THE SOCIO-ECOLOGY OF A SPOTTED HYAENA *CROCUTA CROCUTA* CLAN IN THE KRUGER NATIONAL PARK

by

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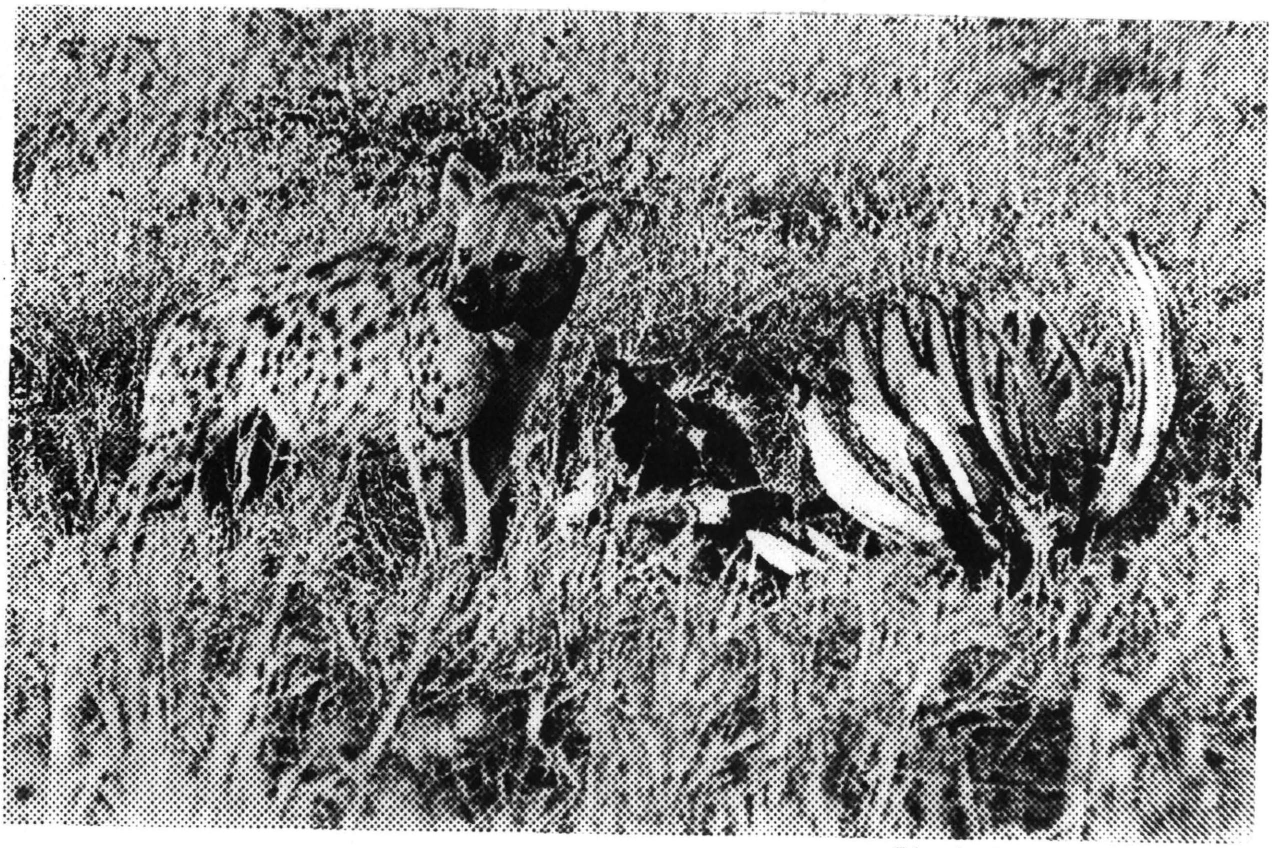

Photo: I.A.Henschel

Far away from home Crocuta wandered,
In his wake I followed and wondered,
He called into the lonely night,
The others met him with angry might.

To safety and food back home he fled,
By morning to show a hole in his head.
Why he did wander puzzles me,
What does he know that eye cannot see?

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ABSTRACT

A clan of spotted hyaenas was studied for 27 months in the Kruger National Park with the purpose of describing its structure, social organization and members' dispersal patterns, and to relate these to resource procurement, environmental factors, prey selection, spatial organization and diet.

Five social classes were recognized within a clan, namely, females, cubs, resident natal males, a central immigrant male and peripheral immigrant males. The clan was organized in a linear dominance hierarchy, which was most strongly expressed at food to the benefit of dominant individuals. Females were philopatric, dominant to males and maintained amicable relationships amongst each other and their offspring. Males emigrated, joining adjacent clans, where they had precarious social relationships, except a central immigrant male, which attended females closely and gained

unrivalled breeding status. Different key resources for each sex explain ecological differences, especially foraging behaviour, interspecific interactions, territory defence, space utilisation and food consumption.

Events that preceded the decline of the study clan in month 24 indicated that the lack of litter synchrony neccessary for communal denning, may have led to high cub mortality and failure to compensate for natural adult mortalities. This could be a fortuitous result of earlier culling in the area.

Foraging behaviour was opportunistic, explaining small group size. Most carcasses were scavenged, often after interacting with other carnivores. While occasional harrassment of large prey could sporadically enable hyaenas to kill, their hunting behaviour concentrated on vulnerable ungulate species of medium size, indicating an ability to discriminate between more and less profitable potential food sources.

The $130km^2$ territory was intensively patrolled and scent-marked, but its defence depended on the presence of resident females. Regional differences in prey abundance, vulnerability and lion activity strongly influenced hyaena space utilization and resulted in patchy food distribution, which could have determined territory size.

Various techniques of diet determination were compared. Although scavenged carcasses of very large ungulates, particularly buffalo, contributed heavily to hyaena diet, occasional killing by hyaenas, especially of more vulnerable medium-sized ungulates was essential, a pattern that was evident throughout the Kruger National Park.

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1: INTRODUCTION

PERSPECTIVE

Introduction

The second largest extant carnivore in Africa, the spotted hyaena, *Crocuta crocuta* Erxleben 1777, has evoked the interest of many authors. Its specific name originates from the Libyan *crocotta*, a word which describes its bristly appearance (O.Keller 1920), and came into common usage since Pliny's (A.D.23-79) "Natural History" (Bostock & Riley 1890). Although reference had been made to the hyaena's feeding habits, appearance of exterior genitalia and vocalizations, little was known about spotted hyaenas' social life, except that they are gregarious (Matthews 1939a,b) until a more comprehensive study was conducted by Kruuk (1966; 1972) in the late 1960's.

In the last decade, more has become known of the social organization (Tilson & Hamilton 1984; Mills 1984a,1985a), feeding habits and diet (Bearder 1975, 1977; Tilson, von Blottnitz & Henschel 1980; Skinner & van Aarde 1981; Mills 1984a,b), feeding behaviour (Tilson & Hamilton 1984), energetics (Green, Anderson & Whateley 1984), spatial organization (Bearder 1975; Bearder & Randall 1978; Whateley & Brooks 1978; Whateley 1981; Tilson & Henschel 1986), endocrinology, particularly virilization of female genitalia (Racey & Skinner 1979; Lindeque 1981; Lindeque & Skinner 1982a,b; Frank 1983; Frank, Davidson & Smith 1985; Frank, Smith & Davidson 1985; Gombe 1985; Lindeque, Skinner & Millar 1986) and bone collecting habits (Mills & Mills 1977; Henschel, Tilson & von Blottnitz 1979; Hill 1980; Brain 1981; Skinner, Henschel & van Jaarsveld 1986).

Although in Pleistocene times, spotted hyaenas occurred in central and western Eurasia and Africa (Thenius 1966; Sutcliffe 1969), this species is today confined to Africa (Smithers 1983). In the Republic of South Africa, viable populations occur only in the Kalahari Gemsbok National Park of the northern Cape (numbering 85; Mills 1984a), in the Umfolozi-Hluhluwe Game Reserve of Natal (about 265; Whateley & Brooks 1978; Whateley 1981) in the Kruger National Park in the eastern Transvaal Lowveld, which is estimated to contain 1269 to 3886 spotted hyaenas (Mills 1985a) and in reserves adjacent to the Kruger National Park.

As hunters and scavengers, spotted hyaenas are renowned for their efficiency in dealing with carcasses to the extent that they can utilize all parts of a dead animal except hair, hoof and horn. They feed mostly on medium-sized to large ungulates i.e. gazelle to buffalo, which they kill or scavenge. They are also known to consume a wide variety of items ranging from indigestible substances, like plastics, to small mammals or birds and fruit and even members of their own species. Their diet overlaps with that of other large carnivores, especially lions.

Hyaena social organization is based on a matriarchal system of clans, comprising four to 80 adults. Where prey availability is relatively constant, these clans are fairly stable and territorial. Territory occupation is indicated vocally and olfactorily, involving defaecation, pasting vegetation with anal gland secretions, and pawing the ground to apply interdigital gland secretions. Within the home range of 25-1000 km^2, a clan is often subdivided into small groups of solitary individuals, which sometimes meet other individuals or congregate, to cooperate in territory defence and food procurement. This flexible system has neccessitated complex mechanisms to frequently renew or reaffirm social relationships. Communication therefore involves a large repertoire of vocalizations, postures and odours.

Adult females dominate males, are heavier than males, and their external genitalia resemble those of males. They give birth to one or two offspring, which they keep in communal dens and nurse for nine to 18 months.

The central theme of the present study was to examine three facets of hyaena social organization, namely dispersal, dominance and cooperative behaviour and to relate these to resource procurement and space utilization. An outline of current knowledge of hyaena social organization and some relevant theoretical concepts of socioecology is provided prior to the study objectives being outlined in detail.

Resource Procurement

Wrangham (1980) uses the term "key resource" to describe the most important asset that affects an individual's fitness in the sense of natural selection. A key resource can be most readily identified if access is restricted and individuals compete for it directly. Thus, an alternative to measuring fitness, is to quantify individual access to a limiting resource. Since opportunities for siring offspring are usually restricted, access to fertile females can be regarded as a key resource for males. The importance of this in influencing male behaviour has been recognized long ago (Darwin 1859). In contrast, female reproduction is not usually limited by the availability of mates, but by environmental resources, such as food or nursery sites. Therefore, the effects of ecological variables on females are thought to be ultimate factors in determining selection pressure on social units (Emlen & Oring 1977; Wrangham 1980). The relative ease of identifying factors that may influence food procurement of large carnivores, makes this resource a convenient starting point to examine this suggestion.

Of the large Carnivora, the Hyaenidae (except *Proteles cristatus*) have the best anatomical adaptations for scavenging large mammal carcasses: strong jaws and teeth to crush bones and cut hide and the capacity to walk long distances between meals. As the largest, most powerful, and most social of the extant Hyaenidae, *Crocuta* does not only have a greater ability to contest possession of carcasses, but can also hunt regularly. The availability of a comparatively richer and patchier food source in the form of large fleshy carcasses could conceivably play a role in intraspecific relationships of *Crocuta*, both within and between social units.

Dominance

A dominance-subordinance relationship can be defined (Kaufmann 1983; p2) as: "a relationship between two individuals in which one (the subordinate) defers to the other (the dominant) in contest situations...and is affected by different, usually unknown, combinations of inherited, maturational, and learned components." It is generally accepted that such relationships affect access to resources in such a way that direct conflict is reduced, enabling an increase in the efficiency of resource utilization (Gauthreaux 1978).

Dominance can be regarded as a fundamental aspect of territoriality, which favours an individual's access to resources within, but not outside, a certain fixed area of its home range at a given time (Eibl-Eibesfeldt 1970; Owen-Smith 1977; Kaufmann

1983). By emphasizing dominance, rather than exclusion, this view of territoriality differs slightly from Kruuk's (1972) description of a hyaena territory as an area from which all hyaenas except clan members are excluded. Accordingly, a hyaena clan could be redefined as a group whose members occupy a common area in which they dominate intruders.

Social rank is a convenient way of describing cumulative effects of dominance-subordinance relationships on a member of a social unit and can be measured by the outcome of observed agonistic interactions between group members, in which the submissive individual (loser) shows evasive tendencies or ritualized displays of deference, but the dominant individual (victor) need not neccessarily display aggression (Rowell 1974). A neccessary component is the ability of an observer to recognize critical resources, even if fitness cannot be measured (Kaufmann 1983). Observations that social rank in some species may differ when competing for different resources, or that social rank did not appear to correlate with access to a resource (Syme 1974), or might be caused by artificial circumstances of observation (Rowell 1974), emphasize the need for an observer to correctly identify dominance-subordinance behaviour patterns and the resource being competed for by such behaviour.

Different studies on the brown hyaena *Hyaena brunnea* described a gradation of dominance-subordinate behaviour in this species, depending on the nature of the food supply. No hierarchy was recognized in the southern Kalahari, where scavenged food is widely scattered (Mills 1981; 1984a), but a weak non-linear hierarchy was evident along the coast of the Namib desert, where clumped food was abundant (Goss 1986). In situations where clumped food was limited in supply (Owens & Owens 1978; Bosman 1982), aggressive enforcement of strong linear hierarchies was witnessed. Similarly, while Kruuk (1976) found no dominance hierarchy among free-ranging striped hyaenas *Hyaena hyaena*, which have highly opportunistic and slightly omnivorous feeding habits, Rieger (1975) found a hierarchy among captive individuals. Such relationships to the type of food source could also have influenced the social evolution of *Crocuta*.

Kruuk (1972) recognized that spotted hyaena females usually dominated males and adults dominated immatures, but explained that no simple dominance rules were evident as the social history of individuals was not known. Although in the large clans of Ngorongoro, scramble competition over food appeared to be more important for gaining a share than agonistic interactions, Kruuk (1972) indicated that females sometimes gained better access to food through dominance behaviour. The latter was found to be much more important in small clans of the Namib desert (Tilson & Hamilton 1984), where hyaenas usually fed in rank-orderly succession, and females ensured that their offspring had feeding priority over adult males.

In a large East African clan, Frank (1983) found that the effects of dominance expression became progressively more evident as a carcass was consumed and dominant females excluded all but their offspring. He speculated that, despite this, the principal benefit of female dominance was not food itself, but the ability to raise sons of superior fitness.

Unlike its effects, determinants of social rank are often difficult to quantify, as it may depend on a history of relationships, such as mother-offspring protection, besides physical and physiological developments. The latter has recently been examined for hyaenas. Racey & Skinner (1979) found that peripheral testosterone levels of both sexes were similar, unlike many other mammals, where males dominate (Bardin & Catterall 1981). This led Racey & Skinner (1979) to propose a hormonal basis for dominance relationships in spotted hyaenas. These hormonal comparisons in hyaenas were substantiated by Lindeque (1981), Gombe (1985) and Lindeque *et al* (1986), who found that adult female testosterone levels were not abnormally high, but that male levels were lower than expected by comparison with other species. However, Frank *et al* (1985a,b) found that the same did not appear to be true for total androgen levels.

Cooperation and Social Affiliation

Wittenberger (1981) points out that one of the most cogent criticisms of social dominance theory is its emphasis on aggression rather than affiliation as basis of social relationships. Examples from studies of large social carnivores, where cooperation, in the form of alloparental help, as well as dominance relationships have been described are wild dogs *Lycaon pictus* (Frame, Malcolm, Frame & van Lawick 1979; Reich 1981; Malcolm & Marten 1982), wolves *Canis lupus* (Mech 1970; Peterson 1977; Zimen 1981) and brown hyaenas (Owens & Owens 1978; Bosman 1982; Goss 1986).

In *Crocuta*, amicable social activities appear to favour cooperation between clan members, especially between females when hunting and during other interspecific interactions and affect the efficient utilization of available carcasses (Kruuk 1972; Mills 1985a). However, in contrast to alloparental behaviour found in many other carnivore species (Macdonald & Moehlman

1982), spotted hyaenas do not help each other in providing cubs with food (Kruuk 1972; Mills 1983; 1985a).

Many behaviour patterns have been described that are thought to facilitate close social bonds among spotted hyaenas (Kruuk 1972). These include various soft vocalizations, social sniffing, other contact behaviours and an elaborate greeting ceremony, ending in the display and mutual inspection of erect phalluses between individuals of both sexes and all ages. Indeed, the evolution of an enlarged clitoris in females has been postulated to be an adaptation for the latter behaviour (Kruuk 1972; Hamilton, Tilson & Frank 1986). However, contrary opinion holds this anatomical development to be an exaptation for the greeting ceremony (Gould 1981; Gould & Vrba 1982), an incidental product of pre-natal testosterone secretion by female foetuses (Lindeque & Skinner 1982a), a characteristic which could have been fixed due to its affect on adult female aggression leading to dominance.

Hyaena Dispersal

In areas where hyaena clans and territories are clearly defined, as in the Ngorongoro crater (Kruuk 1972), the Hluhluwe-Umfolozi Game Reserve (Whateley & Brooks 1978; Whateley 1981) and the Kalahari Gemsbok National Park (Mills 1985a), territorial intrusions are usually resisted by a clan. However, some authors have previously detected temporary or long-term shifts of members between clans.

During three and a half years in the Ngorongoro crater, Kruuk (1972) observed 15 permanent shifts between clans, only one of which was by an adult female, eleven by adult males and three by unsexed subadults. Kruuk reported that a marked male associated temporarily with two clans for about six months before settling permanently with one of these. Another marked male from the crater, where hyaena clan territories have a diameter of 5-10km, was later seen 20km outside of the crater, but returned four months later. Van Lawick-Goodall (1970) observed a Ngorongoro male repeatedly moving into the territory of a neighbouring clan and associating with residents there, before returning to his clan of origin. In the Hluhluwe-Umfolozi Game Reserve in Natal, Whateley (1979a) resighted a male, 40km from the site where it had been marked some fifteen months earlier. Mills (1984a) reported that in four years in the Kalahari, nine males left their natal clan upon attaining adulthood, at least one of which joined another clan, while others ranged widely. Two other males, whose origin was not known, were observed to immigrate. Similarly, Frank (1983) found that in four years, eight males, one female and 18 individuals of unknown sex, that were born into a large clan in Kenya, disappeared at puberty. Although transient males sporadically appeared in this clan on 74 occasions, their origin and fate was unknown.

Some of the 22 cases of territory intrusion other than immigration observed by Kruuk (1972) in the Ngorongoro crater, were interpreted as being related to fluctuations in the local abundance of ungulates. But Kruuk (1972; p42) stated that "it was sometimes impossible to guess why a hyaena should go so far from his home grounds, just for a short visit, when there were many (prey) animals in his own range and when he ran the risk of encountering the rightful owners of the territory."

Inter-clan movements are more difficult to interpret in areas, such as the Serengeti plains, where long-distance migrations of wildebeest and zebra cause large fluctuations in the availability of food (Kruuk 1972); or such as the Namib desert, where temporary water depletion sometimes imposes limits on the ability of hyaneas to exist in a particular locality (Tilson & Henschel, 1986). In these areas, a section of the hyaena population migrates or disperses with the resource. Although Namib desert hyaenas are grouped into less territorial clans, whose membership changes little, Tilson & Henschel (1986) noted some shifts, including a male which was once seen alongside other hyaenas about 20km from its clan of origin and an unsexed subadult which joined one of the study clans. In another case, an intruding male was killed by residents.

These reports suggest that males are more inclined to change clans than females are. As a corrollary it can be assumed that females tend to remain in natal groups, and may be closely related (Ralls 1976; **Mills 1985a**). This consideration was apparently overlooked by Bertram (1980), when he concluded that the average degree of relatedness among members of a spotted hyaena clan was low, which he used to explain the apparent lack of direct cooperation in the rearing of young.

Mutualism

Three differences between the sexes, outlined above, may appear to be characteristic of hyaena social organization: a) female dominance over males; b) closer cooperation between females than males; c) male dispersal, but female philopatry. In a species, which, as scavenger and hunter can obtain bulk meat, with limited access (patchy food source), and scattered lower-quality skin and bones, with less restricted access, such social relationships might be expected to have bearing on an individual's diet, and hence, foraging behaviour, interspecific relationships and space utilization. However, the dispersal, dominance and cooperative patterns of *Crocuta* require substantiation and explanation, and their ecological implications should be explored.

Cooperation between philopatric females and less cooperation between immigrating males are reported for numerous primate species (Wrangham 1980). Social units with such patterns, recognizable by females having a differentiated network of aggressive, greeting and contact interactions, which reinforce affiliative bonds between them, and improves female access to rich patches of food, are called female-bonded groups.

Mutualism occurs when two or more individuals cooperate and thereby simultaneously fare better than they would by acting alone. Various forms of mutualism have been identified long ago in interspecific relationships (reviewed by Boucher, James & Keeler 1982; Addicott 1982), but have only recently been proposed for intraspecific relationships (Wrangham 1982). Where mutualism is the basis of a social unit, it offers many opportunities for altruism in such a way that interactions have greater short-term benefits than costs for all participants. Moreover, in a social unit, there are frequent opportunities to reinforce mutualistic relationships by repeated interactions. Kin groups can arise as a result of mutualism, because opportunities for forming such relationships arise early in an individual's life e.g.during social play. For this reason, affiliative bonds are expected to be best developed among kin.

Mutualism is thus a suggested connection between theoretical views of an ecological basis of group formation (Crook 1970) and genetic factors that may influence an individual's relationship to kin (Hamilton 1964). Ecological factors (Kruuk 1972; 1975; Lamprecht 1978; 1981) and kinship (Mills 1985a) have both been independantly described previously as bases of *Crocuta* groups.

OBJECTIVES

1) To describe *Crocuta* social organization in terms of cooperative, dominance and dispersal patterns and to identify their effects on resource procurement.

2) To describe how *Crocuta* foraging behaviour, space utilization and social organization operate within the limits of environmental parameters.

3) To describe *Crocuta* diet in terms of prey availability, hyaena preference and requirements, as indicators of their ecological role in a woodland habitat.

4) To express these findings in terms of conservation requirements.

STUDY CONSIDERATIONS

As an alternative approach to Kruuk's (1972) study, which covered a wide area, many clans and different environments, it was decided to conduct intensive observations of members of a single clan to facilitate the efficiency of obtaining sufficient information on the above topics.

As one of the three areas in South Africa, where natural populations of spotted hyaenas exist, the Kruger National Park was chosen for a number of reasons: a) Difference in habitat from those of previous observations on open plains or desert environments; b) The availability of some previous knowledge of spotted hyaenas in the Transvaal Lowveld; c) Requirements of National Parks Board to gain knowledge of the ecological role of spotted hyaenas in that area.

The structure of this dissertation is as follows: After outlining the study framework (Chapter 2), a desciption of clan structure is given (see Table 1) in relation to amicable, dominance and dispersal behaviour (Chapter 3), and depiction of some limiting ecological factors which could be identified in a changing social environment (Chapter 4). Social and other behavioural responses to environmental parameters that relate to food procurement are examined with reference to foraging behaviour, interspecific interactions (Chapter 5), territoriality, space utilization, food distribution (Chapter 6) and diet (Chapter 7). Finally, an outline is presented of how these factors appear to be interrelated, and how they relate to conservation considerations (Chapter 8).

Table 1: Abbreviations for members of different social classes of *Crocuta*, which are defined in Chapter 3.

	ABBREVIATION	
Social Class	Collective	Individual
Female	FEM	F*
Cub	JUV	J*
Resident Natal Male	RNM	R*
Central Immigrant Male	CIM	C*
Peripheral Immigrant Male	PIM	P*

* followed by lower case letter to identify individual.

2: STUDY AREA AND METHODS

STUDY AREA

Location

The upper catchment area of the Mavumbye River ($24^{o}20$'S; $31^{o}45$'E), referred to as the Mavumbye area, 5-15km north of Satara in the Central District of the Kruger National Park (Fig.1), was selected as the main study area for a number of reasons:-

a) Relatively open woodland conditions with few rocky outcrops and few stretches of broken country (e.g.river and vlei) enabled direct observations of free-ranging hyaenas to be made by vehicle. A network of roads (19km) and tracks (53km) facilitated accessability into the area (Fig.1).

b) **Heterogeneous** vegetation structure (12 ecotopes) within two landscape types, a high diversity of ungulate prey and high density of lions made the area suitable to examine habitat and prey selection by hyaenas.

c) Management considerations emphasized the need for a hyaena study to be conducted in areas, such as the Mavumbye area, affected by zebra and wildebeest migrations within the Central District of the Kruger National Park (Joubert, Pienaar, van Wyk & Smuts 1974).

d) The social unit of hyaenas residing in the Mavumbye area, henceforth referred to as the Mavumbye clan, initially comprised 11 members (8 adults, 2 subadults, 1 cub), which was considered to be a suitable number for intensive observations of all clan members.

The outer limits of the main study area, the Mavumbye area, were defined by the territory boundaries of the Mavumbye clan,

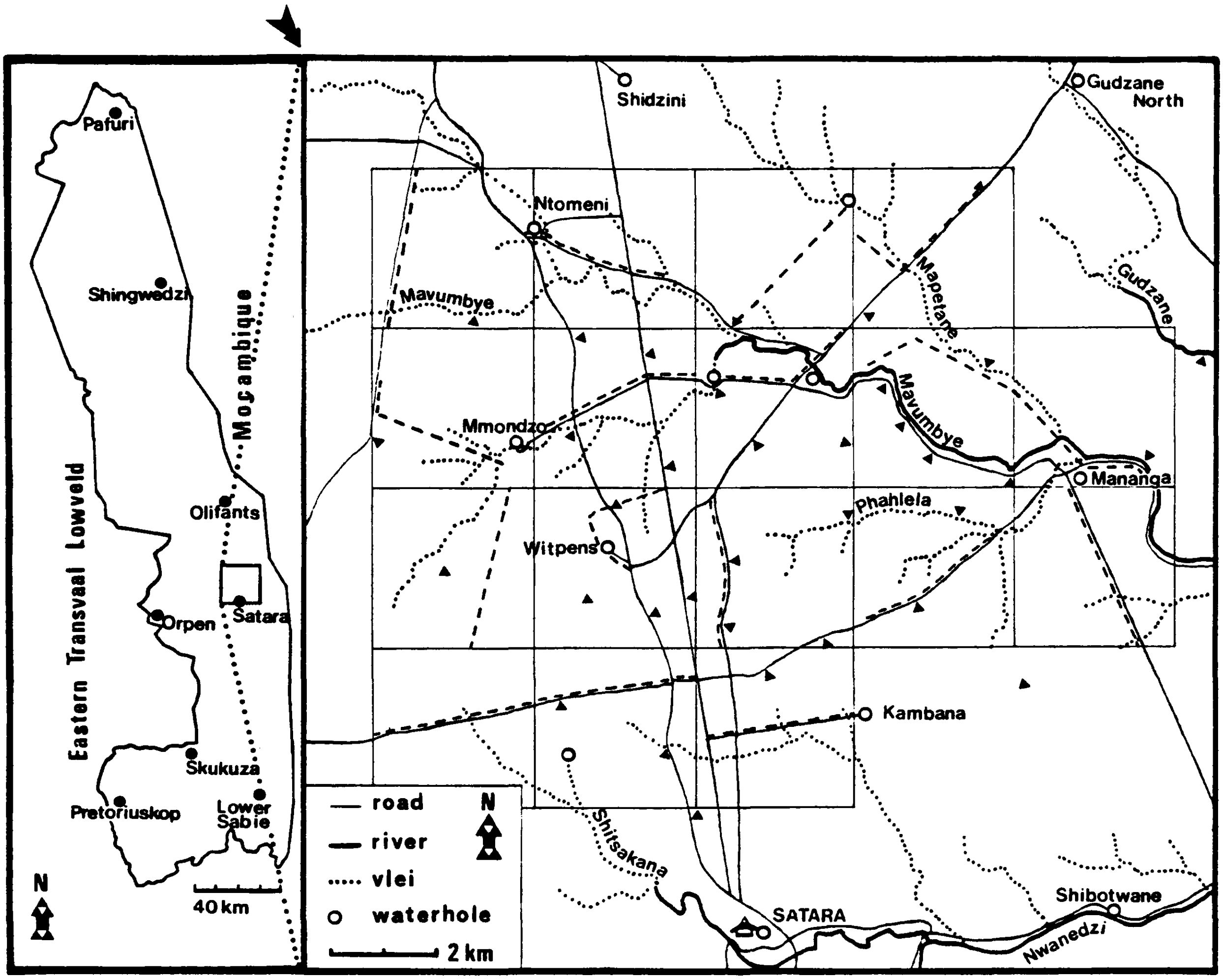

Figure 1: Map of the Kruger National Park and of the study area, showing places mentioned in the text, subdivision of study area into $9km^2$ sample squares and locations of line transect routes (dashed lines). Landmarks are at road, river and vlei junctions and at places marked with a triangle. The arrow indicates the viewing angle used for three-dimensional graphs.

within which ecological parameters were measured. Surrounding areas (in a 10km radius) were less intensively studied, but data applicable to interclan relationships were collected.

Climate

Below average rain fell during the first year of the study (Table 2). At Satara, 322mm were recorded between July 1982 to June 1983, compared to the long-term annual average of 548mm (Gertenbach 1980). The onset of perennial rains was three to four months late during the wet season of that year. Rainfall was above-average during the following year, 573mm being recorded at Satara. Even more rain fell at Mmondzo, in the Mavumbye area, where 729mm were recorded between July 1983 and June 1984. Not only was the rainfall in the second year heavier, but it fell more frequently, giving rise to a high field layer and muddy ground, which made fieldwork conditions difficult.

Rainfall records were used to divide the study period into five periods of alternating dry and wet seasons (Table 2). Differences in ungulate distribution, hyaena behaviour, diet and space utilization between these periods are examined in the relevant sections.

Temperatures ranged from 4 to 40^{o}C (Table 2). During spring to autumn, night temperatures remained above 15^{o}C. Humidity was often high during these seasons, explaining why midnight temperatures of up to 34^{o}C were recorded. During winter, the temperature usually declined below 15^{o}C at night to a minimum of 4^{o}C. Fogs prevailed during winter, often blanketing the eastern half of the Mavumbye area at night.

Climate was monitored continuously during observations, using descriptive characteristics (Table 3).

Table 2: Monthly rainfall at Satara and Mmondzo and minimum to maximum temperatures at Mmondzo during the study period.

	RAINFALL			TEMPERATURE		DURATION
	Satara		Mmondzo	Mmondzo		of season
MONTH	mm	N	mm	Min	Max	in months
Jun 82	0	0	-	-	-	
Jul 82	0	0	-	-	-	
Aug 82	0	0	-	-	-	
Sep 82	10	1	-	-	-	
Oct 82	16	3	-	-	-	
Nov 82	9	2	-	-	-	
Dec 82	4	1	-	-	-	
SEASON 1	39	7	-	-	-	7
Jan 83	93	4	-	-	-	
Feb 83	7	2	-	-	-	
Mar 83	144	5	-	-	-	
Apr 83	3	1	-	-	-	
May 83	36	4	-	-	-	
SEASON 2	283	16	-	-	-	5
Jun 83	0	0	-	-	-	
Jul 83	1	1	1	6	29	
Aug 83	30	2	30	11	31	
Sep 83	0	0	0	9	39	
Oct 83	32	6	35	14	39	
SEASON 3	63	9	66	6	39	5
Nov 83	123	9	189	21	39	
Dec 83	84	8	73	21	36	
Jan 84	94	5	141	18	40	
Feb 84	39	3	59	20	33	
Mar 84	125	7	154	16	36	
SEASON 4	465	32	616	16	40	5
Apr 84	36	1	45	12	31	
May 84	0	0	0	9	31	
Jun 84	9	2	2	4	34	
SEASON 5	45	3	47	4	34	3
Jul82-Jun83	322	16	-	-	-	12
Jul83-Jun84	573	44	729	4	40	12

Table 3: Climatic conditions monitored during hyaena observations.

Light	Condition
Dark night	less than quarter moon
Bright night	more than quarter moon
Twilight	1h before and after dawn and dusk
Dark day	early morning or cloudy
Bright day	sunshine

Wind	Condition
Calm	still air
Breeze	gentle wind
Windy	strong wind to gale

Moisture	Condition
Dry	low humidity
Humid	high humidity
Wet	after rain
Raining	during precipitation

Temperature	°C
Cold	<15
Cool	15-25
Warm	25-35
Hot	>35

Water Availability

The Mavumbye river was fed by a permanent spring, situated near the confluence with the Mmondzo vlei (Fig.1). The Mavumbye area enclosed 8km of this river. Four permanent natural waterholes (along the Mapetane, Mmondzo and Shitsakana vleis) and five artificial watertroughs (at Ntomeni, Mavumbye, Mananga, Kambana and Witpens; fed from the Olifants-Satara waterpipe or from windmills) were situated in the area. The maximum distance from permanent water sites was 3,7km.

Surrounding areas within 10km were drained by the Timbavati river to the west, the Gudzane river to the east, the Shitsakana (spring-fed) to the south-west, and the Nwanedzi river to the south. A network of artificial waterholes likewise covered these surrounding regions.

Landscape Description

The vegetation and soils in the Mavumbye area are classifiable into two different landscapes (Fig.2). The southern two-thirds of the region was *Sclerocarya caffra / Acacia nigrescens* Savanna (marula-knobthorn; Landscape 17; Gertenbach 1983), or Non-vertic Tropical Semi-arid Basaltic Lowveld (Coetzee 1982), while the northern section is classified as Dwarf *Acacia nigrescens* Savanna (stunted knobthorn; Landscape 18; Gertenbach 1983), or Vertic Tropical Semi-arid Basaltic Lowveld (Coetzee 1982). In both regions the terrain is gently to moderately undulating.

The soil in the marula-knobthorn landscape consists of Sabi River Basalts, with relatively poor drainage and good water retention. A melanic or orthic pedocutanic A-horizon soil-type usually overlies non-calcereous lithocutanic B-horizon soil. Most of the soil contains 15-35% clay, which has been classified into the Mayo mayo, Bonheim dumasi and Glenrosa williamson Series (Coetzee 1982).

In the dwarf knobthorn landscape, the basalts are rich in amygdal and olivine, with dark calcereous versitols of the Arcadia arcadia Series with a self-mulching to weakly crusting surface and a clay content of 35-60%. However, the central high plateau has non-vertic, non-calcereous soils of the Mayo mayo and Bonheim dumasi Series with 30-65% clay (Coetzee 1982).

A detailed vegetation survey was not conducted in the present investigation. Emphasis is here put on hyaena visibility range and freedom of movement, factors which are largely affected by the vegetation cover and structure in the lowest 1,5m above the ground (Table 4).

Table 4: Indices for grass height, shrub density and degree of cover surrounding a hyaena.

Grass Index	Height	Hyaena Cover
1	< 10 cm	below ankles
2	10- 40 cm	below chest
3	40-100 cm	below eye-level
4	>100 cm	above eye-level

Shrub Index	Visibility	Freedom of Movement
1	>150 m	unimpeded
2	30-150 m	unimpeded
3	3- 30 m	some hindrance
4	< 3 m	impeded

Cover Index	Place	Degree of cover
1	open patch	none
2	in grass	partly
3	against shrubs	partly
4	under low canopy	complete
5	in water	partly
6	inside hole	complete

The general distribution, structure and major constituents of different communities, or ecotopes within each landscape unit, were examined crudely and compared to a previous phytosociological study by Coetzee (1982; indicated by C# in the text). The vegetation patterns of twelve different ecotopes are described below. The associated fauna is described in Chapter 5. Regions refer to the study area shown in Fig.2.

1) *Sclerocarya caffra - Acacia nigrescens - Themeda triandra* Treeveld with scattered to moderate shrub cover (C#6.3). Hyaena visibility indices were usually grass:2-3 and shrub:2. This ecotope features prominently throughout the central and southern sections of the study area.

2) *Sclerocarya caffra - Acacia exuvialis - A.nigrescens - Themeda triandra* Treeveld with moderate tree and shrub cover (C#6.6), usually having visibility indices of grass:3 and shrub:3. Such a vegetation pattern is found in the south-western and central regions.

3) *Acacia nigrescens - Grewia bicolor - Terminalia prunioides - Combretum apiculatum* Brushveld with shallow soil and rocky outcrops (C#6.7). The vegetation structure was moderately to densely shrubby, normally giving indices of grass:3 and shrub:3-4. Two regions, in the centre and in the south are covered by this vegetation.

4) *Acacia nigrescens* Brushveld (C#6.12) of sparse to moderate shrub cover and visibility indices of grass:1-3 and shrub:2-3. A patch of this type is situated in the south-eastern region.

5) *Acacia nigrescens - Panicum maximum - Setaria woodii - Ischaemum brachyaterum - Digitaria eriantha* Brushveld (C#7.3) with indices of grass:1-4 and shrub:2-4. *A.nigrescens* dominated

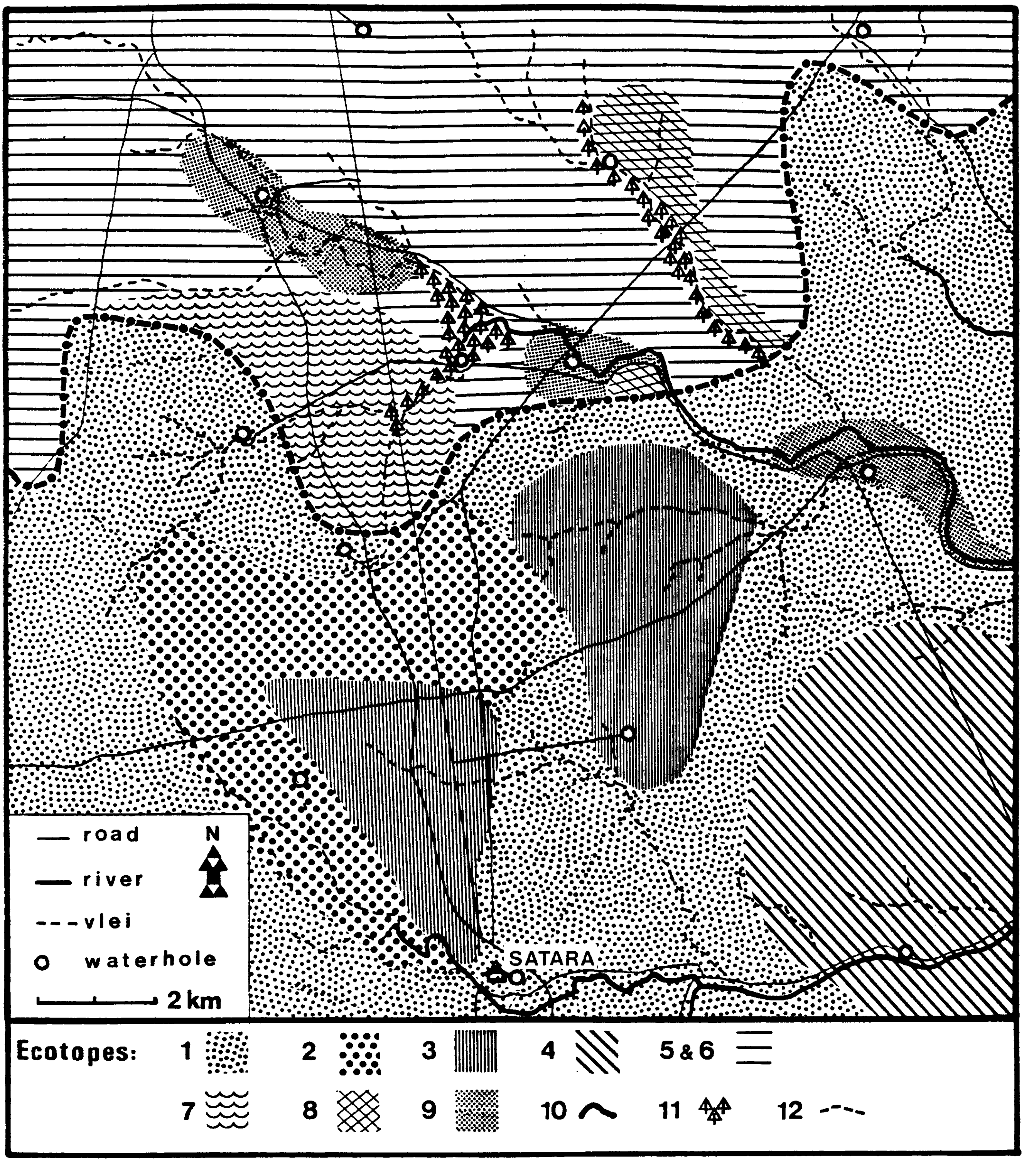

Figure 2: Landscapes of the Mavumbye area, showing the locations of twelve ecotopes described in the text. The bold dashed line indicates the border between landscapes.

from shrub to tree level. Most of the vegetation in the northern regions had this pattern, interspersed with open patches of ecotope 6.

6) *Panicum maximum* - *Setaria woodii* Grassland (C#7.4), with no shrubs, of visibility, grass:2-4 and shrub:1. This occurs in small patches along the lower slopes in the northern region.

7) *Acacia nigrescens* - *Themeda triandra* - *Bothriochloa radicans* - *Digitaria eriantha* Grassland on high plateaus (C#7.1), which have sparse shrub cover and visibility of grass:1-2 and shrub:2. The occurrence of numerous forbs was indicative of a disturbed veld type. Most of this veld was burnt in 1981 and subsequently grazed and trampled heavily for a number of years. This ecotope is found in a region north of central.

8) *Tetrapogon mossambicensis* Grassland with *Acacia borleae* scrubclumps on poorly drained broad bottomlands (C#7.5). Visibility is grass:4 and shrub:1 or 4. Two patches of this type (2,9km^2) are situated along the Mavumbye river and Mapetane vlei.

9) *Grewia bicolor* - *Acacia tortilis* - *Acacia nigrescens* - *Dichrostachys cinerea* Brushveld of heavy-grazed bottomlands (C#6.9), giving indices of grass:1-2 and shrub:2. Such patterns are found along the Mavumbye river.

10) River Complex, with numerous species of trees, shrubs and grasses (C#6.14). *Maytenus senegalensis* often dominates to form impenetrable thickets. Where grazing and trampling has not cleared the dense cover, visibility indices are grass:3-4 and shrub:2-4. Such vegetation was found in the marula-knobthorn landscape along rivers with permanent water, i.e. the Mavumbye, Gudzane, Shitsakana and Nwanedzi rivers and the middle reaches of the Mmondzo vlei.

11) *Lonchocarpus capassa* Treeveld (C#7.6) is found on levees in the dwarf knobthorn landscape, along the Mmondzo and Mapetane vleis, forming dense stands, with little grass. A relatively large patch of these trees occurs at the tributary of the Mmondzo and Mavumbye rivers.

12) *Sporobolus consimilis* Grassveld (C#7.7) occurred along vleis throughout the area, forming tall stands of 2m height. 25km of such vleis occurred in the Mavumbye area.

None of these ecotopes was subjected to fire for the duration of the present study, but the effects of a previous fire remained evident in ecotope 7. Major changes in the degree of cover in the field layer occurred only due to rains following the drought of 1982. During the drought, the grass indices were lower by one or two units than indicated above.

MATERIALS AND METHODS

Fieldwork

Trips into the study area were made with a Toyota (Hi-lux 4x4) on 456 workdays (noon to noon), covering 3061h and 21751km over a two-year period between 29 June 1982 and 9 July 1984.

