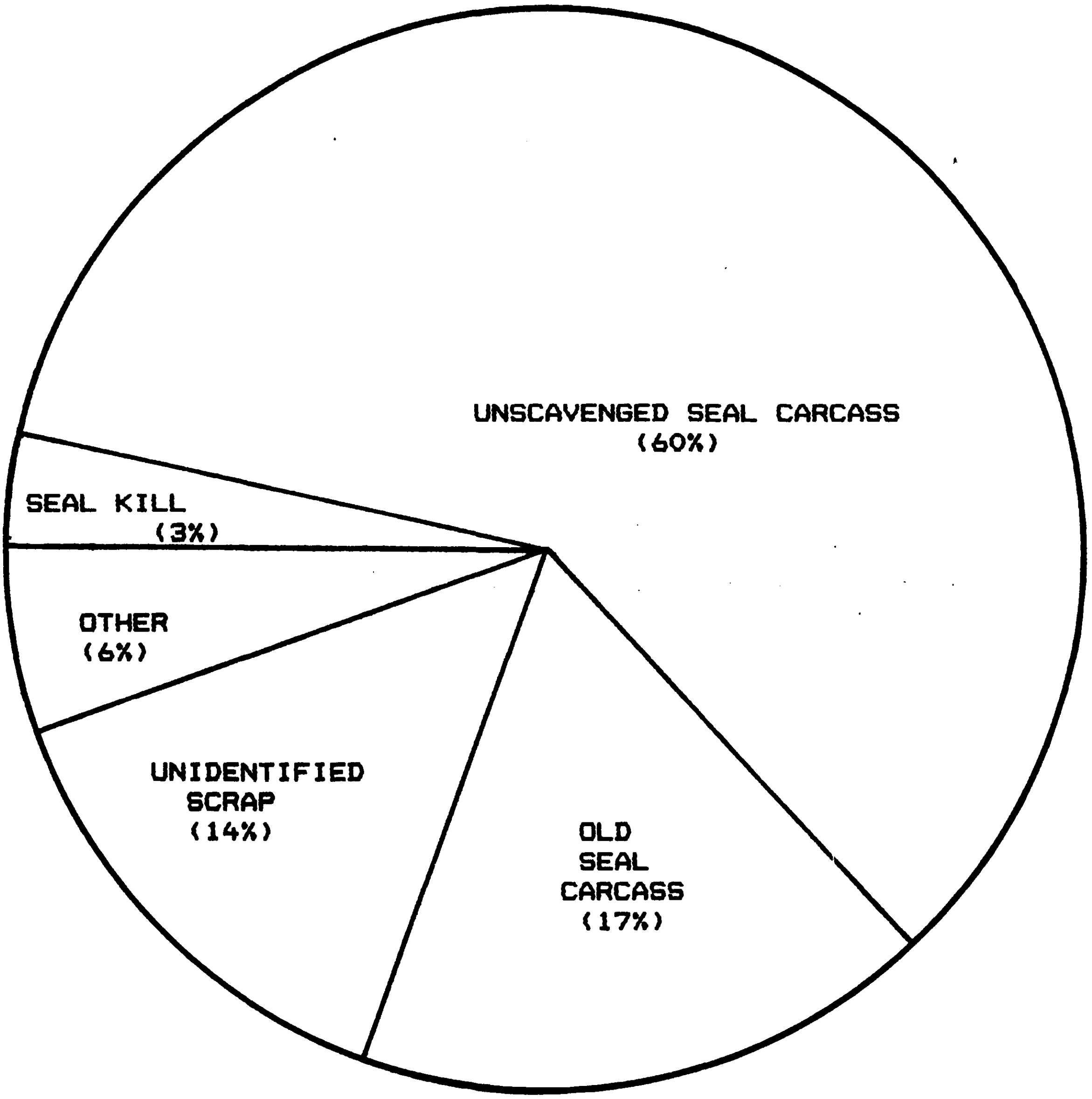


FIGURE 21. PIE CHART OF FREQUENCY OF OCCURRENCE OF VARIOUS DIETARY ITEMS IN THORA'S DIET.

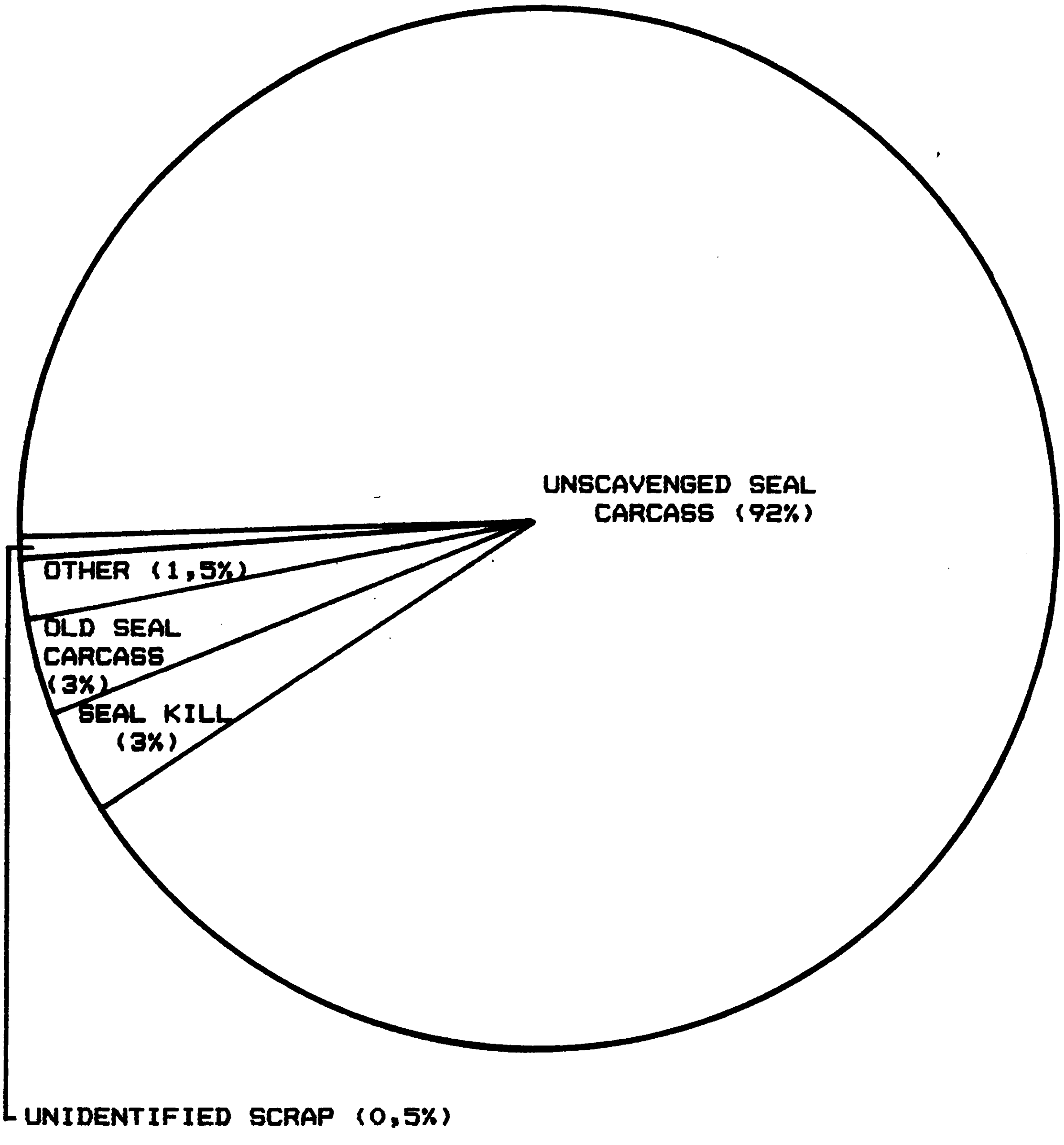


FIGURE 22. PIE CHART OF TIME SPENT BY THORA EATING VARIOUS DIETARY ITEMS.

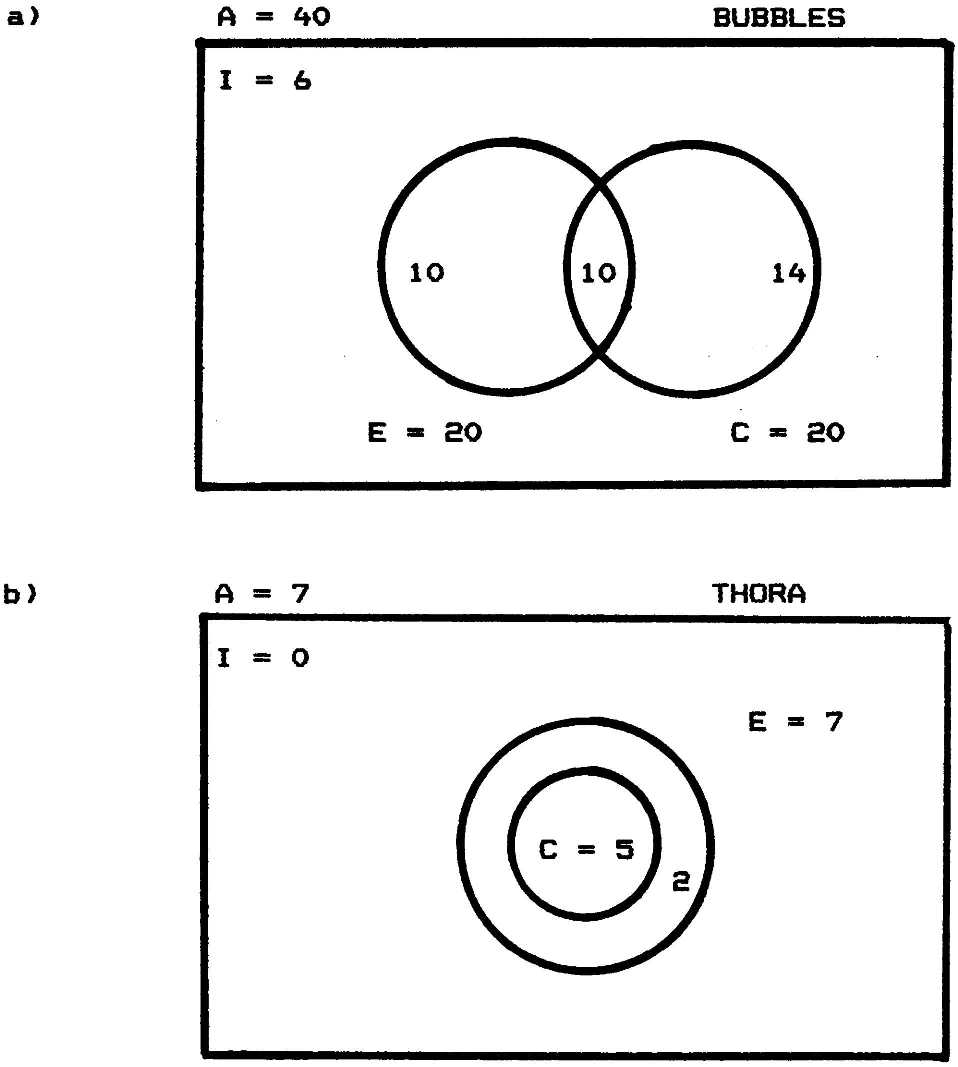
of "supplied carcasses" in Thora's diet to 70%. Further details with regard to the part that various individuals played in maintaining Thora at the den are supplied and discussed in Chapter 5.

e) Caching Behaviour

Figure 23a is a set diagram showing the total number of "cachable" (as defined in Materials and Methods) food items encountered by Bubbles. The number which were ignored, eaten at the location site and cached are indicated. The overlap between E and C represents those items which were first eaten, before being cached by the hyaena. Of the "potentially cachable" items encountered, 15% were ignored, while 50% were eaten on site. Sixty percent were cached and 42% of these were first eaten on site. Of those eaten on site 50% were subsequently cached.

Figure 23b shows the same data for Thora. The food items considered here are those which the hyaena located herself, i.e. those that were supplied to her at the den were not considered to be "potentially cachable". No carcasses were ignored by Thora, and all those that were located were eaten on site. Of those located 71% were cached. All the carcasses cached by Thora were carried to the den and then cached there.

FIGURE 23. SET DIAGRAMS OF CACHING BEHAVIOUR BY BUBBLES AND THORA.



KEY
A : "POTENTIALLY CACHABLE" FOOD ITEMS ENCOUNTERED
I : IGNORED
E : EATEN/ PARTIALLY EATEN AT LOCATION SITE
C : CACHED

f) Drinking

During the course of the present study, no naturally occurring fresh water was available to the hyaenas. Rainwater was the only natural water source in this area, and, since very little rain fell, only very little, if any, water would have been available to the hyaenas from this source. The animals were observed to drink from artificial sources near to Lüderitz e.g. leaking pipes and valves, and drainage outlets.

Thora drank from these sources on 13 occasions over 26 full 13 h observation periods i.e. once every two nights, on average. The average time which she spent drinking was 3,75 min (±1,04). Drinking data are scant and unreliable in the case of Bubbles, since she tended to frequent water sources which were hidden from view, thus making relaible observation impossible.