Hyaena Capture

Sixty-four nights (538h) were devoted to hyaena immobilizations, using a Cap-Chur CO-2 pistol and rifle (Palmer Chemical and Equipment Co., Atlanta, U.S.A.) and Cap-Chur type 1cc darts (National Parks Board, Skukuza, R.S.A.). However, readiness to immobilize was maintained on each fieldtrip throughout the second year of study (in an attempt to capture immigrant males). Mavumbye hyaenas were captured and released on 18 occasions (Table 5). Two immigrant males died under

Table 5: Darting record of Mavumbye clan hyaenas. Booster dosages follow a '+' sign. Mean dosages and times are for successful attempts only.

						DURATION (hours:min)		
Hyaena	Mass	Drug	Dosage: mg	mg/kg	Rompun	Recumbant	Recover	Release
Fm	68	Sernylan	80	1,2	40	0:09	7:55	52:00
Cg	66	"	80	1,2	40	0:22	7:40	DEAD
Rz	54	"	80	1,5	40	0:00 #	7:40	52:00
Mean	63	Sernylan	80	1,3	40	0:16	7:45	52:00
Fu	70	Ketamine	750 + 400	10,7	40	0:09	3:50	5:50
Fa		"	500 + 200		35 + 28	0:07	1:09	3:00
Rz		"	2x500+3x300		35 + 21	not effective		
Rw		"	2x660		32	"	"	
Pk		"	660		35	lost out of sight		
Pk		"	660		35	" " " "		
Mean	65	Ketamine	625 + 300	10,7	38 + 14	0:08	2:30	4:24
Rf	70	Tilazol	165 + 3x100	2,4	-	0:08	1:19	1:49
Pc	60	"	225 + 75	3,8	-	0:02	1:00	2:43
Fl	81	"	250 + 100	3,1	-	0:04	0:35	2:00
Fh	71	"	250 + 2x100	3,5	-	0:03	1:14	3:04
Cb		"	250 + 250		-	0:05 *	1:15	1:40
Cb	65	"	250 + 200	3,8	-	0:09	1:13	2:46
Rw	63	"	250 + 250	4,0	-	0:01 *	1:39	3:27
Fm	77	"	240 + 200	3,1	-	0:03	1:48	4:40
Ps	56	"	200 + 40	3,6	-	0:05	0:54	2:04
Pc	59	"	250 + 200	4,2	20	0:02	1:34	3:55
Fh		"	250		-	not effective		
Pd		"	250		-	"	"	
Pk		"	250		-	"	"	
Mean	67	Tilazol	233 + 181	3,5		0:04	1:15	2:48
Fp	54	Etorphine	3	0,056	30	0:02	0:41	0:49
Rw	65	"	3	0,046	30	0:01	Fluothane	
Fp	55	"	3	0,055	30	0:03	Fluothane	
Rw		"	3			lost out of sight		
Pn		"	3			" " " "		DEAD
Mean	58	Etorphine	3	0,052	30	0:02		

dart entered jugular vein
* recumbent only after booster dart 30 min later

anaesthesia (Chapter 4). Five times, darted hyaenas did not become recumbant and four times they were lost out of sight in rugged terrain or dense vegetation after being darted. Immigrant males (Chapter 3) were most difficult to capture, because of their shy nature, avoidance of other hyaenas at bait and tendency to bolt when darted.

The effects of phencyclidine hydrochloride (Sernylan; Parke-Davis Laboratories (Pty) Ltd, Cape Town, R.S.A.) in combination with the tranquilizer, xylazine hydrochloride (Rompun; Bayer Pharmaceuticals (Pty) Ltd., Johannesburg, R.S.A.) have been discussed previously (Whateley 1979; Mills 1981), but the long period of recovery experienced in the present study (>52h), was undesirable. Although ketamine hydrochloride (Ketalar; CI-581; Parke-Davis) and rompun were better suited for short-term immobilizations (Smuts 1973), they were often not effective, despite potent applications to members of the Mavumbye clan (Table 5) and five other hyaenas. Tiletamine hydrochloride (Tilazol; CI-744; Parke-Davis) was found to be the most reliable drug, with a short induction time, and smooth recovery phase. As tilazol was in short supply at the end of the study, etorphine hydrochloride (M99; Ricket & Coleman Pharmaceuticals, Cape Town, R.S.A.) and rompun was used (van Jaarsveld, McKenzie & Meltzer 1984), which had the shortest induction time, but led to a hyperactivity phase before recumbancy, during which a hyaena could vanish.

Radio collars (LA12 transmitters; A.V.M. Instrument Co., Dublin, U.S.A.) with two beta-lights each (MP105/G/900; Saunders-Roe Dev.Ltd., Middlesex, England) were fitted on twelve occasions and thrice colour-coded sterkalite collars were fitted. Data collected from immobilized hyaenas included sex determination, age class assessed by examining toothwear of the lower PM_3 (Kruuk 1972), body size by shoulder height along extended legs, and length from nose to base of tail, measures of bulkiness by mass and chest girth, and an indication of relative jaw strength by maximum head circumference across the masseter muscles. An objective index of relative age by toothwear of lower PM_3 was obtained from plaster-of-paris tooth impressions or post-mortem material, when skulls of dead individuals had been recovered. The method of Lindeque & Skinner (1984) was modified to project a 256X magnified image of the PM_3 occlusal surface onto paper using a microscope drawing tube, and thrice measuring the magnified surface area with a planimeter, before converting the mean result back by its magnification factor.

Telemetry

Eight radio collars (150,72-151,06MHz; Table 6) were fitted onto 11 Mavumbye hyaenas (Table 7; Fig.7). With a hand-held Yagi antenna, radio-reception range varied with transmitter strength and type of terrain (moderately undulating) which allowed a maximum reception range of 2-4km, but normally only 1,0-1,5km for an active hyaena and 0,1-0,8km for a hyaena resting in open terrain. In favourable terrain outside the study area, the same equipment gave a maximum reception range of 12km for a transmitter held 0,3m above the ground, indicating that the shorter range in the study area was mainly due to terrain. These limitations affected the ability to locate hyaenas, the selection of focal animals, and the ability to keep in contact with fast-moving hyaenas.

Table 6: Radio frequency, maximum reception range of transmitters held at 0,3m height above ground level in open terrain and use of radio collars on Mavumbye clan members.

Frequency (MHz)	Max.Reception Range (km)	Collared Hyaena (code)	Period used (dates)
150,72	1,1	Fm, Fa	20.08.82-01.05.84
150,77	1,4	Fz	20.08.82-
150,82	4,5	Fu, Fl	20.08.82-09.11.83
150,87	1,3	Pc, Jp	07.10.82-17.04.84
150,92	1,3	Fh, Rw	17.12.82-
150,97	1,5	Rf	11.09.82-26.02.84
151,01	0,2	Cb	26.06.83-
151,06	0,8	Fm	30.08.83-09.07.84

Table 7: Identity codes, sex and estimated age (Kruuk 1972) of Mavumbye clan members. Age was backdated to July 1982. Duration and distance of observation and number of months that individuals were clan members and were radio-collared as members and non-members (brackets) are indicated.

	1982 AGE					
	Age	Kruuk	OBSERVATION		MONTHS	
Hyaena	(yrs)	Class	Time(h)	Distance(km)	Member	Collared
Fm Female	6-16	IV	771	632	24	22
Fl "	6-16	IV	339	248	17	13
Fa "	?	?	254	139	22	6
Fh "	1- 3	II	61	86	8	3
Fu "	>16	V	37	43	3	1
Jp "	< 1	I	378	289	22	4
Rw Male	1- 3	II	601	484	24	12
Rz "	1- 3	II	421	462	24	22
Rf "	3- 6	III	198	253	16	14 (3)
Cb "	3- 6	III	372	354	18	12
Cg "	3- 6	III	67	69	2	-
Pk "	-	-	41	74	12	-
Pd "	-	-	37	55	8	-
Pc "	6-16	IV	35	65	5	2(10)
Ps "	1- 3	II	4	16	2	-
Pn "	6-16	IV	2	0	3	-
Po ? *	-	-	3	1	4	-
TOTAL			3678	3317		

* Sex was not confirmed, but assumed to be male from behaviour.

Hyaena Observations

All 17 Mavumbye clan members were individually recognizable by distinctive body characteristics, especially spot patterns, and radio frequency of collar. Sightings of hyaenas that disappeared before they could be identified were not recorded. Usually individuals were located by radio-tracking, then followed visually by vehicle, using a spotlight (Q-Beam Blue Max, 20000cp with red filter; Q-Beam Corp., Dallas, U.S.A.) to which they became habituated. Fieldnotes were spoken onto tape recorder and transcribed later.

Mavumbye clan members were sighted on 1578 occasions on 328 workdays and were followed for 2053h over 1862km giving a total of 3678h and 3317km of focal animal samples (Altmann 1974). Most observations were done at night, during the hyaenas' main activity periods. Four females and four males were each observed for 198-771h, but seven immigrant males and two females were each observed for less than 70h (Table 7). Hyaenas of adjacent clans were sighted 86 times and were observed for 46h over 44km.

By noting the initial location of a hyaena relative to a known point and recording the distance by vehicle odometer and direction of movement determined by compass or stars in 45° intervals, a hyaena's movements could be plotted to the nearest 0,1km on a 1:50000 Universal Mercator gridded map. Data on activity of a focal animal were recorded on computer entries, each of which contained the following parameters: time, identity of focal animal, location (grid reference), distance travelled since beginning of observation, environmental parameters of climate and vegetation, activity (Table 8), other participants in activity (e.g.hyaena identity, prey species or food item) and

Table 8: List of *Crocuta* activities. Social behaviour patterns follow Kruuk's (1972) description.

ACTIVITY	BEHAVIOUR
Resting	Lying inactive, usually sleeping.
Foraging	Exploring, usually wandering with many deviations.
Feeding	Posture and jaw action indicate food quality: Tear meat with front teeth while pulling with neck, shoulders and front legs; Cut hide with the carnassial shear while tilting head sideways; Crack bones audibly with the large premolars while flexing the masseter muscles.
Maintenance	Drink, urinate, regurgitate, groom, stand or sit.
Territorial	Patrol by directional moving between latrines with few deviations; Scent-mark by defecating, pasting with the anal gland, or scratch-marking by pawing the ground to deposit interdigital secretions.
Interspecific	*Nearby*: Approach to 50m of other species without apparent interaction. *Aggressive*: Threaten, displace, chase (>30m), bite or kill other species. *Evasive*: Show nervousness, retreat or flee from, or wait aside of other species.
Socialize	*Agressive*: Threaten, bite, displace or chase. *Evasive*: Display submissive posture, retreat, flee, wait aside of other hyaena. *Greeting*: Social approach, head-sniffing, greeting ceremony, sniffing non-erect genitals. *Contact*: Social sniffing, nudging, mouthing, body contact, allogrooming or playing. *Mating*: Pre-mating behaviour and copulation. *Maternal*: Digging den, parturition, nursing.

spacing from other hyaenas (Table 9). Entries were labelled according to observation status (Table 10). Distinction was made between random and non-random sightings. The former were not influenced by prior knowledge or expectancy of a hyaena's location, or by observations of a current focal animal.

When a moving hyaena was out of sight for 2-15min, the activities at last sighting and at first resighting were each assumed to have taken up half of the period (Lehner 1979), except when a change in radio signal indicated a change in activity (e.g.end of pursuit in a hunt). Observations were terminated at the last visual sighting if contact was lost for longer periods. When the distance a hyaena moved while out of sight was less than the distance moved around obstacles by the vehicle, mapped distances, rather than odometer readings were used.

Table 9: Indices of spacing between hyaenas.

Index	Distance (m)	Spacing
1	0 - 1	Close
2	1 - 30	Nearby
3	30 - 150	In sight
4	150 -1500	In hearing
5	>1500	Remote

Table 10: Types of observation status recorded for hyaenas.

A) Instantaneous Sighting (5min or less)
- Random: not influenced by predictable factors
- Incidental (non-random): predictable

B) Continuous Observation
- Random beginning: not predictable
- Non-random beginning: predictable
- Continuous observation
- Last activity before lost out of sight
- Assumed activity while out of sight
- Activity when resighted in less than 15min
- Observations end.

Observations over 24h were made on 55 occasions. These covered entire nocturnal activity periods, but visual or radio contact was not always maintained countinuously during the hyaenas' diurnal resting periods (08h00-17h00). Because adults (except a dam) did not appear to use a particular lair, it was assumed that focal animals had remained resting all day if contact was resumed at the same locality before sunset.

Data Analyses

All observation, census, environmental and other data were loaded onto computer at the University of Pretoria. An SAS package (Statistical Analysis System 1982, SAS Institute Inc., Cary, North Carolina, U.S.A.) was used for most data manipulation and analyses. Observation data (especially continuous sampling) usually violated the assumptions for parametric statistics (Sokal & Rohlf 1981). The following tests were applied (Siegel 1956; Sokal & Rohlf 1981): Pearson's correlation (r), Spearman's correlation (r_s), Kendall's Tau (τ), Chi-square test (χ^2), Mann-Whitney U test (U) and the R-square test (r^2). Other tests are outlined in the text. Where multiple correlation tests are cited, only the minimum or maximum r-value or both are cited together with the lowest significance value.

Computer software for the production of three-dimensional graphs of spatial distribution (unweighted peaks and troughs) was developed using the DISSPLA package (Integrated Software Systems Corp. Graphics, San Diego, California). A suitable viewing angle (from NW to SE) was chosen and adhered to throughout.

3: SOCIAL RELATIONSHIPS AND DISPERSAL PATTERN

INTRODUCTION

The way in which a member of a social group gains or maintains breeding status can be described by its retention of or transfer between one of the following five dispersal states (Brown 1983): a) nonbreeder in natal unit; b) breeder in natal unit; c) floater outside any breeding unit; d) nonbreeder in another unit; e) breeder in another unit. The cumulative effects of the individual dispersal strategies determine the constitution of a social unit and, hence, the history of social relationships between its members.

Spotted hyaenas are organized into clans characterized by social integration, hierarchical relationships, solitary as well as cooperative food acquisition and territory defence by all members (Kruuk 1972; Tilson & Hamilton 1984; Mills 1985a). It has been suggested that a dominance hierarchy in spotted hyaenas may affect feeding priority (Frank 1983; Tilson & Hamilton 1984). In order to support or modify this hypothesis, the following information is necessary: a) The effects of amicable relationships, which would influence the nature of coalitions. This could be as important as dominance behaviour (Wittenberger 1981). b) Confirmation of the assumption that the social hierarchy within a group is the same at food as elsewhere, and that its principal function is to regulate access to food. c) The actual benefits of feeding priority.

Results of previous studies (van Lawick-Goodall 1970; Kruuk 1972; Whateley 1979; Frank 1983; Mills 1984a; 1985a; Tilson & Henschel 1986) suggest that a system of male dispersal and female philopatry prevails in *Crocuta*. However, the frequency, causes and effects of dispersal have not been previously examined. Frank (1983) and Mills (1985a) assumed that an immigrant male which became a resident gained mating rights, but did not present data on the origin of mating males or on the various stages of dispersal, the associated social and other behaviour patterns and how they relate to agonistic territorial behaviour.

The Mavumbye clan was studied to examine social relationships and their importance for changes in clan membership. The succession of dispersal states followed by individuals was identified and the behaviour of males before, during and after immigration observed. Although this clan was in a state of decline at the end of the two-year study (Chapter 4), this would not have affected conclusions made in the first 17 months when sufficient numbers of both sexes were present. Conversely, events that led to clan demise emphasized factors underlying the dispersal pattern of free-ranging hyaenas. Support is presented for the hypothesis that spotted hyaena clans are matrilocal, extended family groups (Ralls 1976; Mills 1985a) which conform to the definition of female-bonded groups (Wrangham 1980).

METHODS

The following criteria were used to distinguish clan members from non-members: a) Frequent resightings of a member in the territory of the clan over a period of at least two months; b) Mutual tolerance and amicable social interactions between clan members.

RESULTS

Clan Membership

In July 1982, the Mavumbye clan comprised five adult females, one female cub (nine months), three adult males and two subadult males. During the next two years, none of the six females emigrated out of this clan and no others immigrated into it. However, females died respectively after 3, 9, 17, 22, 23 and 25 months of the study (Chapter 4). Of eleven males that associated with the Mavumbye clan, only three did not either immigrate into or emigrate out of this social unit in the first 17 months. One of these had died in August 1982, while the other two were subadults at the beginning of the study and were presumably born into the clan.

On the basis of resident status and behaviour (described below), five social classes could be recognized within this clan:

i) permanently resident females;

ii) dependent cubs (<2yrs);

iii) resident natal males (RNM), which were born into the clan;

iv) central immigrant males (CIM), which became residents;

v) peripheral immigrant males (PIM), which associated with the clan temporarily.

One Mavumbye female (Fa) had badly damaged teeth and fed solely on scavenged soft food, some of which she obtained from a restcamp refuse dump situated 5km outside the Mavumbye clan territory. She did not associate with other hyaenas at the dump and returned to the Mavumbye territory after feeding. This behaviour was no longer observed after February 1984, explaining her death by starvation in April 1984. Because of her unusual behaviour, Fa has been excluded from most of the analyses that follow.

Amicable Relationships

Females formed the social nucleus of the clan (Fig.3), and were located in more than 30% of the observations within a radius of 150m of members of each class except PIMs, and only 16% of the time alone. An older cub and CIMs spent most of their time (90% and 78% respectively) in the company of females, but RNMs and PIMs usually moved alone (56% and 77% respectively). A dam tolerated only females, an older offspring, or a CIM in the close vicinity of very young cubs.

Amicable social interactions observed included head, body or genital sniffing, the greeting ceremony, social sniffing, allogrooming, muzzle wrestling and playing (Kruuk 1972). Most of these interactions (N=2191) were seen between females, cubs and RNMs (Table 11a).

Table 11: Occurrence of amicable contact interactions between social classes of the Mavumbye clan; a) all interactions; b) full greeting ceremonies. Figures in brackets indicate number of individuals in each social class.

	actor	recipient					
		Fem	Cub	RNM	CIM	PIM	Total
a)	ALL INTERACTIONS						
	Fem (5)	281	125	275	74	10	765
	Cub (1)	156	-	171	44	5	376
	RNM (3)	301	174	140	79	33	727
	CIM (2)	116	45	83	-	11	255
	PIM (6)	12	6	35	10	5	68
							2191
b)	FULL GREETING CEREMONIES						
	Fem (5)	69	25	48	16	3	161
	Cub (1)	29	-	22	8	0	59
	RNM (3)	51	21	27	8	4	111
	CIM (2)	16	7	11	-	0	34
	PIM (6)	3	0	6	0	0	9
							374

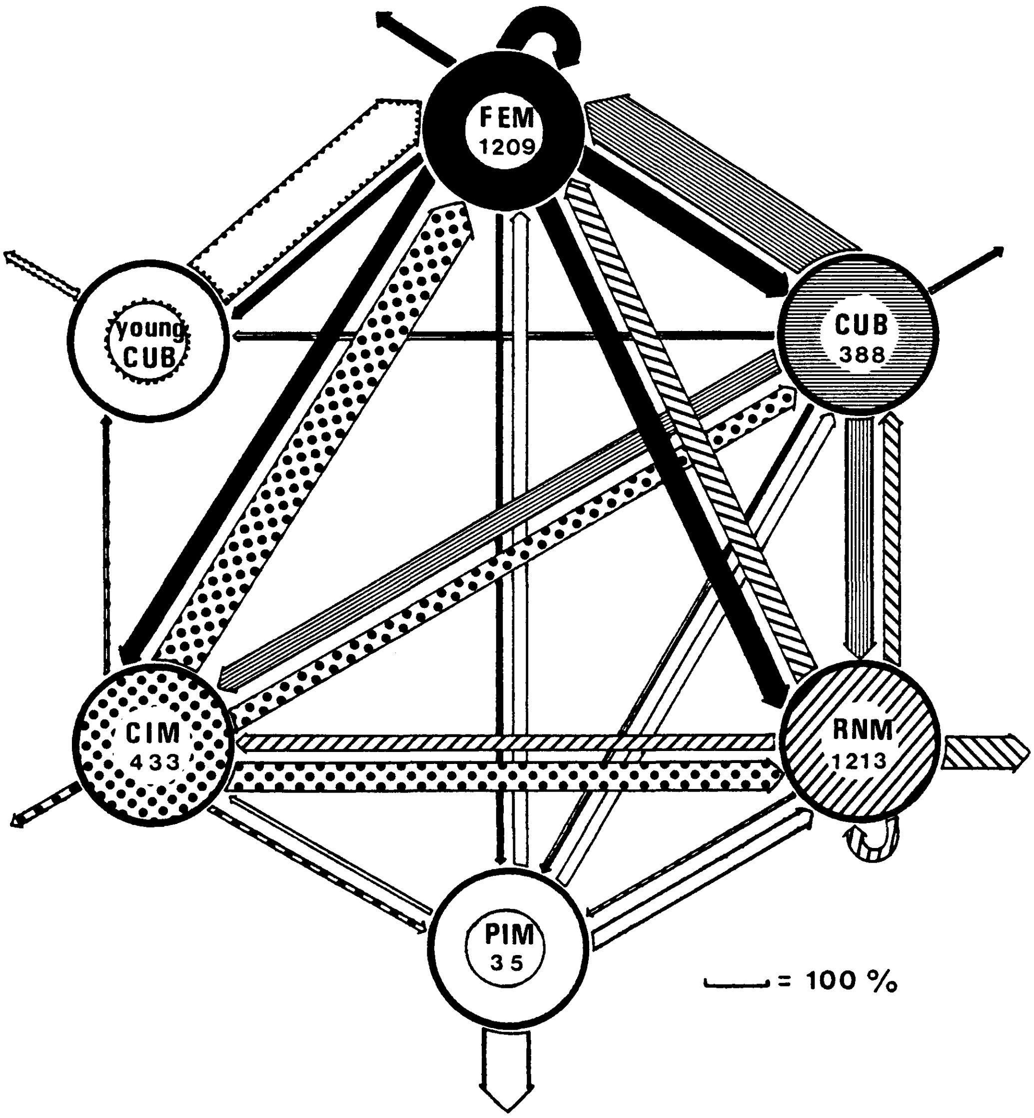

Figure 3: Time that members of each social class of the Mavumbye clan spent within sight (<150m) of other clan members. The numbers in circles indicate the duration (h) of observation. The thickness of arrows represents % time observed. Arrows pointing outwards represent time spent alone. Young cubs were less than two months old. Results obtained from a toothless female (254h), which spent 66% of the time alone, are excluded. Most observations of uncollared PIMs (86h) were not representative samples and are omitted here. The results shown here were obtained from one radio-collared PIM.

When hyaenas were active and together with others, such interactions occurred at a significantly higher frequency between females, cubs and RNMs than between this group and immigrant males or between immigrant males themselves (1,87±0,51/h cf. 0,66±0,29/h; $U_{9;8}=4$; $P<0,05$). Although body sniffing was performed most frequently (26 times) by a CIM towards females, this behaviour pattern was also often seen (86 times) among and between all other classes except PIMs.

Similarly, the last stage of the greeting ceremony (Table 11b), involving a participant presenting an erect clitoris or penis for another to sniff (N=374; 86% mutual presentations), was performed at a higher frequency by females, cubs and RNMs than by immigrants while they were active together (0,33±0,12/h cf. 0,08±0,06/h; $U_{9;8}=0$; $P<0,05$). PIMs were observed presenting towards females only three times. Although individuals sometimes sniffed a female's non-erect clitoris (N=22), they rarely sniffed a non-erect penis (N=2). These differences in behaviour reflect a higher degree of social intimacy among females and their offspring than that experienced by immigrants with other clan members.

Social Rank

The social rank of each hyaena was determined by recording the occurrence of submissive or evasive postures shown by one hyaena during interactions with another (Fig.4). This included the following elements (Kruuk 1972): crouching, creeping on carpal joints, tail curled under belly, head held low often at an angle, ears flat, teeth partly bared, retreating upon being displaced, fleeing when being chased, or standing adjacent while waiting to gain access to a site occupied by another hyaena. The

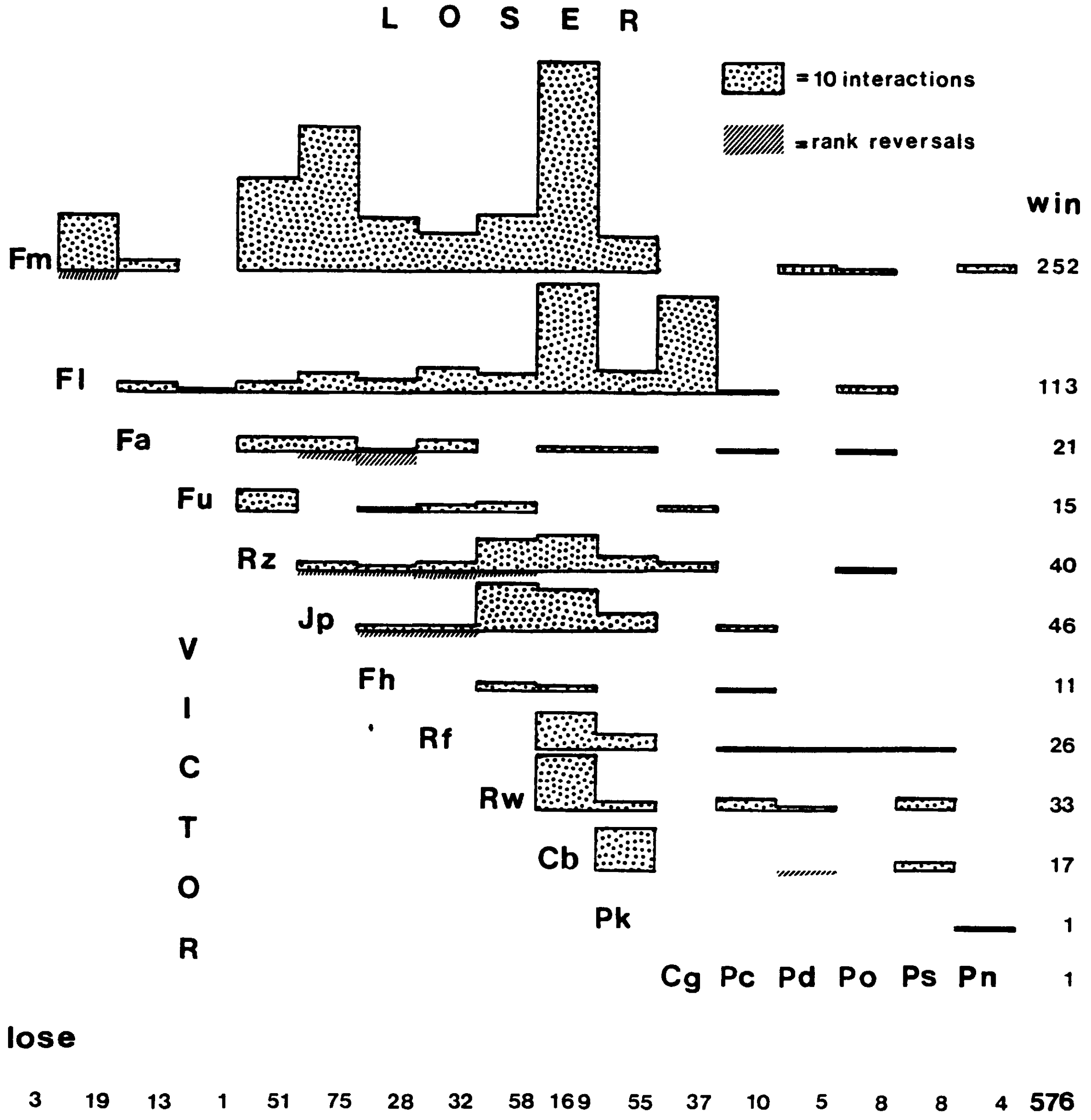

Figure 4: Dominance matrix for members of the Mavumbye clan, determined from displays of submissive postures in one-to-one interactions.

latter could or could not display aggressive intentions.

The clan was organized in a near-linear social hierarchy (Kendall's coefficient K=0,84; N=10; P<0,005; Appleby 1983), with mature adult females being dominant, followed by other natal members, then CIMs and PIMs in rank order (Fig.4). Immigrant males entered the social hierarchy at the bottom and lost all agonistic interactions against one or more residents (N=295).

Social rank bore no simple relationship to relative age (indicated by toothwear) and relative body size (Table 12), but body mass correlated significantly at a low level with social rank of all clan members (τ=0,48; P<0,05) and shoulder height correlated with social rank among adult females (τ=0,73; P<0,05).

Table 12: Age class (Kruuk 1972), occlusal surface area (mm^2) of the lower third premolar, body mass, shoulder height, chest girth and maximum head girth of Mavumbye hyaenas, correlated (Kendall's Tau) with relative social rank of all hyaenas and of females only. Significance (P<0,05) is indicated by '*'.

Hyaena	Rank	Kruuk Age Class	PM_3 surface area (mm2)	Mass (kg)	Shoulder Height (cm)	Chest Girth (cm)	Head Girth (cm)
Fm	1	IV	30,04	73	81,0	98,5	56,0
Fl	2	IV	34,10	81	84,5	95,5	55,0
Fa	3	- no teeth	-	-	80,0	94,5	54,0
Fu	4	V	47,07	70	80,0	96,0	56,0
Rz	5	II	-	64	80,5	91,5	-
Jp	6	I	8,61	55	75,0	86,5	54,5
Fh	7	II	13,92	71	78,0	95,5	54,0
Rf	8	III	-	70	77,5	96,0	55,5
Rw	9	II	12,19	63	78,5	94,5	53,0
Cb	10	III	-	65	83,0	95,0	55,0
Cg	10	III	15,71	66	83,0	94,0	-
Pc	11	IV	-	60	79,0	86,5	53,0
Ps	11	II	-	56	78,0	88,0	53,0
τ: TOTAL		-0,06	-	0,48*	0,15	0,38	0,16
τ: FEMALES		0,20	0,20	0,40	0,73*	0,33	0,33

Furthermore, adult females were heavier than males (73,8±5,0kg cf. 63,4±4,5kg; $U_{4;7}=4$; $P<0,05$) and of more sturdy build, indicated by chest girth (96,0±1,5cm cf. 92,2±3,7; $U_{5;7}=4$; $P<0,05$), although they were not taller (shoulder height: 80,7±2,4cm cf. 79,9±2,3cm; $U_{5;7}=12$; $P>0,1$). The only rank reversal among the two dominant females was observed when the top-ranking female deferred to the other thrice during one night during late pregnancy of the latter, suggesting that reproductive status may influence rank temporarily.

Feeding Priority

Agonistic interactions (N=692) occurred more frequently at food than when hyaenas were active together elsewhere (5,4/h cf. 1,6/h). In 252 such interactions at food, the social ranks correlated significantly with that determined by means of 237 interactions away from food ($\tau=0,79$; $P<0,005$; Fig.5).

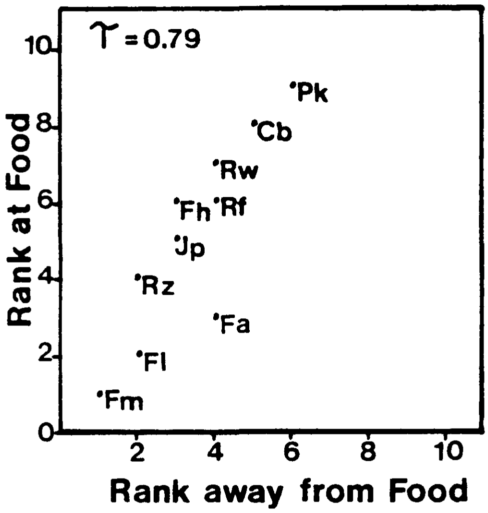

Figure 5: Comparison of social rank of ten Mavumbye hyaenas at food and elsewhere determined by the number of clan members dominated by an individual.

Rank equality could be determined for a single pair at food, but for five pairs away from food. These data indicate that the hierarchy was more clearly defined at food.

Feeding priority was determined by the outcome of disputes at carcasses, scored as displacement or retreat. With females and RNMs, feeding priority depended mainly on relationships between single individuals and only infrequent (7% of 152) displacements of an individual by groups of two or more were observed. In comparison, immigrants were displaced by groups in 37% of the interactions (N=190; X^2=41,1; P<0,001), reflecting a low tolerance of residents towards them. PIMs were completely excluded from feeding on 93% of the occasions (N=30), and CIMs on 41% of the occasions (N=49), when they were present at carcasses together with females or RNMs. In contrast, none of the females and RNMs were excluded by others. However, in 11 cases when females or RNMs kept at a distance of more than 30m from a carcass to which access was made dangerous by another species, such as lion, an immigrant male was observed feeding at the carcass during this period of low intraspecific competition.

The quality of food obtained by a feeding hyaena was indicated by its posture and jaw action: meat was gripped with the front teeth and torn by pulling with the neck, shoulders and front legs; hide was cut with the carnassials at the side of the jaw; bones were cracked audibly with the premolars. When all feeding observations were categorized by this means, it was calculated that females spent 79,8±10,9% of 118h and males 57,7±14,1% of 150h eating meat ($U_{6;6}$=5; P<0,05). These differences can be explained by the higher feeding rank of females. Twenty-four hour observations (N=55) indicated that males may have compensated for this lower high-protein intake by foraging over greater distances than females (23,6±10,4km cf. 16,5±10,4km; $t_{53}=2,45$; $P<0,05$), and eating more low-quality food items than females (2,9 cf. 1,2; $\chi^2=9,23$; $P<0,01$) per night.

Territory Intrusion

The Mavumbye clan defended a 130km^2 territory and scent-marked this area by scratching, pasting or defaecating, often using latrines for this purpose. On fourteen occasions, when non-immigrant intruders were observed to encounter Mavumbye hyaenas in their territory, the former immediately returned to their own territory upon being challenged. Mavumbye hyaenas ventured out of their territory on 40 occasions (Fig.6) for various reasons (Table 13), but females immediately returned to their own territory on all seven occasions when they were challenged. Similarly, non-immigrant intruders into the Mavumbye territory fled from its tenants at fourteen encounters.

Table 13: Reasons for territorial intrusions.

Reason	N
Access to Food	13 *
Land Dispute	8
Prospective Immigration	13
Unknown	6

* excluding the toothless female.

In contrast, prospective immigrant males did not leave the area immediately upon encounters (N=10). Initially, they made their presence conspicuous by vocalizing (whooping) or seeking out members of the resident clan. When challenged, they lay down prone or sought shelter, but did not flee over long distances. The attacking group surrounded the intruder, sniffing, nudging and biting it for one to thirty minutes, sometimes repeating this several times in a night ($\bar{X}$=2,3). On the 23 occasions (with seven prospective immigrants) when such interactions were witnessed, no serious injuries were inflicted, although the victim sometimes emerged limping and bleeding. Disparity in the proportion of males older than six years (8,6% of 35) compared to females (37,8% of 37; χ^2=8,5; P<0,005), of 11 Mavumbye clan members and of 61 other hyaenas from a nearby area (Lindeque 1981), may indicate male-biased mortality which could result from such attacks on prospective immigrant males.

Male Immigration

All instances of male immigration reported here occurred during the first 17 months of this study while there were still at least four females in the Mavumbye clan.

Events leading to the acceptance of one Mavumbye RNM into another clan were observed. Over a period of three weeks, this male explored and scent-marked far into the adjacent territory and had agonistic encounters with its residents on at least five occasions. Finally, an encounter between him and a female and subadult of the other clan resulted in lengthy sequences of cautious approaches while sniffing air and ground (paw marks) until he retreated, repeated sixteen times over three hours. The culmination was the first amicable social contact (mutual head-sniff) between the antagonists, after which the male was no longer prevented from accompanying members of this clan, thus becoming a PIM of the new clan. When he once temporarily reappeared in the Mavumbye clan a month later, his relationships towards females and other RNMs appeared to be unchanged from their former amicable status.

Different stages of this behaviour sequence were seen with ten other Mavumbye males. At different times, six PIMs remained in the clan for 6,0±3,4 months before disappearing. Four of these were each seen once in amicable association with members of other clans, indicative of previous contact. However, because these timid PIMs could not be fitted with radio collars, they could not be observed more intensively. One CIM joined the clan permanently (>18 months) three months after the death of another adult male that had shown CIM-like characteristics (relatively low social rank and close attendance on females). Neither of these were seen to cross into other territories. Two RNMs remained Mavumbye clan members, but were observed initiating contact with three adjacent clans on eight occasions before returning to the Mavumbye clan within three nights.

As a consequence of these movements, RNMs and PIMs ranged over larger areas and spent relatively more time outside the Mavumbye territory than did females and CIMs (Fig.6; maximum diameter: 35 cf. 16km). RNMs had extraterritorial ranges of $70{,}0 \pm 30{,}8\text{km}^2$ compared to $11{,}4 \pm 8{,}8\text{km}^2$ for females and CIMs ($U_{3;7}=0$; $P<0{,}05$).

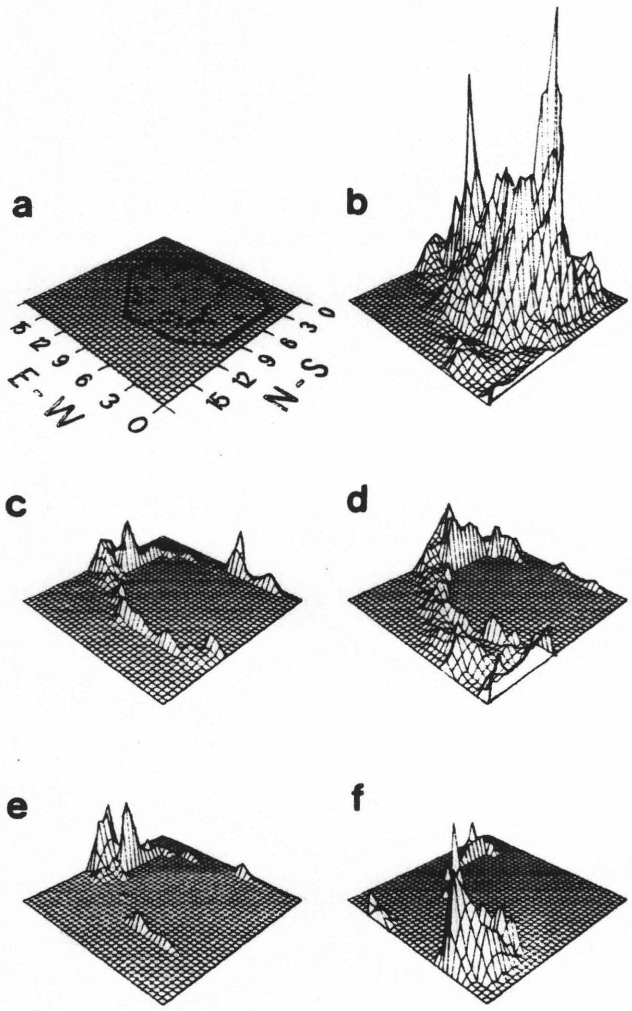

Figure 6: (a) Location of Mavumbye clan territory boundary and latrines compared to the three-dimensional representation of (b) distance moved per km^2 grid square by all hyaenas and (c–f) the extraterritorial movements of adult social classes: (c) Females, (d) RNMs, (e) CIMs, (f) PIMs.

Mating

On three occasions when mating attempts were witnessed, a CIM was associated during pro-oestrus. Approach - retreat behaviour, strong submissive postures towards the female, followed by mounting (Kruuk 1972), characterized such associations. Late pregnancy was once detected by palpation after 13 weeks, while another female, which had lost her cubs two weeks prior to mating, gave birth 17 weeks later. This corresponds to the gestation period of *Crocuta* in captivity (Schneider 1926) and in the wild (Lindeque 1981).

Direct agonistic competition between males for mating opportunities was not observed. Despite the presence of three RNMs during the three periods of several days when a CIM attempted to mate, the RNMs showed no interest in the female. The precarious social status of PIMs precluded them from approaching near enough to a female to attempt mating, although these males sometimes followed females at a distance. As a result, CIMs were observed to be the only suitors of females in oestrus. Only once was an RNM observed to mount a female in his natal clan. This incident differed from others in that the male showed no characteristic premating behaviour and the female was in early lactation and therefore probably anoestrus.

DISCUSSION

Cooperation amongst adult members of a spotted hyaena clan is important for the defence of a group territory and for the procurement of large carcasses, but social relationships determine how carcasses are divided. This confirms Frank's (1983) and Tilson & Hamilton's (1984) findings and contrasts with Kruuk's (1972) observations of scramble contests in large East

African clans. Feeding priority was determined by social rank, which could be influenced by many factors, including the social history of an individual, dependant rank inherited from the mother (Rowell 1974), or by endocrinology (Racey & Skinner 1979). Reproductive condition could also play a role, as was indicated by the rank reversal of a parturient female in the present study, and of a lactating female reported by Tilson & Hamilton (1984).

The present study showed that as a result of priority of access to carcasses, females generally obtained a higher proportion of meat than males did. Males compensated by moving over greater distances when foraging, consuming more low-quality food and feeding more readily in adverse conditions. It is suggested that this feeding behaviour resulted in the nursery unit receiving the greatest benefits at the expense of other population sections. Since growing cubs and lactating or parturient females require a high protein intake, this system assures optimal food distribution (Gauthreaux 1978). This difference in consumption might explain why adult females were heavier and more sturdy than the males, in agreement with Matthews (1939a), Kruuk (1972) and Hamilton *et al* (1986).

Crocuta cubs depend solely on their mother's milk for some 12-14 months (Kruuk 1972). In the Kruger National Park, where hyaenas breed aseasonally, females have litters at intervals of about 16 months (Lindeque & Skinner 1982a), and a mature female, which raises litters in succession, can be expected to lactate for about 75% of her reproductive lifespan. Under such circumstances, individual selection is sufficient to explain female dominance, whereas kin selection (Mills 1985a) would explain cooperation in food acquisition by subdominant individuals (except PIMs) and exclusion of immigrants.

Intimate social contact and olfactory examination, including body sniffing and the greeting ceremony, contribute to the maintenance of coalitions along cooperative lines. In this respect, present observations do not agree with Frank's (1983) description of body sniffing for the sole purpose of males identifying female reproductive status, and contradict the hypothesis of Hamilton *et al* (1986) that one of the principal functions of displaying an erectile penis or clitoris was the signalling of subordinate social rank.

The reluctance of females to emigrate is epitomized by the case of the Mavumbye female which had damaged teeth and depended on the availability of refuse in the territory of a neighbouring clan. In contrast, 11 cases of male immigration or emigration into or from the Mavumbye clan were noted during the first 17 months of observation, while there were still at least four females in the clan. It is suggested that these differences between the sexes reflect different dispersal patterns.

Only one immigrant male, which succeeded in maintaining close contact with females, obtained unrivalled mating opportunities. I hypothesize that the three social classes, RNM's, PIM's and CIM's, respectively represent the three dispersal states, nonbreeders in their natal clan, nonbreeders in another clan and breeders in another clan, and that both of the former classes attempt to attain the latter. Frank (1983) had suggested that prospective immigrants, which he called transient males, might be nomadic and were expelled from their natal clan similar to dispersing wolves *Canis lupus* (Messier 1985). However, present observations indicate that prospective immigrants and

PIMs were also members of a neighbouring natal clan which they left voluntarily and to which they later occasionally returned as a temporary escape from attacks by members of the new clan. Mortality during immigration could contribute to the observed disparity in the age structures of the sexes, as is expected in a species with a male-biased dispersion (Greenwood 1980).

As a result of female clan fidelity, male immigration and a polygynous mating system, the Mavumbye females were probably closely related, as had previously been found for clans in the southern Kalahari **(Mills 1985a)** and contrary to an earlier suggestion for East African clans (Bertram 1980). Consequently, social units of spotted hyaenas should be regarded as extended family groups (Ralls 1976), or harem groups of long duration (Crook, Ellis & Goss-Custard 1976), to which cousins or more distantly related males attach themselves from adjacent groups. One of the genetic advantages of this system is that mating opportunities are distributed in such a way as to optimize outbreeding (Bateson 1983).

Most reports of male immigration in spotted hyaenas (van Lawick-Goodall 1970; Kruuk 1972; Whateley 1979; **Mills 1984a;** Tilson & Henschel 1986) did not identify its relationship to **paternity. My finding confirms Frank's (1983) and Mills' (1985a)** hypothesis to this effect and that only one immigrant at a time attains mating status. The present interpretation differs from that proposed by Frank (1983) that mating rights are determined by aggressive interactions among males. It is argued that such an arrangement should have led to selection for male dominance in a clan, as is the case in wolves (Zimen 1981). Rather than agonistic rivalry between spotted hyaena males, the emphasis is placed on the ability of an immigrant male to establish amicable relationships with females and to mate with them without affecting the latter's access to food. Even if a male with breeding status is the highest-ranking immigrant, this agonism is related to feeding priority rather than mating rights. Closest attendance on females distinguishes the central immigrant male from dominant natal males and from peripheral immigrant males.

As a corollary of the conclusion that mutualism (Macdonald & Moehlman 1982), associated with communal denning, appears to be important for spotted hyaena reproduction (Chapter 4), the present study indicates that the benefits of cooperation, especially between females, extend to food acquisition. This is characteristic of a female-bonded system (Wrangham 1980) in which males cooperate less than females in food acquisition and transfer between groups in order to mate, in a similar manner as described here for spotted hyaenas.

4: SOCIAL AND ECOLOGICAL FACTORS UNDERLYING CLAN DECLINE .

INTRODUCTION

Spotted hyaenas are organized into clans, whose members share a common territory (Kruuk 1972) and form a breeding unit. Clan size is believed to be related to the availability of prey (Macdonald 1983; Chapter 6), comprising mainly medium to large ungulates in the size range between Thomson's gazelle (*Gazella thomsoni*) to giraffe (*Giraffa camelopardalis*) (Kruuk 1972; Bearder 1977; Mills 1978; Tilson *et al* 1980), that can be acquired by solitary or cooperative hunting or scavenging (Kruuk 1972; Lamprecht 1978).

Recently, Mills (1985a) found that the composition of foraging spotted hyaena groups in the Kalahari desert could be explained by kin selection theory. Cubs are usually kept in communal dens (Deane 1962; Kruuk 1972; Mills 1983; Tilson & Henschel 1986), but cooperation between related individuals does not appear to accrue direct benefits to the rearing of young (Mills 1985a) as is found in some other carnivore species (Macdonald & Moehlman 1982). This raises questions concerning indirect benefits of communal denning, or the degree of breeding synchrony required for it, or subsequent social connotations and whether these can be explained as a form of mutualism (Wrangham 1982; Macdonald & Moehlman 1982).

Here I describe some of the ecological and social factors that influenced membership of the Mavumbye clan, which occurred in a region where hyaenas and lions had been culled seven years previously to temporarily reduce effects of predation on wildebeest and zebra (Joubert *et al* 1974; Smuts 1975; 1976a; 1978a). In this clan, recruitment did not balance natural mortalities, eventually leading to the sudden decline of the clan towards the end of the study. Events that occurred in this unusual situation enabled the identification and examination of some of the variables affecting natural mortality and recruitment, which ultimately influence the maintenance of clan integrity or its decline in a natural environment.

By examining some long-term effects of population management and comparing them with other studies of undisturbed populations elsewhere (Hornocker 1972), three possible explanations for hyaena group demise are considered: a) that changes in the environment brought about a resource shortage (Tilson & Henschel 1986); b) that once hyaenas were reduced below a "threshold density" (= small group size), they were unable to compete effectively with lions and conspecifics, so that adults suffered a food shortage and high combat mortality (Smuts 1978c); c) that the breeding unit depended on expansion from within because of the lack of female immigration (Chapter 3), but that cub mortality agents were more severe in a small clan than in a larger clan in the same ecological context. Finally, a model of hyaena social organization is examined in the light of previous studies.

METHODS

Cause of death of adult hyaenas was determined by carcass inspection, which revealed either a cracked vertebra, scratched skin and large bite marks caused by lions, or numerous small bite marks and skin tearing caused by hyaenas, or goring and bone fractures caused by prey.

The methods used to determine ungulate abundance and biomass are described in Chapter 5.

RESULTS

Hyaena Density

In July 1982, the Mavumbye clan comprised five adult females, one female cub (nine months), two subadult males and three adult males. The density of hyaenas older than 18 months from the Mavumbye clan and three adjacent clans was estimated as 7,5-9,8/100km^2 (Table 14).

Excluding the losses of orphaned cubs, a total of 375 hyaenas were destroyed in the Central District between December 1974 and January 1980 (Table 15). The Mavumbye clan and three adjacent clans lived in Area 2 (Fig.7) of 397km^2 in which 67 adults and subadults (23 males, 42 females, 2 unknown sex) and 36 cubs (<18 months; Smuts pers.comm.) had been culled in January and February 1975 , leaving some survivors (Smuts 1978a). Some culled hyaenas could have come from outside the cropping area. Judging from behaviour observed in the present study, hyaenas in this region have restricted movements because of territoriality, but sometimes stray several kilometers into adjacent territories (Chapter 3). Culling could therefore have affected an additional area, the width of the radius of clan territories (6km), around the periphery of Area 2 (except where it borders onto Area 3; Fig.7). By including this area, the maximum size of the Area 2 impact region was calculated as 780km^2. It is thus estimated that 8,6-16,9/100km^2 adults and subadults were removed from Area 2 from an original density of some 16,1-26,7/100km^2 (culled + 1982 numbers).

Area 2 was bordered by regions in which density reductions had taken place (Fig.7). To the south, in Area 3 of 288km^2, 153 hyaenas were culled over a five-year period. To the north, in the

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<u>Table 14</u>: Number of adult and subadult members (>18 months old) and minimum size of non-overlapping territories of four adjacent clans (Fig.7), determined from sightings of known hyaenas.

CLAN	Members	Min.Territory Size (km^2)	Density (no./100km^2)
Mavumbye *	10	130	7,7
Nghotsa	9	115	7,8
Gudzane	9	60	15,1
Satara	11	92	12,0
Total +	39	397	9,8
Total ++	39	520	7,5

* Determined with certainty
\+ Maximum density (assuming minimum territories)
++ Minimum density (assuming 130km^2 territories)

<u>Table 15</u>: Number of spotted hyaenas destroyed in the Central District of the Kruger National Park between December 1974 and January 1980.

(1) Area Code	Date	Cause of Death	<u>Adults & Subadults</u>			(2) Cubs	TOTAL	(3) Source
			Male	Female	Unknown			
3	Dec74-Jan75	Culling	29	26	4	32	91	a,c
2	Jan75-Feb75	•	23	42	2	36	103	a,c,e
B	Dec75-Oct76	•	2	1	0	0	3	b
A	Dec75-Oct76	•	4	7	0	5	16	b
?	Dec75-Oct76	•	4	4	17	2	27	b,c
5	Dec76	•	23	23	0	17	63	c
3	Dec78	•	9	9	28	0	46	d
Nghotsa	1979	Electric Shock			10		10	d
3	Dec79-Jan80	Culling	7	9	0	0	16	d
							<u>375</u>	

(1) Area codes (after Joubert *et al* 1974):
2=Satara-Nwanedzi; 3=Sweni-Lindanda; 5=Kingfisherspruit; A=Manzimahle-Manzimhlope; B=Mmondozi-Rietpan.

(2) Cubs (<18 months old) culled at dens and bait, not counting orphan cubs that died (e).

(3) Data sources: a = Smuts (1975); b = Smuts (1976a); c = Smuts (1978a); d = National Parks Board (unpubl.); e = Dr GL Smuts, Anglo-American Corp., Box 61587, Marshalltown, 2107.

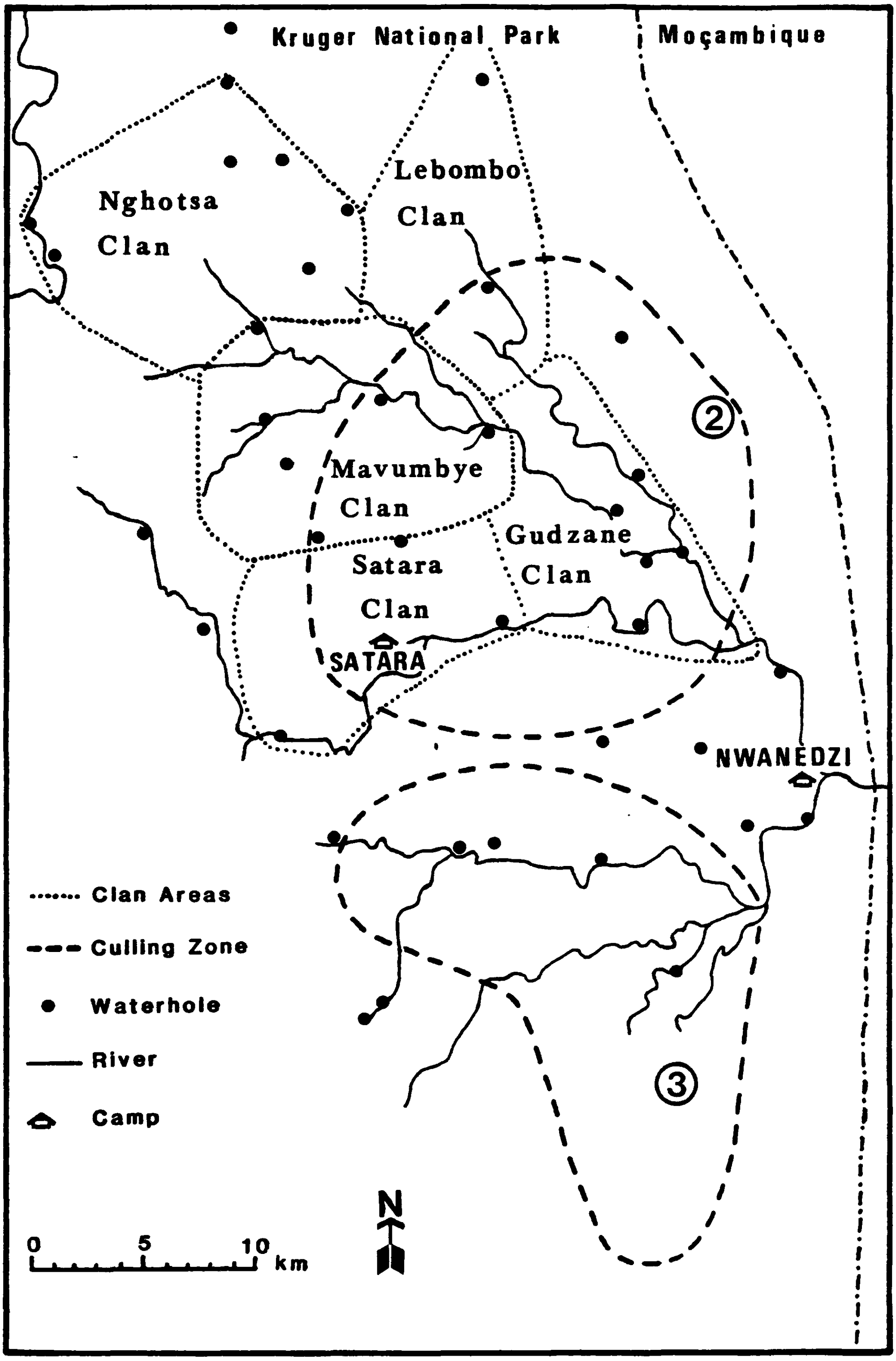

Figure 7: Map of culling Areas 2 and 3 in the Central District of the Kruger National Park. The territory of the Mavumbye clan and approximate clan ranges of surrounding clans are indicated.

territory of the Nghotsa clan, ten adults were inadvertently killed by electric shock in 1979 (Table 15).

Water and Food Availability

In their territory, Mavumbye clan members were never further than 3,7km away from the nearest permanent source of water (Fig.7). Ungulates constituted 94,6% of the observed hyaena diet (223,6 meals). The mean biomass of ungulates smaller than 1000kg was 2267 kg/km^2, ranging from 520 kg/km^2 in summer to 3222 kg/km^2 in winter. The Mavumbye territory contained 67,6 tons of these ungulates at the leanest period in midsummer 1983/84. Assuming a food requirement of 4,0 kg/hyaena/day (Chapter 7), the annual food requirement of the Mavumbye clan (11 members) would amount to only 5,5% of the mean biomass of ungulates smaller than 1000kg.

Relationship with Lions

In 1983, the lion density (16,2/100km^2; 7 prides in 588km^2; Whyte pers.comm.) was slightly higher than before culling in 1974 (12,6/100km^2; Smuts 1978b). Whereas the bulk of hyaena food, 50% of 223,6 meals, was from own kills, only 8% of the food originated from lion kills (Chapter 7). However, the cause of death was not known with certainty for 65% of 147 ungulate carcasses, which made up 18% of the observed hyaena diet. The majority of these were probably lion kills. It is estimated that lions contributed about 20% to the hyaena diet.

Six of the ten natural deaths of hyaena that were recorded in the Mavumbye clan and other clans, were caused by lions. In interactions between hyaenas and lions, it was evident that lions were usually dominant and that hyaena aggression increased with their group size (Chapter 5).

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Clan Size

Of eleven Mavumbye clan members that were present in July 1982 and six immigrant males that appeared later (Fig.8), nine died (Table 16) and five emigrated (Chapter 3). Despite the deaths of a male and two females in the first 17 months of the present study, clan size remained fairly constant at ten, with immigration balancing emigration and mortality. The deaths of six members during the seven months that followed, caused the rapid demise of the clan (Fig.8). In July 1984, four males but no females remained and the clan (= breeding unit) was regarded as non-viable.

Table 16: Causes of death of Mavumbye clan members.

Date	Sex	Age (yrs)	Cause of Death
Aug 82	Male	3-6	Phencyclidine hydrochloride anaesthesia
Sep 82	Female	6-16	Lion
Mar 83	Female	3-6	Unknown
Nov 83	Female	6-16	Hyaenas (territorial dispute)
Jan 84	Male	6-16	Hyaenas (?)
Mar 84	Male	3-6	Etorphine hydrochloride anaesthesia *
Apr 84	Female	2	Lion (?)
Apr 84	Female	?	Malnourishment ++
Jul 84	Female	6-16	Lion

* see van Jaarsveld *et al* (1984)
++ damaged dentition, depended on soft food

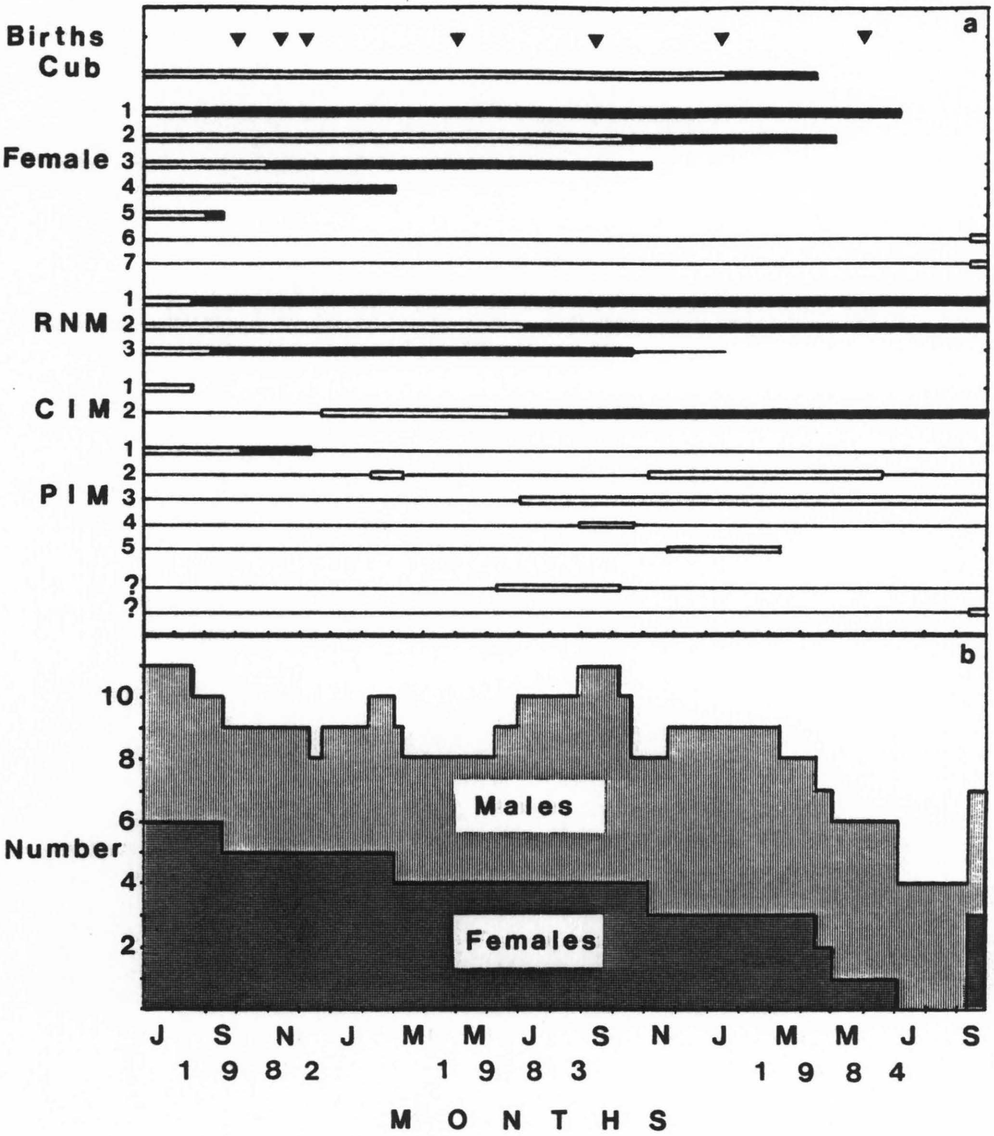

Figure 8: Spotted hyaenas of the Mavumbye clan. (a) A thick line indicates the time when a hyaena was a member of this clan without (light) or with a radio collar (shaded). A line stops when a hyaena was confirmed dead. (b) Number of male and female clan members between July 1982 and September 1984.

Births and Cub Mortality

A low recruitment rate prevailed within the Mavumbye clan for a few years prior to this study and in 1982 only six of its members (55%) were younger than six years (Table 17), compared to 80% established for 61 other Kruger Park hyaenas ($\chi^2=3,4$; $P<0,1$).

Of litters born during the study period, only one survived for longer than two weeks, but the cause of death was never established. All of the cubs were kept in two non-communal dens, which the dams had adapted from actively used aardvark (*Orycteropus afer*) holes. These only had one large main tunnel (height x width = 0,3 x 0,3m), but no side-passages (Skinner *et al* 1986). Observations over 24h periods indicated that the dam gave the cubs considerable attention (Appendix B) and spent only 3,1±3,4 h/day (N=9) away from the den compared to her usual 6,7±2,7 h/day (N=7) period of activity (t=2,32; $P<0,05$). In one instance, a litter was lost while the dam chased a member of another clan away from the den (see Appendix B). This loss could have been caused by hyaenas from a neighbouring clan. The dominant female (Fm; Chapter 3) gave birth to five litters of one or two cubs at a mean interval of 135,2±6,0 days. In addition, pregnancy was detected by palpation in two other females on three occasions, but their litters were never seen (Fig.8).

Table 17: Age structure of the Mavumbye clan during July 1982 compared to the age structure of a sample of 61 other hyaenas from the Kruger National Park (Lindeque 1981).

Sample	Age (yrs)	Males	Females
Mavumbye	<6	4	2
	>6	1	4
Other KNP	<6	28	21
	>6	2	10

DISCUSSION

The density of adult and subadult hyaenas in the study area and surrounding regions was two to three times as high prior to culling in 1975 (16,1-26,7/100km^2) than in 1982 (7,5-9,8/100km^2). These estimates are comparable to the 20,6/100km^2 in 1975 estimated by Smuts (1975) and 6,0-18,2/100km^2 in 1984 by Mills (1985b) for the Central District of the Kruger National Park.

Hyaenas have been culled in this park throughout this century (Pienaar 1969). The present study confirms the earlier indication (Smuts 1978c) that the hyaena population appears to have failed to recover from the latest density reductions. Wolves (Fritts & Mech 1981) and lions (Smuts 1978c), increase immigration and recruitment rate following culling, because a reduction in intraspecific competition for food and space, increases the probability of immigrants and weaned juveniles surviving and achieving breeding status. In contrast, hyaenas lost most offspring before weaning and females did not immigrate (Chapter 3). This appears to have been fundamental to the demise of the Mavumbye clan.

The capacity of an exploited population to increase is ultimately influenced by the way recruitment is affected (Laws 1973). Thus, causes of adult mortality and the relationship of hyaenas with lions (Smuts 1978c), can be regarded as secondary in importance. As in East Africa (Kruuk 1972), lions were major agents causing mortality of hyaenas in the present study, but in the Mavumbye clan, losses were not replaced. Although scavenging from lions was important for subsistence between hyaena kills, the difficulty of a small hyaena group displacing lions at a carcass (see also Lamprecht 1978) did not limit resouce availability to the clan.

In response to changes in the environment, which create a food or water shortage, hyaena clans have been reported to decline by dispersing and abandoning cubs (Kruuk 1972; Tilson & Henschel 1986). Although prey abundance varied seasonally in the present study (Chapter 5), a resource shortage did not occur, females did not disperse (Chapter 3) and cubs were not abandoned. The sudden disappearance of apparently healthy cubs could not be explained by deficiencies in maternal care or the existence of endemic diseases.

Because of the lack of alloparental help and no provisioning of solid food to *Crocuta* cubs (but for one recorded exception; Hill 1980), they rely solely on milk from their mother for sustenance over an extensive period (Kruuk 1972). According to Mills (1983), alloparental help would be difficult to accomplish because of the distribution of large carcasses, the competitive nature of adult feeding behaviour and the competitive advantage larger (older) cubs would have over small cubs at provided food. Instead of helping each other, as do brown hyaenas, *Hyaena brunnea* (Mills 1982; Owens & Owens 1984), and striped hyaenas, *Hyaena hyaena* (Kruuk 1976), a number of *Crocuta* females can breed simultaneously, but have small litters (usually two cubs; Matthews 1939a; Kruuk 1972; Smuts 1975; Lindeque 1981).

Spotted hyaenas are polyoestrous non-seasonal breeders (Lindeque & Skinner 1982) and can conceive two to three weeks after the loss of cubs (Grimpe 1916). The short litter interval of 19 weeks was evidence of this in the present study and represents a maximum production of cubs for a female. All of these cubs were kept in non-communal dens and none survived.

With a two-week longevity of solitary litters, the probability of one of the three reproductively active females having cubs at any given time was low (P=0,1), so that parturition by any two females was unlikely to occur within the same fortnight (P=0,03). This could be the reason why a communal den was not established by the Mavumbye clan during the study period.

It is suggested that solitary litters were more vulnerable than cubs in communal dens, such as were found in more densely populated areas of the park. In East Africa, 83 to 100% of cubs occurred in communal dens (Kruuk 1972). An advantage of such dens is that older cubs could act as guards while adults are out foraging. This factor could explain why Watson (1965) found older cubs holding young cubs in a firm grip, when he excavated their den. Kruuk (1972) noted that cubs were efficient excavators of tunnels too small for adults to enter. Unlike 10 of 11 other natural dens examined in the Kruger National Park (Skinner *et al* 1986) and numerous dens described elsewhere (Matthews 1939b; Sutcliffe 1970; Kruuk 1972; Henschel *et al* 1979; Brain 1981), the two Mavumbye dens had no narrow passages, or retreats for small cubs, the tunnels being large enough to permit human entrance into the extremities. Thus, these non-communal dens probably offered less protection to very young cubs against physical threats (e.g. foreign hyaenas or black-backed jackals, *Canis mesomelas*) than evidenced at communal dens elsewhere.

The present study indicates that the survival of a cub may not only depend on the well-being of its own mother, but could be affected by the ability of the clan to establish a communal den, which requires a degree of breeding synchrony between females.

Mutualism (Wrangham 1982; Macdonald & Moehlman 1982) may thus favour the establishment of large breeding units of related females (Mills 1985a; Chapter 3). This may account for the apparent lack of social constraints on maximum clan size in spotted hyaenas, which ranges from four (Tilson & Henschel 1986) to 80 adults (Kruuk 1972), within the limits of ecological factors (Macdonald 1983). Such a system, where cooperation is expected to benefit females more than males, would account for the observed pattern of male dispersal and female philopatry (Chapter 3), as is found in female-bonded primate groups (Wrangham 1980).

Conversely, factors which affect the survival of new-born cubs in a certain area, such as the availability of suitable den sites and the presence of predators of hyaena cubs, could determine the minimum group size of a viable reproductive unit of spotted hyaenas in which the probability of achieving breeding synchrony is less dependant on the timing of parturition and offspring survival of each mature female than in a small group. It is suggested that the Mavumbye clan was reduced to a low probability of breeding synchrony, so that recruitment was too slow to compensate for natural female mortalities.

5: FORAGING BEHAVIOUR AND INTERSPECIFIC INTERACTIONS

INTRODUCTION

Important considerations for foraging predators are when, what and where to search and how to procure food. Principles of food procurement by a predator can be examined by observing factors affecting its activity pattern, by gaining knowledge concerning its search patterns relative to potential food sources and by investigating interspecific interactions that could affect the availability of a potential food source.

Foraging behaviour of spotted hyaenas has previously been examined in East Africa by Kruuk (1972), who found that the group size of foraging hyaenas could affect interspecific interactions, and conversely, that the relative abundance of prey species could affect hyaena foraging behaviour. In previous investigations on the relationships of spotted hyaenas with other canivores (Kruuk 1972; Bearder 1975), it was found that this may depend on the relative abundance of the various species, their relative body sizes and possibly on the history of previous interactions.

In this chapter, I intend to identify some factors that limit foraging behaviour, to examine the hyaenas' response to factors that relate to food availability, such as the effect of a drought on other species, to examine the hypothesis that social relationships affect hyaena foraging behaviour, and to compare foraging behaviour and interspecific relationships with studies elsewhere.

METHODS

The abundance of ungulates of impala size and upwards was determined by means of five biennial aerial censuses (National

Parks Board unpubl.). Total counts were made, but the sampling accuracy for each species was not known, although apparent (unrealistic) numerical fluctuations of resident species, such as kudu (*Tragelaphus strepsiceros*), emphasized the need for such tests.

Between June 1983 and June 1984, all ungulates and other mammals were counted at night on twelve line transect censuses (over 46 nights) conducted along 17 routes of 3km length (total 51km; Fig.1). These data served as an independant measure of the probability of encountering organisms in the present observation framework. The abundance of small ungulates (<20kg) and other mammals with small group sizes, which were sighted more than 20 times at different localities on line transects, could be computed using the Fourier series estimator multiplied by mean group size (Burnham, Anderson & Laake 1980).

Records were kept of all casual sightings of carnivores, and nocturnal mammals (>1kg) in the study area to indicate their relative abundance. Individual recognition of some jackals *Canis mesomelas*, lions *Panthera leo* and leopards *Panthera pardus* facilitated abundance estimates.

Biomass was calculated using census results, ungulate age and sex ratios for the area (Mason 1983, 1984, 1985; Mason & van der Walt 1984) and mean mass for age and sex (Meissner 1982; Smithers 1983).

RESULTS

Hyaena Foraging Behaviour

Exploratory behaviour by sniffing, listening and looking at surroundings while moving with many deviations at an average speed of 3,9km/h, that did not relate to the location of dens, other social attraction points, or latrines, but presumably to the locating of food or available prey, was recorded as foraging. In response to auditory stimuli, hyaenas sometimes moved at considerable speeds. In four instances where these could be followed, speeds were 36,0km/h over 3,0km, 18,9km/h over 4,1km, 15,5km/h over 4,9km and 15,0km/h over 5,0km.

During 24-h observations (N=55), 3,7±2,2h were spent foraging in a total activity period of 6,6±2,7h. Most of the remaining time was spent on territory patrol (1,2h), feeding (0,9h) and social activities (0,6h). Foraging periods were usually longer for males than for females (4,5±2,1h cf. 3,0±2,1h; $t_{53}=2,10$; $P<0,05$), accounting for the differences in total activity patterns (7,2 cf. 6,0h in 24h). These differences were reflected by distances travelled (males: 23,6±10,4km; females 16,5±10,4km; Chapter 3). Consequently males located more food items per night than females did (2,9 cf. 1,2; Chapter 7) and encountered more other mammals per night than females did (6,9 cf. 5,4), although the mean distances travelled between mammal encounters were the same (3,1km) for both sexes.

During all observations, adult females seldom foraged alone (29% of time), except for the toothless one (Fa; 79%). A female cub spent only 6% and two CIMs 14% of their foraging time alone. In contrast ($U_{7;4}=1$; $P<0,05$), RNMs (66%) and a radio-collared PIM (89%) usually foraged alone, so that their interspecific encounters were less likely to be influenced by the activities of other classes.

Hyaenas were mostly nocturnal with only 11% of their total activities being by twilight or daylight (Fig.9). Activity pattern varied much from night to night, but no general patterns

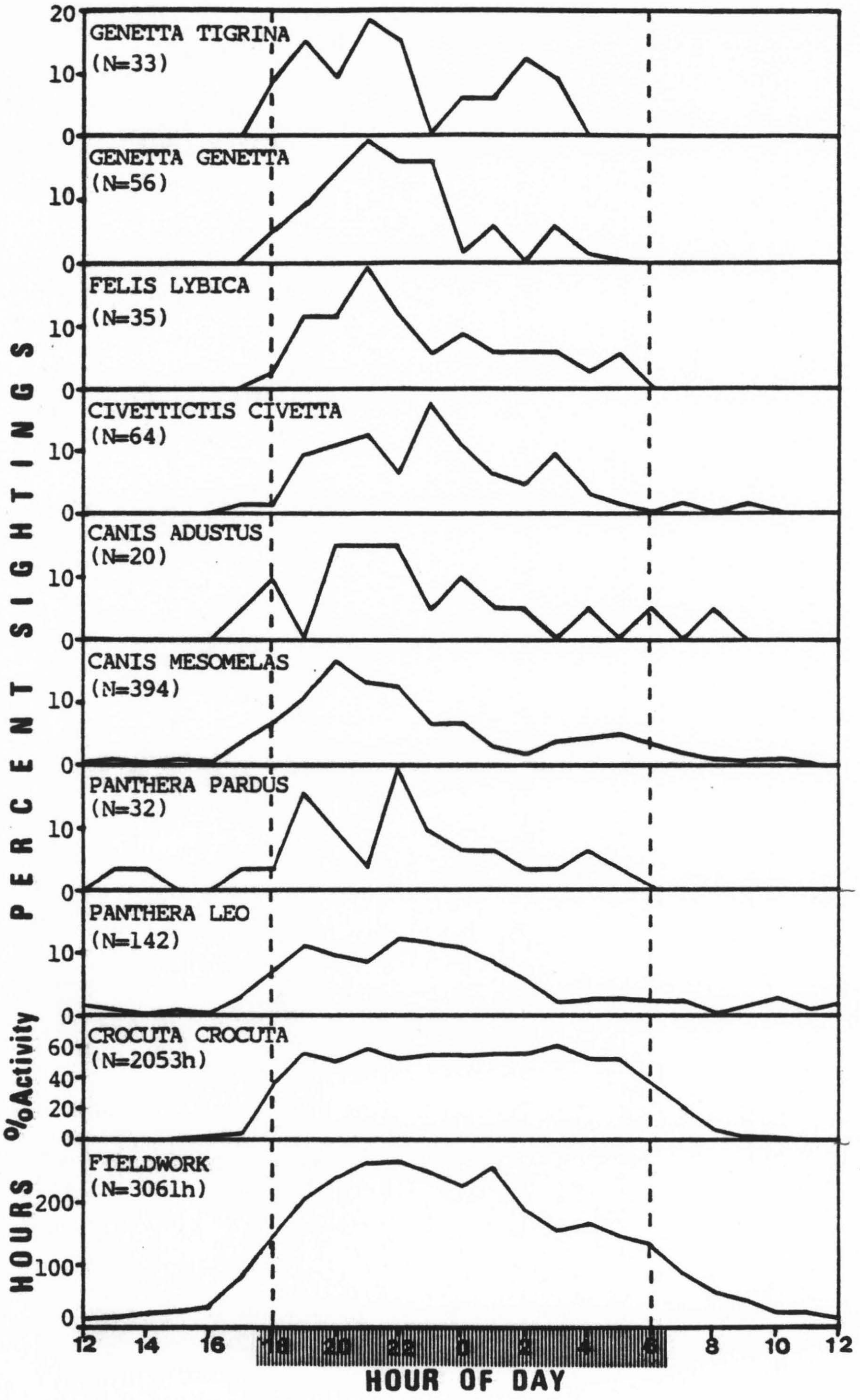

Figure 9: Time of day when carnivores were sighted, compared to the activity pattern of spotted hyaenas (% time observed) and the pattern of fieldwork in the study area.

of activity variation depending on time of night were evident. Climatic factors had similar effects on foraging as on other activities (Fig.10). These did not differ between social classes (maximum χ^2-values: light=2,47; wind=2,68; moisture=5,24; temperature=2,86; d.f.=3; P>0,1).

By day, foraging activity declined strongly with increasing light intensity (χ^2=18,80; d.f.=2; P<0,05) and increasing temperature (χ^2=16,82; d.f.=3; P<0,05). These effects were so strong that possible influences of wind or of moisture were obscured. At night, the presence or absence of moonlight and changes in temperature appeared to have no effect on foraging behaviour (χ^2<0,41; P>0,1; Fig.10).

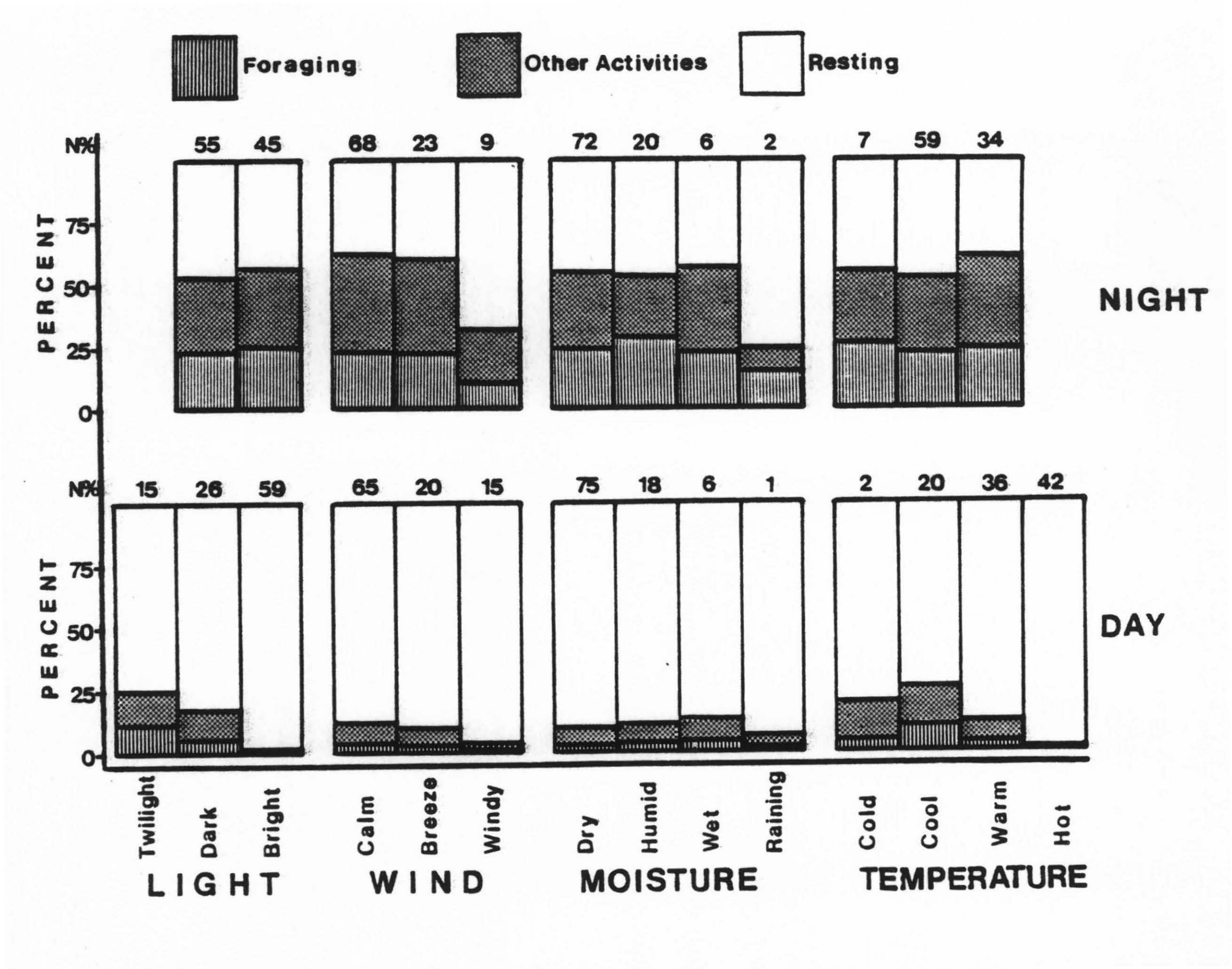

Figure 10: Diurnal and nocturnal activities of hyaenas in various climatic conditions.

In contrast, wind strength was important (χ^2=6,25; d.f.=2; P<0,05), as activity was much reduced during strong wind. Similarly, rain inhibited activity, although this was not significant for foraging behaviour (χ^2=3,41; d.f.=3; P>0,1), but was for all activities combined (χ^2=15,60; d.f.=3; P<0,05). These effects of strong wind and rain were important independant of each other. Likewise, no other climatic conditions presented different conclusions in combination than alone.

It is thus evident that foraging activity was limited by climatic conditions for less than 10% of the time at night, but that daytime conditions were seldom favoured for such activities.

Populations of Other Species

Eighteen ungulate species, numbering 1804 (844-2218), inhabited the 153km^2 Mavumbye area during the study period (Table 18). Abundance was similar in seasons 1, 2, 3 and 5 (r_s>0,67; P>0,05). The only major seasonal differences were evident in the second wet period, season 4 (correlation with season 3: r_s=0,27; P>0,1), when lower numbers of wildebeest *Connochaetes taurinus*, buffalo *Syncerus caffer*, zebra *Equus burchelli* and impala *Aepyceros melampus* were counted than in other seasons (Table 18). These trends were less pronounced in the first wet period, season 2, which followed the severe drought of 1982.

Several species, mainly buffalo, kudu *Tragelaphus strepsiceros*, warthog *Phacochoerus aethiopicus* and impala, appeared to be in poor body condition and suffered losses during the 1982 drought, but these could not be quantified by aerial census, as differences were within the unknown margins of census error (Table 18). Nevertheless, some 34-40% fewer buffalo, kudu, impala and warthogs were counted in the Central District during mid-1983 than during mid-1982, whereas differences were less pronounced for other ungulates (National Parks Board unpubl.). I found nine buffalo and two kudu carcasses that appeared to be the result of starvation along the Mavumbye and Gudzane rivers in December 1982 and January 1983, but fatalities among kudu, impala and warthog may easily have been overlooked. The warthog population in the study area declined considerably from an unknown size to two boars, three sows and a few subadult offspring after the drought.

Table 18: Abundance of ungulates in the Mavumbye area (±153km2) during five successive seasons. Mean body mass was calculated from age and sex ratios of each species. Census methods: 1=aerial; 2=line transect; 3=casual sightings.

	Mass	Seasonal Abundance						Census
Species	(kg)	1	2	3	4	5	Mean	Method
Elephant - *Loxodonta africana*	3000	31	20	89	11	5	31	1
White Rhino - *Ceratotherium simum*	1500	0	0	1	1	1	1	3
Hippo - *Hippopotamus amphibius*	1400	3	2	2	2	2	2	3
Giraffe - *Giraffa camelopardalis*	791	41	49	43	38	67	48	1
Eland - *Taurotragus oryx*	500	0	3	2	0	4	2	1&3
Buffalo - *Syncerus caffer*	447	571	142	522	4	131	274	1
Zebra - *Equus burchelli*	290	397	405	629	125	982	508	1
Roan - *Hippotragus equinus*	180	5	0	0	0	0	1	1
Waterbuck - *Kobus ellipsiprymnus*	154	31	14	43	48	42	36	1
Sable - *Hippotragus niger*	150	0	3	0	14	0	3	1
Wildebeest-*Connochaetes taurinus*	147	283	612	320	105	330	330	1
Gr.Kudu- *Tragelaphus strepsiceros*	132	102	40	110	83	171	101	1
Tsessebe - *Damaliscus lunatus*	108	3	0	6	4	0	3	1
Reedbuck - *Redunca arundinum*	70	6	6	6	6	6	6	3
Warthog- *Phacochoerus aethiopicus*	50	30	20	20	20	20	22	1&3
Impala - *Aepyceros melampus*	42	183	68	60	18	75	81	1
Common Duiker - *Sylvicapra grimmia*	18						22	2
Steenbok - *Raphicerus campestris*	11						343	2
							1804	

The relatively low density of impala in the Mavumbye area (0,53/km^2) distinguished this area from most other regions in the Central District of the Kruger National Park ($\bar{X}$=8,25/km^2 for total district 1982-1984; National Parks Board unpubl.). Zebra, steenbok *Raphicerus campestris*, wildebeest and buffalo were respectively the most abundant species in the study area (Table 18), and the highest mean biomass was recorded for zebra (963kg/km^2), buffalo (800kg/km^2), elephant *Loxodonta africana* (608kg/km^2) and wildebeest (317kg/km^2).

The Hyaenidae in the study area were represented by three species, namely *Crocuta crocuta*, which were most abundant (7,5-9,8/100km^2; Chapter 4), the brown hyaena *Hyaena brunnea*, of which one sighting was reported (Mills 1985b), and the aardwolf *Proteles cristatus*, of which at least one individual had a den in the Mavumbye area (Table 19).

Besides the Hyaenidae, I sighted 17 Carnivora species in the area (Table 19). Most of these (13) were crepuscular or nocturnal (Fig.9) and only 7,8% of all carnivore sightings occurred between 06h00 and 18h00. Black-backed jackals *Canis mesomelas* were the most abundant species (30,7/100km^2), with an estimated 47 individuals in 13 social units of adult pairs with or without subadult offspring or pups (Fig.11c). Other canids, side-striped jackals *Canis adustus*, and wild dogs *Lycaon pictus*, were rare. The Mavumbye area overlapped with home ranges of four lion prides (Fig.11b), which together numbered at least 25 adults and an average of 14 cubs and subadults. In a nearby area, the lion density was estimated at 16,2/100km^2 (Whyte pers.comm.). Other large Felidae were about seven leopards *Panthera pardus*, including three cubs, and at least two cheetahs *Acinonyx jubatus*.

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Table 19: Frequency of sighting per 100h nocturnal fieldwork (N=2866h) and estimated abundance of carnivores and some other mammals (>1kg) in the Mavumbye area (153km^2). Census methods were line transect (Fourier series estimator), casual sightings and individual recognition. Population estimates represent a minimum. Young individuals were recognized by size. Species where counted individuals were known to also frequent areas outside the Mavumbye area are indicated by '*'.