DISCUSSION

At Wolf's Bay, approximately 4,5km to the south of the southern boundary of the hyaenas' territory (as indicated in Fig. 1), there is a Cape fur seal colony. About 11,0km further south, at Elizabeth Bay, another colony exists, and the number of seals at these two colonies has been estimated at between 400 000 and 500 000 animals (Division of Sea Fisheries, pers. comm.). These colonies would together produce an annual pup crop of approximately of 200 000.

Natural mortality (largely at sea) can be conservatively estimated at about 10%, yielding about 20 000 first-year-pups for the hyaenas along the coast to scavenge on. Large numbers of these carcasses would undoubtedly be washed out to sea or spread along a very large part of the coastline. However, as a result of the colony being the focus of activity for the seals, the highest density of carcasses is at the colony itself, and it decreases with distance from the colony. With the prevailing winds and current from the S.E., bays, coves and beaches with this orientation appeared to have more carcasses than the rest of the coastline.

This spatial trend in food availability is clearly reflected in Figs. 11, 17 and 18, which indicates that the hyaenas obtained most of their food on the S.W. coastal region (see discussion in Chapter 2). The only other area of any importance in this respect is the area around Lüderitz. This high foraging success rate in the S.W. was not simply a result of the hyaenas traversing this area more frequently, since values were still highest here, even when presented as a function of distance moved by the hyaenas (Fig. 18).

The extreme importance of the seal pups in the hyaenas' diet is apparent from Figs. 19 - 22 and in Tables 5 and 6. Seals made up only 42% of Bubbles' diet, by frequency of occurrence, but 84% by volume (i.e. time spent eating). In the case of Thora, the figures were 80% and 90% respectively. These data reinforce the notion that the hyaenas had a food supply which was sufficiently large and predictable to allow them to eat small, unusual items either out of curiosity or because of their palatability and to vary their diet. This appeared to be the case, particularly in the vicinity of Lüderitz. Bubbles, with no offspring-related responsibilities, was particularly prone to this feeding pattern, whilst Thora was forced, through circumstances, to concentrate on the larger food items i.e. seal carcasses. The relatively large proportion of small items in Bubbles' diet may also have been as a result of the fact that she was more active than Thora, and thus encountered many more small items around Lüderitz and in the interior than Thora, whose walking was largely in the direction of the "food-rich" S.W. or a return path to the den. Thus, although there may have been differences in degree, seal pup carcasses were clearly the major factor which allowed the hyaenas to inhabit what was otherwise a very unproductive environment. This factor also allowed the hyaenas to explore once their hunger was satisfied thus improving their chances of taking advantage of new and transient food sources which may become available. The importance of unscavenged, and partially scavenged carcasses, is particularly evident in Figs. 20 and 21. The greater importance of unscavenged carcasses in Thora's diet was largely due to the provision of these food items to her at the den by other group members.

Comparing the mean time required to eat food items (Tables 5 and 6), it is apparent that there is a clear correlation between the size of the item and the time spent feeding on it. The fact that very little time was spent on the small items, means that although many of them were unindentifiable and occurred relatively frequently in the animals' diet (Figs. 19 and 20), they were very unimportant in terms of the amount of time which the hyaenas spent on them. Care should, however, be taken when comparing these means, since the range and standard deviation is relatively large in all cases.

When hyaenas encounter the carcass of a land mammal they normally start eating by disembowelling it.The hyaenas in the present study however,generally ate a seal pup carcass in a specific manner: in 89% of the 34 cases in which an intact seal carcass was eaten, the hyaena would start at the head, and, once this had been crushed and largely eaten, would peel back the skin, pulling upwards on the skeleton with its jaws whilst holding the skin under its paws. As the skin was peeled back, so the meat and softer bones and organs would be eaten, until all that was left was the skin (literally turned inside out) and core of the skeleton. This specialised feeding method was probably imposed by the very thick fur and tough skin of the seal pups.

Brown hyaenas reputedly favour canid meat in their diet (Skinner, 1976, 1980; Mills 1977). In the present study the hyaenas were observed to eat Canis familiaris carcasses on four occasions. The mean time spent on these carcasses was approximately 10 min most of which was spent mutilating the carcass. This time is equivalent to that spent on an old/well-scavenged seal carcass, whereas there was certainly a great deal more meat on the dog carcasses than on the seal carcasses i.e. very little of the available meat on the dog carcasses was eaten. In the case of the dog which was probably killed by the hyaena, she dismembered and disembowelled the carcass, but ate virtually nothing off it. A jackal which was killed by Thora at one of the maternity dens, was also disembowelled but left virtually uneaten.

The particular hyaenas in the present study do not appear to support the view that hyaenas prefer canid neat. The killing of canids may be a reaction to a species which is a competitor and which can be relatively easily overcome, the amount of the carcass eaten being only enough to replace the energy expended in the kill. Hyaenas were also observed to roll on old canid carcasses (n = 9) and never rolled on any other type of carcass.

The flamingo and gecko which were killed were also left uneaten. In the case of the flamingo, the hyaena spent 15 min dismembering and disembowelling the carcass, but appeared to eat very little, or nothing at all. This inherent killing instinct thus seemed to be very strong in the brown hyaena, but, whether the prey was subsequently eaten or not appeared to depend on the palatability of the food item and/or the animal's hunger-state at the time.

The hyaenas showed an intense interest in any artificial object which they came across. Plastic pipes, wire, various plastic containers and glass bottles were frequently chewed on for substantial periods of time, and when using a set route, they would predictably and invariably chew on the same artificial objects as they encountered them. Food containers which were picked up and which still contained remnants of food, were licked and chewed until all the contents had been removed. Most of the human refuse found by the hyaenas was in the vicinity of the municipal rubbish dump, but, as reflected in Figs. 20 and 22, this source was unimportant in terms of volume i.e. (time spent eating).

The social implications of a female hyaena with young cubs being provisioned at the den by other group members are discussed later, but the importance of this phenomenon to Thora can be gauged by the fact that such a large proportion (70%) of her food intake was acquired in this way. Her activity budget (discussed in Chapter 3) can be clearly related to this : a large part of her time was spent resting at the den, with very little time spent foraging or walking.

Thora's concentration on the acquisition of large food items, and the very specific way in which she dealt with them, is further highlighted in Fig. 23. When she undertook a foraging trip, she went directly to the S.W. coast, where she was most likely to locate a seal pup. She would then eat approximately half the carcass before returning to the den with the remainder. She followed this pattern on five of the seven occasions on which she located a seal pup. Twice, she ate the entire seal pup (excluding certain parts of the skeleton) before returning to the den. The fact that she never ignored a carcass, whilst Bubbles ignored 15% of those she encountered, would seem to indicate that Thora was probably driven by hunger to leave the den and her cubs to embark on a foraging trip. Bubbles' more variable reaction to large prey items was presumeably due to the fact that she was not under the same pressure as Thora, who was compelled to return to a specific site some distance away from the food source. Her 60% caching rate was, however, comparable to the 71% found in the case of Thora. Food storing has been well-documented in the brown hyaena (Mills, 1977; Owens & Owens, 1978). By removing food from the area in which it was found i.e. normally a "food-rich" area, which would be well-frequented by competitors, the hyaenas prevent the food from being discovered by these competitors. Although quantification of this aspect was difficult, it did appear that a jackal would regularly follow a hyaena to the point at which it cached its food, and then steal it after the hyaena's departure. Thus, although the mechanism of hiding food was undoubtedly successful, it was rendered less efficient by the jackals' having learnt the advantages of following a hyaena which was carrying food in its mouth.

The hyaenas, in turn, have had to modify their caching behaviour by staying with the food that they have moved from the shore (where it was more likely to have to have been defended against other hyaenas). This behaviour applied to all of the cases in which Thora cached food, and to 76% of Bubbles' caches. In these cases, if a jackal was present, it would often remain near the hyaena whilst it ate, and would attempt to steal small pieces of food. It would then eat off the carcass once the hyaena had left. Although jackals were only observed to follow a hyaena which was caching food on 27% of the occasions, jackals were present at 59% of the caching sites. This suggests that caching may be a mechanism to avoid intra rather than interspecific competition in the brown hyaena. Owens & Owens (1978) comment on the fact that jackals did not take advantage of the hyaenas' caches in the central Kalahari even though there was intense competition for food between the two species. Other hyaenas were observed at all of Thora's caching sites i.e. the maternity dens (which were focal points for the group anyway) and at only 8% of Bubbles' more conventional and less conspicuous caching sites.

The brown hyaena has been reported to be able to survive for long periods without water in the southern Kalahari (Mills, 1977), in the central Kalahari (Owens & Owens, 1978) and in the Namib Desert (Skinner & Van Aarde, 1981). In the present study the animals certainly utilised artificial fresh water sources to some extent, but it can be reasonably assumed that water is not a limiting factor in the distribution of the hyaenas in the Namib Desert, since they occur in areas where no permanent water exists at all (Skinner and Van Aarde, 1981). The fact that there are no water-rich fruits in the area (such as the tsama melons (Citrullus lanatus) of the Kalahari) is a disadvantage to the animals, but they have the advantage of having fresh mammal carcasses (seal pups) with their high water content as the major part of their diet. The effect of the high salinity of these marine mammal carcasses would be another important, but as yet unquantified aspect of the hyaenas' water relations in this area.

5. SOCIAL STRUCTURE & INTERSPECIFIC RELATIONS

INTRODUCTION

The social system of brown hyaenas has been reported ,on in some detail in the southern Kalahari by Mills (1981, 1982a, 1982b, 1983a, 1983b), in the central Kalahari by Owens & Owens (1978, 1979a, 1979b, 1984) and in captivity by Bosman (1982). Brown hyaenas were found to live in small social groups (Mills, 1978a, 1981, 1983b; Owens & Owens, 1979b) and co-operate in feeding the young (Mills, 1982b, 1982c; Owens & Owens, 1984). The clan will defend a territory which is demarcated by scentmarking using an anal gland and by the use of latrines (Mills, 1978a, 1981, 1983a; Owens & Owens, 1978, 1979b). In the southern Kalahari, non-territorial, nomadic males do the mating (Mills, 1982b). Members of the clan forage alone (Mills, 1978a; Owens & Owens, 1978) but may congregate to scavenge large food items. Under such conditions individuals typically feed in turn (Mills, 1978a,1981; Owens & Owens, 1978).

Mills (1981) found no suggestion of a dominance hierarchy, whilst Owens & Owens (1978, 1979) found a stable rank order existing which was maintained by ritualised fighting. In captivity Bosman (1982) concluded that the hyaenas were organised in a dominance hierarchy which was maintained by aggressive and submissive displays. The brown hyaena appears to differ from the spotted hyaena (*Crocuta crocuta*) in this respect. Tilson & Hamilton, (1984) indicate that *Crocuta* has a more rigid, near linear dominance hierarchy in the Namib Desert where food is in very short supply, and that, in the Serengeti, with its abundant food supply, hyaenas have a non-linear hierarchy, with scramble competition at carcasses (Kruuk, 1972).

Rowell (1974) has stated that dominance is essentially a term used to indicate the probability of a correct prediction being made of the outcome of an interaction or potentially competitive situation involving individuals or groups. The same author has cautioned against ascribing any particular recognisable function to intraspecific dominance, and stresses the importance of the submissive element in any dominant-subordinant relationship or interaction. Others have warned against assuming that, if a dominance hierarchy exists, transitivity is assumed to apply, and that the hierarchy is taken to be linear (Appleby, 1983). Various procedures for producing rank orders can also produce quite different results from identical sets of observations (Boyd & Silk, 1983).

Kaufman (1983) defines a dominance-subordinance relationship as one in which a subordinate animal defers to a dominant animal in contest situations. The author sees the function of a dominant-subordinant relationship as saving both individuals time, energy and risk of injury; also, immediate priority of access to resources is gained by the dominant animal. Territoriality is thus a form of social dominance.

Dominance may be absolute or relative, and some species may exhibit both types of dominance; e.g. social mammals which have rigid hierarchies within a specific group (absolute dominance) and reciprocal territoriality between groups (relative dominance) (Kaufman, 1983).

Dominance-subdominance relationships may have related behaviours such as aggressive and submissive displays, ritualised fighting as a test of competence, mutual avoidance through temporal or spatial separation and policing by high-ranking individuals (Rowell, 1974).

The concepts of "ecological niche" and "competition" are of great importance in modern ecology and population biology. An ecological niche can be viewed as a multi-dimensional system of relations between a functionally specified taxonomic unit and the environment (Rejmánek & Jenik, 1975). Where two species occupy niches which overlap to any extent, potential exists for competition (Cameron, 1971). Many biologists now believe, however, that, through the principle of competitive exclusion, (i.e. that there can be no more than one species per niche or limited resource) and the corollary that communities live at competitive equilibrium, no examples of competition are to be found in natural systems today. Thus, competitive interactions have been resolved either through one species being victorious or through mechanisms having evolved to ensure spatial or temporal displacement of activity, thereby reducing contact between the species eg. (Murie, 1971; Colvin, 1973; Randall, 1978; Glass & Slade, 1980).

A major problem in accepting the above, is the acceptance of the assumption that equilibrium conditions exist in natural communities. Variation in environmental factors which are ecologically significant, and non-equilibrium in population numbers are both aspects which emphasize the dynamic, non-equilibrium nature of ecosystems (Alley, 1982).

There is growing evidence to back up the idea that true competitive equilibrium occurs rarely, if at all, in natural situations (Huston, 1979). Two species of woodrat *Neotoma fuscipes* and *N. lepida* exploit a common food source under certain conditions. Direct competition, is, however, reduced to a significant extent by the behavioural dominance of *N. fuscipes* over *N. lepida* (Cameron, 1971).

Interspecific territoriality has been shown for a number of birds, and recently in mammals, where two sympatric species of *Peromyscus* spp. displayed interspecific territoriality with dominance being site-specific as opposed to species-specific (Wolff, Freeburg & Dueser, 1983). This phenomenon may well reduce direct competitive interactions between the two species, with the possibility of escalation as a major threat to both species. Cranford & Derting (1983) also found that two species of voles *Microtus* spp. had substantial niche overlap in the wild, and suggest that behavioural interactions between the two species may contribute towards their segregation into different microhabitats.

Thirty three carnivore species living in the Transvaal were compared on the basis of their daily activity regimen, food and habitat preferences, geographical distribution and social structure. The majority of co-existing species avoided interspecific competition primarily by utilising different food sources, different sized prey items, or differential use of habitat types (Rautenbach & Nel, 1978).

Several studies have shown that, where closely related carnivores are sympatric, the smaller species tend to avoid areas utilised by the larger (Schaller, 1967; Kruuk, 1976; Seidensticker, 1976; Skinner & Van Aarde, 1981; Mills & Mills, 1982; Mills, 1984).

Alley (1982) points out the differences between relativley direct or "interference competition" as opposed to indirect or "exploitation competition". The author also quotes Pianka (1976) : "niche overlap is neither a necessary nor a sufficient condition for interference competition; moreover, overlap is only a necessary but not sufficient condition for exploitation competition." Thus, in summary, competition would appear to tend towards minimisation through the evolution of behavioural responses as communities tend towards equilibrium, but, in non-equilibrium or dynamic conditions, competition may well be strongly in evidence.

Brown hyaenas, as carnivores, utilise relatively high energy, high quality food packages. This, together with a scavenging way of life and a heavy reliance on other predators, means that the hyaenas have frequent exposure to other, potentially competitive carnivores. Owens & Owens (1978) ranked the large carnivores of the central Kalahari in the following order, with regard to their dominance : lion - spotted hyaena - wild dog - brown hyaena - leopard - cheetah. As mentioned earlier, size seems to play a large part in determining interspecific social status. In the southern Kalahari, Mills (1982a) found spotted hyaenas to be the brown hyaenas' most serious competitor for the remains of vertebrate kills. He also found brown hyaenas avoided areas of comparativley high density of spotted hyaenas and lions (Mills, 1981). Apart from this interference competition which appears to affect brown hyaenas to a large extent, exploitation competition between black-backed jackals and hyaenas probably exists, since there is a great overlap in the diet and mode of existence of these species (Owens & Owens, 1978). Mills (1977, 1978a) reports severe interference competition for food between black-backed jackals and brown hyaenas.

The behavioural mechanism used by brown hyaenas to avoid confrontation with dominant species seems to be one of discreet avoidance. When a confrontation does occur, extensive pilo-erection may occur (Mills, 1982b). Another adaptation to its inferior social status in certain areas e.g. the Kalahari, is its ability to live off a diverse food source including small or low quality items such as fruits, old bones and insects (Skinner, 1976; Mills & Mills, 1978; Owens & Owens, 1978).

Man and his domestic animals may also be regarded as both competitors and providers for brown hyaenas. Skinner (1976) refer to accounts of brown hyaenas killing livestock and domestic dogs, and Skinner & Van Aarde (pers. comm.), report hyaenas foraging on offal in towns such as Pretoria and Lüderitz, and from farms in the Magaliesberg area. Interference and exploitation competition exist between man and the hyaenas in most areas of sympatry.

MATERIALS AND METHODS

All the data in this chapter were collected by direct observation. The group size was estimated by means of individual recognition of the animals. Animals which could not to be recognised were always assumed to be the same individual, thus giving a minimum estimation of group size. The ages of the animals which were immobilised were determined as outlined in Chapter 1.

All interactions with conspecifics were timed, and behaviour recorded in as much detail as possible. These data was then interpreted using descriptions of displays, vocalisations and postures by Owens & Owens (1978, 1979b) and Mills (1981, 1983a) in order to determine whether an animal was dominant over another in any given encounter. Once the outcome of all encounters had been decided upon, the data were analysed and a dominance matrix and hierarchy constructed, following Brown (1975). The degree of linearity in the hierarchy was then established following Appleby (1983). It was not possible to use more sophisticated analysis techniques, such as that of Boyd & Silk (1983), which assigns cardinal dominance ranks to individuals, because of the relatively small data base and resultant large number of unknown relationships. This situation arose as a result of the fact that most of the data were from only two of the seven animals which were considered, and because of the relatively low frequency with which the animals encountered one another.

Data on all social aspects related to denning and the raising of offspring was obtained from direct observation. In order to elucidate details of the hyaenas' territorial maintenance behaviour, the number of defaecations and scent-marks per night was noted; the location of all scent-marks was mapped, and the density of the marks over the territory portrayed using the DISSPLA program, with the number of marks in each ¼km^2 grid block for Bubbles, Thora, and for both combined being indicated on the vertical axes of the three-dimensional maps. The total number of marks per grid block was then calculated as a function of the distance moved in each grid block, in order to yield a marking index for each block in the territory. This was also displayed three-dimensionally, using DISSPLA. The number of marks per km moved by the hyaena under observation on each night was also calculated, in order to compare the marking intensity on various nights' activities as categorised in Chapter 3. All latrines which were known to exist, or which were used by the hyaenas were mapped, and the animals' behaviour recorded each time a latrine was visited.

All details with regard to any interspecific encounter were noted in order to elucidate the hyaenas' relations with other species in the area. Data were too sparse to enable detailed analysis for the existence of hierarchies, but impressions gained from the field observations do provide significant insight into this aspect.

RESULTS

a) Group Size and Composition

The minimum group size was estimated to be five adults, four subadults and three cubs of approximately three weeks of age when first observed. Brown hyaena cubs' ears become upright at approximately four weeks (Schultz, 1966) and this criterion was used to estimate their age. Of the adults, two were female, one was male, and two were unsexed. Two subadults were female, one was male and one was unsexed.

This estimation of group size is conservative, but is probably not substantially lower than the actual group size since the unidentified individuals (which were always assumed to be the same adult and subadult) were randomly observed with roughly the same frequency as the other animals in the group. If there were several unidentified animals, an unidentified animal would probably have been seen with a frequency which would be dependent on the number of unidentified hyaenas in the group i.e. more frequently than those which were able to be identified.

b) Intraspecific Dominance and Related Behaviour

Reference to previously reported social behaviour patterns enabled the outcome of all agonistic encounters to be satisfactorily determined. On two occasions a behaviour was observed which has not been described by previous workers on this species : rapid, extremely exaggerated licking at the base of a subordinate animal's back (almost on the pelvis) and upper thigh by a dominant animal was observed to take place. On one occasion, a dominant adult male greeted with an adult female; the male then mounted her for approximately 90 sec, without penetration taking place. After dismounting, the male licked the ground behind the female, while she stood motionless with head held very low, and back hunched. He then began licking her back and upper thigh at the rate of about one lick per second and with the head being thrown rapidly up and backwards with each lick, in a very distinctive and exaggerated manner. This licking continued for approximately 30 sec after which the male moved slowly away, leaving the female still standing in the position described above.

The second time that this behaviour took place was after Bubbles had greeted an unidentified adult hyaena in a typically subordinate manner. She then lay down and the other animal sniffed briefly at her genitals before licking her in exactly the same way, and for about the same period of time as described above. Bubbles then got up and the two animals moved apart.

The significance of this particular behaviour pattern is not clear; it does, however, appear to be associated with the enforcement of dominance and was possibly related to situations when sexual interplay took place between the individuals.

Figure 24 is a matrix which best represents the order of dominance within the group. This has been constructed according to Brown's (1975) guidelines. From this, each individual's total number of wins and losses in its encounters with other individuals can be calculated, and a dominance hierarchy can be shown to exist (Fig. 25). Note that no assumptions are made about transitivity in the construction of this hierarchy. Landau's (1951) index of linearity, (h), can be calculated in order to ascertain the extent to which the hierarchy is linear. A perfectly linear hierarchy has an h value of one, and an h value of zero indicates complete absence of linearity in the hierarchy. The low h value of 0,75 reflects the high degree of nonlinearity in this case. When one considers the four adults only, an h value of 0,6 is obtained.

The number of circular triads (d) was calculated to be 8,75, following Appleby (1983), and was not significant, even at P = 0,1, illustrating further that the hierarchy cannot be said to be linear. The same author's degree of linearity, K, was

LOSER

		THORA	FLOPPY EAR	BRUNO	BUBBLES	MARGY	YORICK	THICK EAR	TOTAL WINS	TOTAL LOSSES
WINNER	THORA		–	8	6	1	2	10	27	0
	FLOPPY EAR	–		–	2	–	1	–	3	0
	BRUNO	0	–		5	–	–	2	7	8
	BUBBLES	0	0	0		3	7	10	20	13
	MARGY	0	–	–	0		3	2	5	4
	YORICK	0	–	0	0	0		–	0	16
	THICK EAR	0	0	–	0	0	–		0	24

FIGURE 24. MATRIX OF DOMINANCE INTERACTIONS FOR ALL IDENTIFIABLE GROUP MEMBERS

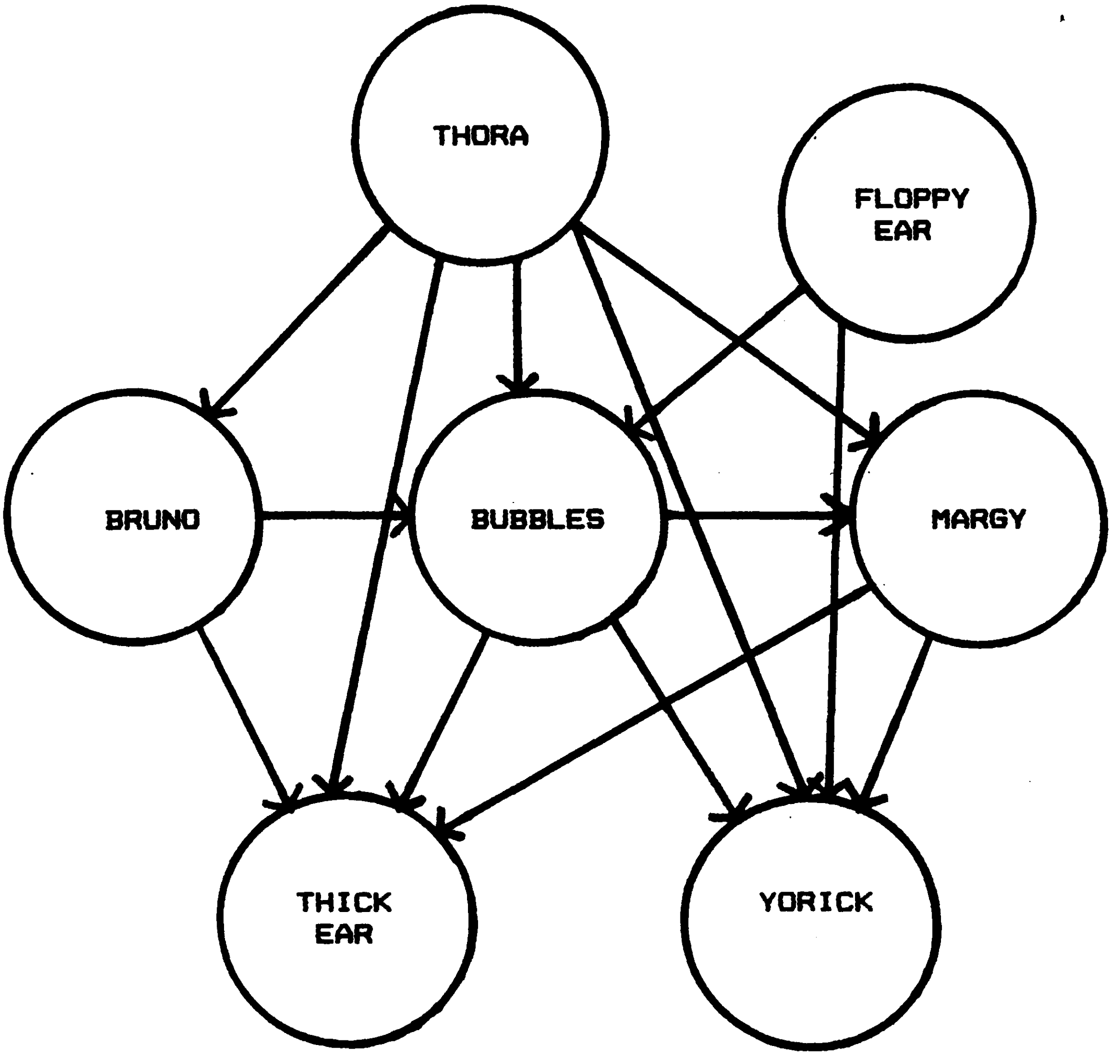


FIGURE 25. HIERARCHICAL ORGANISATION OF ALL IDENTIFIABLE GROUP MEMBERS.

found to be 0,375.