Species	SIGHTINGS		GROUP SIZE			ABUNDANCE	
	Total	/100h	Range	Mean		Total	Young
NOCTURNAL CARNIVORES							
Spotted Hyaena - *Crocuta crocuta*	1578	55,1	1-11	1,97	*	11	3
Lion - *Panthera leo*	142	5,0	1-18	3,65	*	39	14
Leopard - *Panthera pardus*	32	1,1	1- 2	1,13		7	4
Bl.Bkd.Jackal - *Canis mesomelas*	397	13,9	1- 9	1,66	*	47	21
Sd.Str.Jackal - *Canis adustus*	20	0,7	1- 3	1,25		3	-
Civet - *Civettictis civetta*	64	2,2	1- 2	1,05	)		1
Ratel - *Mellivora capensis*	11	0,4	1- 2	1,27	)		3
Wildcat - *Felis lybica*	35	1,2	1	1,00	)		1
Lrg.spt.Genet - *Genetta tigrina*	33	1,2	1- 2	1,03	)	57	1
Sm.spt.Genet - *Genetta genetta*	63	2,2	1- 2	1,02	)		4
Wh.tl.Mongoose-*Ichneumia albicauda*	9	0,3	1	1,00	)		-
Mell. mongoose-*Rhynchogale melleri*	1	0,0	1	1,00		1	-
Aardwolf - *Proteles cristatus*	6	0,2	1	1,00		1	-
Serval - *Felis serval*	2	0,1	1	1,00		1	-
TOTAL	830	29,0				167	
DIURNAL CARNIVORES							
Vultures - Accipitridae	48		1-300	32,10	*	?	
Crocodile - *Crocodilus niloticus*	5		1	1,00	*	1	
Cheetah - *Acinonyx jubatus*	5		1- 3	1,60	*	2	
Wild Dog - *Lycaon pictus*	3		6- 8	7,33	*	8	
Marabou - *Leptoptilos crumeniferus*	fairly common				*	?	
Slend.Mongoose-*Galerella sanguinea*	fairly common					?	
Dwarf Mongoose - *Helogale parvula*	fairly common					3	troops
Banded Mongoose - *Mungos mungo*	rare				*	1	pack
OTHER TERRESTIAL VERTEBRATES (>1kg)							
Ostrich - *Struthio camelus*	22		1- 4	2,00		4	
Aardvark - *Orycteropus afer*	9	0,3	1	1,00		3	-
Porcupine-*Hystrix africaeaustralis*	43	1,5	1- 3	1,30		17	5
Pangolin - *Manis temminckii*	1	0,0	1	1,00		1	-
Hare - *Lepus saxitilis*	common		1- 3	1,10		189	-
Baboon - *Papio ursinus*	fairly common				*	2	troops
Canerat - *Thryonomys swinderianus*	rare					1	colony

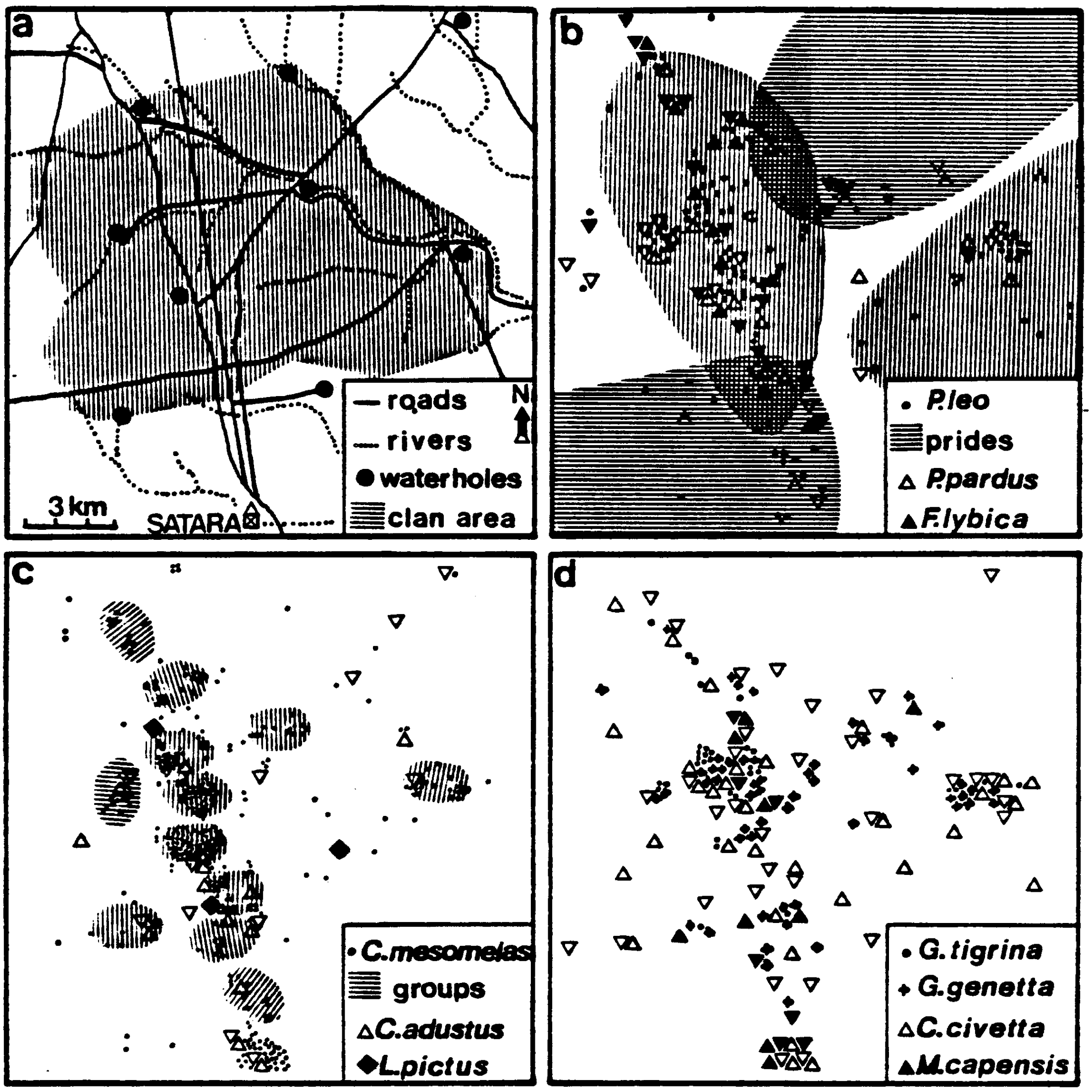


Figure 11: Locations of carnivore sightings in the Mavumbye area. (a) Map with *Crocuta* clan territory; (b) Felidae, showing approximate *Panthera leo* pride ranges; (c) Canidae, showing approximate group territories of *Canis mesomelas*; (d) Viverridae and Mustelidae.

Among the Viverridae, Mustelidae and small Felidae, which collectively were estimated to number 57 (37,2/100km^2; Table 19; untruncated line transect method), small-spotted genets *Genetta genetta* and civets *Civettictis civetta* appeared to be most numerous (Fig.11d).

Using fixed 10m transect width on open ground, the abundance of scrub hares *Lepus saxitilis* (189) and porcupines *Hystrix africaeaustralis* (17) were estimated. Other mammals besides small rodents were rare (Table 19).

Vultures, mainly white-backed vultures *Gyps africanus*, but also hooded vultures *Necrosyrtes monachus*, whiteheaded vultures *Trigonoceps occipitalis* and lappetfaced vultures *Torgos tracheliotus*, were sighted in the Mavumbye area on 48 occasions, totalling 1540 individuals. Because their local abundance fluctuated a great deal, abundance estimates in such a relatively small area were difficult to make, and were considered to be meaningless. However, it should be noted that these scavengers were periodically rare or absent, especially during culling operations conducted by National Parks Board in other areas, while at other times, considerable numbers of up to 300 ($\bar{X}$ =32,1±60,9) assembled at carcasses.

<u>Ungulate Interactions</u>

Mavumbye hyaenas were observed to encounter ungulates 416 times (Table 20). The rate at which ungulates were seen in the presence of hyaenas (22,3/100km; 4,0/24h) was much lower than on line transects (77,3/100km). However, encounters with the main species, giraffe *Giraffa camelopardalis*, buffalo, zebra, waterbuck *Kobus ellipsiprymnus*, wildebeest, kudu, impala and steenbok, were proportionally similar to transect sightings

Table 20: Encounters of spotted hyaenas with other species over 1862km compared to frequency of encounter on 612km of line transect censuses and estimates of mean abundance, and hyaena behaviour at interspecific interacions.

	ABUNDANCE		ENCOUNTERS				INTERACTIONS			
	Estimate*		Census*		Hyaena		Neutral	Evasive	Aggressive	Kill
	N	%	N	%	N	%	%	%	%	N
UNGULATES								distance < 50m		
Elephant	31	1,7	8	1,7	16	3,9	87,5	12,5	0,0	0
Hippo	2	0,1	0	0,0	4	1,0	50,0	8,3	41,7	1
Giraffe	48	2,7	15	3,2	24	5,8	34,4	26,9	38,7	(2)
Buffalo	274	15,2	10	2,1	15	3,6	42,3	11,5	46,2	2
Zebra	508	28,2	98	20,7	55	13,3	69,2	6,2	24,6	2
Waterbuck	36	2,0	17	3,6	11	2,7	63,6	0,0	36,4	0
Wildebeest	330	18,3	84	17,8	90	21,7	54,2	11,2	34,6	3
Kudu	101	5,6	41	8,7	58	14,0	48,5	1,5	50,0	4
Reedbuck	6	0,3	6	1,3	1	0,2	100,0	0,0	0,0	0
Warthog	22	1,2	0	0,0	9	2,2	25,0	41,7	33,3	2
Impala	81	4,5	10	2,1	38	9,2	64,4	0,0	35,6	4
Steenbok	343	19,0	178	37,6	94	22,7	65,4	1,0	33,6	6
Duiker	22	1,2	6	1,3	1	0,2	0,0	0,0	100,0	0
CARNIVORA								distance < 30m		
Lion	39	23,4	11	13,1	78	35,6	34,4	42,2	23,4	0
Leopard	7	4,2	3	3,6	14	6,4	52,2	4,4	43,5	0
Jackal	50	29,9	41	48,8	104	47,5	71,9	2,3	25,8	0
Other	60	35,9	29	34,5	23	10,5	54,2	0,0	45,8	2
Spt.Hyaena	11	6,6	8							
OTHER								distance < 20m		
Man ++	-		-		7	-	28,6	71,4	0,0	0
Hare	189		72	85,7	21	36,8	52,2	0,0	47,8	0
Mouse	-		-	-	21	-	23,8	0,0	76,2	13
Other Mammal	21		8	9,5	12	21,4	50,0	0,0	50,0	1
Vultures	?		2	2,4	20	35,1	59,3	7,4	33,3	0
Ostrich	4		2	2,4	2	3,5	50,0	0,0	50,0	0
Small Bird	-		-	-	60	-	45,3	0,0	54,7	8
Crocodile	1		0	0,0	2	3,5	50,0	50,0	0,0	0
Other Reptile	-		-	-	3	-	0,0	66,7	33,3	1
Other Vert.	-		-	-	22	-	0,0	0,0	100,0	22
Arthropod	-		-	-	38	-	33,3	8,3	58,3	22
UNGULATES	1804		473	73,8	416	60,1	54,3	9,5	36,2	24
CARNIVORA	167		84	13,7	219	31,6	53,1	19,1	27,7	2
OTHER	-		84	13,7	57	8,2	40,5	6,3	53,2	67
GRAND TOTAL	-		641		692		553	125	394	93

* Percentages are calculated only for species that were censused.
160 close encounters with other organisms are excluded from totals.
++ Man, other than observer (e.g.tourist on road).

(r=0,85; P<0,01), but were not similar to their proportions in the population (r=0,56; P>0,1). The main differences were more than expected encounters with impala and kudu, and less with zebra and steenbok (Table 20; Fig.14).

Hyaena foraging behaviour was often suggestive of spoor tracking that sometimes took them to kudu resting concealed in dense vegetation. In contrast, hyaenas seldom reacted to audible zebra activity closeby. Such differences in behaviour were not quantified, and were less noticeable with other species, but may explain why some species were encountered at greater or lesser frequencies than expected.

Flight distance from hyaenas of most ungulates appeared to be short (<50m) in cases where the observer's influence was not evident. Hunting behaviour, characterized by directed approach, followed by chasing in excess of 30m, occurred in 34% of close approaches by hyaenas to ungulates smaller than buffalo (N=422; sometimes repeated several times at an encounter). This was seen more frequently (50%) in kudu interactions (N=68), and only with cows and calves, than with other species (<37%), especially zebra (24.6%).

At encounters with these ungulates, hyaena group size was not different from that during all 395h of foraging observed (χ^2=0,8; d.f.=3; P>0,1; Table 21). Foraging hyaenas spent 61% of their time alone and most (53%) aggressive interactions towards ungulates smaller than buffalo involved single hyaenas.

Table 21: Hyaena group size while foraging, at ungulate encounters, and when chasing ungulates for short or long distances.

ACTIVITY	GROUP SIZE				N	MEAN
	1	2	3	>3		
Foraging	60,9	18,7	10,5	10,1	395h	1,81
Ungulate encounters	60,0	21,6	10,4	8,1	416	1,67
Chase < 100m	54,9	23,9	15,5	5,6	71	1,72
Chase > 100m	72,2	13,9	6,9	6,9	72	1,48

Readiness to chase steenbok upon an encounter was higher by a single hyaena than by two or more, but the trends were opposite for bigger species, especially for impala and kudu (Fig.12). This difference was probably related to prey size. When a dominant female in a group caught a steenbok, she consumed it alone without interference from others, but when a low-ranking male killed one, it was appropriated by a dominant hyaena.

In half of the observed chases, these were terminated in 100m or less, but some chases (9,4%) were in excess of 1km (Fig.13). Kudu were the only species for which most chases (76,9%) exceeded 100m in distance. Single hyaenas appeared to be more persistent during pursuit so that mean hyaena group size was smaller (1,48) for chases longer than 100m than for shorter chases (1,72; X^2=8,5; d.f.=3; P<0,05; Table 21). Maximum chase distances that were recorded without losing radio contact with the hyaenas, were 1,1km for impala, 4,0km for steenbok, 5,0km for kudu and 5,1km for wildebeest, with speeds ranging from 14,0-32,0km/h.

Hunting success was difficult to determine, as visual and radio contact was often lost. Of 143 chases of ungulates smaller than buffalo, seven (4,9%) definately terminated in kills after 30m-5,1km ($\bar{X}$=1,4±2,1km), but three kills were made without a chase and the chase distance was unknown for another eight such ungulate kills. Most of the latter were found by following focal animals that were attracted to carcasses. Hunting success was highest for steenbok, of which three (9,4%) were caught in 32 chases, and another three without chasing.

Aggressive behaviour towards hyaenas was sometimes shown by zebra stallions (N=4), wildebeest bulls (N=12) and warthogs

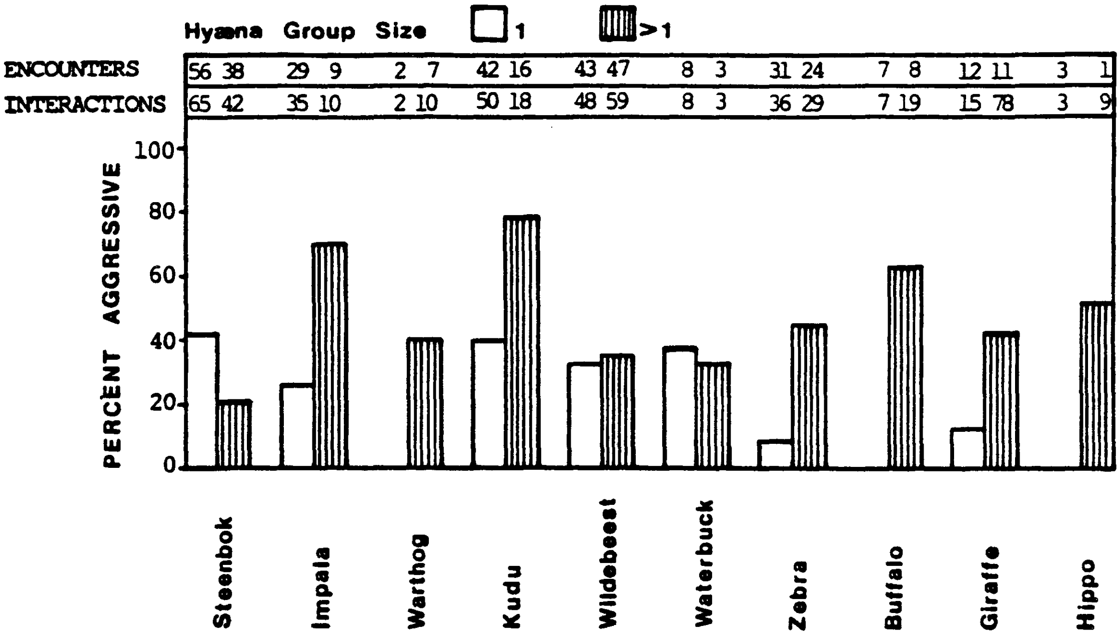


Figure 12: Aggressive interactions with ungulates by one hyaena compared to groups of two or more hyaenas.

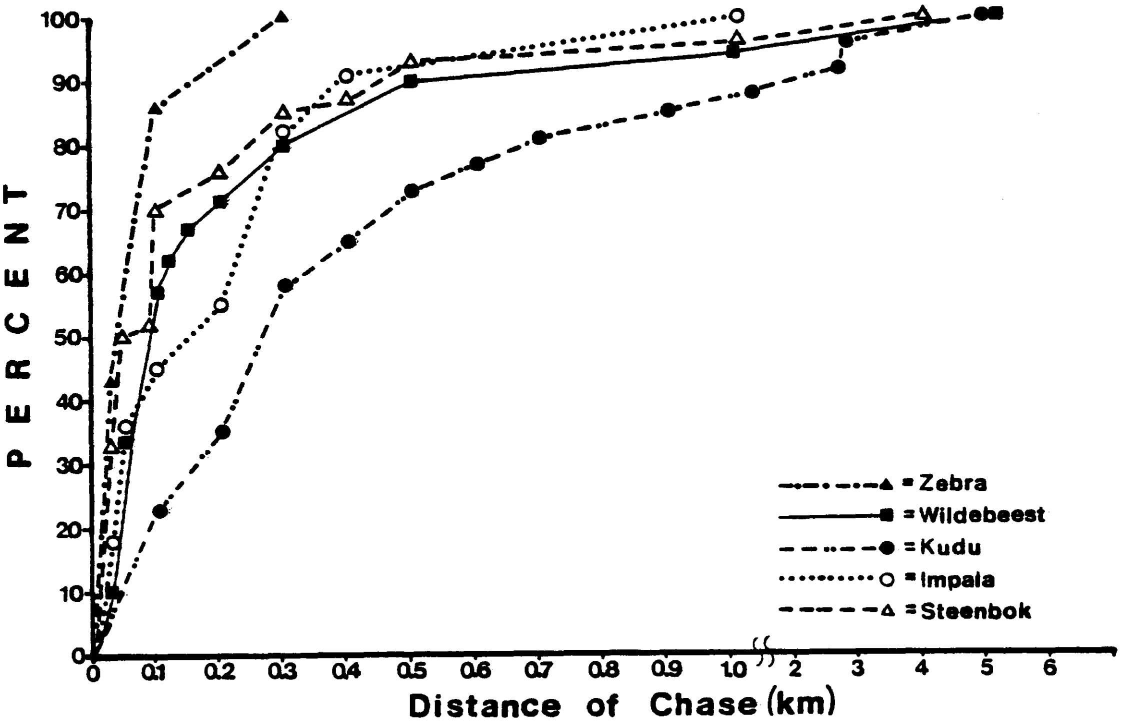


Figure 13: Distances (>30m) that steenbok, impala, kudu, wildebeest and zebra were chased by hyaenas.

(N=5). A warthog sow once chased a hyaena for 1,5km by day.

Buffalo and larger ungulates were usually (92%) only attacked or harrassed by groups of two or more hyaenas in repeated sequences of rapid approach, bite and retreat. This was seen six times with buffalo, giraffe and hippopotamus *Hippopotamus amphibius*. Two injured buffalo reacted by retreating backwards into thorny vegetation, but hyaenas succeeded in killing one by persistent repetition of harrassment over a week. When three hyaenas harrassed a hippopotamus from the rear, it slipped and dislocated its shoulder, enabling the hyaenas to kill it. On three occasions, giraffe calves were harrassed. Once, two hyaenas enticed a female giraffe to cause the death of her newborn calf, when she kicked it over while trying to strike at the hyaenas. Indications were that another giraffe calf died under similar circumstances.

Although hyaenas of different social classes encountered ungulate species at similar frequencies ($r>0,83$; $P<0,01$), there were some differences, notably with kudu, impala and wildebeest (Fig.14). The latter two species were encountered more often by hyaena females and central immigrant males (CIMs) than by resident natal males (RNMs), which had more encounters with kudu than the other classes had. The probability of attacking ungulates upon encounters was of the same order between females and CIMs ($r=0,55$; $P<0,1$), but dissimilar with RNMs ($r<0,15$; $P>0,1$). Too few observations were made of peripheral immigrant males (PIMs) to enable valid comparison. In general, RNMs appeared to be more ready to attack steenbok, impala, kudu, wildebeest and zebra than other classes were (Fig.14), and accounted for most ungulate chases observed for single hyaenas.

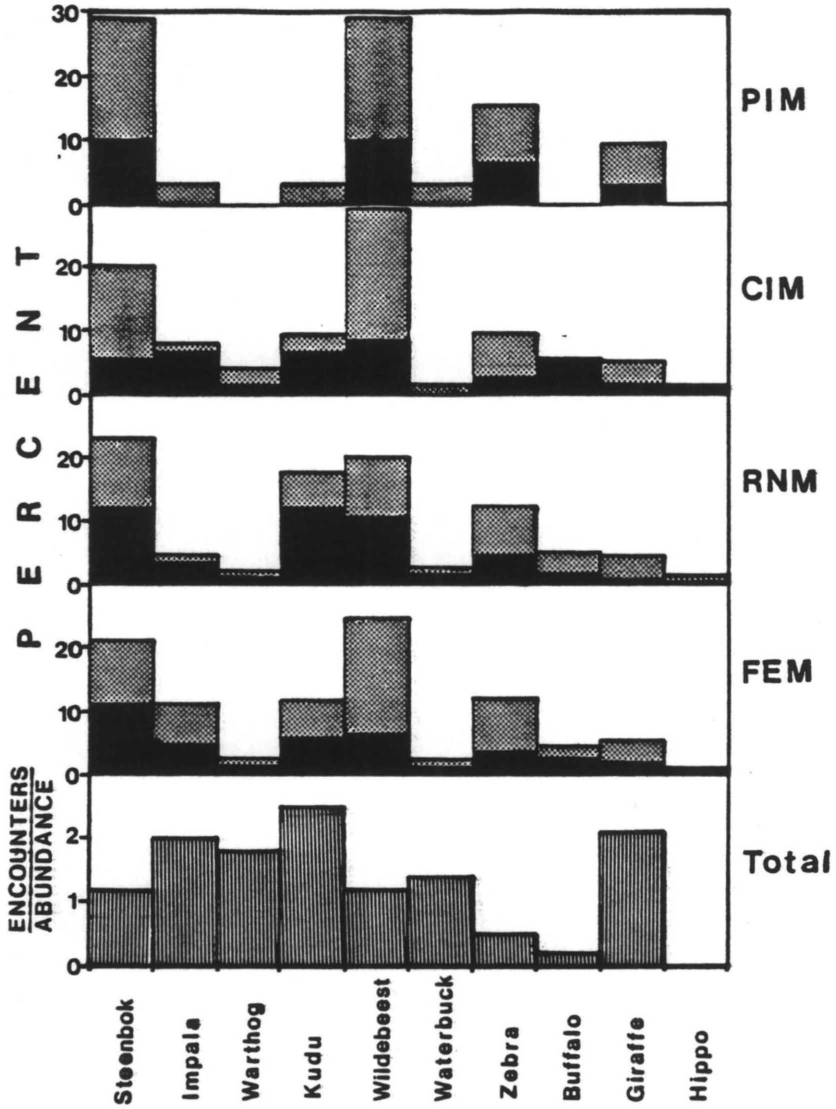


Figure 14: Encounters (dotted shading) and aggressive interactions (black shading) of different hyaena social classes with ungulate species compared to the total rate of encounters relative to the abundance of each ungulate species (line shading).

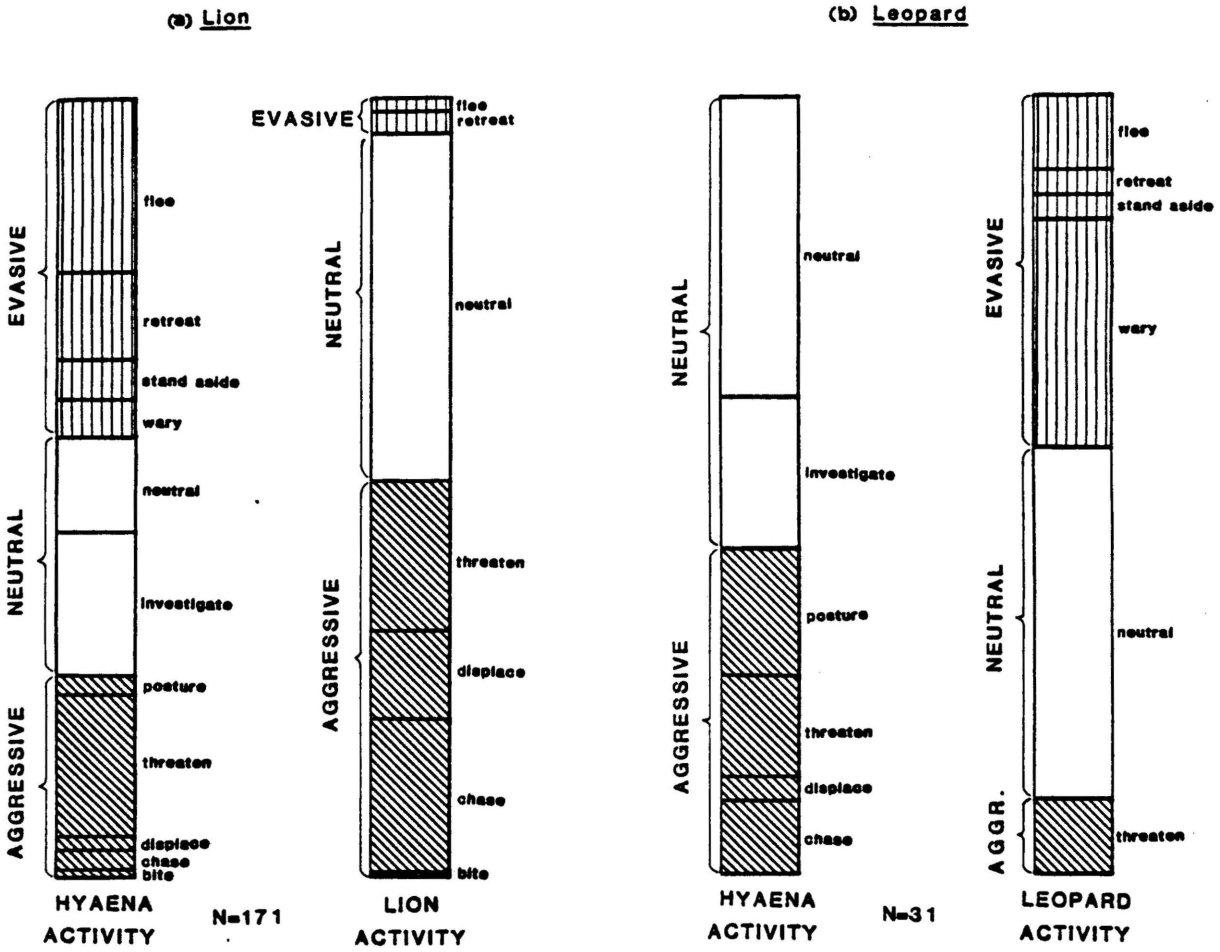
Carnivore Interactions

Hyaenas did not encounter carnivores with the relative frequency to be expected for chance encounters (Table 20; χ^2=57,6; P<0,001). Lions were encountered more than twice as frequently than expected and leopards slightly more often, with 71% of encounters with lions and 85% with leopards being in the vicinity of a carcass. In all such cases, the common interest appeared to be the carcass, except once, when a leopard caught a black-backed jackal alongside a feeding hyaena. In contrast, encounters away from food were less frequent for lions (1,0/100km) and for leopards (0,1/100km) than expected (1,5/100km and 0,5/100km respectively). Observations indicated that hyaenas avoided lions if perceived before sighting (e.g. hearing roars) and that leopards avoided hyaenas. Twice, hyaenas found leopards by investigating alarm-calling black-backed jackals.

In 51% of 171 interactions between lions and hyaenas (Fig.15a), the former were aggressive, approaching threateningly, displacing hyaenas from food, chasing, biting or pawing them. Although hyaenas showed evasive tendencies in 42% of the interactions, they were sometimes aggressive (26%), displacing, chasing or biting the lions on nine instances.

Readiness to attack one to four lions was directly proportional to hyaena group size (Fig.16). Packs of one to three hyaenas showed aggression on 7,4% of close encounters, packs of four to six in 16,2%, and packs larger than six in 42,5% of encounters. Hyaena group size appeared to be unimportant in interactions with smaller species.

The observed behaviour during mornings of groups of 4,8±3,2 hyaenas always dispersing in various directions away from fleshy



(a) Lion

(b) Leopard

Figure 15: Hyaena interactions with (a) lions and (b) leopards.

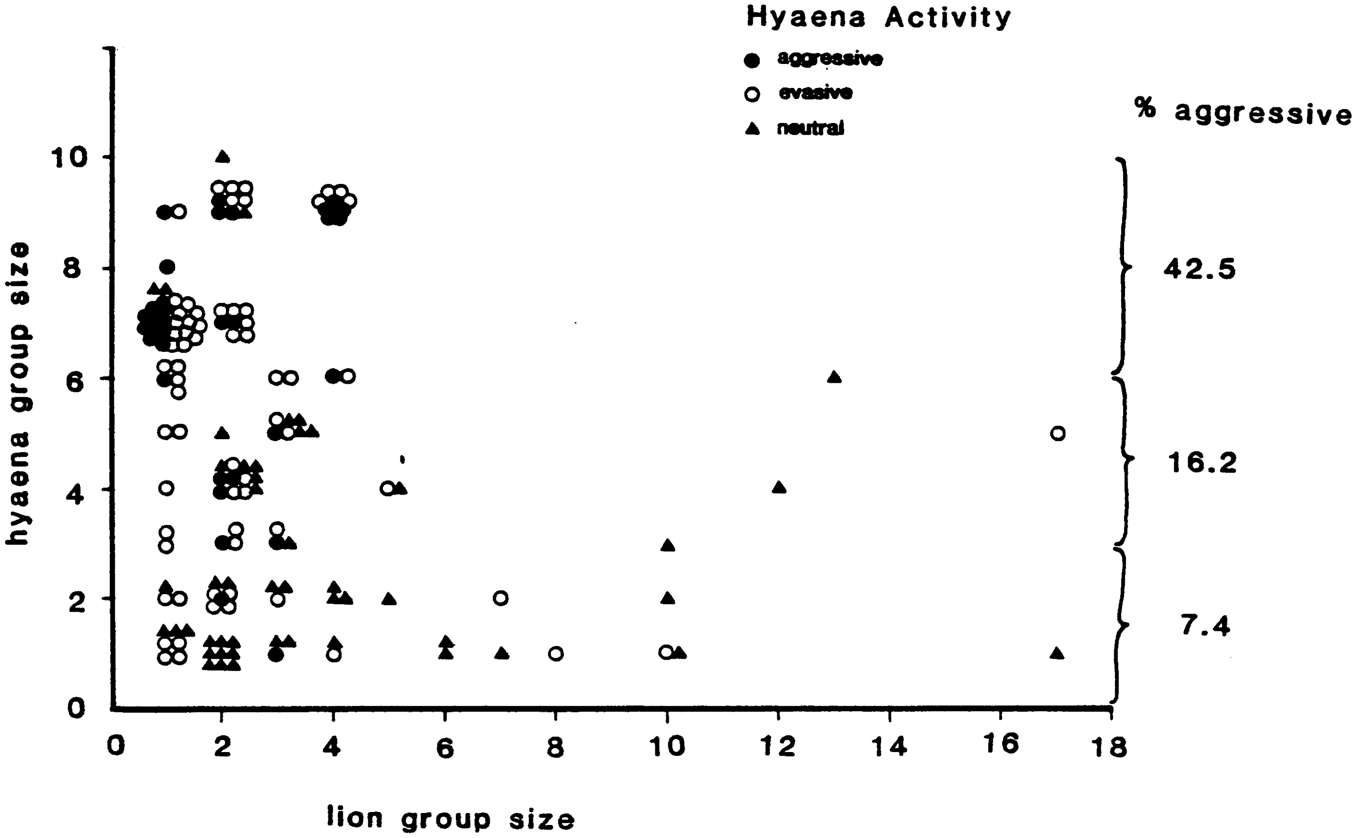


Figure 16: Behaviour of different group sizes of hyaenas towards lion groups.

carcass remains at which they had been feeding (N=21), to spend the day resting in lairs at least 2km away, could be related to the vulnerability of sleeping hyaenas to lions. Hyaenas sleep soundly by day as witnessed by a number of close approaches on foot without waking them.

Hyaenas never showed evasive tendencies in interactions with leopards (N=23), but usually approached closely (Fig.15b). Thrice, hyaenas showed aggressive behaviour (e.g.vocalizations) towards a leopard with a carcass in a tree, and four times chased one away from a carcass on the ground, but once, a single hyaena tolerated a leopard feeding alongside it for an hour on a hyaena-killed zebra.

Of all carnivores, hyaenas encountered black-backed jackals most frequently (5,6/100km), probably due to the jackals' behaviour of following, investigating hyaena activities, or associating with them at food. Hyaenas usually ignored jackals (N=92), but responded threateningly when harrassed by them (N=33). Observations indicated that jackals may have benefitted from the hyaenas' greater ability to dismantle a carcass, as jackals often stood close alongside a feeding hyaena and snatched up morsels dropped by the hyaena, but stopped feeding when the hyaena did so.

Wild dogs and cheetahs were rare in the area and no interactions with hyaenas were seen. During censuses, Viverridae, Mustelidae and small Felidae were sighted at a much higher frequency than when following hyaenas, probably due to differences in the searching behaviour by the observer. Hyaena behaviour towards these carnivores indicated that they may sometimes have been regarded as prey (46% of 24 interactions).

The only carnivores observed to be killed by hyaenas were two African civets *Civettictis civetta*. When surrounded and threatened by five hyaenas, a honey badger *Mellivora capensis* adopted a defensive threat posture and growled, which deterred the attackers. Other small Carnivora fled when threatened, usually up a tree. Four times, African civets, which are not known to climb trees, escaped attacking hyaenas by ascending straight treetrunks, using lateral leg pressure.

When hyaenas were feeding during early morning hours, they dominated vultures, that also began to feed (N=22), but always abandoned carcasses as the day progressed. No instances of hyaenas using vultures as indicators of the whereabouts of carcasses were observed.

Interactions with Other Species

Interactions with most other vertebrates indicated that they were regarded as potential prey (Table 20). Chases of hares (N=10) were always short, abrupt and unsuccessful. Small rodents were usually ignored (not recorded), but during one night, a hyaena, searched, flushed up and caught eight mice, more than half the total of rodents observed to be killed (Table 20). After six lengthy interactions, porcupines escaped, but a pangolin *Manis temminckii*, that curled itself up, was bitten through the scales until it could be killed an hour later. A tortoise *Testudo pardalis*, was killed by cracking its shell central dorsally, similar to the damage seen on two other tortoise shells found.

Reactions to man other than the observer were usually evasive. On five of seven occasions when other cars approached, hyaenas moved some 50m off the road before resuming their activities. After habituation in the first two months, such behaviour was not shown towards the observer. Although roads were frequently used at night (Chapter 6), active hyaenas usually avoided them after the onset of tourist activities at dawn.

DISCUSSION

The unimodal activity pattern of spotted hyaenas in the Kruger National Park, which, on average, spanned all dark hours, without pronounced activity peaks at particular hours, differed substantially from the bigeminus or two-peak pattern observed by Kruuk (1972) for spotted hyaenas in East Africa. Furthermore, activities of other carnivores in the Mavumbye area were also bigeminus, as appears to be characteristic for many nocturnal species (Aschoff 1966). The absence of such a pattern has been reported for brown hyaenas, which forage for scavenged food (Mills 1978a), or which utilize predictable food resources (Goss 1986). The highly opportunistic foraging behaviour of Mavumbye hyaenas, with which irregularly available carcasses were scavenged or occasional kills of a wide variety of species were made (see Table 20), required more temporal flexibility and longer activity periods than the more regular hunting with higher success, concentrating on relatively few species, observed for spotted hyaenas in East Africa. This prompts the conclusion that hyaena activity patterns are environmentally induced.

Mavumbye hyaenas were predominantly nocturnal. Although both temperature and light appeared to influence this pattern, their interdependance confounds interpretation. As hyaenas were seldom active later than two hours after sunrise, irrespective of weather or season, but could select different resting sites, such as shady lairs, bare patches of ground, or water pools, depending on climate, it is concluded that light intensity was the main factor inhibiting activity, but that an affect of this was avoidance of high temperatures. Exceptions were noted when hyaenas were disturbed by day, particularly by human activities.

When foraging, Mavumbye hyaenas appeared to rely mostly on olfactory and auditory senses to locate potential food sources, or to sense the proximity of lions. A reduction of the distance that they could smell and hear during wind and rain, explains their decline in activity during such times. Once potential food was located, the hyaenas relied on their visual senses, running stamina and endurance in prolonged interspecific interactions to procure it, unless it could readily be scavenged.

In a study of lion foraging behaviour, Van Orsdol (1984) examined how they responded to numerous environmental factors to maximize their hunting success. He found that lion activity was influenced by light levels, not only between day and night, but also between moonlit and dark nights. Apart from opportunistic kills made at any time, lions foraged mostly when and where those prey species, which offered the highest returns for effort, were most vulnerable. Similarly, it was recognized in the present study that some aspects of hyaena foraging behaviour could provide optimal returns for effort. These include:

a) Hyaenas foraged at night, when ungulates were more likely to make mistakes when harrassed or tested (e.g. separate from herd, stumble over obstacles, or accidentally strike at own calf).

b) Chases or harrassment of ungulates and interactions with lions at carcasses were short and were terminated when it became apparent that they would not be profitable.

c) Foraging group sizes were small (1,8; 61% solitary) and comparable to records for nearby areas (Bearder 1977; Mills 1985b). This is expected in this area where the hyaenas kill less regularly than in East Africa, the Kalahari and the Namib deserts (Kruuk 1972; Mills 1984a; Tilson & Henschel 1986). Scavenged food is not located more easily by a group than by solitary individuals (Mills 1978a; 1981) and opportunistic killing, as observed with Mavumbye hyaenas, relies less on coordinated group activities than on the ability to identify opportunities. This is maximized by individuals spreading out over a wide area. Furthermore, by using the long-distance vocalizations, hyaenas could communicate over the entire territory on windless nights, clan members were usually within earshot, and could rapidly converge at a carcass site. The inter-regional comparison of hyaena group size supports the hypothesis that the size of food items, rather than hunting efficiency or interspecific competition *per se*, may determine optimal group size, as has been described for lions (Caraco & Wolf 1975).

d) Judging from distances and time spent travelling, and behaviour at interspecific encounters, hyaena males spent more energy when foraging and hunting than females did, although, as a consequence of differences in feeding priority (Chapter 3), females could benefit more from carcasses at which several hyaenas were present. This ensures optimal use of resources.

e) Although it is suspected that hyaenas might increase their hunting success of small (<15kg) and agile species, such as steenbok, by coordinated hunting in a group, they were more reluctant to attempt catching such prey when they were together with other hyaenas than when they were alone. It would not benefit a subordinate to participate in such a hunt, because prey of such size, which presents a meal for only one hyaena, would be appropriated by the dominant individual in a group. Such inhibition of hunting behaviour was not seen in interactions with larger species, where the probability of hunting increased with group size.

f) Encounters and interactions with ungulates indicated that hyaenas did not forage randomly, but demonstrated a preference for more vulnerable prey species, as is described below.

Severe drought conditions prevailed throughout the Kruger National Park at the end of 1982. Besides my casual observations of a decline in body condition of buffalo, kudu, impala and warthog, with some observed fatalities among buffalo and kudu, National Parks Board staff conducted a number of surveys that indicated the nature of the short-term and long-term effects of the drought. A search for drought victims along watercourses in the Southern District of the park conducted by rangers between 8-19 November 1982 (National Parks Board unpubl.) indicated that heavy mortalities occurred among impala (1083 carcasses) and some among kudu (18), warthog (21) and buffalo (7). Casual observations suggested that buffalo mortalities were probably an order of magnitude higher in the Central District. In contrast, wildebeest, zebra and giraffe appeared to be unaffected by the drought. These data were reflected by the results of aerial censuses.

In this area, impala and warthog have short peak birth seasons in November and December and kudu in January and February (Fairall 1968). This period coincided with the extreme end of the drought during 1982/1983. This would explain why Mason (1984; 1985) found that kudu, impala and warthog recruitment had been considerably less in the marula-knobthorn landscape during the 1982/1983 breeding season than during the 1983/1984 season (juveniles per 100 mature females during August 1983 cf. August 1984 for kudu: 26,3 cf. 58,2; impala: 7,9 cf. 36,3; warthog: 29,2 cf. 188,5). These results were consistent with those from the whole Kruger National Park, where recruitment (juveniles:100 ♀♀) was 2,0-3,3 times higher for impala, 1,6-3,2 times higher for kudu and 5,5-6,5 times higher for warthog during 1984 and 1985 than during 1982 and 1983 (Mason 1983; 1984; 1985; pers.comm.).

In a study of kudu in the Kruger National Park, Owen-Smith (1986; pers.comm.) found that only 10% of calves survived the 1982/1983 drought, whereas survival rate was 41-74% in the subsequent year with higher rainfall. He noted that, although adult females had been in bad physical condition during the drought, with an increase in their mortality rate from 10% to 18% per annum, the more telling effect of the drought may have been its effect on juvenile condition.

Malnutrition during early life could result in retarded development, as Peterson (1977) had found with Isle Royale moose *Alces alces*, which were subsequently selected by hunting wolves over a number of years. This may explain the present observations of spotted hyaenas having more than expected encounters with kudu cows and calves and a high probability of making hunting attempts, which were more persistent than with other ungulate species. Furthermore, hyaenas consumed kudu carcasses more frequently than expected (Chapter 7). Although impala and warthog were relatively scarce in the study area, similar relationships were evident (see Chapter 7). These conditions prevailed throughout the two-year study period, suggesting that hyaenas

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were responding to vulnerable sectors of the prey population.