Only one positive encounter between individuals of different groups was observed. This interaction took place on the southern boundary of the group's territory, on the coast. Bubbles encountered a male from the neighbouring group, and was, throughout the interaction, absolutely submissive. Although the male was dominant, no overt aggression or neck-biting took place. On one other occasion, Bubbles was in the same area, and, after sniffing the air briefly, she suddenly turned rapidly in her tracks, running fast in the direction from which she had come i.e. northwards. Soon thereafter an adult female from the neighbouring group came walking along the beach; Bubbles had quite clearly taken evasive action on discovering the presence of the other female. Active avoidance by one of the subadults in the group of an unidentified adult near the northern edge of the territory was also observed. In this case, the subadult smelled the other animal and immdediately hid itself behind a sand hummock, lying absolutely still and pressed close to the ground. After the adult had passed by, unaware of the presence of the subadult, the latter ran extremely fast in the opposite direction from the adult's direction of travel.

Mills (1981) and Owens & Owens (1978) suggest evidence of active avoidance between members of groups, and implicate scentmarking as one of the major mechanisms involved. Bubbles also discovered a strange subadult, of unknown sex, well within the limits of the territory, in the S.W. As a result of her larger size she was easily able to overcome the younger animal. She then continually mauled the animal very severely around the neck and head, and would easily have been able to kill or seriously injure it, had she not been restrained by her very ritualised behaviour pattern. The subadult was allowed to scramble away to safety, up a very steep cliff, after approximately 10 min of this neck-biting and mauling (which resulted in the animal losing a substantial amount of blood from her neck, head and shoulder).

c) Denning and Related Social Behaviour

Thora was collared when her three cubs were approximately three weeks old. Over the next five weeks, she moved the cubs four times. The moves were 1,0km, 1,2km, 0,5km and 1,8km respectively, and the dens were all within a 3km area. On the first three occasions, the cubs were carried individually, with the mother making separate trips between the two dens for each cub. The last, and longest move, was undertaken when the cubs were approximately eight weeks old, and, on this occasion, the mother moved all three at once -carrying one while the other two followed behind; all three had a chance to be carried.

The dens were caves under rocky ledges. Two were near the top of ridges which were almost inaccessible by vehicle, although it was possible to walk up to them without too much difficulty. The den entrances were too small for an adult hyaena to pass through, in all but one case, and Thora regularly dug sand away from the entrances in order to allow easy passage for the cubs. Only two of the dens looked as if they had been used for maternity purposes to any substantial extent in the past; this was recognisable by the existance of bone accumulations around the entrances, and large latrines nearby.

As discussed in the previous chapters, Thora was observed to spend a very large proportion of her time at the particular den in use : 75% of the night (18h30 - 07h30) and 82% of the total 24 h period. Most of this time was spent resting within a few metres of the den entrance, but, time spent interacting with the cubs or other animals and time spent eating, is also included in these figures. Suckling normally took place with the mother lying down on her side (n = 51), but on a few occasions (n = 3) the cubs suckled from her while she stood. The average duration of suckling was 14,1 min (±4,9), and, on eight occasions, the babies suckled three times over the 13 h observation period; on 14 occasions they suckled twice a night.

Whilst Thora was at the den, the cubs would spend long periods playing with each other, with Thora and with inanimate objects such as sticks or bones. The cubs only rarely slept outside the den, and, apart from the times when they were being moved from one den to another, they did not venture more than approximately 20m from the den. At about five weeks of age, the cubs began to chew on pieces of seal lying in the vicinity of the den, but would have obtained little or no nourishment from this source. At this age, they were also observed going through the motions of scent-marking on various objects, but once again, this behaviour was certainly not functional at this stage (Mills, 1983b). At seven weeks, the cubs began to eat off seal carcasses, and, within 10 days of this time, they were ingesting significant quantities of meat, and fighting and competing over available carcasses, although no decrease in the amount of time spent, or frequency of, suckling was apparent.

Thora was supplied with food at the den by other group members. As stated in the previous chapter, she was provided with 16 unscavenged carcasses and one gemsbok skull, representing 70% of her food intake. Of the 16 carcasses provided, one was supplied by an unidentifiable group member, and three were supplied by animals which were never seen. Two were provided by Thick Ear (a subadult male), and 10 by Bruno (an adult male). Bruno thus supplied 76,9% of the carcasses which were observed being brought to the den, and Thick Ear 15,4% of these. These two males, then, provided 92,3% of the seal carcasses of which the origins were known, and only three animals (apart from Thora), were seen bringing food to the den.

Judging by Thora and Bubbles' foraging successes (presented in Chapter 3), it would seem likely that these seal carcasses were located mainly on the S.W. coast. Bringing the food to the den would thus have involved a walk of between approximately 6,5km and 10,0km. The carcass was carried in the animal's mouth, with its head held high, in order to prevent the seal pup from snagging on rocks and bushes, and to prevent the hyaena from tripping over it. When the animal arrived at the den, it would normally be seen by Thora, who would run towards it, snarling and with her tail held out horizontally behind her. The provider would drop the carcass as she approached and adopt a submissive posture whilst she snatched the carcass up in an aggressive manner. Thora would then either drop the carcass and chase the individual who had brought the food for 10 or 20m before returning to collect the seal, or would return immediately to the den entrance with the carcass, and start eating. The provider would then either spend some time in the vicinity of the den, resting , (its distance from the den being dependent on the individual), or would continue on its way.

Thora was dominant to all the other group members, and any animal approaching the den was chased off aggressively. Bubbles, in particular, showed a great deal of interest in the cubs, but was never allowed within less that about 2-3m of them by Thora. Generally, any animal approaching to within 30m of the den was chased, with the exception of Thick Ear, who was often tolerated at the den by Thora, and allowed to interact with the cubs to a limited extent.

Group members would take advantage of any food that they could find around the den area, but were never observed stealing any large food item from the den itself. Thick Ear, on one occasion, approached the den in Thora's absence and found a fresh, unscavenged seal carcass at the entrance. He picked the carcass up and then walked slowly away from the den for about 50m, looking over his shoulder two or three times. He then stopped and stood, still holding the carcass in his mouth, for about a minute, before turning and walking back to the den, where he pushed the fully intact carcass back into the entrance, where he had found it. On another occasion, after giving a carcass to Thora, Thick Ear went to some trouble to steal it back from the den entrance, carried it off a few metres and then returned it to where he had found it. Mills (1983b) also reports similar behaviour in subadults who appear to go through a transition period between bringing food to the den and accepting food which has been brought there by other adults.

Up until the age of about seven weeks, the cubs showed fear of all hyaenas except their mother, and would run into the den if any animal approached them while Thora was not close by. From this age on they started showing apprehensive curiosity towards other group members, and would approach them warily. It was normally Thora who terminated these interactions, by chasing the hyaena when it go too close to the cubs.

d) Territory Maintenance

As indicated in Chapters 2 and 3, Bubbles undertook "territorial patrols", during which she behaved in a specific way. She would frequently follow identical routes, visiting the same latrines, and scentmarking in the same places; she would walk fast and her movement would be directional; she would also scentmark very frequently along the way. Other group members were seen exhibiting the same behaviour, and were also presumably patrolling the perimeter of the territory. Thora never undertook these patrols, but moved substantial distances (often along the coast) during which she would scentmark. The density of scentmarking is shown three-dimensionally in Fig. 26 for Bubbles, in Fig. 27 for Thora and in Fig. 28 for both of them. The total number of scentmarks per ¼km^2 grid-block is shown as a function of the total distance moved by the two hyaenas per block in Fig. 29.

The minimum number of scentmarks that Bubbles was observed to perform over a full 13 h observation period was five, and the maximum was 74. For Thora, the minimum was zero and the maximum 49. Bubbles was observed to travel a total of 477km and to scentmark 745 times; she thus marked 1,56 times per km, on average. Thora, however, marked 182 times over a distance of 306km, yielding an overall scentmarking frequency of 0,59 marks per km. This indicates that Bubbles marked over 2½ times more frequently than Thora, and Bubbles would certainly have had a much higher density of scentmarks in the territory, when one considers how much more mobile than Thora she was, as well. No significant difference was found in Bubbles' marking frequency when on a patrol and when engaged in some other activity. When she was in the most southern 1½km of the territory, within 500m of the coast, her marking

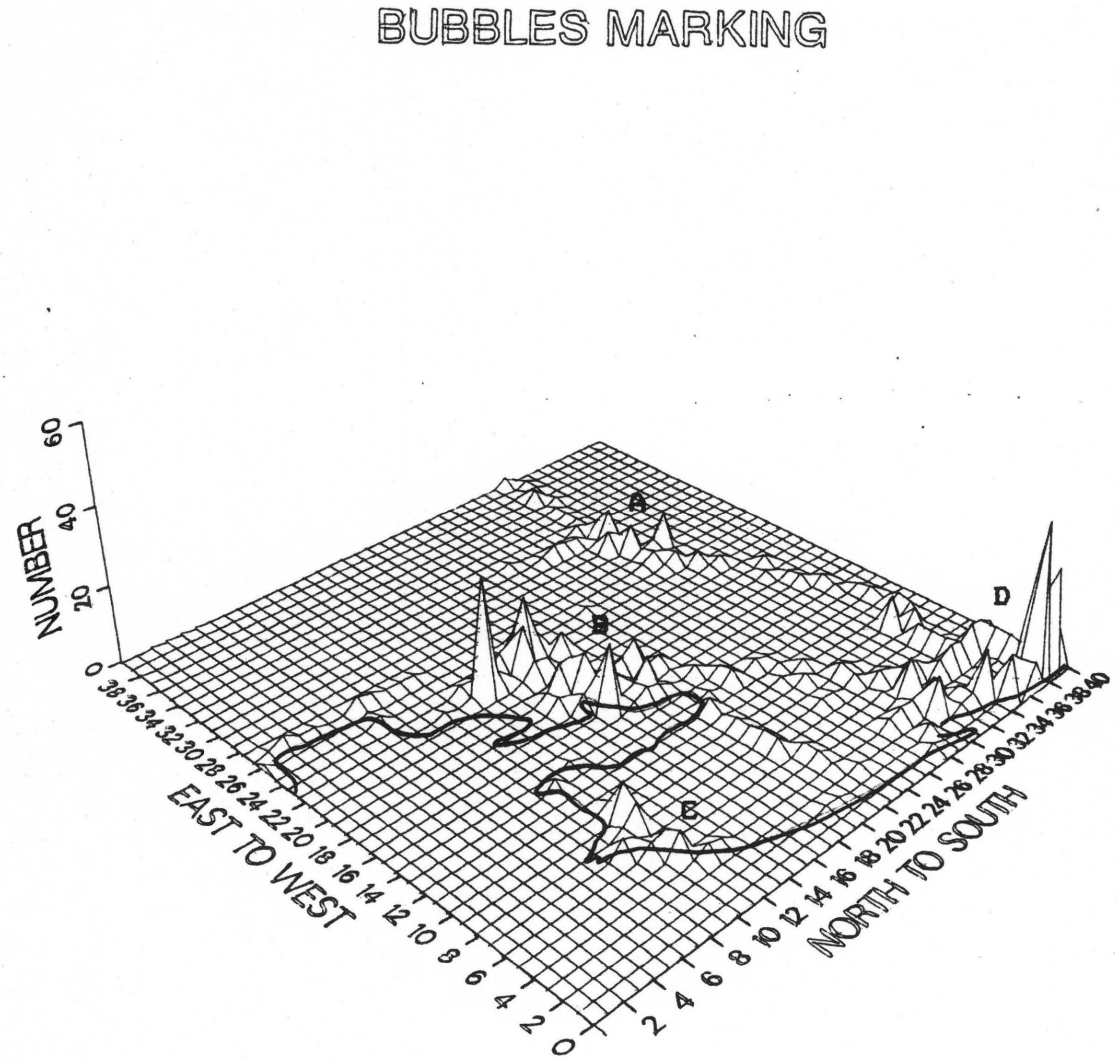


FIGURE 26. THREE-DIMENSIONAL, DISSPLA-GENERATED MAP SHOWING SPATIAL DISTRIBUTION OF BUBBLES' SCENTMARKING.