Carcasses were the common factor that influenced most interactions between hyaenas and other large carnivores, with dominance depending on size and degree of sociality, in agreement with previous reports by Pienaar (1969), Schaller (1972), Kruuk (1972), Bearder (1975), Richardson (1980) and Mills (1984b). The present study confirms previous findings that the relative abundance of lions and hyaenas is fundamental in determining the relationship of these close competitors (see also Smuts 1978b). This species, which was the major provider of scavenged food to Mavumbye hyaenas (Chapter 7), but also the most important mortality agent, may be one of the important ecological factors favouring large hyaena group size (see Chapter 4).

In view of the competitive interspecific interactions seen over large carcasses at night, the observations of hyaenas abandoning these to vultures at dawn are somewhat puzzling, especially as they are capable of keeping vultures off a kill for some time. However, prolonged active carcass defence would be difficult to achieve, because it would be energetically expensive against many vultures and would require continuous vigilance due to the extremely rapid feeding rate of vultures, especially of white-backed vultures (Richardson 1980; Mundy 1982). Furthermore, Mavumbye hyaenas abandoned carcasses by day whether or not vultures were present, probably due to their vulnerability to lions in this position. The only effective way to counter such competition by vultures would be to cache food items. On the 18 occasions that Mavumbye hyaenas cached food (Skinner *et al* 1986), this involved pieces with little meat, which were probably cached to reduce intraspecific rather than interspecific competition.

It is concluded that, although opportunistic, spotted hyaena foraging behaviour and interspecific interactions appears to discriminate between more and less profitable food sources in terms of their availability and defensibility. Similar findings have been made in numerous studies (reviewed by Krebs, Houston & Charnov 1981; Werner & Mittelbach 1981; Pyke 1984), which followed MacArthur & Pianka's (1966) and Emlen's (1966) proposal that animals tend to forage in an optimal fashion. Although the requirements of optimality theory for the observer to independantly guage food availability and profitability could not be fulfilled in the present study, the observed response of hyaenas to potential resources supports this hypothesis.

6: SPACE UTILIZATION

INTRODUCTION

An individual's relationship to space presents a reflection of its relationship to resources. Uneven use of land by an individual and the relative way conspecifics use it, can give an indication of the importance, distribution, richness and accessibility of food. Conversely, by measuring distribution and abundance of different food types, one can obtain an indication of an animal's ability to influence accessibility.

An individual's range must satisfy all of its energetic needs (Gittleman & Harvey 1982). Depending on the distribution of resources, territories may be established in fixed areas at a given time, where resident individuals or groups dominate and limit access to non-resident conspecifics (**Eibl-Eibesfeldt** 1970; Owen-Smith 1977; Kaufmann 1983). For carnivores, food distribution has often been identified as being important in determining territory size, while its richness may influence group size (Kruuk 1978; Mills 1981; Kruuk & Parish 1982; Macdonald 1983). In a comparison between various study areas, Tilson & Henschel (1986) found that this appears to be applicable to spotted hyaenas.

In the foregoing analysis of spotted hyaena social organization (Chapter 3) it was evident that hyaenas in the Kruger National Park are highly territorial, but that differences in relationships between clan members are reflected in differences in their relationships with other clans. In the present chapter, I explore the behavioural mechanisms and factors that relate to the cost and benefits of territory maintenance and I examine how events that could be identified in a changing social environment in the Mavumbye clan, could reveal something about processes that underly the spatial organization of the local poulation of hyaenas.

Furthermore, following up the suggestion put forward in Chapter 5, that hyaena foraging behaviour discriminated between more and less profitable food sources, this is now investigated relative to spatial variation of food abundance and other ecological factors, such as habitat condition, that may affect food accessibility at a locality.

METHODS

During continuous observations of hyaenas, records were kept of activity and major changes in direction (to nearest 45^{0}). Distance (0,1km) travelled in each $1km^{2}$ grid square was calculated by assuming straight-line movements between successive data entries, computing the length of straight line segments moved in each grid, and multiplying by the ratio (>1) of distance that the observer's vehicle travelled in covering the mapped distance between fixes. The proportion of distance travelled in the grid to total distance between fixes was used to calculate the time (min) spent in each grid, assuming equal-velocity movements between data entries.

Total area utilized was determined by the minimum area method (Stickel 1954), which gave a unique convex polygon, linking the outlying points of observation. The 95% and 50% probability areas were calculated from the duration values, by sequentially subtracting grids of least utilization until 5% or 50% of the observations were omitted. These grids were treated as marked cells (Voigt & Tinline 1980) to calculate home range (95%) and core area (50%) respectively. Observation data could not be subjected to the same statistical treatments as independant resightings (Ford & Krumme 1979; Dixon & Chapman 1980; Macdonald, Ball & Hough 1980; Bekoff & Mech 1984), but are considered to be more accurate, especially for determining home range use (Rongstad & Tester 1969; Laundrè & Keller 1981).

Degree of overlap of 95% and 50% utilization areas between any two hyaenas was determined using Cole's (1949) coefficient for measuring associations, following Morgan, Simpson, Hanby & Hall-Craggs (1976):

$$\text{Similarity} = \frac{(\text{grid squares where both hyaenas were recorded})^2}{(\text{grids used by one}) \times (\text{grids used by other})}$$

The boundaries of the Mavumbye clan's territory were defined by the locations of outside latrines at which members were frequently observed scent-marking. These were confirmed as boundary zones in the outcome of 14 observed interclan interactions (Fig.18), during which the rightful land owners were identified (except in the west, where no encounters were seen). The same criteria, regular scent-marking and outcome of interclan encounters, could be used to recognize possible changes in territory boundaries.

All instances of defecation, whether on or off a latrine, could be regarded as scent-marking. For the purposes of this study, a latrine is defined as a place, smaller than $200m^2$, to which hyaenas periodically return to scent-mark by pasting, scratching or defecating. A minimum of 8 visible stools (Bearder & Randall 1978) was not necessarily present, even if a latrine was regularly visited, but this criterion was used to initially identify a latrine at first discovery.

A species-by-species comparison of aerial census data from June 1984 with three complete ground censuses (3x17x3km) conducted in the same week, indicated that distribution data for buffalo, kudu, wildebeest and zebra did not compare well between the two methods (Spearman's $r_s<0,27$; $P>0,2$), and had low similarity for impala ($r_s=0,54$; $P<0,05$). For this reason, only aerial census abundance and distribution data were used for medium to large ungulates in the present study.

A hyaena's environment could be represented by numerous variables. In an attempt to describe their variation within the Mavumbye area, these factors were measured in 19 grid squares of $9km^2$. It was assumed that Mavumbye clan members had freedom of movement within their territory, so that r^2 analysis should help to identify those factors which could influence hyaena space use within this area. The dependance of time and distance of all hyaena activities, time spent foraging and patrolling, and frequency of scent-marking and whooping in each season, were tested for the following variables: a) Physical factors: distances from lairs, grass and bush visibility indices; b) Territorial factors: distances from territory boundary or centre and from latrines; c) Resource distribution: distance from water or carcasses, space use of lions and jackals, total biomass of small to large ungulates (10-1000kg), abundance of buffalo, zebra, wildebeest, kudu, impala and steenbok determined by aerial censuses, line transects and frequency of encounters by hyaenas; d) Social influence: space use of other clan members, distance from social clubs and dens.

All factors were tested separately for each season and for all seasons together (by sequential stringing). Significance and negative or positive signs of r^2 values was tested by Pearson's correlation ($P<0,05$) and relevance interpreted intuitively.

RESULTS

Space Utilization

Most of the clan members' foraging, feeding, scent-marking and resting activities were confined to a relatively small area (Fig.17). The 9-16km^2 and 51-104km^2 areas in which each Mavumbye hyaena spent 50% (core area) and 95% (home range) of its time respectively, were smaller than and nearly completely within the the clan's territory (130km^2; Fig.18). The location of these areas for each individual for which sufficient data was available (>195h observations), were interpreted visually (Fig.19) and analysed with Cole's coefficent (Fig.20).

This indicated that the home ranges of all individuals were similar (>65%), but that it was least similar (<70%) for the RNM (Rf) which left the territory most frequently as prospective immigrant or the female (Fa) that scavenged at a refuse dump in a neighbouring territory (Fig.20a). The relative locations of core areas reflected patterns of social association (Chapter 3; Fig.3), namely: (a) Greatest similarity (>60%) between mother (Fm) and offspring (Jp), between another female (Fl) and a CIM (Cb), and between all of these; (b) Low similarity (<45%) of RNMs and of an injured female (Fa) towards other hyaenas. Core areas of PIMs may have differed (Fig.21f), but observations were too short (total=121,5h) and could seldom be made independantly for this to be determined with certainty.

Total areas (Fig.19) covered by RNMs (178,0±47,3km^2) were much larger than those covered by females (129,9±17,0km^2) and a CIM (118,5km^2), because the former sometimes moved far outside the territory, while CIMs maintained close attendance of females, which seldom went far out of the territory (Chapter 3).

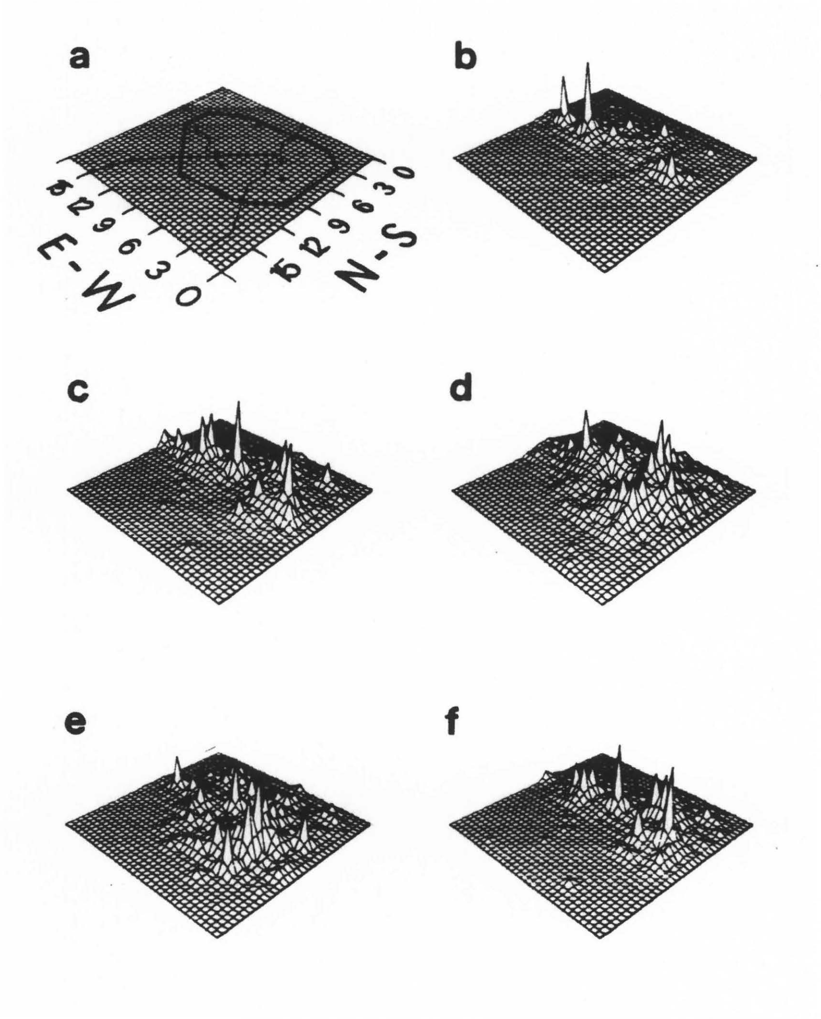
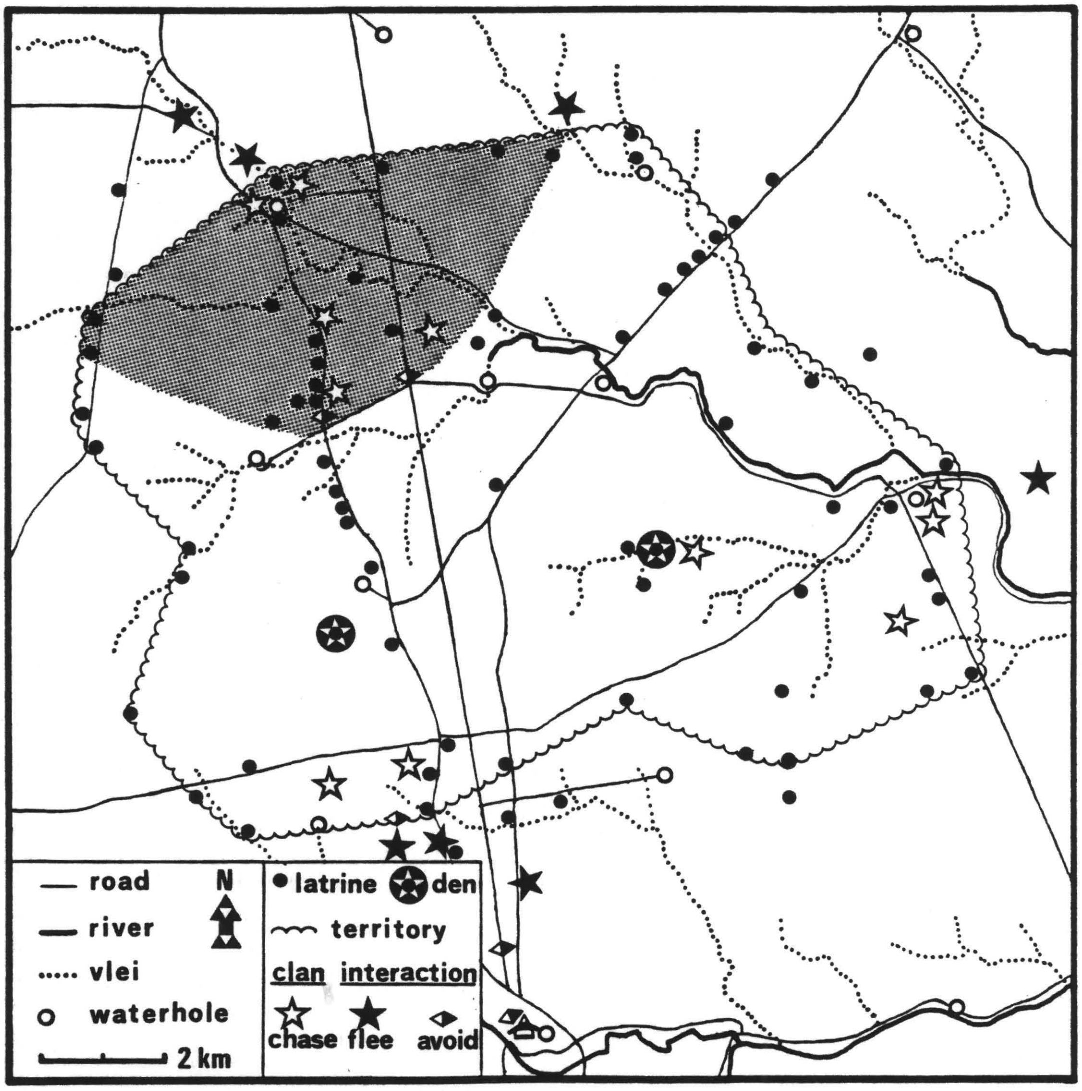


Figure 17: Three-dimensional representation of (a) Mavumbye area map, (b) quantity of food obtained, (c) duration in area, (d) distance travelled in area, (e) distribution of scent-marks, and (f) location of lairs of the Mavumbye clan.



<u>Figure 18</u>: Mavumbye clan territory configuration compared to the location of den sites, latrines, the disputed northwestern sector (shaded area) and the location of interclan encounters (except by prospective immigrants), indicating activity of Mavumbye clan members at encounters.

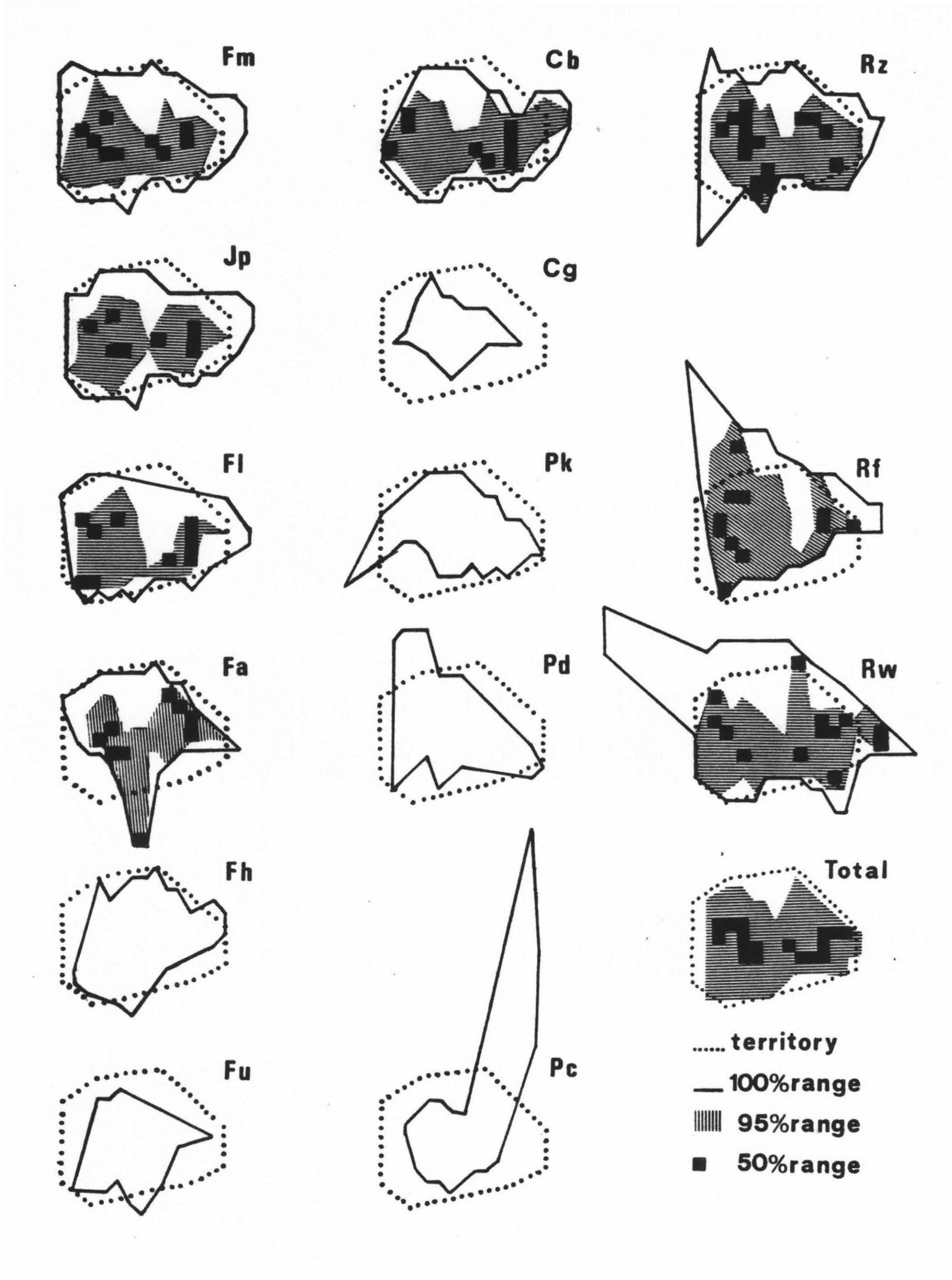
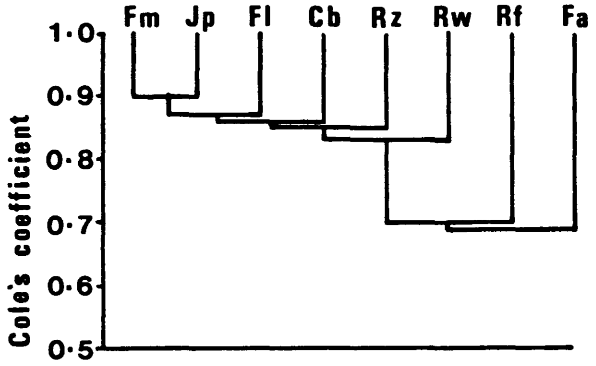


Figure 19: Areas in which Mavumbye clan members spent 100%, 95% and 50% of their time, in relation to the location of the Mavumbye territory.

(a) HOME RANGE



(b) CORE AREA

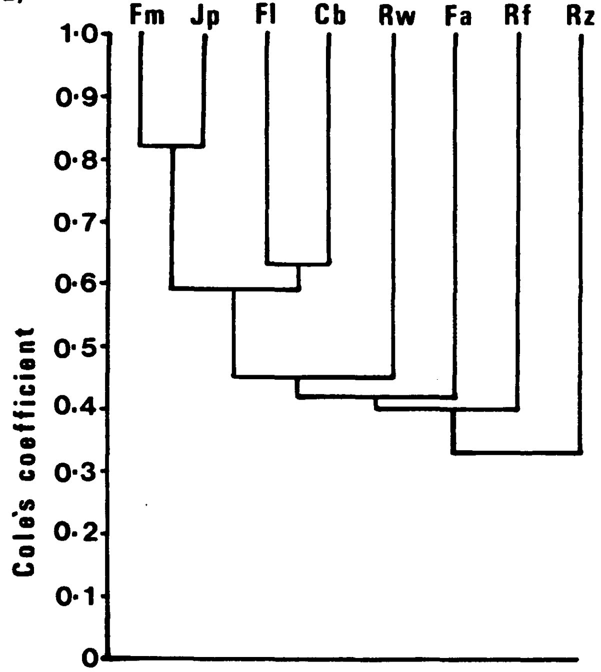


Figure 20: Similarity of (a) home range and (b) core area between Mavumbye clan members.

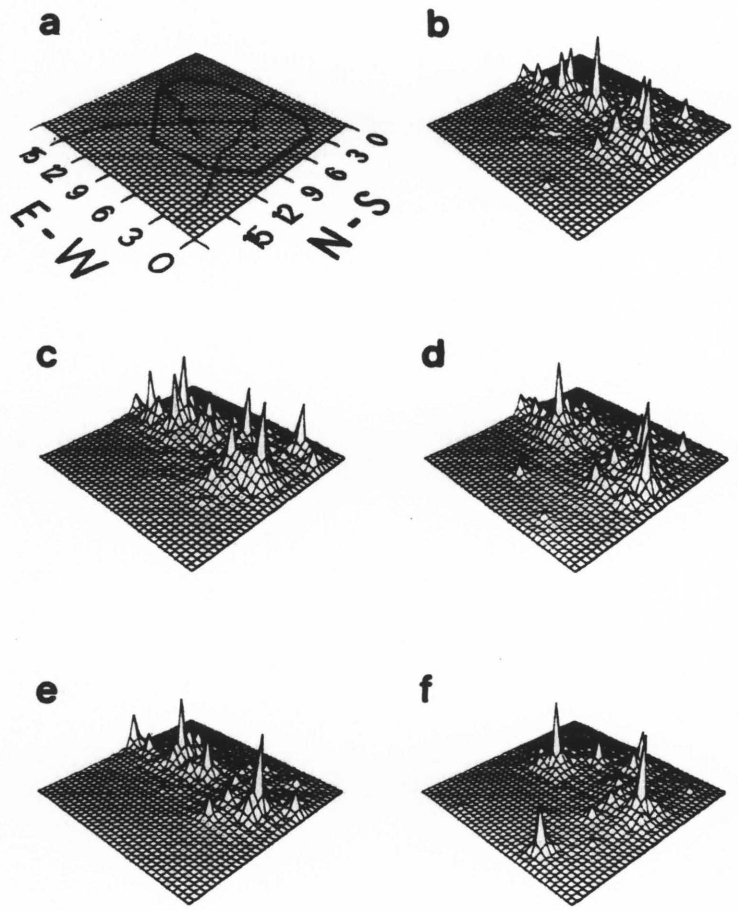


Figure 21: Three-dimensional representation of (a) Mavumbye area map, and the duration spent in areas by (b) all Mavumbye hyaenas, (c) all females, (d) RNMs, (e) CIMs, and (f) PIMs.

An injured female, Fa, was an exception, as she depended on food obtained from a refuse dump in an adjacent territory. Four of the six Mavumbye PIMs were sometimes seen far from the Mavumbye territory in association with members of neighbouring clans (Chapter 3).

A quantitative analysis of intraterritorial space use (of $9km^2$ grids) by RNMs and PIMs showed that this correlated poorly with that of other classes ($r<0,36$). In constrast, space use was more similar between juvenile and adult females and CIMs ($r>0,52$). These social conditions may be important for an interpretation of ecological determinants of space utilization.

Territoriality

Territory patrolling was characterized by directional moving at an average speed of 3,8km/h with few deviations between latrines, and a much higher rate of scent-marking (9,1/h) than during other non-resting activities (0,6/h). In 24h (N=55), an average of 1,2±1,8h (maximum 7,7h) and 4,1±7,0km (maximum 28,0km) were spent on territory patrols, usually longer by females (1,4±2,2h) than by males (0,9±1,4h), although differences were not significant ($t_{52}=0,92$; $P>0,05$). In all observations, group size was bigger during territory patrols (2,5; $\chi^2=16,6$; d.f.=3; $P<0,001$)) and at latrine visits (2,6; $\chi^2=15,0$; d.f.=3; $P<0,01$) than when hyaenas were foraging (1,8; Fig.22).

In 1365h during the present study when hyaenas were active, scent-marking was observed at a rate of 0,93 marks/h and 0,38 marks/km. This was usually higher for females (1,13/h and 0,50/km) than for males (0,76/h and 0,30/km). These differences were not significant (time: $U_{6,7}=9$; distance: $U_{6,7}=12$; $P>0,05$), because the highest rate of scent-marking was by a male (Rf) that

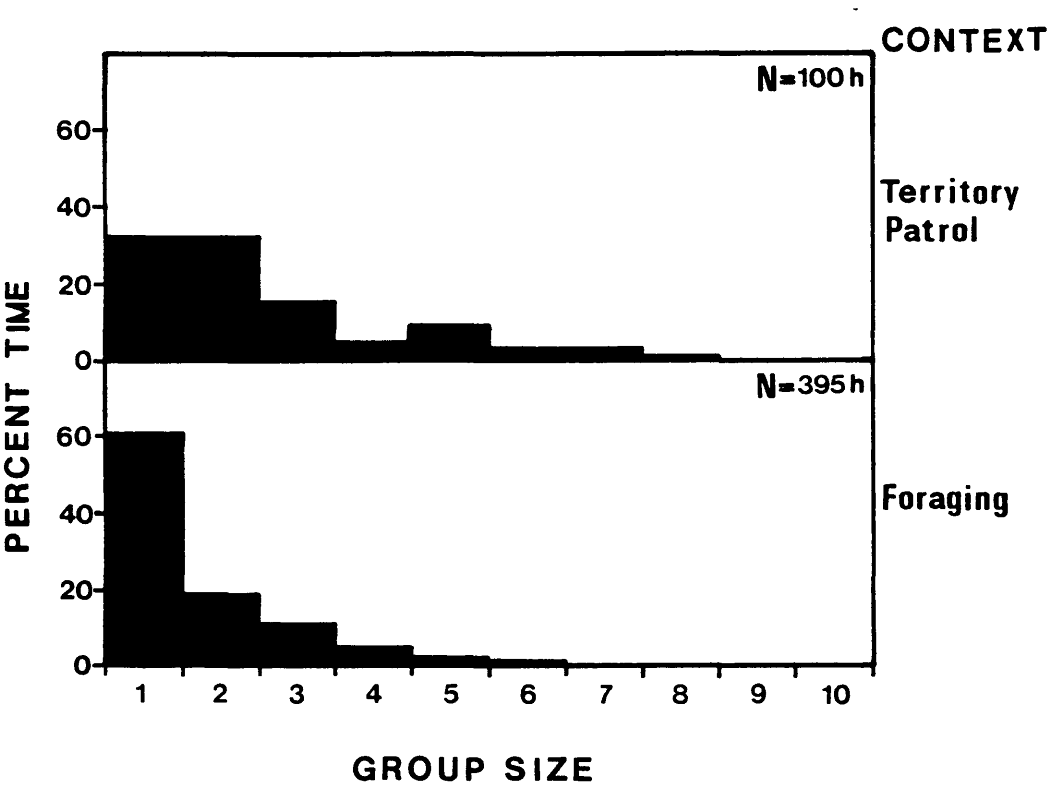


Figure 22: Group size of Mavumbye hyaenas during territory patrol and foraging.

was in the process of emigrating (2,1/h and 0,65/km), whereas an injured female (Fa) seldom participated in territory patrols.

A total of 64 latrines were found in the Mavumbye territory, of which 67% were within 2km distance from the territory boundary and 77% were along recognizable landmarks, such as roads, tracks or watercourses (Fig.18). On 302 occasions, 700 individual latrine visits were made by Mavumbye hyaenas during which they scent-marked 909 times and sniffed intensively without scent-marking 297 times. Pasting was the most frequent form of marking (51%), followed by scratching (35%) and defecating (14%). Hyaenas marked 365 times away from latrines, usually (61%) by pasting, sometimes (26%) by defecating and seldom (13%) by scratching.

Scent-marking took place least frequently in the core area (Fig.23b&c), but the long-distance spacing call, whooping (Appendix A), was emitted most in the core area (r=0,75) and away from the territory border (r=-0,35). Most patrolling (Fig.23d) was done in territory sectors which were otherwise seldom visited (Fig.23e). Thus, territory patrol was the only activity during which space utilization was not similar to that during foraging (for each individual: r<0,21; P>0,1). The north-western and south-eastern territory sectors, into which intrusions by adjacent clans were observed most frequently (Fig.23f; Fig.18), were patrolled intensively by Mavumbye hyaenas (Fig.23d).

On three occasions, when single Mavumbye RNMs encountered intruding females of other clans, the RNMs showed submissive approach behaviour, characteristic of prospective immigrants, until other Mavumbye hyaenas appeared, and chased the intruders away with the cooperation of these RNMs.

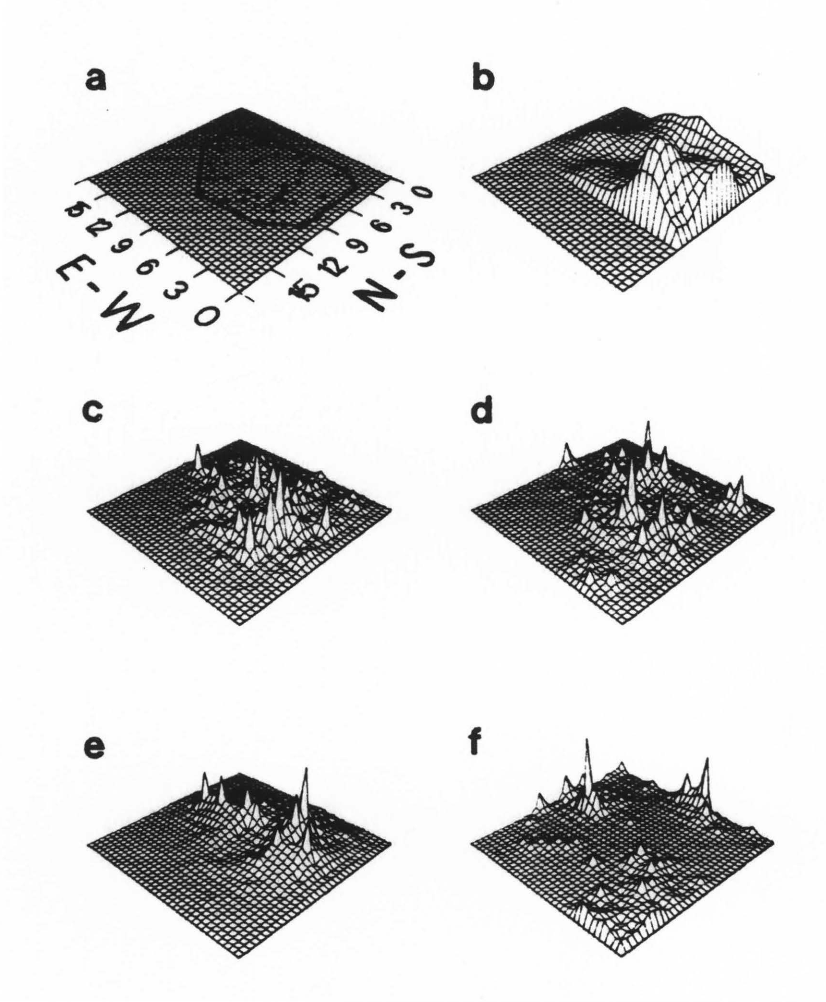


Figure 23: Three-dimensional representation of (a) Mavumbye area map indicating territory boundary and latrine locations, and the distribution of territorial activities measured by (b) counting scats and scratch-marks on latrines, (c) observing scent-marking activity, (d) mapping territory patrols, and the frequency of sighting of (e) Mavumbye hyaenas and (f) members of other clans.

A change in territory size was evident in seasons 4 and 5, when no Mavumbye hyaena, besides two RNMs, that were prospective immigrants to the Nghotsa clan, entered the north-western sector of the Mavumbye area (Fig.18; Fig.24). The only other hyaenas seen four times in this 25km^2 area during that period, were members of the adjacent Nghotsa clan. During two encounters with Mavumbye residents, the latter no longer displayed readiness to challenge the Nghotsa clan, as they had done at eight occasions during seasons 1 to 3 (Fig.18).

During the year following the death of the last Mavumbye female in July 1984 (Chapter 4), members of two adjacent clans (not the Nghotsa clan), including females, were seen at the centre of the Mavumbye area alongside the four remaining Mavumbye males (Van Jaarsveld pers.comm.). This suggests that the latter no longer maintained a territory and that members of adjacent clans expanded their home ranges into this region.

Distribution of Environmental Factors

Bush density, grass height, ungulate numbers and biomass were uneven over the study area (Fig.25). Highest prey numbers and biomass were recorded in the central and south-eastern sectors of the Mavumbye area where bush was open and grass shortest, although, in general, these associations were only significant at a low level for steenbok, impala, zebra and wildebeest ($0,05<r^2<0,16$). Due to the influence of migratory species, buffalo, zebra and wildebeest, prey biomass (ungulates <1000kg) in the 153km^2 Mavumbye area varied much between successive seasons, ranging from 67,6 tons in the wet season to 418,4 tons in the dry season.

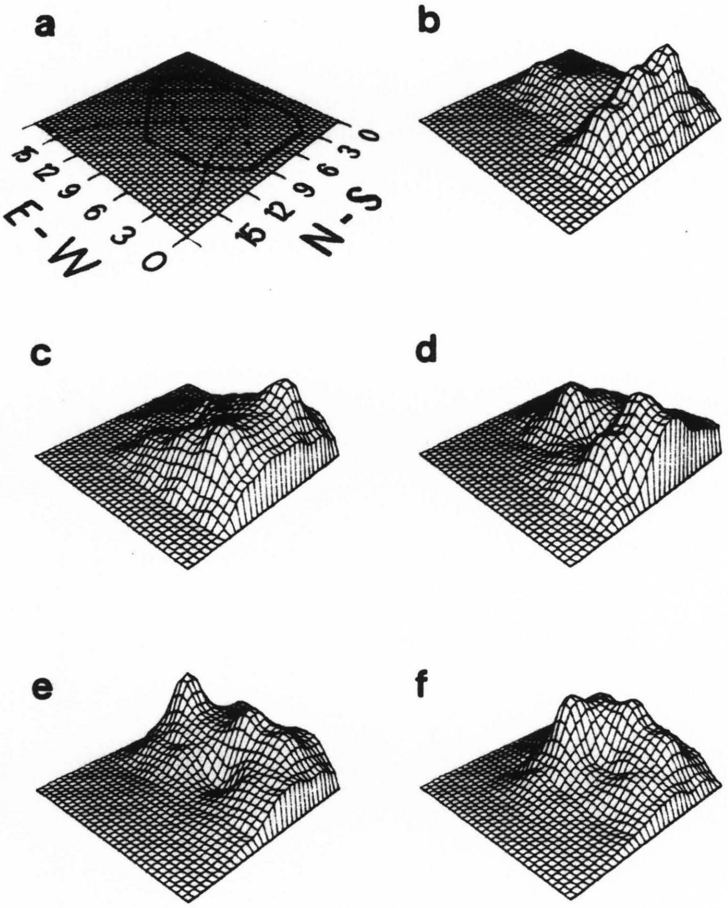


Figure 24: Three-dimensional representation of (a) Mavumbye area map, and distance travelled by Mavumbye hyaenas in (b) season 1, (c) season 2, (d) season 3, (e) season 4, and (f) season 5.

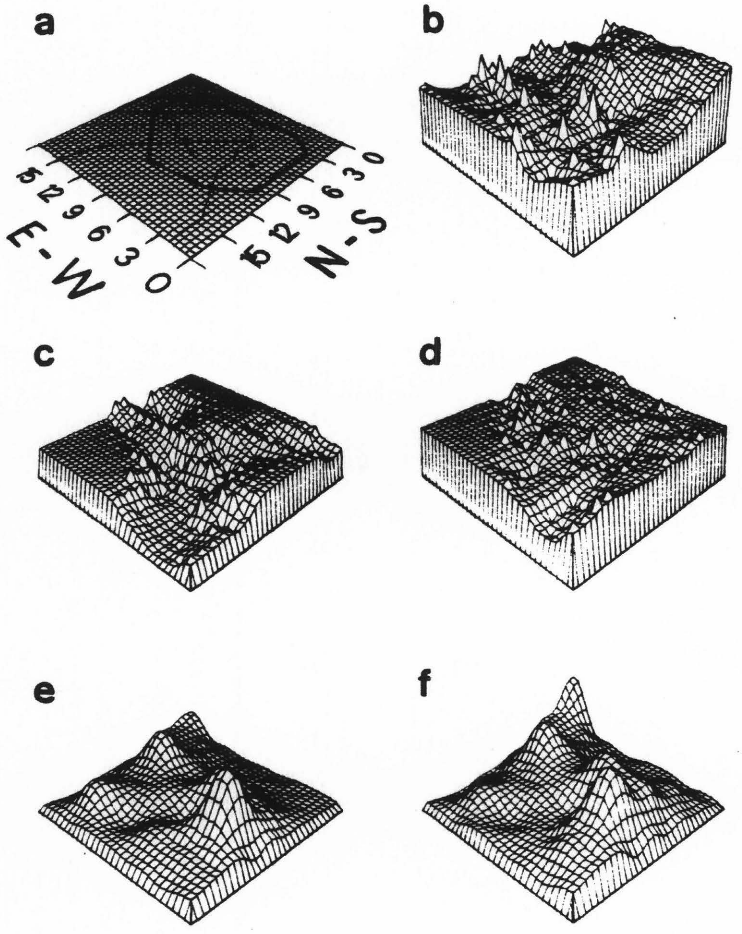


Figure 25: Three-dimensional representation of (a) Mavumbye area map, (b) mean bush density index, grass height in the (c) dry season and (d) wet season, (e) ungulate biomass, and (f) ungulate abundance.

Aerial censuses indicated that the number of ungulates was generally lower in the Mavumbye area than south of it (Table 22). These differences were mainly due to impala and wildebeest. Impala were abundant (7,64/km^2) west, south and southeastward of the Mavumbye area, but were scarce (0,87/km^2) in the area and northwards. During the dry season, wildebeest were abundant in the Mavumbye area (2,03/km^2), which was near the northern limit of the migratory southern population (Whyte pers.comm.), so that usually even higher densities (4,32/km^2) were recorded southwards. This contrasts with the pattern recorded for zebra, which reached peak densities (4,37/km^2) in the Mavumbye area, compared to all surrounding regions (2,38/km^2). The local zebra population did not migrate far but moved between the plains in summer and areas surrounding river courses in winter, in agreement with Smuts' (1972) findings. All species, besides kudu, impala and sable antelope, were less abundant in the Nghotsa area, in which the average ungulate density was 7,37/km^2 compared to 11,67/km^2 in the Mavumbye area, and 16,9/km^2 in its north-western sector, an area which was disputed between the two hyaena clans.

Habitat Use

Mavumbye hyaenas spent disproportionately more time in the *Sclerocarya caffra - Acacia nigrescens* (marula knobthorn) than in the dwarf *Acacia nigrescens* (stunted knobthorn) landscape (Table 23; χ^2=11,59; d.f.=1; P<0,001). This was true for all ecotopes of the two landscapes (χ^2=17,81; d.f.=8; P<0,05), except for ecotope 7, disturbed grassland of the high plateaux in the stunted knobthorn landscape, where hyaenas spent more time than expected.

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Table 22: Mean density (number/km^2) of ungulates in the Mavumbye area and territories of five surrounding clans (Fig.6) determined by aerial census in June of 1982, 1983 and 1984.

SPECIES	CLAN TERRITORIES					
	Mavumbye	Gudzane	Satara	Nsemane	Nghotsa	Lebombo
Area (km^2)	153	153	153	153	153	117
Elephant,Rhino,Hippo	0,26	0,47	0,50	0,31	0,12	0,46
Giraffe	0,33	0,56	0,63	0,56	0,32	0,62
Buffalo	2,67	2,72	0,75	1,41	0,28	1,18
Zebra	4,37	2,37	2,91	2,80	1,56	2,28
Waterbuck	0,25	0,65	0,27	0,10	0,07	0,15
Wildebeest	2,03	5,46	3,17	0,73	1,87	0,79
Kudu	0,84	0,57	0,50	0,59	1,07	1,21
Warthog	0,10	0,18	0,18	0,12	0,12	0,22
Impala	0,69	8,17	7,12	7,63	1,24	0,69
Other Antelope	0,08	0,07	0,05	0,03	0,48	0,04
TOTAL	11,67	21,23	16,10	14,35	7,37	7,87
BIOMASS (kg/km^2)	2267	3161	2134	1979	1174	1509

Table 23: Proportion of Mavumbye territory covered by each ecotope, compared to the time spent and distance moved by Mavumbye hyaenas in each ecotope.

Ecotope Number	Area in territory		Time	Distance
	(km^2)	(%)	(%)	(%)
1	40,2	30,9	39,3	28,6
2	19,5	15,0	17,5	16,6
3	20,5	15,8	20,6	19,8
4	1,7	1,3	1,9	1,5
5+6	24,2	18,6	4,6	7,6
7	11,8	9,1	11,2	16,4
8	2,9	2,2	1,5	2,1
9	7,2	5,5	3,0	5,8
11	2,2	1,7	0,4	1,8

Ecotope 1, *Sclerocarya caffra - Acacia nigrescens - Themeda triandra* treeveld, and ecotope 3, *A.nigrescens - Grewia bicolor - Terminalia prunioides - Combretum apiculatum* brushveld, were especially favoured, and Mavumbye clan members spent 60% of their time in these ecotopes, which together covered 47% of their territory (Table 23).

However, when moving about, hyaenas did not favour ecotope 1, but moved about more than expected in ecotope 3 and 7 (χ^2=13,77; d.f.=8; P<0,1). The high utilization of ecotope 7 obscured other differences between landscapes (χ^2=0,58; d.f.=1; P>0,1). Ecotope 5, the *Acacia nigrescens - Panicum maximum - Setaria woodii - Ischaemum brachyaterum - Digitaria eriantha* brushveld, interspersed with ecotope 6, *Panicum maximum - Setaria woodii* grassland, were the least favoured areas (Table 23), although these were the most widespread ecotopes in the dwarf knobthorn landscape.

When on territory patrol, hyaenas moved about more in open bush (73%) and short grass (28%) than when foraging (67% and 24% respectively), although differences were not significant (χ^2<3,88; d.f.=3; P>0,1). Furthermore, in areas of long grass (>40cm), individuals kept to open tracks or roads more often (32%) when on territory patrol than when foraging (11%; χ^2=13,70; d.f.=1; P<0,05). This was borne out by the location of many latrines along roads (Fig.17). The layout of roads in the study area may thus have had different effects on hyaena space utilization, depending on their activity.

Influence of Space Use by Environmental Factors

Space use during different activities (foraging, resting and feeding) correlated significantly at a low level (r>0,44), but was different when on patrol ($r<0,21$; see above). Therefore only the results of space use during foraging and territory patrol, when hyaenas were most likely to respond to environmental cues, are shown in detail.

Significant correlations of space use while foraging were found for 13 factors (Fig.26). The best correlations were with locations of lairs and carcasses, where hyaenas started and ended searching behaviour. Encounters with jackals ($r^2=0,30$) were influenced by the jackals' active association with foraging hyaenas (Chapter 5).

Distance from social clubs (Kruuk 1972), where hyaenas often met and socialized with other clan members, had an important influence on a hyaena's movements ($r^2=0,23$), especially early in the evening. The territory boundary was usually avoided ($r^2=-0,19$) and most time was spent nearer to the territory centre, except by RNMs ($r^2=-0,05$), which sometimes explored adjacent territories as prospective immigrants (Chapter 3).

The main activity zones of lions influenced hyaenas ($r^2=0,16$), especially by attracting them to lion-killed carcasses (Chapter 5). Steenbok were most numerous in the core area, explaining the apparent association ($r^2=0,19$), but kudu, zebra, wildebeest and impala were also slightly more abundant in the hyaenas' main foraging regions than elsewhere in the territory ($r^2>0,06$; Fig.26).

Most of these factors were important in the first three seasons (Fig.26), during which seasonal differences in space utilization (Fig.24) were less evident (season 1 cf. 2: $r=0,70$; season 2 cf. 3: $r=0,41$; $P<0,1$) than in the subsequent period (seasons 3 cf. 4; $r=0,10$; $P>0,7$). Foraging areas were roughly

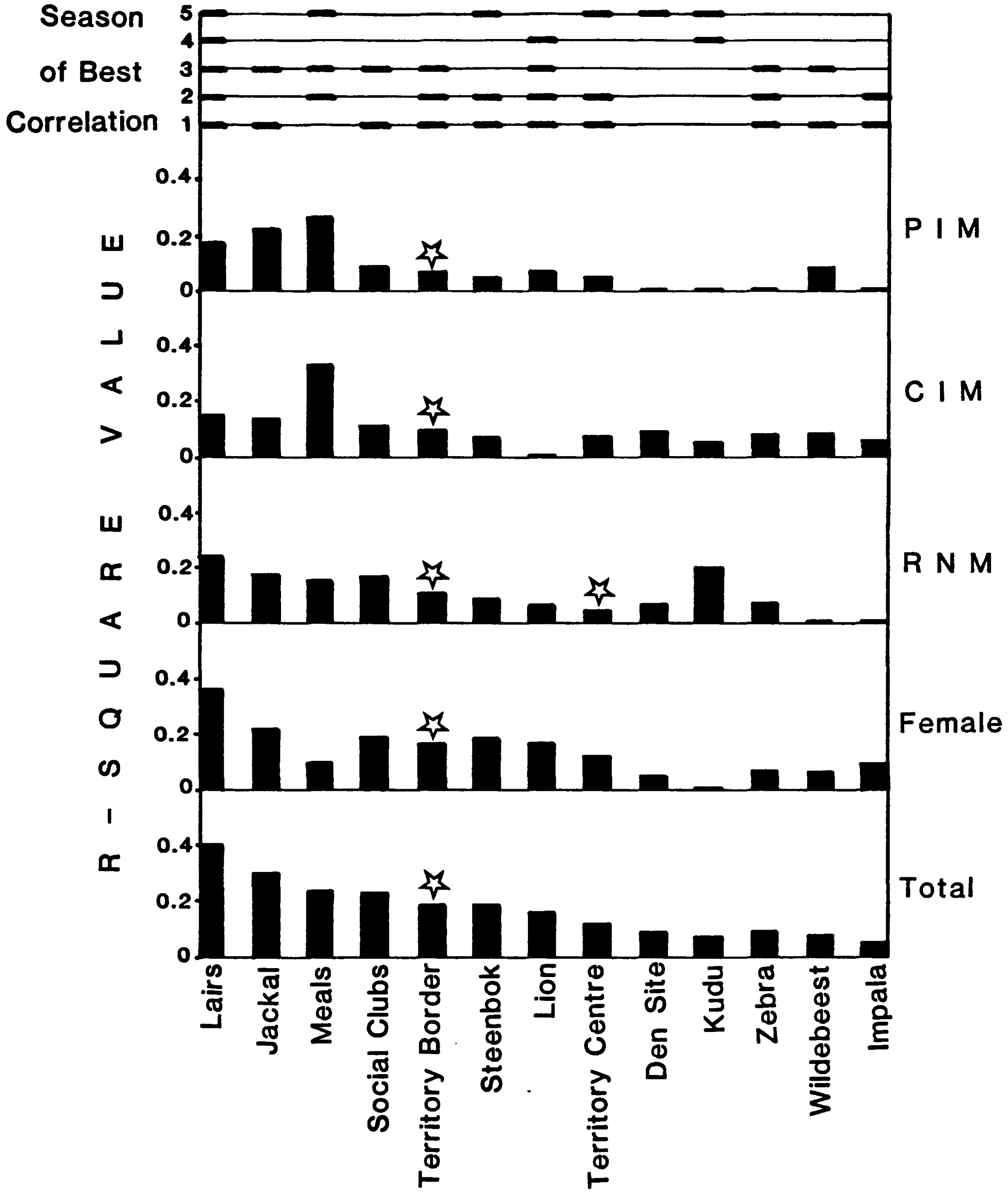

Figure 26: Values of r^2 for factors whose distribution correlated significantly (P<0,05) with Mavumbye hyaena space utilization when foraging. Asterisks indicate negative correlations.

similar between social classes ($0,32<r<0,57$), but differed somewhat in the association with various ungulates and lions (Fig.26). Females were most strongly associated with lions, while RNMs were most strongly associated with kudu, but no trends were evident with other males.

Territory patrols and scent-marking activity were weakly influenced by environmental factors connected with open bush ($r^2=0,05$). Thus, steenbok, wildebeest, jackal and lion, which showed some association with open-bush areas at night ($0,09<r^2<0,26$), were abundant in areas where hyaenas patrolled and scent-marked most.

<u>Food Distribution</u>

In general, the distribution pattern of ungulate carcasses (Fig.27) was more patchy than the distribution of live ungulates (Fig.28). Even within the main hyaena foraging areas, the amount of food obtained varied a great deal. The existence of such a pattern indicates that mortality factors for each ungulate species may not have been consistent over the Mavumbye area.

The relative degree of availability of buffalo, zebra, wildebeest, kudu impala and steenbok carcasses in $9km^2$ grid squares within the Mavumbye territory did not correspond to their relative abundance in the population ($0,12<r<0,35$; $P>0,1$). However, buffalo, zebra, wildebeest and kudu were eaten most frequently in areas where they were encountered alive most by foraging hyaenas (Fig.28; $0,43<r<0,83$; $P<0,05$). Steenbok hunting was so sporadic (Chapter 5) that carcass distribution did not reflect the pattern of their abundance. The low correlation of impala carcass distribution and hyaena encounters with live impala ($r=0,05$; $P>0,8$) emphasizes that, judging from abundance

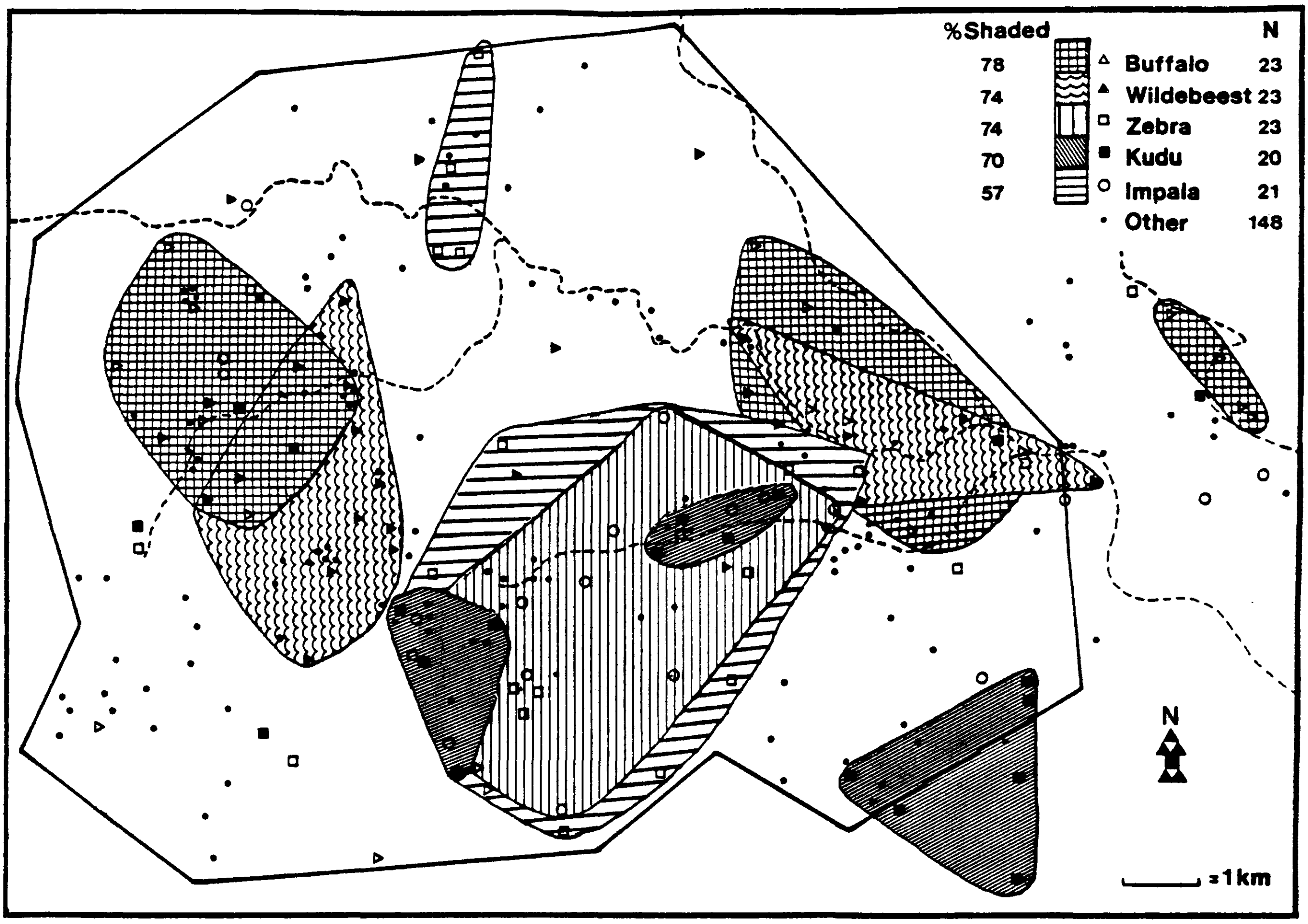

Figure 27: Location of buffalo, zebra, wildebeest, kudu, impala and other carcasses. Shaded areas cover regions where most carcasses of a species were located.

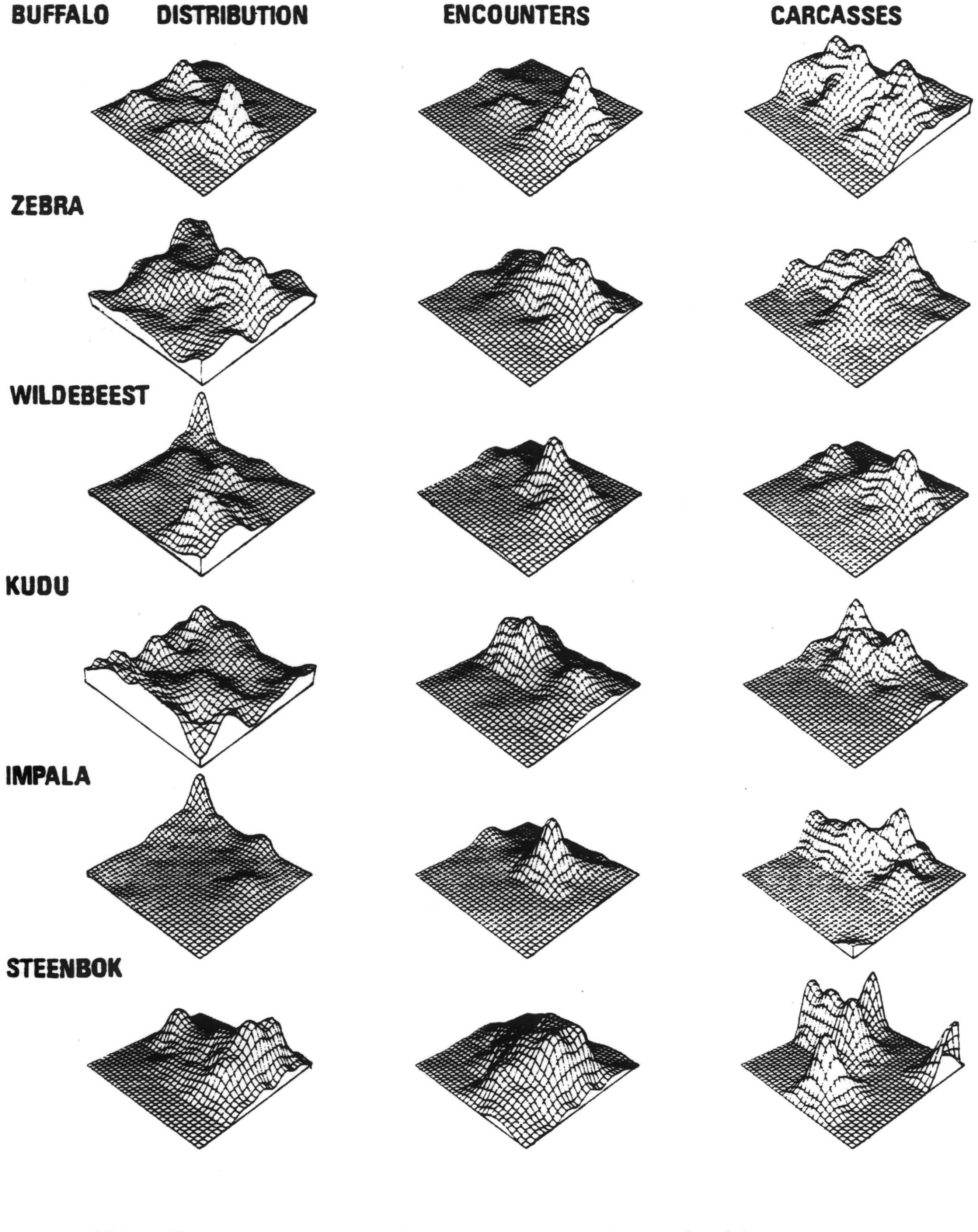

Figure 28: Three-dimensional representation of live ungulate distribution, locations of encounters with hyaenas and carcass localities of buffalo, zebra, wildebeest, kudu, impala and steenbok.

(Table 22), most of the Mavumbye area may have been marginal habitat for this species. It is possible that the few impala in such areas were more vulnerable to predation than those in high-density areas.

DISCUSSION

In defining hyaena *clans*, Kruuk (1972; pg39) noted that "many hyaenas had exactly the same range, whereas others might occupy different areas, these being mutually exclusive". Although in its strict sense this cannot be applied to Mavumbye hyaenas, the present study demonstrated that hyaenas with established social relationships also had home ranges that overlapped by more than two-thirds, but that all of these hyaenas participated in demarkating an identical territory.

Spotted hyaenas in different areas appear to vary much in degree of territoriality. Serengeti hyaenas were not territorial and lived in temporary groups, which aggregated and dispersed along with migrating wildebeest and zebra, and scent-marked along major commuting routes (Kruuk 1972). Hyaenas of the Namib desert, where their main prey species, gemsbok *Oryx gazella* and mountain zebra *Equus zebra hartmanae* were distributed sparsely, lived in small clans of 4-8 individuals, which had large home ranges ($570km^2$), but scent-marked mainly in a common core area and at carcass sites (Tilson & Henschel 1986). In the Kalahari desert (Mills 1984a), this species mainly preyed on dispersed gemsbok and wildebeest, and hyaena territories were very large ($1000-2000km^2$), but details of their scent-marking behaviour have not been reported. In the Ngorongoro crater, hyaena and prey densities were higher than found elsewhere in Africa, with large clans of 35-80 hyaenas defending territories of some $30-40km^2$ and marking mainly along the borders. Small minimum home ranges of 13-39km^2 were found in the Hluhluwe-Umfolozi Reserve, where clans comprised 10-14 members (Whateley & Brooks 1978; Whateley 1981).

Bearder (1977) and Bearder & Randall (1978) recognized that hyaenas in a Transvaal Lowveld woodland were territorial, but did not report the size of territories, except that they were larger than 25km^2. In a one-month survey, in an area situated adjacent to Bearder's previous study area, occupied by a clan of at least 12 adults and six subadults and cubs, I found that some identified females roamed over an area of 60km^2, which compared well with the home ranges of 51-104km^2 of Mavumbye clan members. Not all Mavumbye hyaenas were seen at all extremities of the 130km^2 Mavumbye territory, explaining why this area was larger than the home ranges of individuals. A territory of this size appears to be neccessary to cover enough patches of available carcasses (Fig.27). This fact and the cross-regional comparison support the hypothesis that food distribution may influence territory size (Macdonald 1983), as has been suggested for spotted hyaenas (Tilson & Henschel 1986).

Scent-marking by Mavumbye hyaenas during territory patrols (2,4/km) was at similar rates as brown hyaenas during all activities (Mills, Gorman & Mills 1980), but at much lower rates (0,15/km) when not on patrol. The distribution of most scent-marks away from the main foraging areas can be explained in two alternative ways:

a) The Mavumbye clan maintained a bigger territory than was essential for a group of that size at that time, as was found for brown hyaenas in the Namib desert (Goss 1986). This hypothesis would challenge the validity of the conclusion regarding territory size reached above. The low utilization for feeding purposes but high cost of territorial defence of the prey-rich northern territory sector by Mavumbye hyaenas (see Fig.27) would appear to support this notion. Possession of this area was disputed by a neighbouring clan, whose territory contained a lower density of prey. However, it can be argued that for hyaenas living in an area of variable food supply, this area would be of high value and could have been utilized more by the Mavumbye clan during previous times. This follows Caraco & Wolf's (1975) hypothesis why lion pride ranges are of such a size that a pride survives the leanest period.

b) There was no need to leave scent-marks in those areas where clan members spent most of their time, as they were present in such areas to repel intruders and to advertise their presence by whooping. This explanation supports a suggestion by Bearder & Randall (1978), although scent-marking at feeding sites, which was reported by these authors, was seldom seen in the present study.

When on territory patrol, hyaenas usually traversed open ground or paths to get to latrines with a minimum of energy expenditure. Therefore latrines were often located along roads, tracks, or rivers as found by Bearder & Randall (1978). This distribution of latrines probably maximizes their detection by intruders. The rate at which latrines were passed by without marking was lower (42%) than reported by these authors (60%).

The increased group size of patrolling hyaenas agrees with the finding of Kruuk (1972) in Ngorongoro, but was larger than that reported by Bearder & Randall (1978) for hyaenas marking at border latrines. Large group size probably served as a deterrent to intruders, as these fled from a group upon an encounter without a contest, but did so only after a single resident had rallied other clan members (by fast whooping; see Appendix A). The importance of avoiding contact between groups from different clans was emphasized when the outcome of the only combat recorded in this study was the death of a Mavumbye female (Chapter 4). Following that incident, the increased relative "bullying power" of the Nghotsa clan was evident, against the declining Mavumbye clan, and the disputed Mavumbye territory sector was occupied by the bigger clan.

With the need to defend resources for their nursery unit, females spent much time on territorial activities. Males, including PIMs, participated to a lesser extent in territory patrols, but helped Mavumbye females drive intruders off. However, they were sometimes reluctant to evict intruders when Mavumbye females were not present. This was probably because RNMs that were prospective immigrants to other clans had to reconcile the need to defend the territory of their natal clan, with the need to establish amicable social relationships with an adjacent clan. This would explain why they permitted members of two neighbouring clans to expand their home ranges into the Mavumbye area following the death of the last Mavumbye female.

Mavumbye hyaenas showed a preference for the marula-knobthorn landscape, with most lairs situated in its most densely vegetated regions. These regions were also where most kudu were hunted, but the most favoured foraging area was an open plain on a high plateau in the stunted knobthorn landscape, on which or at the fringes of which most zebra, wildebeest, impala and steenbok were encountered. Most scavenging from lions was done in this region or on moderately open regions of marula knobthorn, while most successful kills by hyaenas were made in dense vegetation. With such a diversity of potential food sources, it is not surprising that Mavumbye hyaenas did not show such strong associations with any particular prey species or any particular habitat type as in Serengeti, where hyaenas had a low preference for woodland (Kruuk 1972). This emphasizes that the pattern of space use in an area may be influenced fundamentally by food distribution relative to regional differences in accessability.

7: DIET

INTRODUCTION

Food can play an important role in many aspects of a spotted hyaena's life, including social behaviour (Chapter 3), relationships with prey and other predators, which in turn influences foraging behaviour (Chapter 5) and spatial organization (Chapter 6). Without knowledge of hyaena diet, some of the conclusions on social, foraging and space-related behaviour would thus not be complete.

Because of the importance for understanding big game management and the relative ease of data collection, diet of spotted hyaenas has been studied most (Deane 1960; 1962; Eloff 1964; Kruuk 1966; Pienaar 1969; Kruuk 1972; Eloff 1975; Bearder 1975; 1977; Smuts 1979; Tilson *et al* 1980; Skinner & van Aarde 1981; Mills 1984a,b; Skinner *et al* 1986). However, it has been emphasized that findings in one region cannot be extrapolated to another ecological region without conducting an independant study (Kruuk 1972).

The methods that have been used previously to determine spotted hyaena diet, have varied from direct observations, detailed analyses of prey remains in scats, regurgitations, or at dens, to spoor tracking or macroanalysis of stomach contents. These methods differ in accuracy and sampling biases. Kruuk (1972) attempted to counter sampling bias experienced in tallying hyaenas observed feeding at carcasses, by comparing these results with an analysis of hyaena scats. However, this does not test the robustness of the observation method *per se*. This would be best accomplished directly, using other variables collected during observations.

The objectives of the present study were:

a) To compare and test the validity of five different methods of diet determination, namely, counting carcasses fed on by hyaenas (Pienaar 1969), counting numbers of feeding hyaenas (Kruuk 1972), measuring feeding duration (Tilson & Hamilton 1984), estimating relative quantity consumed, and identifying prey content in hyaena faeces (Kruuk 1972; Bearder 1977; Tilson *et al* 1980);

b) To examine the diet of spotted hyaenas in the Mavumbye area and other regions in the Kruger National Park relative to prey availability and hyaena foraging behaviour;

c) To examine some environmental and social factors that could influence diet, especially prey abundance, prey size, causes of prey mortality, seasonal availability and social relationships between clan members;

d) To discuss the possible role of food in influencing spotted hyaena social organization (Kruuk 1972, 1976; Lamprecht 1978, 1981; Tilson & Hamilton 1984; Chapter 3).

METHODS

Prey abundance

The mammal fauna (>2kg) in the Mavumbye area comprised 18 ungulate, 16 carnivore, one primate, one lagomorph, one tubulidentate, one pholidote and two rodent species (Chapter 5). These, and to a lesser extent all other vertebrates occurring in this region, were regarded as potential food items of hyaenas. The mean abundance of ungulates was determined in five biennial aerial censuses by National Parks Board over the 25-month study period, June 1982 to June 1984 and twelve line transect censuses conducted between June 1983 and June 1984 (Chapter 5).

Observed Diet

Most information on diet was obtained by direct observations of free-ranging hyaenas of the Mavumbye Clan. Data on hyaenas feeding on 12 ungulate carcasses that originated from human activities, such as culling (5), providing bait to facilitate hyaena capture (6) and road accidents (1), and data collected in the week after the availability of unnatural carcasses were excluded from the present analyses. Parameters recorded during observations are defined as follows:

a) Carcass species, identified from horns, hooves, fur, skull and general appearance;

b) Feeding events, or number of nights that individual hyaenas were observed feeding from each carcass. Several feeding bouts in a night on one carcass count as one feeding event, but feeding bouts on different carcasses count as different feeding events.

c) Feeding hours, or duration (to nearest minute) that each individual was observed feeding;

d) Meals, or estimated quantity compared with a meal to satiation obtained by each hyaena from each carcass during a night, recorded as a substantial meal (1,0), a small amount (0,2 meals; skin and bone or little meat) or a morsel (0,01 meals; e.g.small rodent or brief gnawing of skin and bone). This method is designed to distinguish between opportunistic tasty morsels, subsistence diet and bulk food. Although this estimate is subjective, the scale is crude enough for easy recognition;

e) Food quality, recorded as meat (soft parts), skin and bone, or other parts.

f) Cause of death, established from direct observation of a kill, or by the carnivore species present, their dietary status, number, appearance and behaviour at a very fresh carcass (not older than 1h; Kruuk 1972), or from the nature of body marks on a fresh carcass left by the predator during a kill (e.g. muzzle bite marks made by lions when suffocating prey; Schaller 1972), or from the absence of any signs of violence on the decomposing remains of a natural death. Observed interactions between hyaenas, lions and leopards indicated that an observer's interpretation of the situation could depend on the stage at which observations began, so that in the absence of other signs, cause of death was recorded as "unknown" if the carcass was older than 1h.

Consumption

A method to visually estimate the quantity eaten by a hyaena is outlined. In the Namib desert (pers.obs.), the quantity that hyaenas consumed in each of 63 meals was measured by weighing gemsbok, mountain zebra and provisioned goat carcasses before and after hyaenas had fed. It was found that a hyaena ate 8,7±3,3kg (range=2,1-16,8kg) of meat a night. When only skin and bone were available, each hyaena was estimated to obtain only about 2kg. These findings suggested that, on average, a substantial meal of meat could be computed as 9kg and a small meal of skin and bone or little meat as 2kg. When this was done for the meals observed to be consumed by a clan of Namib hyaenas over 29 days, the calculated amount was in close (95,6%) agreement with the known amount, thus validating this method for a visual estimate of consumption in the present study of the Mavumbye clan.

Scat analysis

A separate estimate of the diet of the Mavumbye Clan was derived from an analysis of food remains contained in 25 faeces, or scats, collected monthly from latrines within the Mavumbye area between September 1982 and June 1984, giving a total sample of 525. The scats were pulverized to enable hair and other undigested remains to be extracted and stored in numbered vials. Some fresh (N=20) and air-dried (N=100) complete stools were weighed with a triple-beam balance.

Various methods of identifying mammal species hair have been used previously. Kruuk (1972), Bearder (1977) and Tilson, von Blottnitz & Henschel (1980) determined hyaena diet by examining the gross structure and colour of hairs from scats and comparing them to reference hairs of known species. However, this technique cannot be used in regions with a high mammal diversity, such as the Central District of the Kruger National Park, because of the similarity of hairs from many species when examined in this way.

The possiblility of using scale patterns of hair imprints (Keogh 1979; 1983), was investigated with reference hairs, but the scale patterns of many ungulate species were found to be too similar to enable accurate identification by this method alone.

Features of hair cross-sections were found to present a more satisfactory technique of hair identification, especially for ungulates. The plate method of sectioning described by Brunner & Coman (1974) and Keogh (1983) was adapted, using white rabbit hair as packing material and collodion (Collodion Flexible B.P., Lennon Laboratories, Port Elizabeth, R.S.A.) to bind the hairs. Ease and speed of use made this technique preferable to the Hardy microtome method of sectioning (Hardy 1933 in Hilyard 1983), which was tested.

Existing keys to hair of South African mammals (Dreyer 1966; Keogh 1979, 1983; Buys 1983; Hilyard 1983; Buys & Keogh 1984), did not suffice to cover the spectrum of appearance of hair from different parts of a body. It was therefore neccessary to obtain reference hairs, which were cut from various parts (head, shoulders, flanks, mane, rump, belly, chest, legs and tail) of mammal skins stored at the Transvaal Museum. Reference sections were photographed (Fujichrome 125ASA), and colour prints assembled in an index. It was found possible to identify some species from few hairs only (notably impala, buffalo, wildebeest, steenbok, warthog, tsessebe, scrub hare, aardvark, brown- and spotted hyaenas), but usually the appearance and combination of a spectrum of hairs of various cross-sectional structure, size and colours provided diagnostic features rather than single hairs *per se* (especially for kudu, zebra, waterbuck, giraffe and most carnivores).

The identification of ungulates, carnivores, primates, lagomorphs, larger rodents (>2kg) and Tubulidentata was to species level, whereas smaller rodents (<2kg), birds (except Struthionidae), reptiles, insects and plants were only identified as such. No hairs (besides spotted hyaena) in a scat, or insufficient representation of a spectrum of hair shapes, were recorded as "unknown".

Diet in Other Regions

Scats were collected from three adjacent latrines in each of six other regions of the Kruger National Park, within 10km of Pretoriuskop, Lower Sabie, Orpen, Olifants, Shingwedzi and Pafuri (Fig.1). From each region, 25 scats were collected during October

1982 and 25 during April 1983, giving a total sample of 300. Prey hairs were identified, and the results compared to the numbers of ungulates counted in aerial censuses during June 1982 and June 1983 in a 153km^2 area surrounding each sample region, except Pafuri, for which comparable census data were not available.

RESULTS

Comparison of Observation Methods

Four methods of estimating diet were compared (Table 24). Three of these, involving direct observations, were based on the same data of carcasses fed on, each emphasizing different variables. Despite differences with very large ungulate prey (>1ton) and of non-ungulate prey, the similarities between estimates of the major portion of hyaena diet, namely small to large ungulates, were striking (Fig.29).

The number of feeding events on ungulates compared favourably with feeding duration ($r=0,98$; $P<0,0001$) and the quantitative estimate of meals ($r=0,93$; $P<0,001$). Despite some shortcomings (Table 24), this validates the use of feeding event results for comparison with different studies.

Scats

Fresh scats obtained from focal animals had a moisture content of 45,8±9,7% (N=20) and a dry mass of 96,7±62,6g (Range=8,1-348,0g; N=100). Most samples from the Mavumbye area (N=525) contained only one prey species (81,2%), but some had two (16,1%) or three (2,7%) species, besides hyaena hair, which was found in 36,2% of all scats.

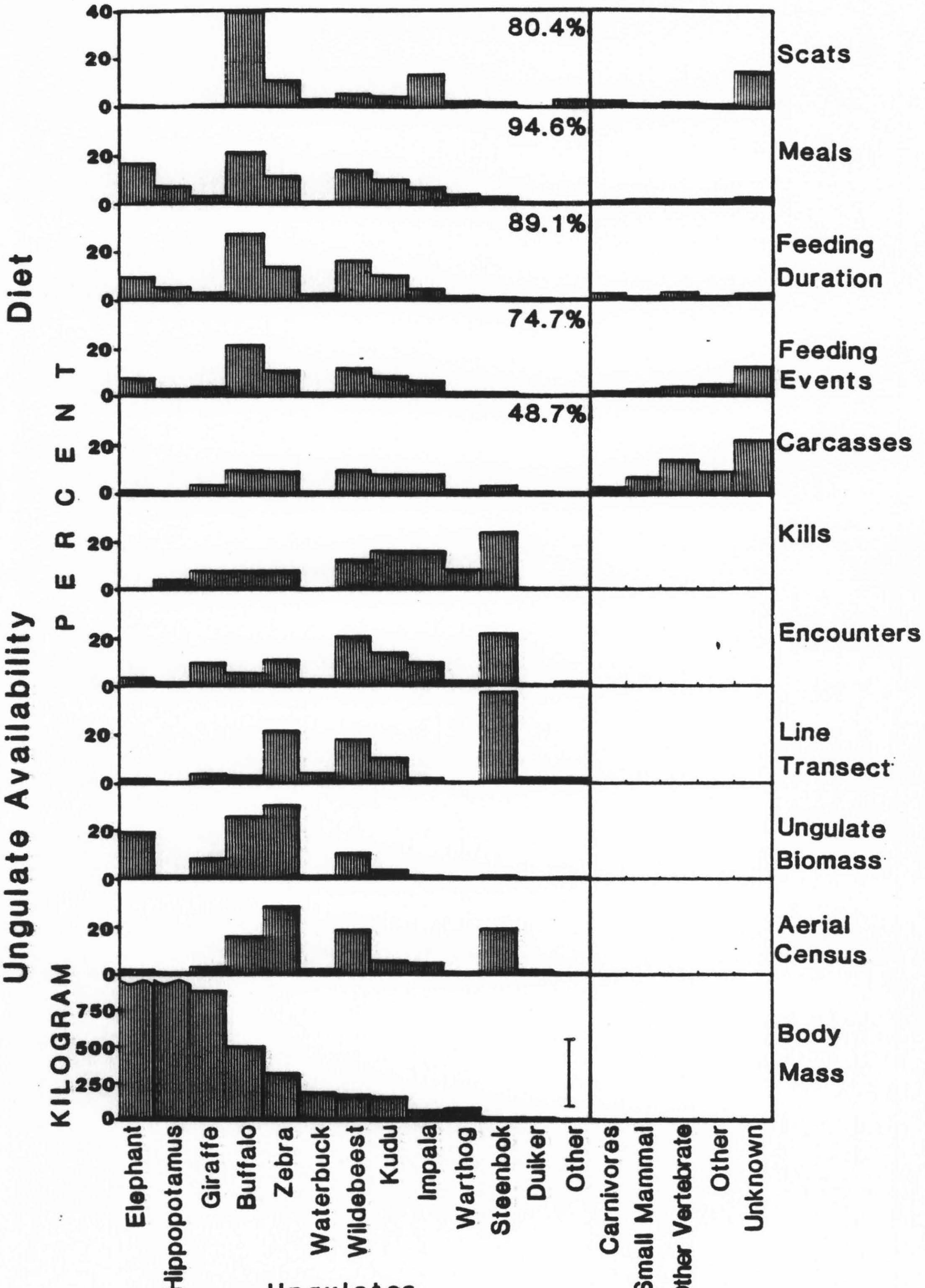

Figure 29: Ungulate abundance, biomass, frequency of encounter on transects and by hyaenas, number of kills made by hyaenas and hyaena diet, estimated by five methods.

Table 24: Comparison of five methods of diet determination.

Method	Correlation		Problem		
	Meals	Scats			
A) Carcasses	0,34	0,55	Effect:	a)	Indicates prey availability.
				b)	Fundamental to all observation methods.
			Problem:	a)	Small items consumed rapidly in dense grass can be overlooked.
				b)	Small items remain unidentified before consumption.
B) Events	0,86	0,86	Effect:	a)	Indicates prey selection.
				b)	Easy to record.
				c)	Enables analysis of individual prey preferences.
			Problem:	a)	Same as for (1).
				b)	No compensation for differences in prey size.
				c)	Measure is independent of size of meal.
C) Duration	0,94	0,78	Effect:	a)	Feeding time budget.
				b)	Indicates relative importance of food items.
			Problem:	a)	Differences in feeding rate.
				b)	Number of focal animals is limited by ability of observer.
				c)	Neccessity of being close to focal animal(s), which differ in degree of habituation.
D) Meals	-	0,65	Effect:	a)	Best estimate of prey utilization.
				b)	Alleviates problems of A, B & C.
				c)	Allows comparison of individual differences in prey utilization.
			Problem:	a)	Subjective.
				b)	Categorizing intermediate-sized meals.
E) Scats	0,65	-	Effect:	a)	Identification of major prey.
				b)	Indicates number of mammal species eaten as minor prey.
				c)	Easiest and cheapest method.
			Problem:	a)	Poor measure of prey importance, besides "major" and "minor".
				b)	Unequal representation of scavenged cf. hunted, large cf. small and hirsute cf. naked prey.
				c)	Ability to identify prey differs between species.

In 25 separate tests, the results obtained from random samples of 100 scats compared well with random sub-samples of 25 scats when examining all species ($r > 0,90$; $P < 0,001$) and the three main species, buffalo ($r = 0,69$), zebra ($r = 0,77$) and impala ($r = 0,74$) separately ($P < 0,001$; Fig.30).

The largest discrepancies between diet determined from scats and observations ($r > 0,65$; $P < 0,001$) were overestimates of buffalo and impala in scats and a consequent underestimate of other medium to large ungulates. Observations indicated that hyaenas often obtained a higher skin to flesh ratio from buffalo, which were usually scavenged, and from impala, which were the smallest major prey species, than they obtained from other medium to large ungulates. The low occurrence of wildebeest relative to zebra did not tally with observations (Fig.29).

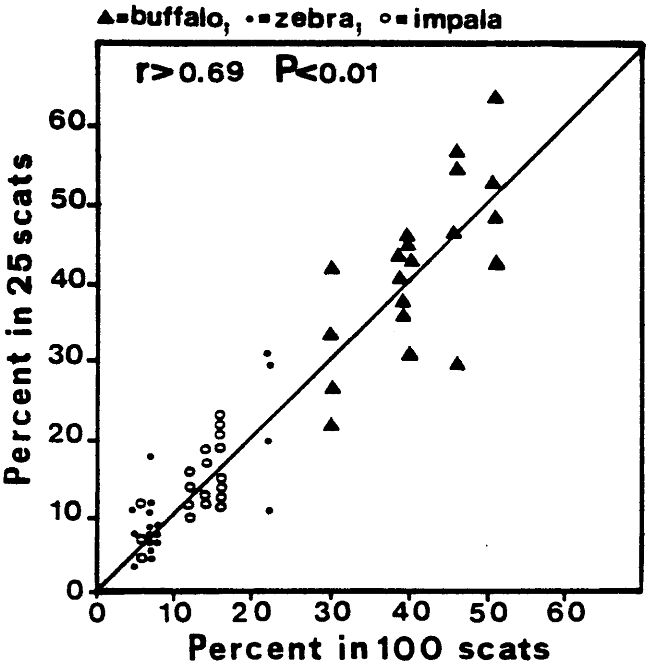

Figure 30: Occurrence of buffalo, zebra and impala hair in 100 scats compared to subsamples of 25 scats.

Diet of the Mavumbye Clan

Fifteen ungulate species represented 48,9% of all items (N=267) that hyaenas fed on. Many other vertebrates were eaten (Table 25). Hyaenas ate more carcasses of the common species of ungulates than of the uncommon species ($r=0,75$; $P<0,001$). However, they consumed similar numbers of carcasses (20-23) of each of the common species, buffalo, zebra, wildebeest, kudu and impala, although these species differed in mean abundance (81-508; $\chi^2=25,07$; d.f.=4; $P<0,001$).

Ungulates formed the bulk of hyaena diet, representing 94,6% of the meals obtained. Buffalo were the most important species, followed by wildebeest, zebra, kudu and impala. One elephant and one hippopotamus were consumed entirely by the Mavumbye clan over an extended period of time, so that these species were represented disproportionately in the present diet estimate. Although more than half of the carcasses were small mammals, other vertebrates, invertebrates or unknown items, these presented very little mass and were not important (Fig.29).

Although grass was often found in scats, hyaenas were never observed to eat it. The only plant they ate once, was a thistle, *Blepharis subvolubilis*. Other vegetable matter might originate from prey rumen contents.

Cannibalism was recorded twice in the Mavumbye clan, and once elsewhere, but the feeding pattern was unlike that witnessed at prey. Hyaena carcasses were often shifted without being dismembered and were consumed gradually over a period of several days. Three other hyaena carcasses were not eaten by hyaenas. One was eaten fresh by vultures, but hyaenas did not feed from the other two, although they were aware of their presence. These were

Table 25: Natural diet of the Mavumbye clan determined by recording carcasses fed on, carcasses killed by hyaenas (figure in brackets), feeding events, feeding duration (hours) and size of meals obtained, compared to an analysis of 525 scat samples.

			Feeding			
Species	Carcasses		Events	Hours	Meals	Scats
Elephant - *Loxodonta africana*	2		43	23,8	37,63	4
Hippo - *Hippopotamus amphibius*	1	(1)	15	12,9	15,00	0
Giraffe - *Giraffa camelopardalis*	7		18	6,7	6,04	5
Buffalo - *Syncerus caffer*	23	(2)	120	66,2	46,79	262
Zebra - *Equus burchelli*	22	(2)	60	32,8	24,16	66
Waterbuck - *Kobus ellipsiprymnus*	1		7	5,5	1,40	16
Sable - *Hippotragus niger*	0		0	0,0	0,00	2
Wildebeest - *Connochaetes taurinus*	23	(3)	66	40,3	31,07	29
Tsessebe - *Damaliscus lunatus*	0		0	0,0	0,00	4
Kudu - *Tragelaphus strepsiceros*	20	(4)	47	24,9	21,86	24
Reedbuck - *Redunca arundinum*	0		0	0,0	0,00	9
Warthog - *Phacochoerus aethiopicus*	3	(2)	9	1,8	8,01	13
Impala - *Aepyceros melampus*	20	(4)	35	10,1	14,51	80
Duiker - *Sylvicapra grimmia*	1		2	0,4	0,02	0
Steenbok - *Raphicerus campestris*	7	(6)	9	1,0	5,23	5
Hyaena - *Crocuta crocuta*	2		9	5,1	0,09	10
Lion - *Panthera leo*	1		1	0,1	1,00	0
Jackal - *Canis mesomelas*	1		1	0,1	0,01	0
Civet - *Civettictis civetta*	2	(2)	3	1,1	1,21	0
Genet - *Genetta* sp.	0		0	0,0	0,00	1
Mongoose - *Ichneumia albicauda*	0		0	0,0	0,00	2
Scrub Hare - *Lepus saxitilis*	1		1	0,1	0,01	1
Porcupine - *Hystrix africaeaustralis*	1		1	1,3	1,00	1
Pangolin - *Manis temminckii*	1	(1)	1	0,5	1,00	0
Mouse - Cricetidae & Muridae	13	(13)	13	0,5	0,13	4
Ostrich - *Struthio camelus*	2		2	0,3	0,21	0
Frankolin - *Francolinus natalensis*	3	(3)	1	0,3	0,20	0
Sandgrouse - *Pterocles bicinctus*	1		1	0,1	0,01	0
Dove - *Streptopelia senegalensis*	3	(2)	3	0,1	0,03	0
Buttonquail - *Turnix sylvatica*	2	(2)	2	0,1	0,02	0
Small Bird - Passeriformes	1	(1)	1	0,1	0,01	6
Marsh Owl Eggs - *Asio capensis*	4		2	0,1	0,02	-
Tortoise - *Testudo pardalis*	1	(1)	1	1,4	0,20	0
Snake - Serpentes	1		1	0,1	0,01	1
Frog - Anura	1	(1)	1	0,1	0,01	-
Barbels - *Clarias gariepinus*	21	(21)	7	2,1	1,40	-
Insect - Hexapoda	20	(20)	6	0,2	0,06	2
Spider - *Nephilia* sp.	2	(2)	2	0,1	0,02	-
Thistle - *Blepharis subvolubilis*	1		1	0,1	0,01	2
Lion Faeces - *Panthera leo*	7		7	0,4	0,07	-
Hyaena Regurgitation	4		4	0,2	0,04	-
Artifacts	5		5	2,3	2,41	2
Unknown	58	(2)	69	6,8	3,73	95
Total	267	(95)	576	248,4	223,6	646
% Ungulate	48,7		74,7	89,1	94,6	80,4

consumed by maggots. The difference between the latter two carcasses and those that were eaten by hyaenas, was that they had not been members of the clan on whose territory they died. All observations of cannibalism involved carcasses of previous members of the resident clan.