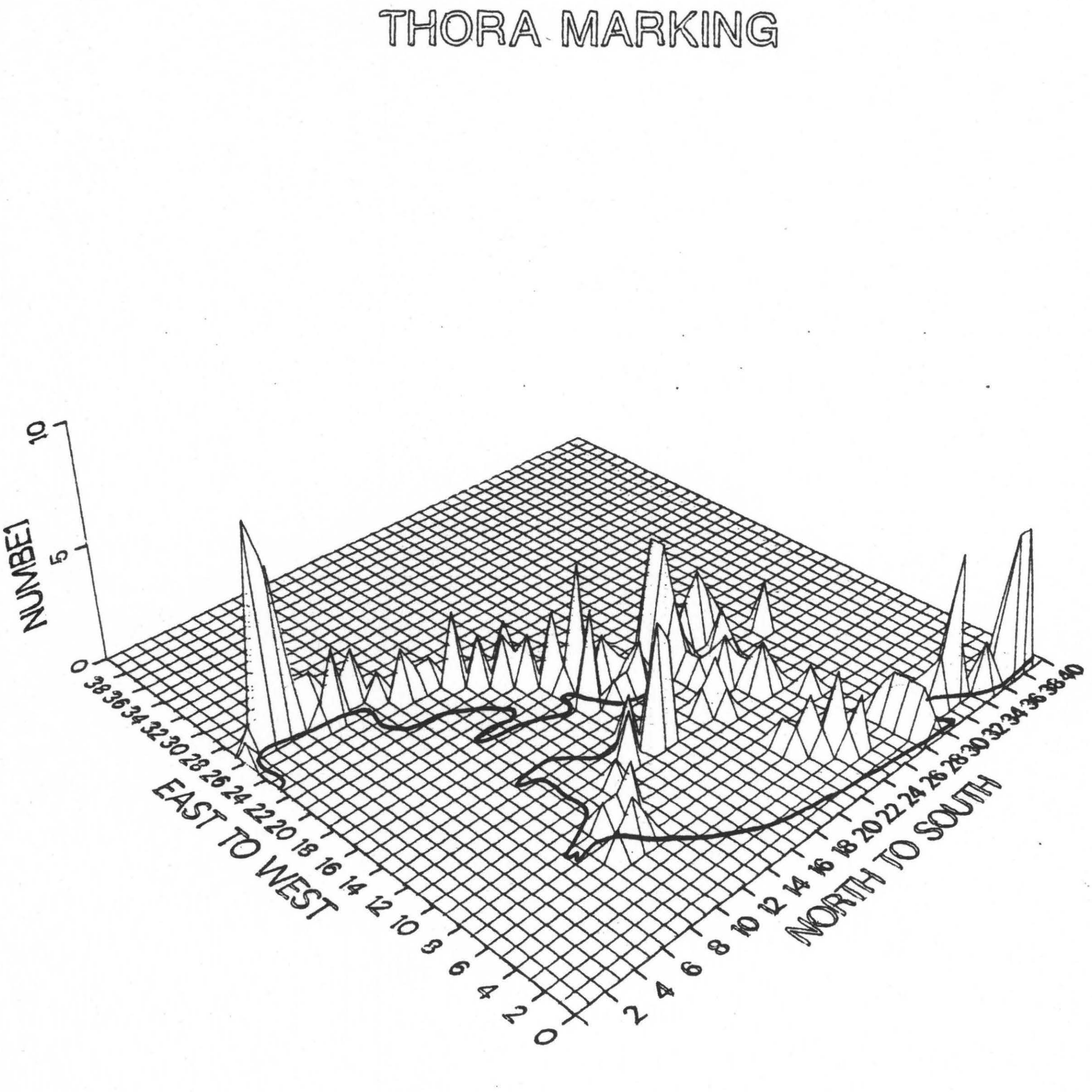
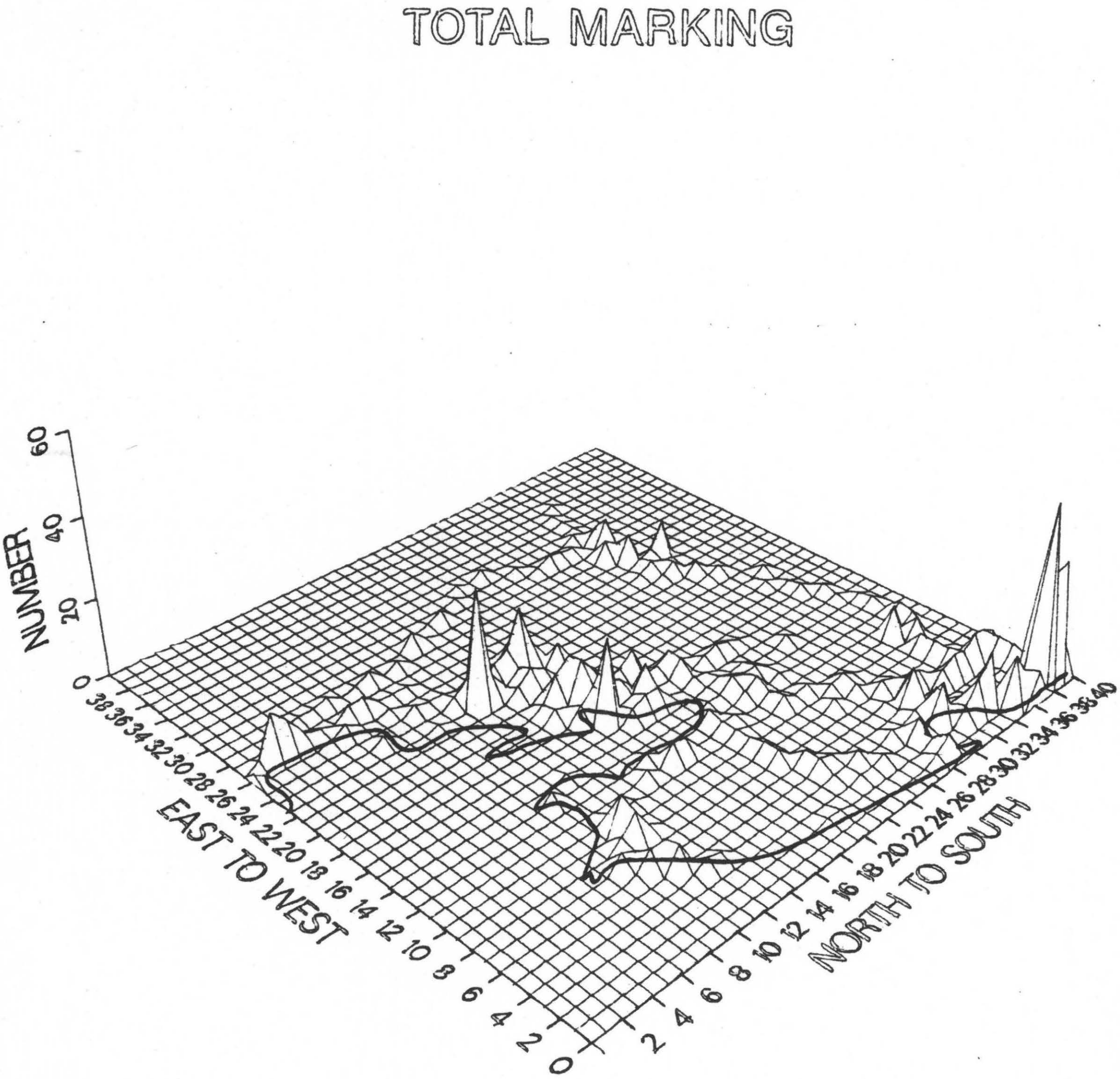


FIGURE 27. THREE-DIMENSIONAL, DISSPLA-GENERATED MAP SHOWING SPATIAL DISTRIBUTION OF THORA'S SCENTMARKING.



TOTAL MARKING

FIGURE 28. THREE-DIMENSIONAL, DISSPLA-GENERATED MAP SHOWING SPATIAL DISTRIBUTION OF THORA'S AND BUBBLES' SCENTMARKING.

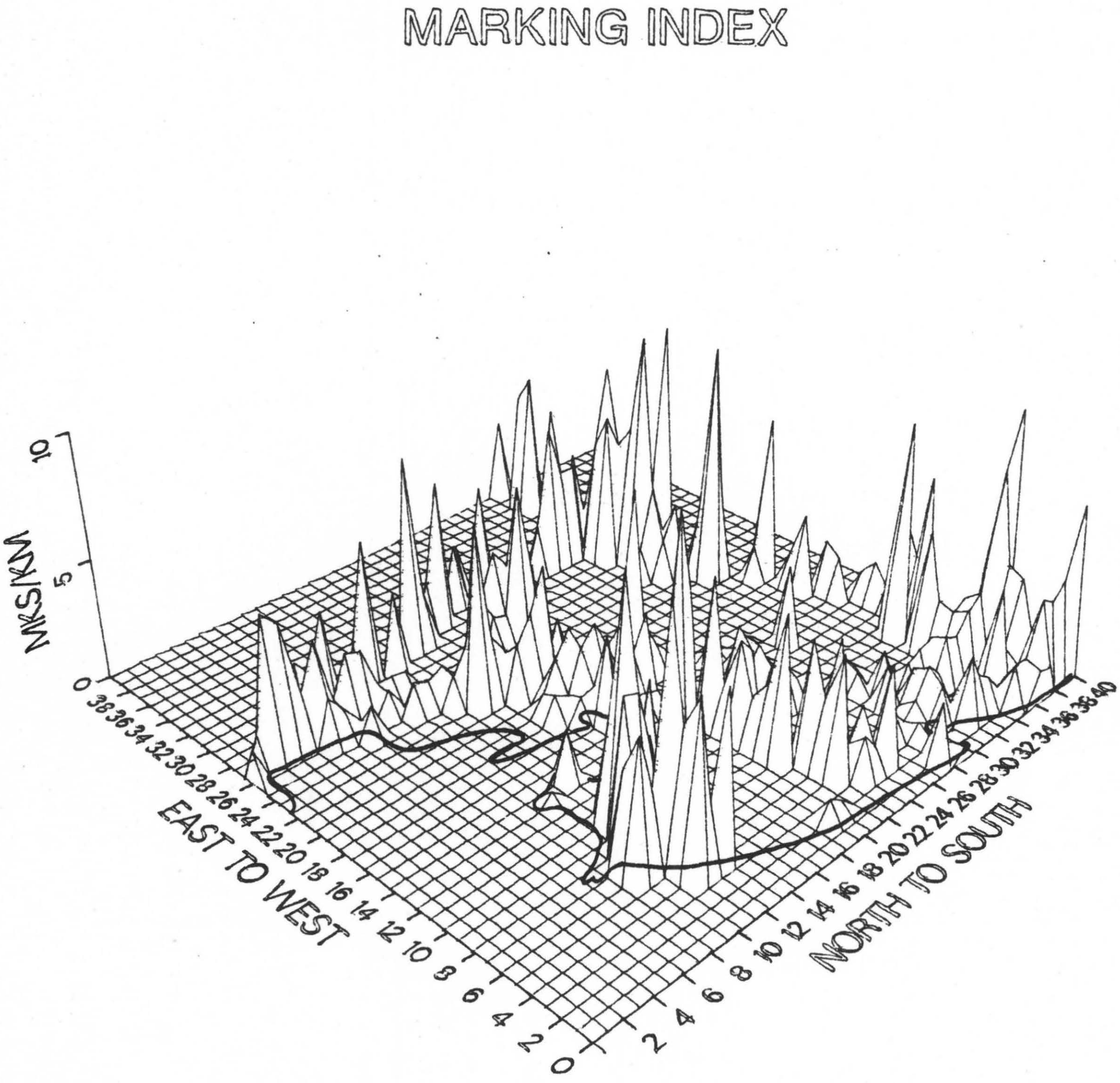


FIGURE 29. THREE-DIMENSIONAL, DISSPLA-GENERATED MAP SHOWING SPATIAL DISTRIBUTION OF THORA'S AND BUBBLES' SCENTMARKING, AS A FUNCTION OF DISTANCE MOVED BY THEM IN EACH GRID-BLOCK.

frequency did, however, increase to 4,0 marks per km.

Bubbles performed 39% of her scentmarks within 500m of the territorial boundary (excluding the coastline), 30% within 500m of Lüderitz and 31% in the rest of the territory. In Thora's case, the figures were 20%, 19% and 61% respectively.

As a result of the absence of vegetation, the hyaenas were observed marking on rocks, artificial objects, such as scrap metal or wire, pieces of kelp, bones and even on the ground on occasions. They would, however, always scentmark on vegetation if it was available, and sheltered, well-vegetated gulleys were often very heavily marked for this reason.

The hyaenas regularly defaecated at latrines, which may act as territorial markers or communication centres (eg. Mills, 1981). The latrines are substantially deeper than is the case in the southern Kalahari, and probably in the central Kalahari as well. They reach depths of 60 cm, and are up to 2 m in diameter. These structures are actively maintained by the hyaenas through frequent rolling and digging. A total of 38 latrines were identified in the territory, and their locations are shown in Fig. 30. Bubbles used 30 latrines. She rolled in the hollow in 37% of the cases in which she arrived at a latrine, defaecated in 60%, scentmarked in 23%, dug in 13% and ignored the latrine in 3% of the cases (after passing within 2 m of the latrine). Of Bubbles' defaecations 39% were at latrines.

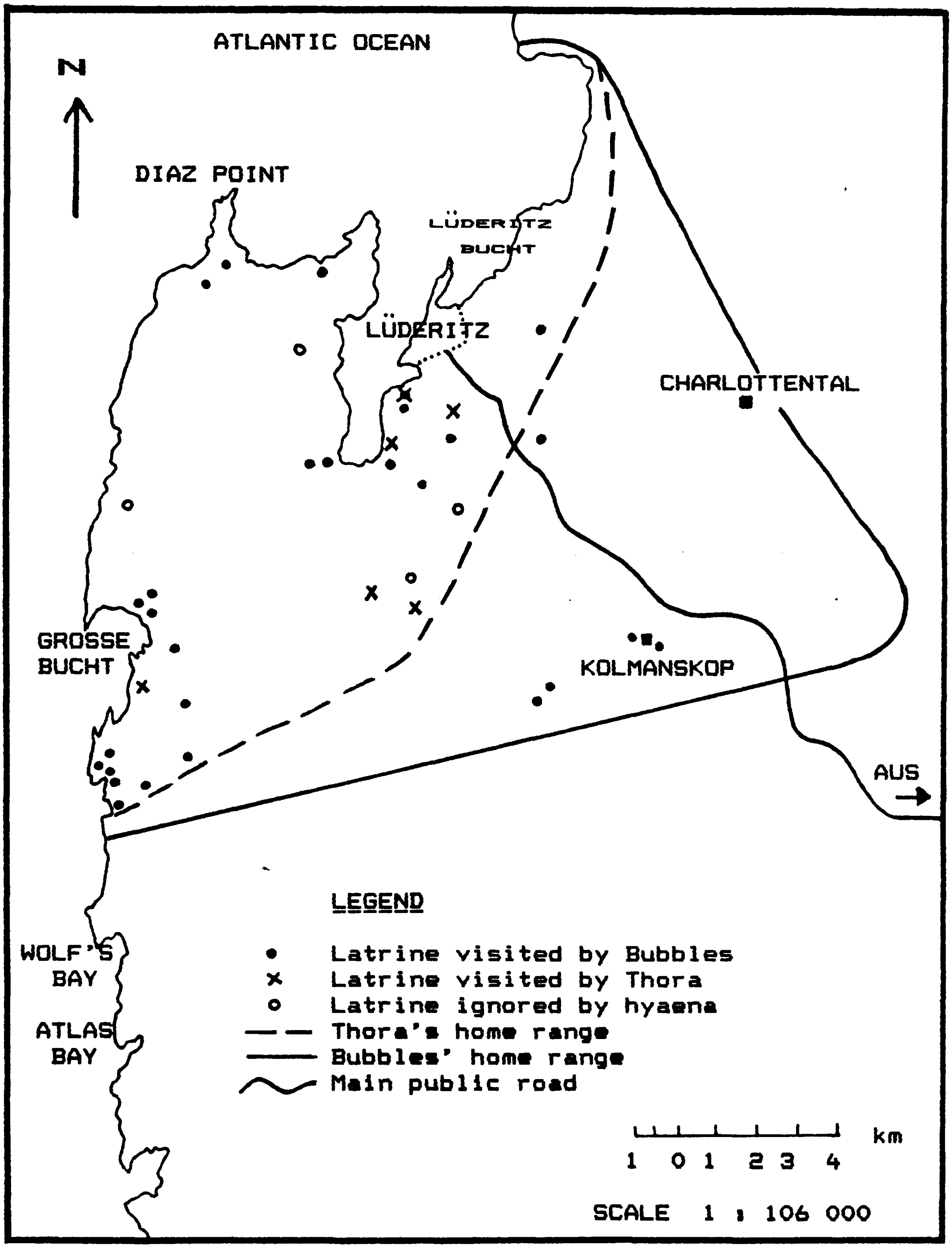


FIGURE 30. MAP SHOWING LATRINE LOCATIONS

Thora encountered a total of nine latrines. She defaecated at these 33% of the time, ignored them 44% of the time, scentmarked 11% and urinated on 11% of the occasions. Of Thora's defaecations 12% were at latrines. Only one latrine was mutually encountered by both Thora and Bubbles. The latrines were often near artificial objects or landmarks such as signposts, ruins, scrap items or road junctions.

e) Interspecific Relations

The brown hyaenas around Lüderitz were extremely wary of humans and would avoid contact with people if at all possible. Only one interaction between man and hyaena was reported during the study. This occurred when a hyaena entered a fenced area at night and was subsequently unable to get out. The animal was discovered when work started the following day; although it was chased and severely traumatised, the animal managed to escape without having an injury inflicted upon it. Only rarely are the animals actively hunted, although a number of road deaths have been reported by local residents over the last few years. Exact mortality figures resulting from human activity could not be ascertained, but an estimate from reports is that five or six animals have been killed around Lüderitz over the last five years. The animals appeared to be aware of the increased danger to themselves when in the vicinity of Lüderitz, and both Bubbles and Thora would become increasingly scared of the observation vehicle as they got closer to the town itself. Once contact was lost with a hyaena, it would run for cover at the next sight or sound of the vehicle. They were probably unable to recognise it as a vehicle to which they were habituated under different circumstances.

Apart form this interference competition around Lüderitz, the hyaenas seemed to be relatively undisturbed by man. Their dens are normally not discovered (on one occasion, when a maternity den was discovered by locals, the female immediately moved) and there is no competition by man for their primary food source, which is seal pups.

Packs of feral dogs, numbering up to eight animals, were known to exist in the area. These animals were, however, only rarely seen, and occurred in low densities. Although they must be sharing the same food supply as the hyaenas, and thus be competing with the hyaenas, no interaction was observed. On one occasion, when a hyaena had been trapped, a group of five dogs were found behaving extremely aggressively towards the caged animal, but these circumstances were obviously unnatural and highly unusual.

Domestic dogs in Lüderitz were extremely aware of the hyaenas. They were scared of the hyaenas, but would bark and howl if they detected the presence of a hyaena. They would normally follow the hyaena, barking excitedly, but would keep a safe distance (50 - 100m) between themselves and the hyaena. The hyaena would ignore the dogs, but was clearly aware of their presence and the fact that they were drawing attention to it, since it would often move to the outskirts of the town once the dogs started reacting to it. On two occasions, large, aggressive dogs were seen to rush out at Bubbles as she walked away. As the dog got to within about 3m of her, she turned towards it with fur raised; the dog immediately turned in its tracks and retreated. Bubbles continued to walk away, with hair raised and more rapidly than she had prior to the encounter; the dog continued to follow her, still barking but keeping about 20m away from her.

Jackals were seen in most parts of the territory (n = 74) but were most frequently seen in the S.W., south of Grosse Bucht and within 2km of the coast i.e. on 43% of the occasions on which they were seen. On 38% of the occasions on which they were seen, they were in the vicinity of the one of the maternity dens, and on 19% of the occasions they were seen elsewhere. Seventy percent of the times jackals were observed alone, 27% in pairs and 3% in threes.

Jackals were observed to follow a hyaena on 14 occasions. They normally kept between 10 and 50m behind the hyaena, but also frequently came up to the hyaena and molested it by nipping it on the heels and tail. Attempts by the hyaenas to spring round and catch the jackal always failed, with the jackals easily anticipating the move, and springing out of the way. The jackals also mobbed the hyaenas whilst they were sleeping or eating, and would sneak up behind them to nip them. The hyaenas were often clearly frustrated, and would move away from the jackal. Once, a jackal was observed to molest a hyaena which was attempting to sleep, for half an hour, before curling up about 5m behind the hyaena and going to sleep itself. This mobbing behaviour put the jackals at considerable risk, since they would undoubtedly have been killed by the hyaena if they had faltered and been caught. A jackal which had persistently molested Thora at the den and attempted to steal food, was found dead at the den entrance after having been severely mauled and disembowelled (presumeably by Thora).

A hyaena was observed to displace a jackal or jackals from a food item on only five occasions whilst there were between one and three jackals almost constantly around the maternity den. They attempted to steal food from the cubs or from the den entrance, in Thora's absence. They also spent a substantial amount of time eating on old carcasses or bones, which had been discarded by Thora. There is a much stronger relationship between jackals and the maternity dens in this area than was described by Mills (1977) in the southern Kalahari. Jackals were also frequently present when Bubbles was eating, and would attempt to snatch bits of food whenever the opportunity presented itself.

The hyaenas' predatory relationship with the seal pups has been dealt with in some detail in Chap. 4. When the hyaenas encountered an adult seal (n = 3) they showed a great deal of interest but approached the animal very slowly and apprehensively. When the hyaena got within about 1m of the seal,the seal would lunge forward in an attempt to bite it.

These interactions lasted between 3 min and 18 min and ended with the hyaena apparently losing interest and moving away.

DISCUSSION

The minimum group size of five adults, four subadults and three cubs is higher than the average group size of five, recorded for five groups in the southern Kalahari by Mills (1981). The study group is, however, very similar, both in composition and size, to a group studied for six years by the above author, when it was at the peak of its fluctuating cycle. Owens & Owens (1978) report a clan size of eight or nine adults; the study group is unlikely to be this large, even with the possible under-estimation of its size. In view of the very large food supply in the Lüderitz hyaenas' territory,one would expect a much larger group size, if this aspect were largely dependent on food availability and quality, as argued by Mills (1982a) and Macdonald (1983). It would thus appear that other factors (most likely social factors) are limiting population growth of the hyaenas, or that some obscure limitation in the food supply (possibly quality or temporal distribution thereof) is making it less advantageous than this study suggests. Long term research on food supply would be required to rule out this unlikely possibility.

The dominance hierarchy which was found to exist (Fig. 25) is largely related to age. Thora and Floppy Ear were older than Bubbles, who was in turn older than the three subadults -

Margy, Thick Ear and Yorick. Bruno appeared to be younger (and smaller) than Thora and Floppy Ear, but larger and probably older than Bubbles. No sexual significance can be attached to this hierarchy. Although certain individuals were certainly dominant over others, the hierarchy showed a high degree of non-linearity when Landau's index of linearity was calculated, and when Appleby's method of testing for linearity was used. This result may be due, to some extent, to the relative paucity of information and large number of unknown relationships.

The existence of individual dominance in the Namib corresponds to the results of Owens & Owens (1978, 1979b) and Bosman (1982). Mills (1981) however, did not find a hierarchy in his study, however. If dominance is related to access to food, as appears to be the case in the central Kalahari, where the hyaenas often feed together off large carcasses, and in captivity, where they are extremely crowded, then one can reasonably expect a hierarchy to exist in the Namib, where the food supply is highly concentrated, as illustrated in Chapter 3. Conditions for the existence of a social hierarchy were not as favourable in this study as was the case in the above two cases. Their high degree of socialising and close physical proximity of the animals in highly competitve feeding situations would certainly have made the existance of a hierarchy advantageous to the animals. Notwithstanding this fact and the fact that no two hyaenas were ever observed to feed together off the relatively small seal carcasses, the high concentration of the food in the

Namib, when compared to the southern Kalahari, would certainly lead to increased social contact and a subsequent necessity for the existence of a dominance hierarchy.

A significant difference in the way in which the hierarchy was maintained existed between the present study and that of Owens & Owens (1978;1979b). In the present study no neck-biting or behaviour of comparable aggression was ever observed between group members. All interactions were highly ritualised and the submissive individual never escalated the aggression beyond muzzle-wrestling. Mills (1981) also reports that neck-biting between group members was never observed.

Thus it appears that the hierarchical situation in the Namib is of an intensity that is greater than that which exists in the southern Kalahari but less than that in the central Kalahari. This may be due to the fact that food is more concentrated here than in the southern Kalahari but less concentrated than in the large carcass situation of the central Kalahari. Competition may also be lessened (resulting in a less intensely maintained hierarchy) as a result of the fact that food is abundant.

The research cited above, in both the southern and central Kalahari, revealed that hyaena cubs were provisioned at the den by their parents and by other group members. In the Lüderitz study the group members were found to provision the mother at the den before the cubs were able to eat and, thereafter, the cubs would eat on carcasses which were brought to the den, but only after the mother had eaten. Coupled with this is the fact that Thora spent so much time at the den (see Chapter 3). Mills (1981) reports the mother to have visited the cubs at sunrise and sunset in order to suckle the cubs, and she was observed to stay away from the den for as long as five days on one occasion. This difference in behaviour is attributable to the fact that food is so abundant on the Namib coast that the cost to a group member of provisioning the den is very low, not only in terms of the time needed to locate food, but also in terms of the value of that food to the individual. This means that much more food can be brought to the den, thus allowing the mother to put a great deal more time into the care of her offspring. This, in turn, should lead to an increased rate of offspring survival.