Diet in the Kruger National Park

The abundance of 14 ungulate species in the Mavumbye area during June 1982 and June 1983 differed significantly ($r<0,55$; $P>0,05$) from that at Pretoriuskop, Lower Sabie, Orpen, Olifants and Shingwedzi, whereas differences between the other five regions were non-significant ($r>0,89$; $P<0,001$). The main reasons for this appeared to be the relatively low abundance of impala and high abundance of wildebeest in the Mavumbye area, compared to all other regions, whereas buffalo, zebra and kudu were important in all regions (Fig.31).

The hyaena diet was estimated by examining 50 scats collected at each locality during October 1982 and April 1983. At Lower Sabie, Orpen, Olifants and Shingwedzi, the diet reflected the ungulate abundance very well ($r>0,93$; $P<0,001$). The diet in these regions and Pafuri was similar ($r>0,85$; $P<0,001$), with impala and buffalo as major prey species. At Pretoriuskop, the correlation was lower between abundance and diet ($r=0,64$; $P<0,05$) and between diet compared with other regions ($r<0,75$; $P<0,01$), and least similar to diet at Mavumbye ($r=0,46$; $P<0,1$), because hyaenas consumed a higher proportion of kudu (27,1%) than the relative numbers of this species counted at Pretoriuskop (6,6%).

At Mavumbye, the significant correlation ($P<0,01$) of diet in September 1982 and April 1983 with ungulate abundance in June 1982 and June 1983 was lower than in other regions ($r=0,76$;

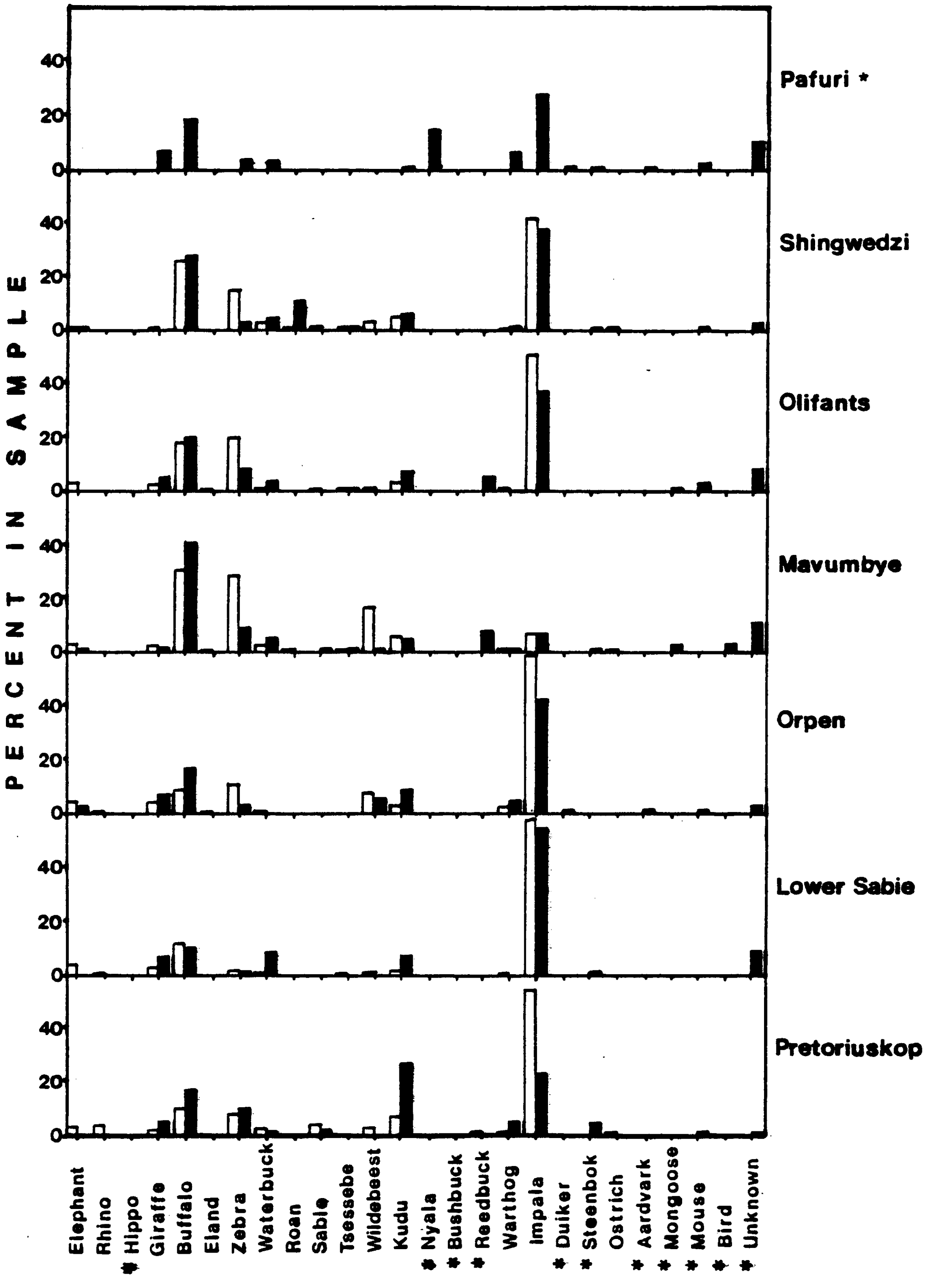

Figure 31: Mean ungulate abundance (white) compared to hyaena diet (black) at seven localities in the Kruger National Park. Aerial censuses were conducted during June 1982 and June 1983 and 50 hyaena scats were collected from each locality during October 1982 and April 1983. '*' indicates lack of census data.

P<0,01) because of the high occurrence of buffalo (40,5%) and low occurrence of zebra (9,5%) and wildebeest (1,4%) in the diet compared to their relative abundance (31,1%, 29,2% and 17,2% respectively). Data from Mavumbye compared poorly with those from Olifants, Shingwedzi and Pafuri (0,54<r<0,61; P<0,05) mainly due to differences in the amount of impala eaten in these regions, although buffalo was important in all (Fig.29). Differences with Mavumbye were most pronounced at Orpen and Lower Sabie (r<0,37; P>0,1), where impala were most abundant (>10/km^2) and were consumed most (>42%) and buffalo was least important of all the regions (<16% of diet).

Seasonal Differences in Diet

The study period was divided into five alternating dry and wet seasons. The abundance of live buffalo, zebra and wildebeest varied between these seasons (Chapter 5). Hyaena diet was compared by meals consumed during observations and prey remains in scats (Fig.32). Although the latter method indicated that buffalo was the principal prey in all seasons and that there was little seasonal variation (r>0,79; P<0,001), this was not confirmed by observation data (r<0,47; P>0,1). The latter were subject to larger sampling bias, especially of hippopotamus and elephant, of which one whole carcass each was consumed by hyaenas. The importance of all other ungulate species in the diet varied seasonally, with some buffalo, zebra, wildebeest and kudu being consumed in all seasons, warthog only in the two wet seasons, and impala only in the first and two last seasons. Buffalo provided bulk food in three seasons only, although skin and bone were eaten in all seasons, explaining why so much buffalo hair occurred in hyaena scats during all seasons.

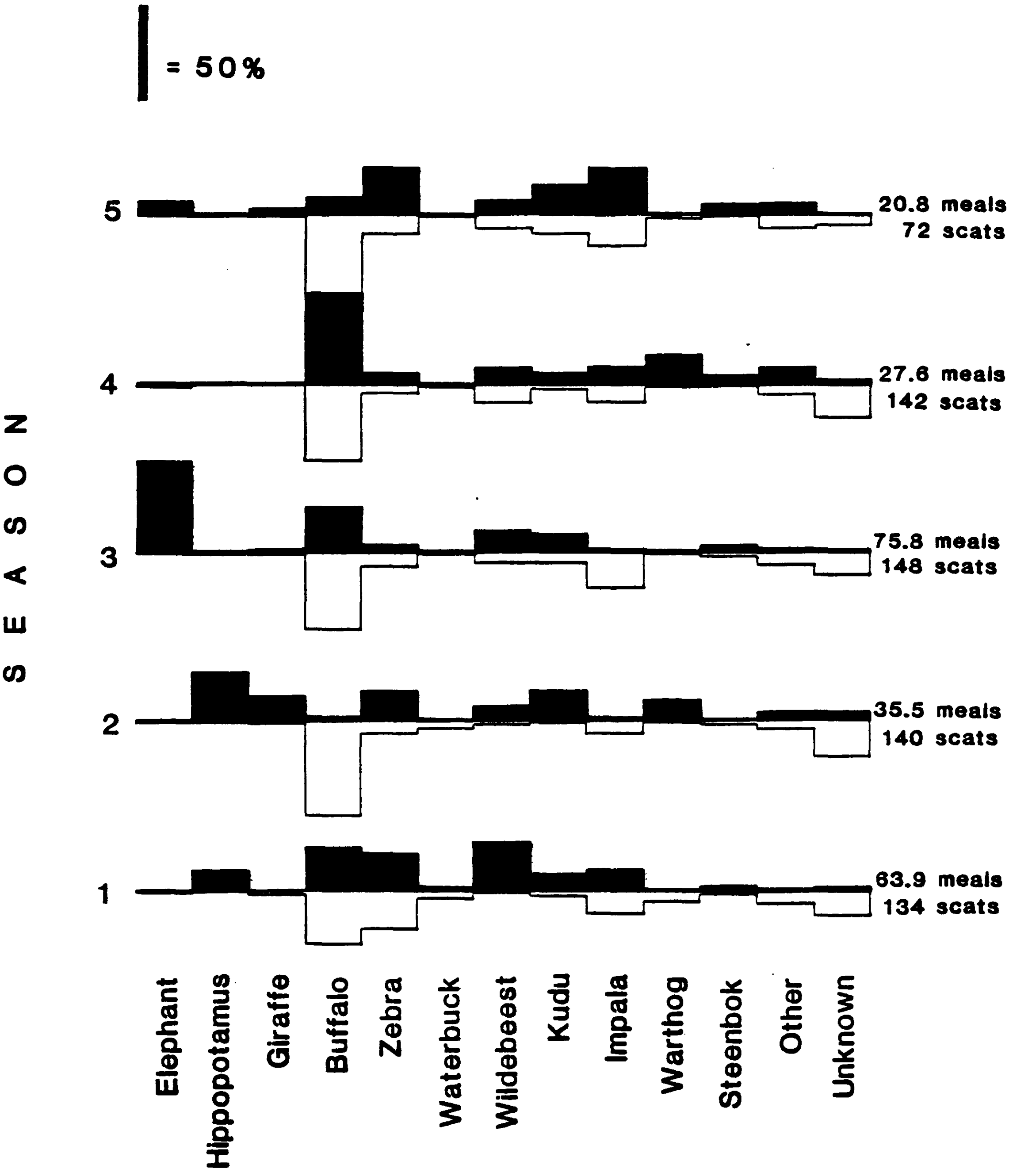

Figure 32: Diet in different seasons as determined by meals observed to be consumed and scats collected in each season.

Food Origin

Cause of death could not be established with certainty for the majority (65%) of ungulate carcasses (N=148; Fig.33). Hyaenas killed at least 24 ungulates (16,2%) themselves, and twice caused giraffe to kill own calves (1,4%). Only 13 ungulates (8,8%) from which hyaenas ate, were known to have been killed by lions, which is probably an underestimate. It was not possible to collect more data on lions, but the impression was gained that besides often hunting wildebeest and zebra, and leaving little for hyaenas, lions frequently killed buffalo, from which hyaenas scavenged. Lions were thus probably the biggest contributing factor (>50%) to the number of ungulates hyaenas fed on. Only thrice (2,0%) did hyaenas get leopard kills. Non-violent ungulate mortalities occurred mainly by starvation during the drought of late 1982, when Mavumbye clan members found seven intact buffalo and two kudu carcasses. Later, an elephant, which apparently died of old age, was entirely defleshed by eleven Mavumbye hyaenas.

Hyaenas killed 85% (N=65; excluding unknown species) of the non-ungulate **animals** themselves. The only such species that was scavenged, besides non-violent deaths, was a bird (sand-grouse *Pterocles bicinctus*) snatched from a jackal that had killed it in front of the hyaena.

The food quality of scavenged material was less than that of own kills, which constituted at least 51% of all meals consumed (223,6 meals; Fig.33). A minimum of 7,8% of the meals were from lion kills, but the actual amount probably exceeded 20%. Ungulates that died of natural causes made up 23% of the meals, consisting of a rich supply of meat, and of skin and bone remains, which were consumed at leisure over many months.

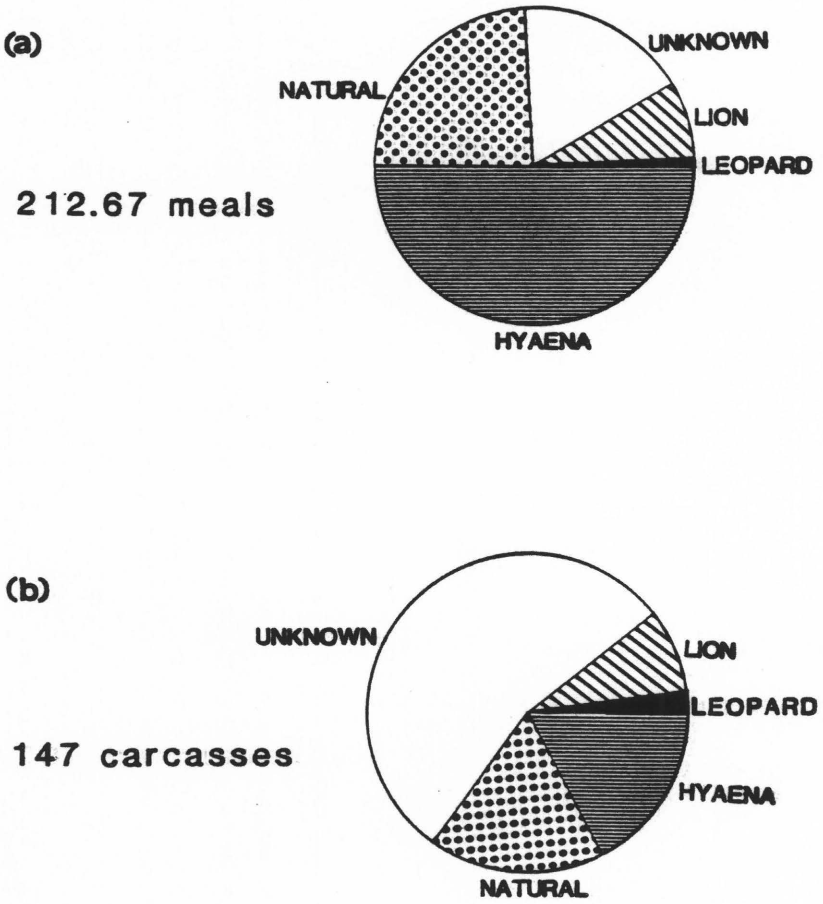

Figure 33: Cause of death of ungulates and their importance in the diet of spotted hyaenas as determined by (a) meals and (b) number of carcasses.

Relative Importance of Prey Species

The relative importance of each ungulate prey species in the diet was determined using the formulas:

% Carcasses Consumed ÷ % Mean Abundance

% Feeding Events ÷ % Mean Abundance

and % Meals Consumed ÷ % Mean Biomass.

The first of these formulas had previously been used by Pienaar (1969), who termed it "prey preference rating". However, this and the other two formulas are functions of many factors which influence hyaena diet, such as the hunting ability of hyaenas, other sources of mortality, relationship with other carnivores, prey abundance and prey availability, besides the effects of prey selection (preference) by hyaenas. Most of these factors are difficult to quantify, except the effect of prey abundance or biomass, which is examined below. These formulas are here referred to as "Prey Importance Ratings".

Ungulates between the size of steenbok and giraffe could be separated into four categories according to their importance ratings (Fig.34). The categories appeared to be related to prey body size, although the underlying factors might not be body size alone. The prey importance ratings of the categories are summarized in Table 26.

Category I were the small agile species, steenbok and duiker. Although they were common (2,39/km^2), they were eaten seldom. Category II comprised kudu (females and calves), impala and warthog (1,33/km^2), which were eaten more often than expected from their abundance and yielded the greatest quantity of food relative to their biomass. This was lower for Category III, zebra, wildebeest and waterbuck. The former two species were

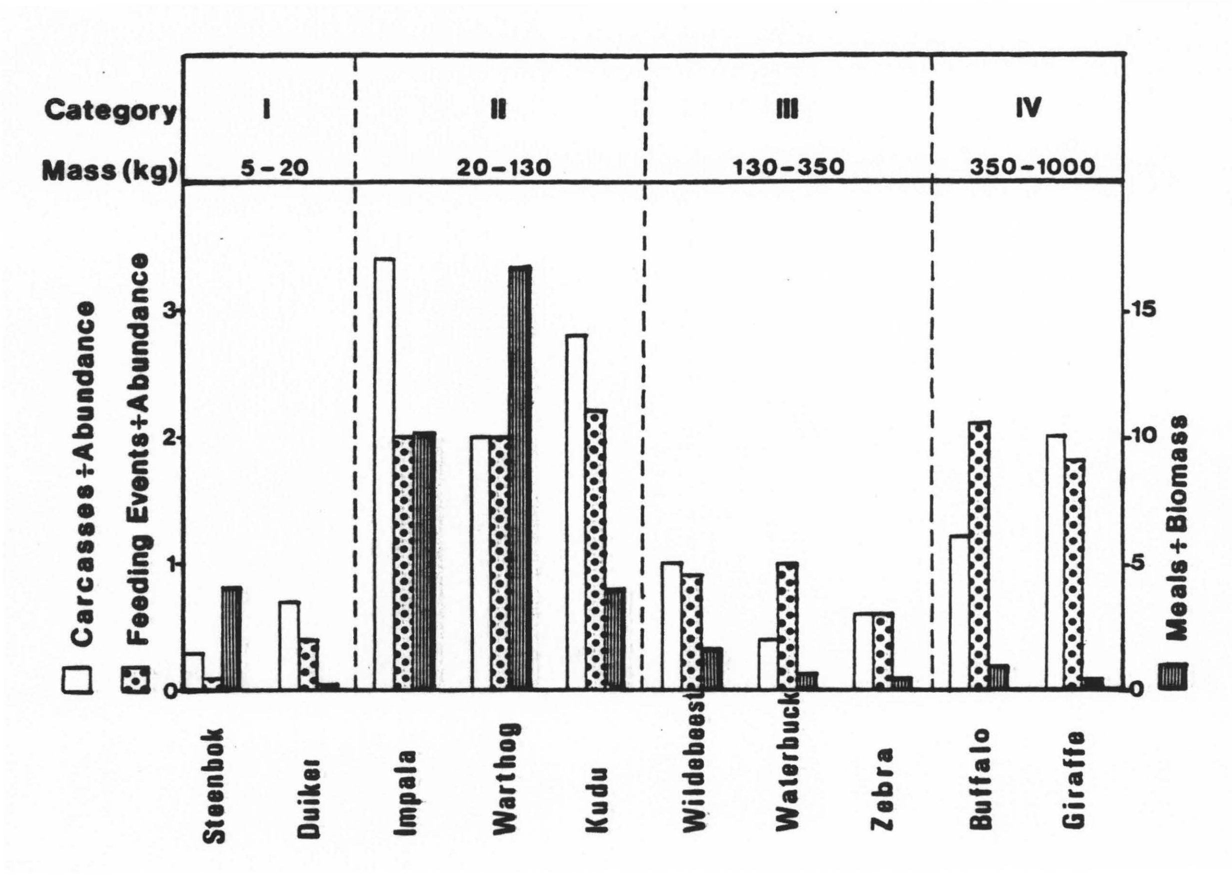

Figure 34: Carcasses÷Abundance, Feeding Events÷Abundance and Meals÷Biomass ratios for different-sized prey consumed by hyaenas. Each category encompasses species with similar ratios.

Table 26: Prey importance ratings for each category of prey.

		PREY IMPORTANCE RATING		
Category Number	Prey Size (kg)	Carcasses÷ Abundance	Feeding Events÷ Abundance	Meals÷ Biomass
I	<20	0,31	0,14	3,09
II	20-130	2,94	2,12	5,91
III	130-350	0,73	0,72	0,68
IV	>350	1,30	2,03	0,80

abundant (about 5,71/km^2), but migrated in and out of the area. Casual observations indicated that buffalo and giraffe that had died non-violently or had been killed by lions, were scavenged more often than the remains of lion-killed zebra and wildebeest, which were sometimes left untouched by hyaenas. Therefore Category IV prey, buffalo and giraffe (2,10/km^2), were eaten often relative to their abundance.

Feeding Behaviour

Although carcasses attracted larger groups of clan members than were seen elsewhere (3,6 cf. 1,8; χ^2=30,85; d.f.=3; P<0,001), the group size of feeding hyaenas was significantly smaller than was present near carcasses (1,6 cf. 3,6; χ^2=42,92; d.f.=3; P<0,001; Fig.35). This can be attributed to limited

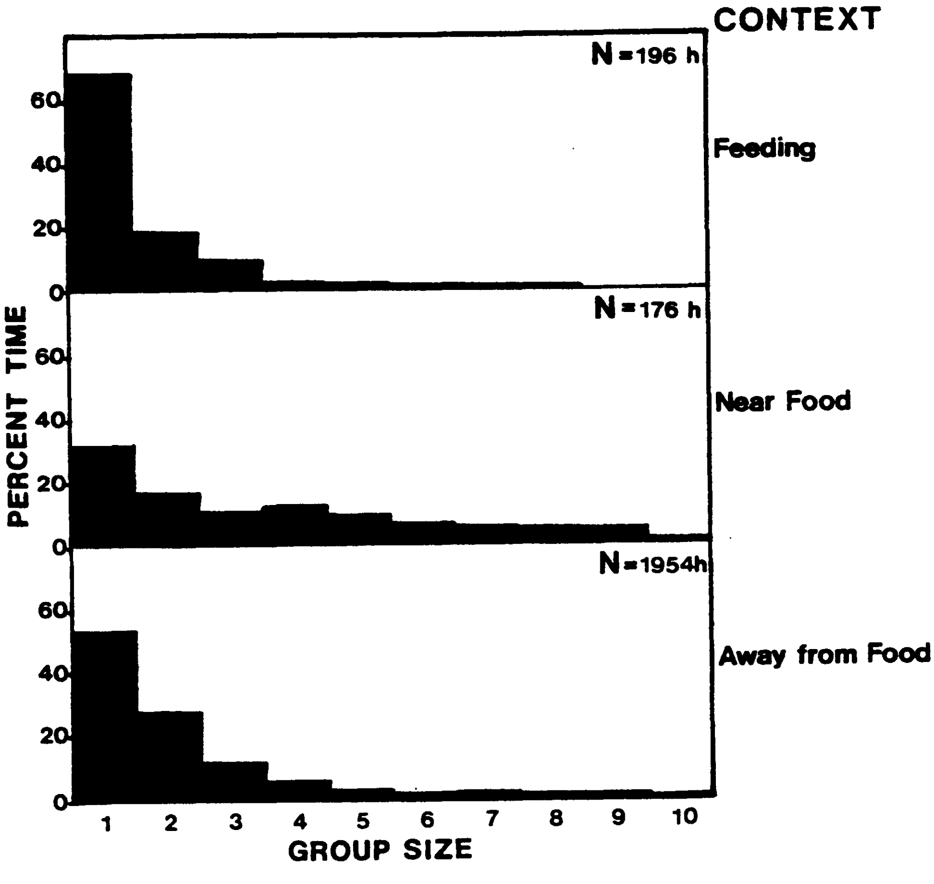

Figure 35: Hyaena group size (% time) while feeding, or near carcasses, or elsewhere.

access to feeding sites, especially at small carcasses, and to agonistic interactions between hyaenas at food, resulting in temporary or complete exclusion of some clan members, to the benefit of others (Chapter 3).

When present at food together with other hyaenas, PIMs (71%), CIMs (55%) and RNMs (46%) more often fed alone than did females (34%; $U_{8;6}=3$; $P<0,05$), which often fed alongside other females, especially at fresh kills. An extreme case of tolerance at food occurred when a 15-month old cub, which had previously fed elsewhere, voluntarily presented a freshly-killed civet to its mother (see Appendix B).

Differences in Diet between Social Classes

When examining all data, the diet (feeding events, duration and meals) of females, juvenile, RNMs and CIMs were very similar ($0,83<r<0,95$; $P<0,001$), but less similar to the diet of PIMs ($0,58<r<0,71$; $P<0,05$), that could only be observed at large carcasses. Males and a cub ate more small carcasses and unknown items than females did, but there were few differences in the consumption of medium to large carcasses (Fig.36). To counter the suggestion that samples (observation periods) were not independant, only data (feeding duration) obtained after random sightings (41% of all data) were compared. This confirmed that, despite some differences in the importance ranking of some prey species (Kendall's tau $\tau=0,20$; $P>0,1$), the diet of males and females was similar ($r=0,82$; $P<0,001$). However, the food quality obtained from these carcasses differed substantially, with females obtaining a higher proportion of meat (80%) than males did (58%) (Chapter 3).

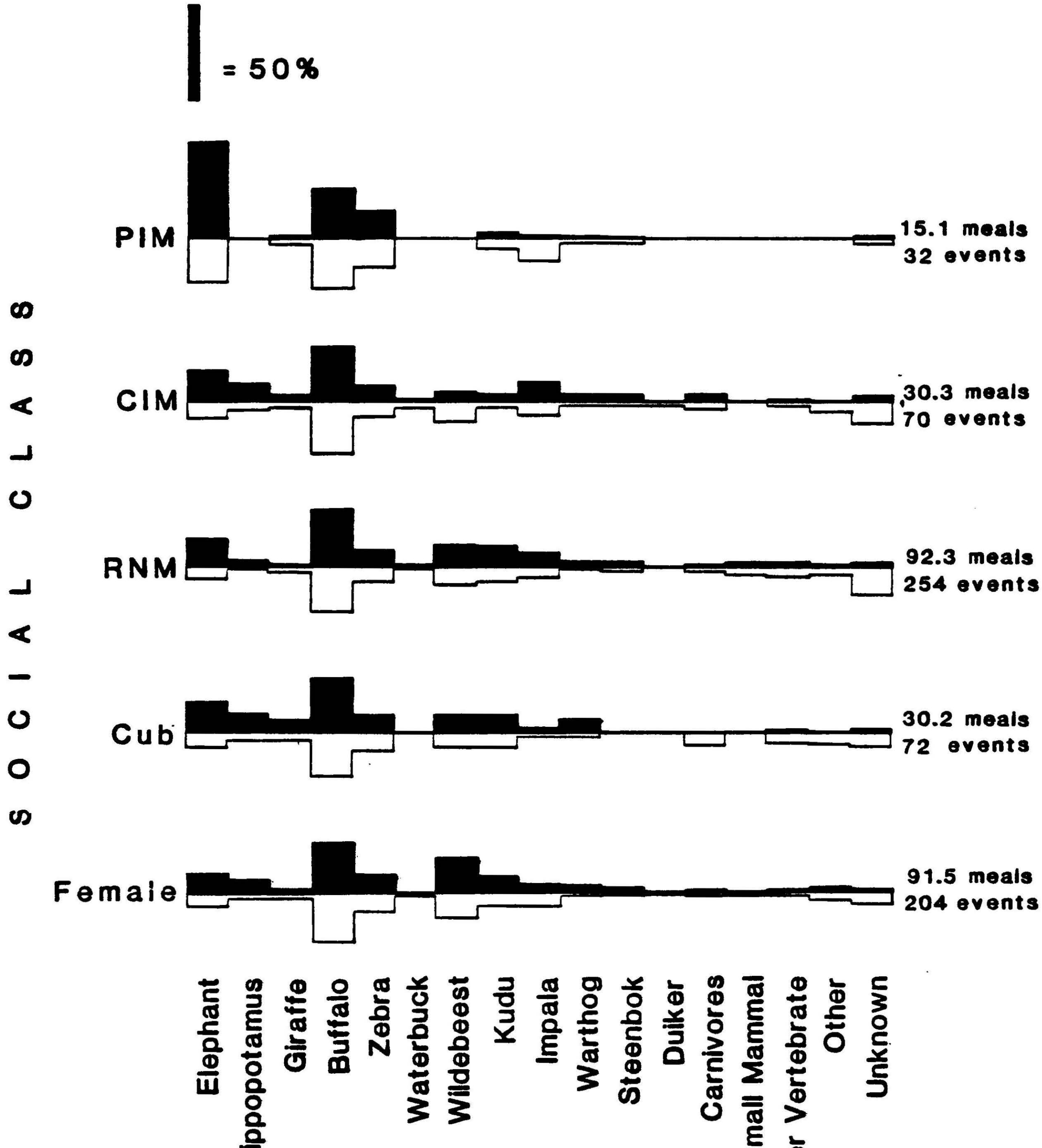

Figure 36: Comparison of diet between different social classes as determined by the number of meals and feeding events.

Consumption

During 55 24h observation periods (27 of females; 28 of males), hyaenas had 115 feeding events, but obtained substantial meals only 12 times and went without food, or only had a morsel on 18 other nights (Table 27). Females spent 48% of the nights without a meal or with only a morsel, once for seven nights in succession without showing ill effects. Males only did so on 18% of the nights, foraged over longer distances and consumed more low-quality items (Table 27; Chapter 3). Observations indicated that males often fed on carcasses abandoned by females, explaining why the consumption of various species was similar between the sexes in the present diet estimate.

Table 27: Feeding records and estimated mass consumed by hyaenas during 24-hour observations (N=55).

	Female		Male		Total	
Nights with	N	%	N	%	N	%
Substantial meal	5	18,5	7	25,0	12	21,8
Small meal	9	33,3	16	57,1	25	45,5
Morsel only	3)	48,1	2)	17,9	5)	32,7
No meal	10)		3)		13)	
Total	27		28		55	

Meals	N	kg	N	kg	N	kg
Substantial	5	45,0	7	63,0	12	108,0
Small	18	36,0	31	62,0	49	98,0
Morsel	10	1,0	44	4,4	54	5,4
Total meals	33		82		115	
Consumed (kg/day)		3,0		4,6		3,8

Assuming the average mass of a substantial meal was 9kg and of a small meal was 2kg and that each morsel represented 0,1kg, the average amount eaten in 24h (N=55) was calculated as 3,8kg. Males consumed more food per day (4,6kg) than did females (3,0kg), as would be expected with the lower-quality diet of males. Although females moved shorter distances in a night than males (16,5km cf. 23,6km; Chapter 3), they obtained substantial meals at similar distance intervals as males did (89km cf. 94km). Assuming the above consumption quantities, males obtained food at a rate of 195g/km and females 185g/km. Considering that females gained a higher proportion of meat and may have consumed greater quantities at a meal due to higher priority of access, it is likely that females had a better nett energy economy than males had.

DISCUSSION

Despite differences in the accuracy of various hyaena diet estimates, similarities in the representation of major prey species in feeding events compared to better quantitative methods, validates the use of this method in feeding studies, and enables comparison of present data with those from previous studies. However, **examinations** of scats tend to overestimate scavenged and small prey and do not appear to indicate diet as accurately for spotted hyaenas as they do for wolves (Floyd, Mech & Jordan 1978). This is in agreement with previous studies (Kruuk 1972; Bearder 1977). The differences in the scat content of zebra and wildebeest hair in the present study, compared to observations of hyaenas feeding on these prey cannot be explained by differences in the ability to recognize their hair. A single wildebeest hair was diagnostic, while zebra hair usually required the examination of a spectrum of shapes for positive identification. For this reason, it would be expected that the results would overrepresent wildebeest relative to zebra, rather than vice versa. Furthermore, sampling bias of scats (Buys 1983) was not a factor, as samples were collected 21 times at monthly intervals.

Mavumbye hyaena diet related to prey size and abundance, but those ungulate species that had been affected most by the drought, buffalo, kudu, impala and warthog (Chapter 5), were consumed more than expected. The former are mostly scavenged, either as drought victims or lion kills. Although the killing agent was uncertain in most cases, the high prey importance ratings of kudu, impala and warthog, confirm the suggestion put forward in Chapter 5 that Mavumbye hyaenas were selectively hunting these species. This preference could be related to the hyaenas' hunting ability and/or to the vulnerability of drought-affected prey.

The results of the scat analysis indicated that, overall, impala and buffalo carcasses were major food items in the Kruger National Park during 1982/1983. Despite the tendency of this method of diet determination to overemphasize the importance of these two species, the consistent high representation of these ungulates in aerial censuses, as well as hyaena diet, supports the conclusion that Kruger National Park hyaenas frequently hunted impala and scavenged buffalo. Kudu and zebra were also consistently represented in the diet in all regions examined in the present study. In contrast, wildebeest appeared to be of minor importance.

Differences in diet between regions appeared to be related to prey availability. The high representation of kudu in scats from Pretoriuskop could reflect a preference by hyaenas that exceeds that observed for Mavumbye hyaenas (but which was not confirmed by scat analysis) and may be related to wide-spread effects of the drought (Chapter 5).

These data differ from those obtained in previous studies conducted in nearby regions in the Transvaal Lowveld (Table 28). Smuts' (1979) visual macroanalysis of stomach contents of 167 hyaenas that were culled during 1974 to 1978 in a region encompassing the Mavumbye and Orpen areas (see Chapter 4), compared poorly to results of the present study (r=0,23; P>0,1). As the accuracy of the different techniques differed, dissimilarities cannot be ascribed to differences in feeding patterns.

Hirst (1975) and Bearder (1977) reported few buffalo, but numerous giraffe and wildebeest in the Timbavati Reserve, adjacent to Orpen, where Bearder (1977) determined hyaena diet by analyses of scats and regurgitations. These differences in ungulate populations from all seven regions examined in the present study were reflected in the hyaena diet (Table 28), so that the results of the different studies did not compare well (Mavumbye cf. Timbavati: r=0,09; Six other regions cf. Timbavati: r=0,61; P>0,05). However, in all Lowveld regions, hyaena diet indicated an emphasis on medium-sized ungulates (<100kg), which were probably hunted, and on very large ungulates (>350kg), which were probably mostly scavenged. This pattern is consistent with observations of the Mavumbye clan.

Table 28: Spotted hyaena diet (%) in the Transvaal Lowveld determined by scat analysis (present study; Bearder 1977), and regurgitations (Bearder 1977).

	PRESENT STUDY				BEARDER		LOWVELD	
	Mavumbye Clan		6 Other Regions		Timbavati		Total	
Species	N	%	N	%	N	%	N	%
UNGULATES								
Elephant	4	0,6	4	0,8	-	-	8	0,4
Giraffe	5	0,8	24	4,9	347	32,5	376	17,2
Buffalo	262	41,2	107	21,9	-	-	369	16,8
Zebra	66	10,4	27	5,5	45	4,3	93	4,2
Waterbuck	16	2,5	19	3,9	9	0,9	44	2,0
Roan	-	-	7	1,4	-	-	7	0,3
Sable	2	0,3	2	0,4	-	-	4	0,2
Wildebeest	29	4,6	5	1,0	127	12,0	161	7,3
Tsessebe	4	0,6	3	0,6	-	-	7	0,3
Kudu	24	3,8	40	8,2	1	0,1	64	2,9
Nyala	-	-	12	2,5	-	-	12	0,5
Reedbuck	9	1,4	10	2,0	-	-	19	0,9
Warthog	13	2,0	13	2,7	-	-	26	1,2
Impala	80	12,6	159	32,6	451	42,6	690	31,5
Steenbok	5	0,8	7	1,4	6	0,6	18	0,8
Duiker	-	-	2	0,4	24	2,3	26	1,2
CARNIVORES								
Hyaena	10	1,5	-	-	-	-	10	0,5
Mongoose	2	0,3	3	0,6	1	0,1	6	0,3
Genet	1	0,1	-	-	-	-	1	0,0
OTHER								
Aardvark	-	-	2	0,4	-	-	2	0,1
Baboon	-	-	-	-	9	0,9	9	0,4
Porcupine	1	0,1	-	-	2	0,2	3	0,1
Scrub hare	1	0,1	-	-	6	0,6	7	0,3
Mouse	4	0,6	7	1,4	8	0,8	19	0,9
Aves	6	0,9	2	0,4	6	0,6	14	0,6
Reptilia	1	0,1	-	-	7	0,7	8	0,4
Hexapoda	2	0,3	-	-	-	-	2	0,1
Plant	2	0,3	-	-	-	-	2	0,1
Artifact	2	0,3	-	-	9	0,9	11	0,5
Unknown	95	14,9	33	6,8	9	0,9	137	6,3
Items	636		488		1068		2192	
N	525		300		727		1552	
UNGULATES		80,4		90,4		94,6	1924	87,8
GROUP IV		42,6		27,6		32,5	753	39,1
GROUP III		18,4		12,8		17,2	316	16,4
GROUP II		19,8		48,0		17,2	811	42,2
GROUP I		0,8		1,8		2,9	44	2,3

In all regions in which diet has been estimated by direct observations, *Crocuta* depend mainly on ungulates larger than 100kg (Fig.37). In Ngorongoro, where hyaenas were the most numerous large carnivores, they often hunted zebra and wildebeest and showed a more specialized diet than on the Serengeti plains, where zebra and wildebeest were often scavenged from lions and sometimes hunted (Kruuk 1972). In the Kalahari desert, where both lions and spotted hyaenas are widely dispersed and consequently meet relatively seldom, the hyaenas relied mostly on gemsbok and wildebeest and some springbok, which they usually hunted themselves (Mills 1984a,b). Prey selection was similar in the Namib desert, where there were no lions, and hyaenas mostly consumed mountain zebra and gemsbok, at least half of which they killed (Tilson *et al* 1980). These patterns contrast with that observed in the Mavumbye area, where lions outnumbered hyaenas and prey diversity was high. Not only did hyaenas scavenge a higher proportion of carcasses than elsewhere, but they occasionally killed a variety of small prey, and thus had a less specialized diet than spotted hyaenas in other regions. The greater reliance on subsistence diet between big meals may explain observed differences in the distance moved between substantial meals by Mavumbye hyaenas compared to Kalahari hyaenas (92 cf. 33km; Mills 1984a).

The feeding behaviour of Mavumbye hyaenas at large carcasses was comparable to that observed in the Namib desert (Tilson & Hamilton 1984). Although rank in feeding priority influenced food quality (Chapter 3), this had little effect on the frequency and

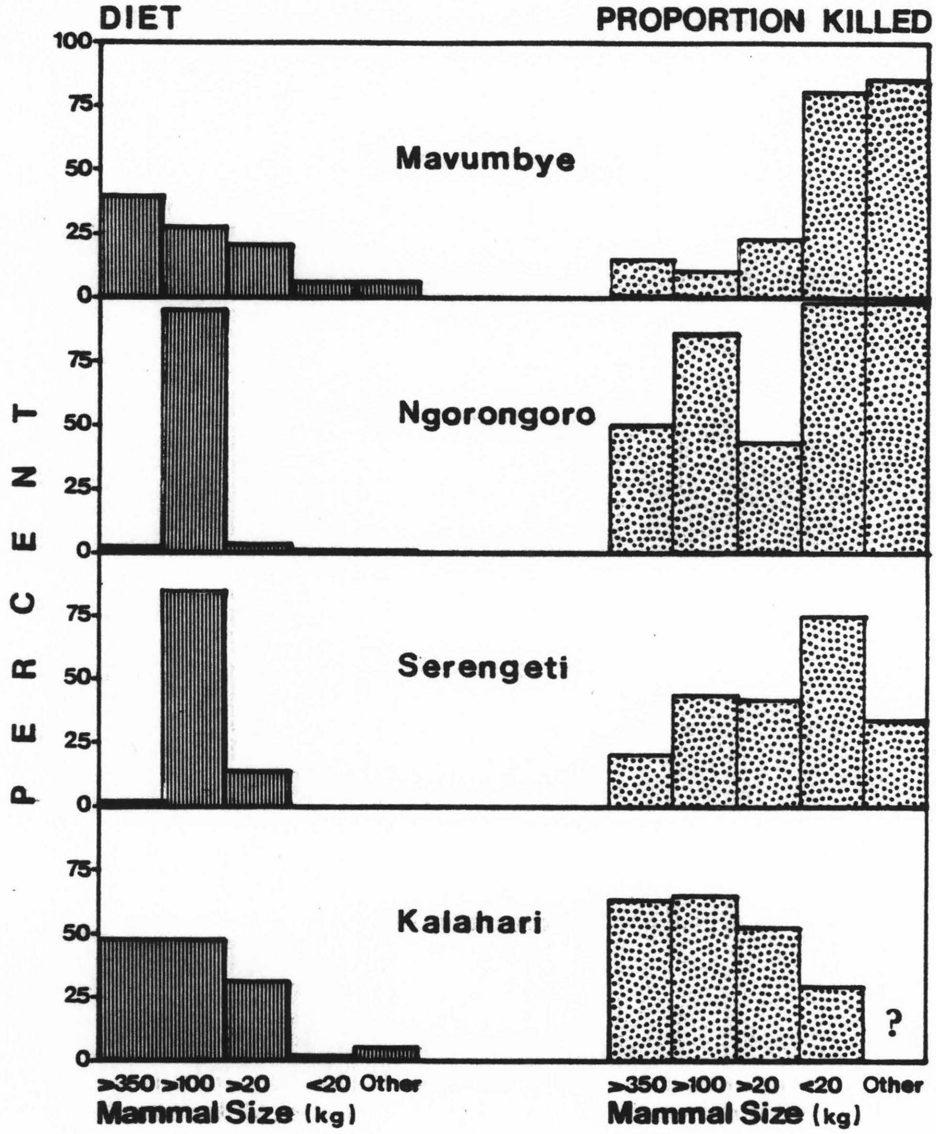

Figure 37: Size class of mammal prey in hyaena diet, estimated by the number of feeding events and the proportion (%) of prey killed by the Mavumbye clan compared to hyaenas in Ngorongoro and Serengeti (Kruuk 1972) and Kalahari (Mills 1984a,b).

duration that hyaenas were seen feeding on various ungulate species, but males and juveniles consumed more small items. This emphasizes that hyaena diet reflects prey availability rather than hyaena preference or energetic requirements *per se*. Consequently, diet can be determined by observing any adult hyaenas living in an area.

Spotted hyaenas can make efficient use of a food abundance, but are also very capable of enduring long periods of over a week without food. At a large carcass, a hyaena can eat substantial meals for a number of nights in succession until all meat is finished. Matthews (1939b) found that few culled hyaenas in East Africa had undigested food items in their stomachs. He concluded that a hyaena keeps food in the stomach for a short time only before it passes to the small intestines. This would enable a hyaena to eat again soon after its last meal. The maximum feeding capacity of hyaenas exceeds 25% of their body mass. Bearder (1977) measured one hyaena eating 18kg, an observation confirmed by the maximum of 17kg measured for Namib hyaenas (pers.obs.). The physiological ability of coping with periods of feast and famine must be of great advantage to a hunter and scavenger whose food availability can be subjected to considerable fluctuations.