Owens & Owens (1984) found that nonparental females provisioned the den on 85,5% of the occasions on which nonparents were observed to perform this activity. This contrasts sharply with the present study, in which males accounted for all the nonparental provisioning. Mills (1981) found females to provision in 59% of the cases in which this was observed, but does not specify whether maternal input is included in these figures. If adult females were most likely to provision the den, Bubbles should have been a prime candidate for this behaviour. She failed to bring any food to the den and was tolerated least at the den by Thora : she was never allowed within about 15m of the entrance and Thora's attacks on her were more aggressive than was the case with other individuals. It is also interesting to note that the subadult male, Thick Ear, who accounted for 15,4% of the provisioning, was most tolerated at the den by Thora, and spent a large amount of time in its vicinity. This behaviour suggests that Thick Ear may have been Thora's son from a previous litter.

The high frequency with which the cubs were moved from one den to another may be a result of the fact that the hyaenas in this area are more apprehensive about humans than those in other areas. This is a consequence of the frequency of agonistic encounters between the two species and my presence at the den may thus have prompted this behaviour. Den moves were much more frequent than was reported by Mills (1981) and Owens & Owens (1984), although the former does record dens having been moved as a result of the observer's presence.

There were no other cubs at dens over the study period, and it was thus not possible to ascertain whether or not the hyaenas in this area denned communally, as was the case in the central Kalahari (Owens & Owens, 1978, 1979a) or not. Mills (1981) speculates that communal denning may be positively correlated with food abundance, and one might thus expect communal denning in this area. The above authors comment on the importance of the den in terms of sociality. This was not the case in this study, and only four of the eight nonparental group members were observed to visit the den area. As mentioned earlier, Thora kept all animals except Thick Ear a substantial distance away from the den itself.

Figures 26 - 28 show the number of scentmarks or pastes which the hyaenas were observed to perform across the territory. When compared to Figs. 3 - 5, these figures indicate that total marking in an area is independant of the total distance which the hyaena or hyaenas move in that area. This is in agreement with the findings of Mills (1981). Owens & Owens (1978) found areas of interest to be more heavily marked than others, and, in Fig. 26, it can be clearly seen that Bubbles marked most in four distinct areas (A, B, C and D). A is the area around Kolmanskop, B is Lüderitz and environs, C is Diaz Point and D is the highly utilised south western area. Thora's marking pattern (Fig.27) was similar to that of Bubbles, with the obvious exclusion of the Kolmanskop area. Note also that the central, highly marked area was around the maternity dens as opposed to Lüderitz which was heavily marked by Bubbles. Thora also marked heavily at the very northern end of the territory, on the coast. The rather small sample sizes associated with Thora's low rate of marking could, however, have lead to dramatic peaks in the figure, which do not have any major significance.

Figure 28 shows the overall importance of the S.W. coastal boundary as a pasting location, as well as that of Lüderitz; the territorial boundary was also largely demarcated by scentmarks. As a generalisation, then, the hyaenas in this area tended to mark important boundary areas heavily ie coastal boundaries. They also tended to mark areas which they frequented out of apparent curiosity, or for unusual food items i.e. Lüderitz, Kolmanskop and the Diaz Point lighthouse.

One might argue that these heavily marked areas were due to the hyaenas spending a great deal of time, and travelling a large distance, in them. This certainly was the case to some extent (as stated earlier), but Figure 29, showing the total number of pastes as a function of distance travelled by the hyaenas, indicates that the hyaenas' marking rate also increased in those areas (described above) which contained a large number of pastes. Mills (1981) also found boundaries to be more frequently marked (although less heavily overall) by the brown hyaenas in the southern Kalahari.

Thora marked predictably less frequently on average (0,59 times/km) than Bubbles (1,56 times/km). This is significantly lower than was the case in the southern Kalahari, where the mean pasting frequency was found to be 3,38 marks/km. Part of the reason for this may be that pastes may not have been recorded as a result of the animals being hidden from view more often in this study than was the case in the Kalahari. The scarcity of vegetation and other objects upon which to scentmark may also have influenced the hyaenas' marking rate.

The location of the latrines in the territory, shown in Fig. 30, is fairly uniform, but there does appear to be some clumping around Lüderitz and in the S.W. The fact that Thora and Bubbles never defaecated at the same latrine is in agreement with the findings of Owens & Owens (1978) but there does appear to have been greater separation betwen the two hyaenas in this case, with only one common latrine being visited. Bubbles encountered, enlarged and defaecated in more latrines than Thora. The reasons for this are twofold: Bubbles' greater activity would inevitably mean that she would encounter more latrines and her more intensive maintenance and use of these is in agreement with her being generally more active in territory maintenance and marking than was the case with Thora.

The difference in structure of the latrines in the Lüderitz area, when compared to the Kalahari, may have a functional significance, in that there are so few landmarks in this area. Both Owens & Owens (1978) and Mills (1981) state that latrines are frequently near trees and are often even on the same side of trees (Mills 1981). This is probably to facilitate location of these latrines by the hyaenas, and this is important since they perform an important communicative function. The deep, large latrines in the Namib Desert may also be more easily located as a result of their depth and size. Alternatively, the reason may be more simple: there is very little movement of sand in the area of the Namib Desert in question; this is because the area has been scoured to the bedrock or gravel surface by the very frequent high winds. Tracks, holes and other marks on the surface are thus extremely long-lived as opposed to the Kalahari, where the wind-blown sand may fill indentations within minutes. The presence of some of the deepest latrines behind beaches and in other areas of sand movement in the Namib Desert makes the former argument more likely.

As discussed in the introduction to this chapter, instability is a pre-requisite for the manifestation of active competition in a system. The recent (in evolutionary terms) introduction of both humans and domestic dogs to the Namib Desert would certainly result in a competitive situation developing. The fact that neither of these species utilise the hyaenas' prime food source to any significant extent does alleviate the competitive intensity. Competition for space is lessened through the temporal spacing of the humans' and hyaenas' activity periods (see Chapter 3) and the fact that human activity is restricted in much of the hyaenas' range. Dogs certainly compete for the hyaenas' supplementary (and apparently highly favoured) food supply in the form of human refuse and pickings from the vicinity of Lüderitz. The aggression between the species and the hyaenas' predation on the dogs are examples of the manifestation of this interference competition.

Jackals have been stated to be the brown hyaena's prime competitors in the Kalahari (Owens & Owens, 1978; Mills, 1981). This is attributed largely to the fact that the two species feed and forage in a very similar manner. This certainly applies in the Namib Desert, too, where the hyaenas will kill jackals if possible and the jackals mob the hyaenas at every opportunity. Mobbing has been reviewed by Bertram (1978) and Harvey & Greenwood (1978) and is almost always associated with a predator/prey situation with very little attention having been given to mobbing in competitive situations. Although jackals are certainly potential prey for the hyaenas, this mobbing behaviour may also be a manifestation of competitive equilibrium at which the two species live.

It is surprising that jackals do not take advantage of the hyaenas' caching behaviour in the Kalahari (Owens & Owens, 1978). In the present study the converse certainly applied (see Chapter 4). There was some evidence for the hyaenas actually being important in enabling the jackals to make use of the food supply in this area: jackals were observed to be unable to kill even a very weak seal pup, whilst the hyaenas manage this easily; the jackals were then able to utilise the remains of the carcass once the hyaena has eaten. The jackals also appeared to have difficulty in penetrating the pelts of seal carcasses, and were unable to crush the skull in order to enter the carcass as the hyaenas did. The extent of the jackals' reliance on the hyaenas was not clear, but it may, in fact, be very much larger than is immediately apparent.

6. EVOLUTIONARY CONSIDERATIONS AND CONCLUSIONS

The conditions in the area in which the present study was undertaken are quite different from those that exist in areas in which the brown hyaena has previously been studied in any detail. These conditions are as follows:

- The existence of a large human settlement within the confines of the hyaenas' territory.
- There are food sources in the territory (in the form of mining towns) which have become totally unproductive in the last fifty years.
- Food production is limited to a very small proportion of the area; only the coastal fringe is productive to any significant extent and even in this zone production is limited to a small stretch of the coastline. The human settlement produces a small amount of apparently favoured food for the hyaenas.
- Food is available in excess, and this is probably the case throughout the year.
- Weather conditions are extremely severe and inhospitable.

In order that they survive under these unusual conditions, one would anticipate specific modifications or adaptations in the hyaenas' behaviour patterns. Physical and physiological adaptations may also take place, but, by its very nature, behaviour is more flexible. It can thus adapt more rapidly than is the case with physical change, which is bound by the unwieldy and slow-moving mechanism of evolution through genetic variation. Subtle physical and physiological adaptations may exist in these animals, but the elucidation of this aspect is beyond the scope of this project.

Behavioural flexibility was discussed in Chapter 2, and some examples were cited. Brown hyaenas, as scavenger and opportunist feeders, are able to exploit a wide range of food sources. The combination of a flexible social system, flexible feeding and foraging habits and a robust physical constitution would certainly enable this species to successfully inhabit the wide range of environments in southern Africa in which it is found today.

What evidence was there in the present study for the existence of flexibility in order to enable the hyaenas to cope with the above-mentioned environmental peculiarities in the study area?

First the hyaenas have managed to survive in reasonable numbers, even in the face of persecution by the human population of Lüderitz. In order to do this, they have learned to avoid confrontation with humans whenever possible. Any evidence of human activity in an area will cause the hyaenas to avoid the area concerned, or to wait, in hiding, until the activity has died down. They appeared to have learned of the dangers of roads and motor vehicles, from which they would shy away immediately. Not only have the hyaenas learned to avoid humans, but they have also learned to utilise their settlement in order to scavenge or hunt preferred and unusual food items. To do this, they have adapted their activity patterns in areas of potential conflict to ensure minimal temporal overlap with the activity patterns of the human population. The ability to remain inconspicuous through secrecy and the alteration of activity patterns, has proved to be one of the hyaenas' major assetts in a subcontinent which is becoming increasingly dominated by man.

There is now growing evidence for the existence of this species over a very wide range (Mills, 1982c; Skinner, 1976) and often in close proximity to large human settlements (Skinner, 1976) or agricultural areas (Skinner & Van.Aarde, 1985). This ability to inhabit areas which are dominated by man is not peculiar to brown hyaenas. Jackals were seen in and around Lüderitz on occasions and urban modes of existence have been described in badgers (Meles meles) (Harris, 1982, 1984) and foxes (Vulpes vulpes) (Harris, 1977, 1980, 1981). Nocturnal activity seems to be a pre-requisite for urban existence in wild, medium-sized and large mammals, but the ability to find shelter during the day is equally important. In the case of brown hyaenas, a relatively undisturbed area (often mountainous or difficult to traverse) is the key to its ability to utilise areas inhabited by human populations as indicated by this study and by Skinner & Van Aarde (1985). The restricted Diamond Area around Lüderitz was ideal in this respect, and arguably essential for the continued existence of the hyaenas in this locality.

Having established the substantial interest which the hyaenas showed in Lüdertiz, one can safely assume that the now abandoned mining towns in the interior would have been at least as attractive to the hyaenas when they were inhabited. The possibility exists that they may even have been much more valuable to the hyaenas at that time, depending on the specific conditions in the area with regard to territorial borders and food availability, both on the coast and in the towns. It would thus appear that, although the hyaenas exhibit flexible behaviour, this may take place over a period of time, and an evolutionary lag will thus exist in response to a changing environment. The existence of a very large, unproductive territory, which encompasses former food sources, may well be a present-day manifestation of this phenomenon.

From an evolutionary viewpoint, a trait, behaviour or physical adaptation which becomes redundant may well continue to exist in the population, if the continued existence of the feature does not confer a selective disadvantage on the individuals in which it occurs i.e. there must be a strong selection pressure in favour of individuals in which the adaptation does not exist. In the case of the Lüderitz hyaenas, the abundance of food may decrease the relative cost to individuals which continue to maintain this "super-territory". The cessation of related behaviour would therefore not benefit the hyaenas to the extent that it would if the energy saved could be expended in a way which bestowed major selective advantages on the animals. This phenomenon may thus be slowing the rate of evolutionary change in this particular case.

In spotted hyaenas it has been suggested that one of the main functions of a hierarchy in the group is to determine individual access to food at large carcasses (Van Lawick & Van Lawick-Goodall, 1970; Kruuk, 1972; Tilson & Hamilton, 1984). Mills (1981) has put this aspect forward as a possible reason for the existence of a hierarchy in the central Kalahari (Owens & Owens, 1978), whilst no evidence was found for the existence of a hierarchy in the southern Kalahari (Mills, 1981). Having thus established that the brown hyaena has developed a hierarchy, it appears that this is only expressed under special circumstances. Tilson & Hamilton (1984) suggest that this may be the case in some groups of social hunters.

How do the environmental conditions in the present study compare with those in the central and southern Kalahari? Food items were small, and no two hyaenas were ever observed to feed off the same item simultaneously. The situation thus appears to be similar to the southern Kalahari, ie the selective pressures of scramble competition and aggression at large carcasses were not present. The important aspect is, in fact, food concentration: a large carcass was an extreme case of a highly concentrated food supply and it was this high concentration which resulted in the expression of the hierarchy. In the study area, the food supply was also concentrated (although not to the same degree as the above case) and a hierarchy is found to be present, as expected. There is no evidence for linearity in this case, and the hierarchy was not as aggressively enforced (through neck-biting) as was found by Owens & Owens (1978) and Bosman (1982). It seems clear then, that food concentration can be positively correlated with the expression of social hierarchies in the brown hyaena and that the entire spectrum of food concentration is covered, resulting in the existence of extremely intense and strongly enforced hierarchies and the total non-existence of hierarchies at all.

In this area on the Namib Desert coast, it appears that food was not a limiting factor affecting population growth. One can reasonably assume that the most likely period of food shortage for the hyaenas would be shortly before seals begin to give birth, or during the calving period itself, in the case of hyaenas which do not have direct access to the colony. The latter part of the study occurred during this period of possible food shortage, and seal carcasses were still available in such abundance that the hyaenas were observed on occasions to ignore fresh carcasses. Social factors were most likely to be limiting population growth, but the details and mechansisms involved remain unclear. The relatively concentrated nature of the food supply and subsequent increased frequency of interaction between the hyaenas would add weight to this argument.

Apart from the effect of environmental conditions on these socially-related behaviour patterns, it is apparent that the individuals' space use, activity patterns and foraging behaviour were well adapted to this particular set of conditions. These adaptations varied between animals of different social status, and in particular between females with young offspring and those without. The adaptive value and functional significance of the particular features which the hyaenas exhibited has been discussed in each chapter, and these have been related to specific environmental conditions where possible. In almost all circumstances the rôle which food source plays was paramount.

I conclude that the brown hyaena does exhibit substantial behavioural flexibility, both in a social and individual context, and that this flexibility can often be related to environmental conditions, with food being the most important of these. There are, however, certainly limits to this flexibility; an example of this is the apparent inability of the animals' social system to accommodate large numbers even when food supply makes this possible. There is also a time-lag in the evolution of adaptations, and this may result in apparent maladaptation during the period of change. The maintenance of an excessive territory is a case in point.

The brown hyaena's most powerful means in the successful colonisation of harsh or rapidly changing environments may be this inherent flexibility in its behavioural ecology.

Summary

The present study investigated aspects of the behavioural ecology of brown hyaenas (Hyaena brunnea) in an environemnt in which they have not previously been studied in detail; namely, the arid coastal region of the central Namib desert in southern South West Africa/Namibia. The prime objective of the study was to establish the extent to which food availability, quality and distribution influenced social organisation and space utilisation by the hyaenas. The effect of the town of Lüderitz on the brown hyaenas' behavioural ecology also received some attention.

Between May and September 1984, two adult females yielded 607 h of direct observation, with the help of radio-telemetry. Other individuals in the group were observed randomly and for short periods; these results were not quantitively analysed.

The home range of the female with cubs, Thora, was found to be 107km^2 whilst the home range of the other female, Bubbles, was congruent to the group's territory which had an area of 220km^2. The territory was largely unproductive with the exception of a 3 km stretch of coast in one corner of the hyaenas' territory which supplied almost all their food requirements in the form of Cape fur seal pups (Arctocephalus pusillus). In the light of this food distribution, the territory is excessively large, and it is hypothesised that the abandoned mining towns in the extreme inland portions of the territory were once food sources which the hyaenas'

ancestors used. The relatively recent disappearance of this food supply has not yet changed the hyaenas' lifestyle, and they are currently maintaining an area which is of little or no apparent benefit to them.

The individual hyaenas' space use patterns differed, with Bubbles mainly utilising the "food-rich" portion of the territory, the area around Lüderitz and the corridor between these two core areas. Thora, however, largely used the area around her maternity dens and the "food-rich" coastal area.

The hyaenas did not appear to be able to defend their territory when the defendability of the area was calculated. Possible reasons for this were: the animals' extremely low intruder pressure along certain boundaries, the tendency of the animals to undertake boundary patrols rather than to encounter the boundaries in a random fashion and a possible under-estimation of group size.

Thora and Bubbles clearly lay up in preferred areas during the day: the former at the maternity den and the latter a few kilometres inland of the rich coastal strip in the south-west of the territory.

The hyaenas were found to spend a large proportion of their time resting: 85% of the 24 h period of Thora and 63% for Bubbles. No clear pattern was apparent in both the animals' nocturnal activity patterns and the sequence of major activities over a number of nights. The very concentrated, over-abundant food source which the hyaenas were utilising appeared to be the major factor influencing the results obtained.

Lüderitz was clearly visited by the hyaenas at times at which human activity reached a nadir in the town. This temporal separation between the two species reduced the potential for possible conflicts which have resulted in trauma, injury or death for the hyaenas.

The hyaenas' diet consisted almost exclusively of seal pups which were normally scavenged but which were also occasionally killed by the carnivores. Other items which were eaten were water birds, dogs (Canis familiaris), fish and the remains of livestock and other human refuse. Seal pups were apparently over-abundant during the period of the study, since the hyaenas were observed to ignore fresh seal carcasses on occasions. A dog (Canis familiaris), jackal (Canis mesomelas), flamingo (Phoenicopterus ruber) and gecko were killed and left virtually uneaten by Bubbles. By volume, seals made up approximately 98% of Thora's diet and 84% of Bubbles' diet.

A well defined linear dominance hierarchy was found to exist. Adults were dominant over subadults and Thora was dominant over all group members. The minimum group size was estimated to be five adults, four subadults and three young cubs. An unrecorded behaviour involving exaggerated licking of one hyaena's back by another was observed on two occasions and appears to have sexual implications.

Thora was provided with 70% of her food at the den, by other group members. Approximately 15% of this was brought by a subadult male and 77% of an adult male.

The hyaenas marked most frequently on the territorial boundaries and on coastal boundaries in particular. The area around Lüderitz was also frequently marked.

Competition between domestic dogs and the hyaenas existed to a limited extent but was quite intense between the hyaenas and black-backed jackals. Jackals often mobbed the hyaenas and took advantage of them in obtaining food. Competition with man was minimal as a result of the restriction on human access to most of the hyaenas' territory and to the food source in particular.

Brown hyaenas exhibit substantial flexibility in their behavioural ecology and, as such, appear to be well adapted to the unusual environment in this hostile, coastal desert.

Opsomming

Die huidige studie ondersoek verskeie aspekte van die ekologie van bruin hiënas (*Hyaena brunnea*) in 'n omgewing waar dit tot dusver nie in besonderheid bestudeer is nie ; naamlik, die droë kusgebied van die sentrale Namib woeatyn in suiderlike Suidwes-Afrika/Namibia. Die vernaamste doel van die studie was om te vestig tot watter mate die beskikbaarheid, kwaliteit en verspreiding van voedsel die bruin hiëna se organisasie en ruimteverbruik beinvloed het. Die uitwerking van die dorp van Lüderitz op die hiënas se gedragsekologie het ook aandag ontvang.

Tussen Mei- en Septembermaand 1984, het twee volwasse wyfies 607 ure direkte waarneming met gebruik van radio-telemetrie, opgelewer. Ander individüe in die groep was vir kort tydperke toevallig waargeneem; hierdie resultate was nie kwantitatief ontleed nie.

Die loopgebied van die wyfie met welpies, Thora, was 107km^2 terwyl die van die ander wyfie, Bubbles, ooreenstemmend met die groep se tuisgebied, met 'n oppervlakte van 220km^2. Die tuisgebied was grootendeels onproduktief met die uitsondering van 'n 3 km strook van die kus in die een hoek van die tuisgebied waar Kaapse pelsrobwelpies (*Arctocephalus pusillus*) waar amper al die hiënas se voedsel benodighede voorsien het. In die lig van hierdie voedsel verspreiding is die tuisgebied uitermate groot en dit word veronderstel dat die verlate myndorpe in die verste binnelandse gedeeltes van die tuisgebied in die verlede kos aan die hiënas se voorvaders verskaf het. Die relatief onlangse verdwyning van hierdie voedsel bron het die hiënas nie tot dusver laat aanpas by hierdie veranderings nie, en dus hou hulle 'n gebied in stand wat van geen of min waarde vir hulle is.

Die individüe se ruimtegebruik het verskil; Bubbles het die "voedsel-ryke" gebied van die grondgebied, die Lüderitz omgewing en die korridor tussen hierdie twee kerngebiede gebruik. Thora het egter die gebied rondom haar kraamholle sowel asdie voedsel-ryk kusgebied intensief gebruik.

Toe die verdedigbaarheid van die grondgebied uitwerk was, skyn dit dat die hiënas dit nie kon nie verdedig nie. Moontlike redes vir hierdie resultaat was: baie lae indringerdruk op party grense, die neiging van die diere om grenspatrollies te onderneem eerder as om die grense op 'n ewekansige manier raak te loop, en die moontlike onderskatting van die grootte van die groep.

Thora en Bubbles het duidelik voorkeur aan sekere gebiede vir gebruik as lêplekke gedurende die dag gegee: Thora het by die kraamhol gerus en Bubbles 'n paar kilometer binneland van die ryk suidwestelike kusstrook.

Die hiënas het vir 'n groot gedeelte van die tyd gerus: 85% van die 24 uur periode vir Thora en 63% vir Bubbles. Geen duidelike patroon was in albei diere se nagtelike aktiwiteitspatrone, en die volgorde van hoof-aktiwiteite oor 'n aantal nagte, sigbaar nie. Die baie gekonsentreerde, oorvloedige voedselbron wat die hiënas gebruik het was blykbaar die hoof-faktor wat die bogenoemde resultate beinvloed het.

Die hiënas het Lüderitz gebruik op tye wanneer die menslike aktiwiteite 'n laagtepunt bereik het. Hierdie skeiding in tyd tussen die twee spesies het die potensiaal vir moontlike stryd wat tot verminking, skok of sterfte van die hiënas kon gelei het, verminder. Die hiënas se dieet het amper uitsluitlik uit robwelpies waarop normaalweg geaas is, maar wat ook nou en dan deur die vleiseters doodgemaak was, bestaan. Ander dinge wat gevreet was, was watervoëls, honde (Canis familiaris), visse en die oorblyfsels van vee en ander afval. Robwelpies was blykbaar oorvloedig gedurende die studie, want die hiënas het by vars robkarkasse op sekere geleenthede verbygeloop. 'n Hond, rooi jakkals (Canis mesomelas), flamink (Phoenicopterus ruber) en geitjie was deur Bubbles doodgemaak. Sy het hulle later feitlik ongevreet gelos.Gegrond op volume het 98% van Thora se dieet en 84% van Bubbles se dieet uit robbe bestaan. 'n Goed gedefinieerde reglynige oorheersingshiërargie het voorgekom. Volwassenes was dominant oor ondervolwassenes en Thora was dominant oor al die ander groepslede. Die minimum groote van die groep is op vyf volwassenes, vier onvolwassenes en drie klein welpies geskat. 'n Onopgetekekende gedrag wat die oorgedrewe lek van een hiëna se rug deur 'n ander behels, is by twee geleenthede waargeneem en het blykbaar seksuele implikasies gehad.

Thora was met 70% van haar voedsel deur ander groepslede by die den voorgesien. Omtrent 15% hiervan is deur 'n onvolwasse mannetjie gebring, en 77% deur 'n volwasse mannetjie.

Die hiënas het mees dikwels op die grense van die grondgebied, en in die besonder op kusgrense, gemerk. Die Lüdertiz omgewing was ook dikwels gemerk.

Kompetisie tussen die honde in Lüderitz en die hiënas het tot 'n beperkte mate voorgekom, maar was redelik sterk tussen die hiënas en rooijakkalse. Jakkalse het die hiënas gewoonlik gemolesteer en het hulle misbruik om voedsel te kry. Kompetisie met die mens was minimaal want toegang tot die meerderheid van die hiënas se tuisgebied en tot die kosbron in die besonder was vir mense streng beperk.

Bruin hiënas het werklike buigbaarheid in hulle gedragsekologie getoon en was as sulks, was blykbaar goed aangepas by die buitengewone omgewing in hierdie vyandige, kuswoestyn.

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TABLE A

3	2	—	—	—	5	1MM
1M	4	—	1M	1MM	—	—
—	—	1m		1MM	1M	3
3	4	5	1mM	—	1	—
—	3	1M	1M	5M	3	4
1MM	2	—	1MM	1M	3	5
4	—	—	—	—	3	—
—	—	—	—	4	3	2
1mM	—	—	—	—	—	3M
—	1mM	1M	3	3	1M	—
—	1mM	5M	—	3	—	3
1MM						

TABLE B

1M	1M	1M	1MM	1M	3	1M
3	—	—	1M	1M	3	1
1M	1MM	—	—	2M	—	2M
—	2M	1	2	1	2	1
3	1	1M	2M	2	3	

M - substantial meal   m - small meal
Figures represent activities; see text for details.

APPENDIX A. CATEGORISED OVERALL NIGHT'S ACTIVITY SEQUENCE FOR THORA (TABLE B) AND BUBBLES (TABLE A).