The estimate of mean food consumption of 3,8kg/hyaena/day in the present study is the same as the amount estimated by Green *et al* (1984) and similar to the 4,0kg/hyaena/day measured in the Namib desert (pers.obs.). In contrast, Kruuk (1972) estimated that East African hyaenas consumed about 1,5-2kg/hyaena/day. Each of the four consumption estimates were obtained by a different method. Kruuk (1972) had counted all kills observed in the territory of a Ngorongoro clan in 38 days, wheras Green *et al* (1984) measured sodium and water turnover rates of three individuals. In the Namib desert carcasses were weighed before and after hyaenas were observed consuming 63 meals in 19 nights (pers.obs.). This could be used to propose a subjective visual estimate of the size of meals obtained by feeding individuals. The latter method was applied in the present study.

Differences between authors could be due to the use of different methods. However, three recent estimates from southern Africa contradict Kruuk's (1972) findings, possibly because:

(a) Adults in East Africa were 20% smaller (52 cf. 65kg) but corrections for this (38,5 cf. 61,5g/kg/day) still do not explain the difference.

(b) Differences between Ngorongoro and Mavumbye in territory size (35 cf. 130km^2), ungulate density (95 cf. 11 ungulates/km^2), activity period (3,8 cf. 6,6h), and daily distance moved (10,1 cf. 20,1km), could contribute to differences in daily energy expenditure.

(c) In comparison with other species, the estimated consumption of adult hyaenas in East Africa was less than expected for a social carnivore of that size, whereas the southern African estimates compared better (Fig.38). It is possible that Kruuk (1972) had underestimated the number of carcasses killed by the Ngorongoro clan, or overestimated the number of individuals that benefitted from observed kills.

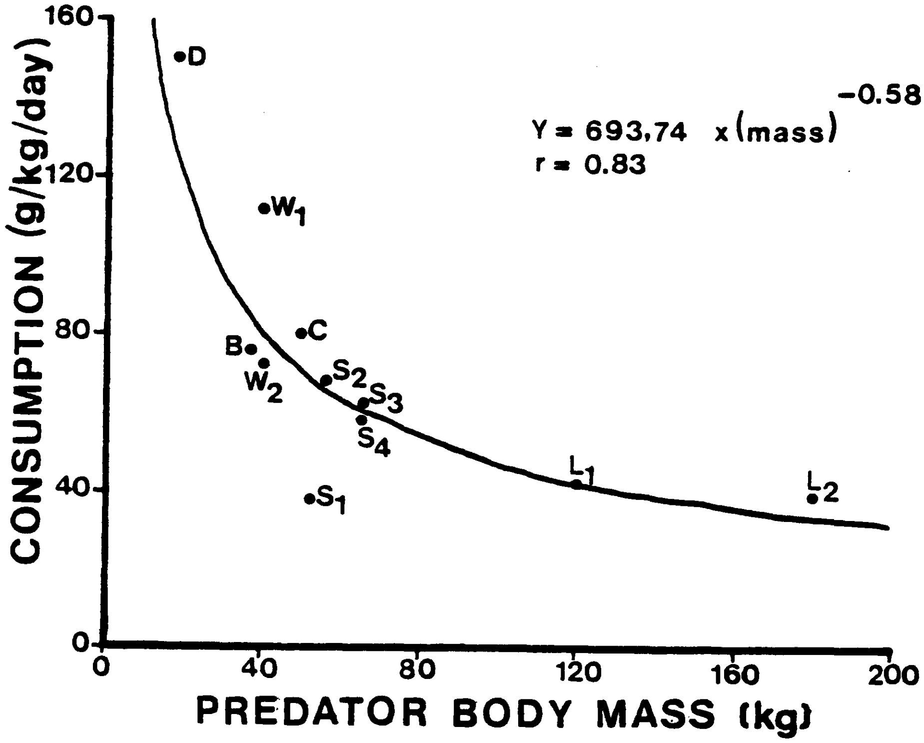

Figure 38: Estimated mean daily consumption by large carnivores relative to their body mass. Species codes are: D=*Lycaon pictus*; W=*Canis lupus*; B=*Hyaena brunnea*; C=*Acinonyx jubatus*; S=*Crocuta crocuta*; L=*Panthera leo*. Data sources are: D=Estes & Goddard 1967; W1=Mech 1970; W2=Fritts & Mech 1981; B=Mills 1977; C=Schaller 1972; S1=Kruuk 1972; S2=Green *et al* 1984; S3=pers.obs. in Namib; S4=present study; L1 & L2=Schaller 1972.

Mavumbye hyaena males and females were estimated to obtain food at similar rates (190g/km), but because females consumed a greater proportion of meat, they may have had a better nett energy economy. Although the present estimate of consumption by each sex is crude, it is supported by much circumstantial evidence from other observations. Not only did females have high feeding priority, often at the expense of males (Chapter 3), but they foraged over shorter periods and distances in a night and located **fewer** food items (or passed by more items), suggesting that they were better satiated and discriminated between high- and low-quality food (Emlen 1966). As females moved about in larger groups than males did, they were more likely to participate in successful hunts (Chapter 5). Although males had larger home ranges than females had for reasons other than food, one of the effects would be that male home ranges contained higher prey biomass. Despite their larger body size, females had smaller home ranges, which satisfied their metabolic requirements (Gittleman & Harvey 1982; Chapter 6), indicating a good dietary status.

8: DISCUSSION: CONSERVATION

Introduction

The tradional view on communities and their subsets, such as predator-prey systems, adopts a deterministic approach. The existence of optimal equilibrium levels of both predators and prey are presumed and are calculated to assess the current status of a system relative to these theoretical levels. This is done especially to establish guidelines for the conservation of wildlife reserves, such as the Kruger National Park, which are subjected to some human influence. The underlying assumptions are that a natural system needs to achieve some degree of equilibrium to preserve its natural state, and that instabilities are detrimental to the system.

Recent theoretical developments in the physical and biological sciences are changing this view of living systems (reviewed by Gutmann & Bonik 1981). According to this approach, non-equilibium is believed to be a fundamental property of biological units, or levels, causing them to maintain a constant readiness to change. At any point in time, all subsets of a system, including interspecific and intraspecific relationships, physical and biotic environments, and so-called artificial man-induced phenonema, form unique ecosystems, which are each separately and combined subjected to selection pressure. Unlike the organism, social unit, population or community, species are not viewed as units of selection, but as organisms with genetic compatability enabling reproduction to take place.

In this Chapter, the role of hyaenas as predators in the Central District of the Kruger National Park is examined in the light of current views of other predator-prey systems. These adopt the premise that living organisms, whether plant, herbivore or carnivore, tend to maximise opportunities of genetic compatibility for reproduction within environmental limits. Relative abundance of various species, as well as observed (social and predatory) relationships between organisms serve as convenient indicators of change in a system. This, in turn, can be useful for an understanding of events that followed the purposeful manipulation of a system as already applied in the Kruger National Park and can be useful to formulate an alternative conservation philosophy.

Predation Impact

Possible influences of predation on prey populations have been discussed extensively. Reports conflict because effects of predation on prey are often complex and differ in various circumstances. In early reviews of the subject, Errington (1946; 1967) expressed the opinion that predators merely accelerate the effects of other mortality factors, such as starvation, disease or old age. Because prey populations tend to compensate for mortalities sustained by predation, the latter probably do not influence prey density levels, except, perhaps, on a very local scale. Food, rather than predation, appears to be the fundamental controlling factor (Lack 1954; 1966; Peek 1980). However, it has been emphasized that predator-prey systems are affected by a multitude of factors, which either determine stability or eruptive cycles during which predator-prey relationships change, so that conclusions change (Lidicker 1978).

Evidence has emerged that, in periods when the densities of some species are reduced due to environmental factors (natural, climatic or man-induced), predation can further depress numbers or affect the ability of prey to increase (Pearson 1964; 1966; 1971; Fitzgerald 1977; Lidicker 1978). Intrinsically regulated predator populations with several alternative prey species can permanently depress the populations of some of their preferred prey species (Liberg 1981; Erlinge, Göransson, Hansson, Högstedt, Liberg, Nilsson, Nilsson, von Schantz & Sylvèn 1983; Erlinge, Göransson, Högstedt, Jansson, Liberg, Loman, Nilsson, von Schantz & Sylvèn 1984). A study of wolves in Alaska demonstrated unequivocally that these predators can further depress or prevent recovery of harvested prey populations following unfavourable weather conditions over a number of years (Gasaway, Stephenson, Davis, Shepherd & Burris 1983). Such situations can be resolved when the predator population and other environmental factors change (Lidicker 1978).

Predation by large carnivores, such as African lions (Schaller 1972; Rudnai 1973), mountain lions *Felis concolor* (Hornocker 1970), wolves (Mech 1970; Hoskinson & Mech 1976; Fritts & Mech 1981; Nelson & Mech 1981) and spotted hyaenas (Kruuk 1972; Tilson *et al* 1980), appears to be influenced, at least to some degree, by prey condition and vulnerability. This may confound controlling effects of predators on prey populations, although it may influence prey behaviour and space utilization (Hornocker 1970). Conversely, the latter may regulate the extent of predation. So, for instance, white-tailed deer *Odocoileus virginianus* living in suboptimal habitat in wolf territory buffer zones, survived best (Fritts & Mech 1981; Nelson & Mech 1981). In Africa, migratory ungulates appear to be subjected to less predation pressure than resident ungulates. For example, in the Ngorongoro crater, where there is a high density of resident wildebeest, spotted hyaena predation was of the same order of magnitude as wildebeest recruitment, whereas the migratory Serengeti wildebeest were affected little by hyaena predation (Kruuk 1972).

Predator-Prey Manipulation

Medium to large ungulate populations of the Kruger National Park are confined within its limits. In the early 1970's, the main migratory species, zebra and wildebeest, were affected by a number of natural and man-induced factors that depressed their densities. The cutting of migration routes with fences, followed by culling, a severe drought, then a number of very wet years that further reduced available food to these short-grass grazers, and possibly increased vulnerability to predation, depressed zebra numbers in the Central District from some 13000 in 1969 to about 7500 in 1975 and wildebeest from 14000 to 6700 in the same period (Smuts 1975; 1978a).

It was felt that after these reductions, predation by lions and hyaenas had lead to the following situation (Joubert *et al* 1974; Smuts 1975):-

1) Zebra and wildebeest, the preferred prey of lions (circumstantial evidence), could not increase their densities again, because they were believed to be in a situation akin to a predator-trap (Caughley 1981) i.e. herbivore-plant interactions became less important than predation in determining population densities.

2) A reduced availability of preferred prey might cause lions and hyaenas to kill more of other species, some of which had a precarious status in the park. The more abundant ungulates would sustain the predator population, and this would maintain

the predator-trap situation on preferred prey.

Since lion and spotted hyaena populations were thought to have the capacity to recover rapidly under favourable food regimes, a temporary reduction by culling was believed to be the best solution (Joubert *et al* 1974). Lions were monitored before and after culling (Joubert *et al* 1974; Smuts 1975; 1976a,b; 1978a,b,c; Bryden 1976; Smuts, Hanks & Whyte 1978; Whyte pers.comm.), but this was not done for hyaenas.

The discussion that follows below, is an attempt to examine some relevant considerations regarding spotted hyaena conservation, based mainly on the findings of the present study. Limitations of this investigation are the small scale (within the boundaries of a single social unit) and that it was conducted only in the post-culling period, during which predator-prey relationships may have changed. Nevertheless, the interactions of spotted hyaenas with ungulates, their food procurement, the nature of social relationships, space utilization and dispersal patterns all have some bearing on the subject.

Importance of Hyaena Predation

The foraging behaviour (Chapter 5) and diet (Chapter 7) of spotted hyaenas in the Mavumbye area indicated that they were largely scavengers, but could benefit substantially from their own kills, which were made occasionally. Although highly carnivorous, these hyaenas had catholic feeding habits, and were the least specialized feeders of any population of spotted hyaenas studied to date. The 49% of all food items (N=267) that comprised ungulates, constituted the bulk (95%) of hyaena diet. Only a few ungulate carcasses (>18%) emanated from kills by hyaenas, but these high-quality items constituted about half

(51%) of the quantity of food eaten, indicating that it was essential for hyaenas themselves to occasionally kill prey. As members of the Mavumbye clan ate full meals at average intervals of 4-5 nights, half of which were from own kills, an individual would be expected to partake of a hyaena kill of steenbok size or larger every 8-10 days.

The high prey importance ratings of kudu, impala and warthog (percent in diet relative to abundance in population = 2,9) indicated that disproportionate mortality factors were acting on these species. Observations of hyaena foraging behaviour support the suggestion that hyaenas were hunting selectively (Chapter 5). Before the possible importance of hyaena predation on these species can be evaluated, it should be noted that large ungulates were the staple food of Mavumbye hyaenas (Chapter 7), because:

a) Buffalo were often killed by lions and some starved during the 1982 drought, leaving much scavenging material;

b) Zebra and wildebeest were very abundant and were consumed regularly, although they had low prey importance ratings (0,7);

c) Very large carcasses, such as hippopotamus or elephant, although rarely available, made a high contribution to Mavumbye hyaena diet.

Mavumbye hyaenas killed a much smaller proportion of their prey than observed elsewhere (Kruuk 1972; Tilson *et al* 1980; Mills 1984b) and those kills that they made, were mostly small to medium-sized ungulates (<100kg) or were obtained fortuitously. In such circumstances, hyaena group sizes were usually small, as would be expected for scavengers and opportunistic predators.

Conversely, if hyaena group size can be used as an indicator of the food regime, small mean group size of hyaenas sighted throughout the Kruger National Park (Mills 1985b) would support the suggestion that this hyaena population led a largely scavenging and opportunistic hunting existence, as in the Mavumbye clan. This was also supported by an analysis of scats, which indicated that large ungulates (>100kg) formed the bulk of hyaena diet throughout the Kruger National Park, except in some regions, such as Lower Sabie and Orpen, where impala were very abundant.

Hyaena predation on kudu, impala and warthog is discussed against this background. Less data are available for impala and warthog than for kudu, but it was indicated (Chapter 5) that hyaena relationships to them were similar as those for kudu cows and calves, on which this discussion focusses.

In their foraging and hunting behaviour, Mavumbye hyaenas showed a preference for kudu (Chapter 5), which was reflected in the high prey importance rating of this species (Chapter 7). Kudu also formed a disproportionately high part of the hyaena diet at Pretoriuskop during 1982/1983, close to an area where population parameters of kudu were monitored. Owen-Smith (pers.comm.) noted that the effects of rainfall on kudu recruitment were mediated mainly by calf survival rather than rapid changes in adult mortality or birth rate. Indications were found (see Chapter 5) that changes in kudu calf survival during and after the drought may have been mediated in part by hyaena predation. However, selective predation appeared to be confined to the 1982/1983 cohort of kudu calves which had endured malnutrition during early life, with much higher recruitment rates being recorded in subsequent years (Mason 1985; pers.comm.; Owen-Smith pers.comm.).

It is concluded that hyaenas were responding to temporary

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environmentally-induced changes in the vulnerability of a prey population sector and were not maintaining a predator-trap that would have prevented prey population growth when favourable environmental circumstances returned again. Similar predator-prey relationships have been identified between wolves and moose on Isle Royale (Peterson 1977). Data on diet (Chapter 7) and group size (Mills 1985b) obtained for hyaenas elsewhere in the Kruger National Park support the suggestion that the general pattern of scavenging and predation reported in the present study was probably not confined to the particular study conditions of the Mavumbye clan, but was broadly similar for the Lowveld population, although the particular prey species involved may have differed regionally.

Similar conclusions can be made for the alleged preference hyaenas may have shown for zebra and wildebeest during the early 1970's. This would probably have been a temporary response to environmentally-induced factors. With their heavy reliance on scavenged large carcasses and flexible predation patterns on a wide variety of species, there is no evidence that spotted hyaenas depressed any of the prey species in the Kruger National Park.

Demography

When several neighbouring spotted hyaena clans were suddenly reduced in size by culling, the population was slow to recover (Chapter 4). This phenonemon may not only be a special condition of the local hyaena population, as reports of other instances of culling suggest similar responses elsewhere (e.g.Nairobi National Park; Kruuk 1972; pers.comm.). Despite limitations of sample size in the present study, some general conclusions can be

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made for the hyaena population in the Central District of the Kruger National Park, based on characteristics which affect recruitment and the maintenance of clan integrity:-

a) Females are philopatric and breed in their natal clan. Despite the existence of a dominance hierarchy among females, which determines relative degree of access to food, all adult females are potentially able to breed at any time (Chapter 3). Litters are small and recruitment rate can be affected by the ability of different females to synchronise births (Chapter 4). Amicable relationships between females and their offspring ensure the maintenance of clan integrity, while their highly developed territorial behaviour ensures them monopoly over local food resources and resists intrusion by members of other clans (Chapter 6).

b) Males leave their natal clan and appear in neighbouring clans as prospective immigrants, or gain membership as peripheral immigrant males or central immigrant males. The latter role appears to be held by only one male at a time, which maintains close attendance on females and achieves breeding status. As a result of the polygynous mating system, individual immigrant males play a minor role in the maintenance of clan integrity (Chapter 3) and territory defence (Chapter 6), and may suffer casualties when moving between clans.

c) Response to live prey and carcass distribution patterns suggest that these determined the land tenure system of hyaenas (Chapter 5 & 6). If the hypothesis regarding the relationship between prey distribution and hyaena territory size is correct, then territory sizes of hyaenas prior to culling in 1974, should have been of similar size as at present and clan sizes bigger.

Although the present hyaena density was probably below the limits of food resources, with the Mavumbye clan annually consuming only some 5,5% of the mean biomass of ungulates smaller than 1000kg (Chapter 7), hyaena population growth appeared to be limited. Ultimate regulation of population density appeared to be determined by factors affecting cub survival, which are thought to be less detrimental in big clans with communal dens. These determine the rate at which losses of adults, for which lions were largely responsible (Chapter 4 & 5), could be replaced.

d) Following the death of all females in a clan, and cessation of territorial defence of the area, permanent re-occupation and re-establishment of the territory by a new clan did not take place. Although some neighbouring clans expanded their territories in the direction of the newly vacated area (Chapter 6), it is apparent that hyaenas are slow to resolve changes in land tenure.

In spotted hyaenas, splinter groups have rarely been reported to part from existing nursery units to form new clans. Although, to date, clan fission has been recorded only once (Mills 1985a), the eventual fate of the splinter group was unknown in that case (Mills pers.comm.). The ability of spotted hyaenas to colonize vacant areas is thus unknown.

Evolution and Conservation Philosophy

It is possible that the social evolution of hyaenas did not involve an adaptation or exaptation to possible catastrophes, because rapid large-scale hyaena population reductions might be very rare in nature. For instance, no reports on outbreaks of epidemic diseases in hyaenas are known to the author, although these animals probably often come into contact with victims of

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diseases.

Fossil records indicate that the large African carnivore fauna underwent a major change around 3,5 million years ago, which marks the disappearance of some species and the appearance of others. Notably, the latter included modern-day spotted hyaenas, striped hyaenas, lions, leopards and cheetahs (Turner 1985). Despite a great degree of behavioural flexibility of extant spotted hyaenas, this is not so large as to span the differences in the ecology of social hunter-scavengers and scavengers that forage asocially, such as *Hyaena brunnea*, differences which are reflected in the morphology. It is therefore reasonable to assume that since its first appearance, *Crocuta crocuta*, which has undergone little morphological change in the last 3 Myr (Turner 1984), has displayed a similar degree of sociality and, hence, similar dietary patterns as seen today. Therefore, it is probable that the simultaneous appearance of *Panthera leo* and *Crocuta crocuta* could have involved a degree of coevolution regarding the utilization of large ungulates as the main food source. With such a long history of relationships, competition between lions and hyaenas should not have resulted in clan demise if hyaena recruitment had been normal.

The question regarding the apparent reduced ability of hyaenas to recover from culling presumes a deterministic approach towards species conservation, which should be avoided. Rather it can be argued that any man-induced or natural changes to an existing ecosystem create new circumstances which can be subject to different selection pressures than those prevailing previously. Therefore, developments that occurred during the post-culling period involved a unique situation, which need not neccessarily return to its previous status. This interpretation places a high degree of responsibility on conservation practises, as the eventual outcome of manipulations may not be predictable and are irreversible.

9: SUMMARY

The aims of the present study of *Crocuta crocuta* were to describe its social organization and dispersal patterns and how these relate to resource procurement, reproduction and clan integrity, to describe how environmental parameters affect foraging behaviour and spatial organization, to describe diet in terms of prey availablity, food preferences and requirements, and to determine how these findings affect conservation considerations.

Fieldwork concentrated on one social unit of 11 spotted hyaenas, the Mavumbye clan, whose members were observed for 3678h over a period of 27 months in an area near Satara, in the Central District of the Kruger National Park.

Membership, social relationships and dispersal were recorded for the Mavumbye clan. Five social classes were recognized, namely, five females, their cubs, three resident natal males (RNMs), six peripheral immigrant males (PIMs) and two central immigrant males (CIMs), although no more than four immigrant males were present simultaneously. The linear dominance hierarchy was strongly expressed at food, but was similar to the hierarchy recorded away from food. Females were philopatric and maintained a network of amicable relationships amongst each other and their offspring. Social dominance assured them priority of access to carcasses, so that they obtained a high proportion of meat. Males left their natal clans and attempted to join neighbouring clans, where they were initially treated as territorial intruders, but could eventually gain membership albeit with low social status, lowest feeding priority at carcasses and precarious social relationships. An immigrant male that maintained close attendance on females, became a central immigrant and gained unrivalled breeding status. This segregation of the clan into cooperative relatives and subordinate immigrants assured an optimal distribution of resources.

The Mavumbye clan occurred in an area where hyaenas had been culled seven years previously, so that the present density of 7,5-9,8 hyaenas/100km^2 in four clans, was about a third to half of that prior to culling. Some fundamental factors that affect clan integrity, were examined in an attempt of explaining the demise of the Mavumbye clan in month 24. It is concluded that the failure of females to synchronize litters and establish a communal den, could have led to high cub mortality, so that recruitment could not offset natural adult mortalities caused by interactions with lions and between neighbouring clans. This emphasizes the importance of mutualistic relationships between *Crocuta* females, as expressed by communal denning. The unpredictability and irreversibility of events following culling stress the need for caution in conservation measures.

Spotted hyaenas were predominantly nocturnal (89%) and were equally active at any time of night, irrespective of lunar phase, but strong wind and rain inhibited activity. Some 56% of the activity period (6,6h/night) was spent foraging singly or in small groups ($\bar{X}$=1,8), shorter by females than by males, which consequently located more food items and had more encounters with other mammals. These differences are explained by differences in feeding priority between the sexes.

Hyaenas could consider any vertebrate smaller than elephant as potential prey. Factors such as rainfall, which affected the vulnerablity of some ungulate species, especially kudu, appeared to influence the hyaenas' foraging behaviour and prey interactions. Frequent availability of scavengable food and an abundance of small prey, whose carcasses were not shared, favoured small hyaena group size. Larger groups could occasionally cause the death of large quarry and more readily attacked lions at carcasses in attempts to appropriate food. Despite rivalry for possession of carcasses between carnivores, with body size and degree of sociality influencing dominance, vultures did not appear to affect hyaena behaviour. This was consistent with the conclusion that, although opportunistic, hyaena foraging behaviour and interspecific interactions discriminated between more and less profitable potential food sources in terms of their availability and defensibility.

All members of the Mavumbye clan shared a common home range, but females most actively scent-marked and defended the $130km^2$ territory, whereas males, except central immigrants, occasionally ventured outside it. Hyaenas spent 18% of their active time on territory patrol, when they traversed the territory peripheries in relatively large groups and scent-marked on 64 latrines. Contact between clans was avoided and individuals spent most time near the territory centre. Social affiliations affected comparative intraterritorial space utilization by individuals, which also appeared to be influenced by a number of ecological factors, namely, distribution of scavengable food, activity centres of lions, prey distribution and inconsistent effects of mortality factors on ungulates in different ecotopes. The resultant patchy distribution of food was probably important in determining the territory size of the clan, which overlapped the borders of the marula knobthorn and dwarf knobthorn landscapes.

However, this relationship was disrupted when clan size decreased in month 17 and a larger neighbouring clan appropriated a territory sector. After month 24, when all Mavumbye females had died, the remaining males ceased to defend the territory against intruders, demonstrating that the defence of the key resource for females, food, underlies the territorial behaviour of *Crocuta*.

Comparison of parameters recorded during observations of feeding, indicated that an estimate of diet determined by counting numbers of feeding hyaenas compared well with better quantitative methods, which measured feeding duration and assessed quantity obtained by each feeding individual. This enabled comparison with other studies. Ungulates formed the bulk (95%) of Mavumbye hyaena diet, with buffalo being the most important species. Kudu, impala and warthog were consumed more frequently than expected from their abundance, probably because of high hunting success on these drought-affected species. Although about 80% of the ungulate carcasses were scavenged, more than half of the estimated quantity consumed was from hyaena kills, emphasising the importance of hunting. However, no evidence was found that hyaenas depressed prey populations. Examination of prey remains in hyaena scats tended to overrepresent scavenged and small prey, but could be used to indicate that hyaena diet elsewhere in the Lowveld also depended on prey availablity, and that buffalo and impala were generally the most important prey species. A crude estimate of consumption supports earlier calculations of average daily consumption of 4kg/individual by southern African hyaenas. This study predicts that females have a better nett energy economy than males have, which may be neccessary to improve their reproductive output.

OPSOMMING

Die doel van hierdie studie van die gevlekte hiëna *Crocuta crocuta* was om die sosiale organisasie en verspreidingspatroon van die spesie te beskryf en om vas te stel hoe dit verband hou met hulpbron bekoming, voortplanting en die integriteit van die familietrop. Verder, is beskryf hoe omgewingsveranderlikkes die soek na voedsel en die gevolglike ruimtegebruik van die hiëna beïnvloed. Die samestelling van die dieet t.o.v. die beskikbaarheid van prooi, voedsel voorkeur en ander behoefdes is ondersoek om te bepaal hoe hierdie bevindings natuurbestuurbesluite mag beïnvloed.

Die Mavumbye familietrop van 11 lede is oor 'n periode van 27 maande vir 3678u waargeneem. Die tuisgebied van die trop was net noord van Satara, in die Sentrale Distrik van die Nasionale Krugerwildtuin geleë.

Lidmaatskap, sosiale verhoudings en die verspreidingspatroon van die Mavumbye familietrop word beskryf. Die trop bestaan uit vyf verskillende sosiale klasse, naamlik, vyf wyfies en hul welpies, drie plaaslik gebore mannetjies, ses periferale immigrante mannetjies en twee sentrale immigrante mannetjies. Daar was egter nooit meer as vier immigrante mannetjies gelyktydig aanwesig nie. Alhoewel die liniêre dominansie rangorde in die trop onder alle omstandighede teenwoordig was, was dit by voedsel merkbaar duideliker sigbaar. Wyfies was gebiedsgebonde en het vriendelike verhoudings onder mekaar en hul afstammelinge in stand gehou. Die besit van 'n dominante sosiale rang het die wyfies bevoorregte toegang tot voedsel verseker, en die individue se dieet 'n relatief hoër vleisgehalte gehad. Mannetjies het hulle familietrop verlaat en probeer om by aangrensende troppe aan te sluit. Alhoewel die mannetjies eers as indringers behandel is, is hulle uiteindelik as lede van die trop aanvaar, hetsy met 'n lae sosiale rang, onsekere sosiale verhoudings en 'n lae toegang by karkasse. 'n Immigrante mannetjie wat die status van 'n sentrale immigrant bereik het, het wyfies aanhoudend vergesel wat tot paringsmoontlikhede gelei het. Die familietrop was dus verdeel in koöperatiewe familielede en ondergeskikte immigrante wat 'n optimale verdeling van hulpbronne verseker.

Die Mavumbye familietrop het in 'n gebied voorgekom waar hiënas sewe jaar gelede op 'n groot skaal uitgedun is. Die huidige bevolkingsdigtheid van die vier aangrensende troppe was 7,5-9,8 hiënas/100km^2, wat omtrent 'n derde tot die helfde van die oorspronklikke getalle is. Sekere fundamentele faktore wat die integriteit van die trop beïnvloed was ondersoek, om die verval van die Mavumbye familietrop, wat gedurende maand 24 plaasgevind het, te verklaar. Die gebrek aan gesinkroniseerde werpsels en die afwesigheid van gemeenskapsskuilplekke het tot hoë mortaliteit van werpsels gelei, sodat die natuurlike mortaliteit van volwassenes, wat veral deur leeus en gevegte tussen hiënatroppe teweeg gebring is, nie deur natuurlike aanwas vervang kon word nie. Dit beklemtoon die belang van mutualistiese verwantskappe tussen *Crocuta* wyfies wat die formasie van gemeenskapsskuilplekke bevoordeel. Hierdie bevindings beteken dat uitdunning tot onvoorspelbare en onomkeerbare gevolge kan lei en beklemtoon die versigtigheid waarmee bestuurstappe benader moet word.

Gevlekte hiënas was oorheersend naglewend (89%) met gelyke aktiwiteit dwaarsdeur die nag onafhanklik van verskillende maanfases. Sterk wind en reën het egter aktiwiteitspatrone onderdruk. Hiënas was vir ongeveer 56% van hulle aktiwiteitsperiodes (6,6u/nag) op soek na voedsel, of alleenlopend of in klein groepies ($\bar{X}$=1,8). Mannetjies moes langer na voedsel soek as wyfies en het dus relatief meer voedselstukke gevind en ook meer met ander soogdiere in kontak gekom. Die verskille in toegang tot karkasse tussen die geslagte verklaar egter hierdie gedragsverskille.

Hiënas kon enige werweldier kleiner as 'n olifant as prooi beskou. Faktore soos reënval wat die kwesbaarheid van sekere hoefdiere, veral koedoes, beïnvloed het, het blykbaar die hiënas voedselbekomingsgedrag en verhoudings met potensiëele prooi beïnvloed. Die relatiewe groot voorkoms van aas en groot getalle van klein prooidiere, wat nie onderverdeel kan word nie, het kleiner hiëna groepe bevoordeel. Groter groepe kon egter geleidelik die dood van groter prooidiere veroorsaak en was meer gewillig om leeus by karkasse aan te val om dit te beroof. Ten spyte van die intensiewe wedywering tussen karnivore oor die besit van karkasse, met dominasie hoofsaaklik afhanklik van liggaamsgroote en groep grootte sowel as sosiale groepering, was die gedrag van hiënas in die verband blykbaar nie deur aasvoëls beïnvloed nie. Hierdie verskynsels dui daarop dat hiënas opportunisties na voedsel soek, en dat hul verhoudings met ander spesies gevolglik deur hul vermoë om tussen meer en minder winsgewende voedselbronne te kan onderskei i.t.v. verkryging en verdedigbaarheid beïnvloed word.

Lede van die Mavumbye familietrop het dieselfde tuisgebied gedeel, maar wyfies het meer aktief gereukmerk en die 130km^2 territorium verdedig, terwyl mannetjies, met uitsondering van die sentrale immigrante, geredelik vêr uit die territorium uitgeloop het. Omtrent 18% van die totale aktiwiteitstydperk was aan territorium patrollies bestee, waartydens hiënas die territorium se grensgebiede in relatiewe groot troppe deurkruis het en op 64 verskillende latrines gereukmerk het. Botsings tussen aangrensende troppe was vermy en die hiënas het gewoonlik hulle tyd in die middelste gebied van die territorium deurbring. Die ruimtelike verbruik van 'n spesifieke individu binne die territorium was beïnvloed deur sy sosiale affiliasies, die verspreiding van aas, jaggebiede van leeus, die verspreiding van prooi en die differensiëele kwesbaarheid van hoefdiere in verskillende ekotopes. As gevolg van hierdie faktore was voedsel oneweredig kollerig versprei, wat tot 'n groot mate die territorium grootte en die posisie van sy grense oor die maroela-knoppiesdoring en dwerg knoppiesdoring landstreke bepaal het. Hierdie verhouding tussen voedselbeskikbaarheid en territorium was in maand 17 versteur, toe die Mavumbye familietrop kleiner geword het en 'n groter familietrop 'n sektor van die territorium aan hulself toegeëien het. Na maand 24, toe alle Mavumbye wyfies dood was, het die mannetjies die territorium nie meer teen indringers verdedig nie. Dit lei tot die gevolgtrekking dat die verdediging van voedselbronne, wat die wyfies se sleutel-hulpbron is, die territoriale gedrag van *Crocuta* tot gevolg het.

Die vergelyking van parameters wat gedurende waarnemings van voedingsgedrag aangeteken is, het daarop gedui dat die bepaling van dieet in terme van die aantal vretende hiënas goed vergelyk met beter kwalitatiewe metodes, wat onderskeidelik die tyd wat gevreet is gemeet het, of skatting gemaak het van die hoeveelheid wat elke individu ingekry het. Dié feit maak vergelyking met ander studies moontlik. Die grooter meerderheid van die Mavumbye hiënas se kos (95%) was hoefdiere. Buffels was die belangrikste spesie. Koedoes, rooibokke en vlakvarke is meer dikwels gevreet as sou verwag word van hulle relatiewe bevolkingsgetalle. Dit dui daarop dat hierdie spesies, wat gedurende die droogte gely het, meer suksesvol deur hiënas gejag is. Omtrent 80% van die hoefdier karkasse is ge-aas, maar meer as die helfte van die hoeveelheid kos wat hiënas gevreet het, is egter van selfgevangde karkasse bekom, wat die belangrikheid van jag vir die diere beklemtoon. Daar bestaan geen bewys dat hiënas die getalle van enige prooipopulasies kon onderdruk het nie. Ondersoek van prooioorblyfsels in hiënaketels oorskat die belang van aas en kleiner prooispesies, maar kon gebruik word om aan te dui dat die dieet van hiënas orals in die Nasionale Krugerwildtuin van prooi bekikbaarheid afhanklik was, en dat buffels en rooibokke in alle areas die mees belangrikste prooispesies was. 'n Rowwe skatting van voedsel inname het goed vergelyk met vorige berekenings van die gemiddelde daaglikse inname van 4kg/individu in suidelike Afrika. Hierdie studie voorspel dat wyfies meer energie ekonomies as mannetjies is en dat dit noodsaaklik is om hul voortplantingssukses te verhoog.

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APPENDIX A: VOCAL COMMUNICATION

INTRODUCTION

One of the most noticeable characteristics of spotted hyaenas is their wide vocal repertoire and the loud amplitude of many of these. However, besides a superficial description given by Kruuk (1972), no detailed investigation of spotted hyaena vocalizations has been published. Descriptions of vocal communication in other Hyaenidae are limited to an initial interpretation of *Hyaena brunnea* sounds by Mills (1981) and of a friendly close range call of *Hyaena hyaena* by Peters (1984). Among the major difficulties in an analysis of *Crocuta crocuta* sounds are gradations in sounds and interindividual variations, which may confuse an observer. However, it is apparent that spotted hyaena vocalizations are much louder and varied than those of other Hyaenidae (Mills 1981; 1984a).

The present study is a preliminary investigation into the types of sounds emitted by spotted hyaenas with the objective of examining their functional significance. To substantiate the hypothesis that the complexity of *Crocuta* vocalizations is related to the socio-ecological role of this species, five facets of behaviour form the basis of this analysis. These are:

a) Amicable close-range signals that accompany contact and greeting behaviour or adult-offspring appeasement and coaxing;

b) Signals that affect access to food by clan members;

c) Long-distance contact and interclan spacing calls;

d) Sounds that could affect the outcome of interspecific interactions;

e) Vocal signals that accompany agonistic encounters between conspecifics.

METHODS

Based on Kruuk's (1972) descriptions and a personal interpretation of sounds heard during six months in the field, a classification of vocalizations was drawn up. On 1157 occasions when calls by members of the Mavumbye clan could be classified while their producers were in sight, these were noted, along with the identity of the producer, and context. However, sounds which could not be subjectively classified in the field, were not recorded. Many soft utterances could have been drowned by engine noise of the observer's vehicle and could have remained unnoticed.

Some sound recordings were obtained during eight months with a UHER-4200 Report Stereo tape recorder on a single track of tape at 19cm/s, using a UHER-M512 hand-held microphone. Recording distance was 3-60m from the caller. Brief notes on producer and context were spoken onto tape after each call. Selected sounds, that were judged to be typical of a certain type, were later analysed on a Sound Spectrograph (Series 700 VII Voice Identification Inc., Somerville, N.J., U.S.A.) at the University of South Africa. A narrow band filter (50Hz) was used throughout. Each sonogram represented a maximum duration of 2,5s and showed sounds of up to 8kHz on a machine-calibrated plot.

In describing sounds, the following terminology was used following Peters (1978), Brady (1981) and Mills (1981):-

Syllable: Duration of one uninterrupted tracing
Bout: Several syllables in short rhythmic succession
Intersyllable: Time lapse between successive syllables
Tonal: Sound energy spread into narrow bands of harmonics
Non-tonal: Sound energy spread over wide band

Frequency range: Lowest and highest frequency of a syllable

Fundamental frequency: Frequency of maximum energy

Staccato: Abrupt, sharply detached syllable

Pitch: General appearance of frequency to human ear

Amplitude: Loudness as perceived by human ear

Context: Accompanying activity following Table 9 (Chapter 2)

Response: Normal reaction of other hyaenas to the utterance.

RESULTS

The description of sounds depended on my subjective ability to distinguish and classify them. This was often difficult because of a continuum of sounds between some categories and because of individual variation. The different sounds are described as they appeared on sonograms and were perceived by me in tone, pitch, amplitude and duration. They are grouped according to the most usual context in which they were heard, as indicated on Table A1. Some vocalizations were emitted more by members of some social classes than others (Table A2). Furthermore, it was evident that hyaenas often emitted the same calls simultaneously at food and interspecific interactions, whereas this was seldom the case elsewhere (Table A2).

1. Amicable Contact and Greeting (Fig.A1)

1a) Groan (Fig.A1a,b&d): Tonal steady "mmmm" sound of low pitch and soft to medium amplitude. *Syllable*=1-5s; *Bout*=1->30 syllables; *Intersyllable*=2-3s; *Context*: Before social contact (Fig.A1a), during close social contact (Fig.A1d), or by a dam calling her cub (Fig.A1b); *Response*: Approach caller or/and repond with groaning or soft whining (1b).

Table A1: Context in which vocalizations were emitted while the producer was under observation. The category "food" lists vocalizations heard when relationships between producer and target were uncertain.

	INTERSPECIFIC		INTRASPECIFIC					
SOUND	Interaction	Food	Aggr.	Evas.	Greet	Contact	Other	TOTAL
Groan	7	2	-	3	40	106	25	183
Soft Whine	-	-	-	8	23	6	1	38
Soft Cry	-	-	-	-	-	12	-	12
Chuckle	-	-	-	-	-	7	-	7
Mewing	2	19	-	52	-	9	-	83
Grunt-Laugh	21	22	-	1	-	-	-	44
Giggle	11	13	-	68	3	1	-	96
Low	92	-	4	-	-	-	2	98
Loud Whine	4	-	-	11	-	-	-	15
Growl	-	9	9	-	1	1	1	21
Whoop	9	-	-	-	5	-	328	342
Fast Whoop	46	1	12	-	-	-	1	62
Loud Squeal	104	1	-	9	-	-	-	129
Yell	3	-	-	1	-	-	-	4
Grunt	2	-	5	-	-	1	1	9
Snarl-Growl	-	-	-	14	-	-	-	14
TOTAL	316	45	29	167	74	143	383	1157

Table A2: Frequency of vocalizing by members of various social classes, total number of occasions on which vocalizations were heard and mean number of hyaenas vocalizing simultaneously. The PIM class includes peripheral immigrant males and prospective immigrants.

	SOCIAL CLASS						
Vocalization	Female	Cub	RNM	CIM	PIM	Occasions	Simultaneous Vocalizations
Groan	81	56	20	26	0	166	1,1±0,4
Soft Whine	9	16	9	1	3	38	1,0
Soft Cry	0	12	0	0	0	12	1,0
Chuckle	-	6	1	-	-	6	1,2±0,4
Mewing	13	28	22	14	5	75	1,2±0,6
Grunt-Laugh	22	2	13	1	1	39	1,0
Giggle	17	21	26	23	8	81	1,2±0,8
Low	39	12	28	13	2	39	2,7±1,5
Loud Whine	1	2	2	1	8	11	1,3±0,9
Growl	16	1	4	-	-	15	1,4±1,1
Whoop	170	81	178	122	86	300	1,2±0,5
Fast Whoop	28	8	16	5	0	24	2,7±1,8
Loud Squeal	54	17	37	18	3	38	3,4±1,7
Yell	1	0	2	1	0	4	1,0
Grunt	8	-	1	-	-	9	1,0
Snarl-Growl	-	-	-	-	14	14	1,0

1b) Soft whine (Fig.A1e): Tonal unsteady "iii" sound of high pitch, often in duet with groaning individual. *Syllable*=0,5-2,0s; *Bout*=1; *Context*: Produced by the younger or lower-ranking individual during close social contact, but probably not related to agonism; *Response*: Usually reciprocal activity, often groaning (1a).

1c) Soft cry (Fig.A1c): Soft whining at very high steady pitch. *Syllable*=0,5-2,0s; *Bout*=1 syllable; *Context*: By a cub while together with other hyaenas; *Response*: Attracts attention of dam.

1d) Chuckle (Fig.A1f): Tonal staccato "he-he" at medium pitch. *Syllable*=0,05s; *Intersyllable*=0,1s;*Bout*=3-10 syllables; *Context*: Playing or wrestling.

1e) Mewing (Fig.A1g&h): Nontonal to hoarse tonal "aae" sound of medium but variable pitch and amplitude, often mixed with elements of loud whining (2e), chuckling (1d), giggling (2c) and growling (2f). *Syllable*=0,5-5,0s; *Intersyllable*=irregular; *Bout*=1->30 syllables; *Context*: Cub close to adult, before and during play or when pleading to gain access to a carcass or to suckle; *Response*: None visible or respond to cub in context.

2. Intraclan Interactios At Food (Fig.A2)

2a) Grunt-laugh (Fig.A2a): Short series of deep fairly soft staccato grunts, whose actual source is difficult to localize. *Syllable*=0,05s; *Intersyllable*=0,05s; *Bout*=5-10; *Context*: Alarm or warning call, especially at food, or when lions are nearby; *Response*: All hyaenas present look up alert or disperse rapidly.

2b) Laugh (Fig.A2b&i): Pronounced loud slow chuckling (see 1d), resembling human laughter, usually with clear tonal qualities. *Syllable*=1,0-1,5s; *Intersyllable*=2s; *Bout*=1-10 syllables; *Context*: When feeding close alongside each other; *Response*: Usually none visible.

2c) Giggle (Fig.A2c-e): Tonal or hoarse staccato chuckling of high pitch, sometimes grading into loud whining (see 2e) and mewing (see 1e). *Syllable*=0,02-0,05s; *Intersyllable*=0,01-1,0s; *Bout*=15-40; *Context*: Appeasement call by subordinate individual which tries to retain its feeding position next to a dominant individual (however, call is not used as measure of rank if not accompanied by visual signals); *Response*: Varies from agonism to tolerance, sometimes lowing (see 2d).

2d) Low (Fig.A2f): Fairly deep tonal bleat. *Syllable*=1-2s; *Bout*=1-5; *Context*: Sometimes uttered by individual standing next to a feeding individual; *Response*: Display of appeasement, giggling, or none visible.

2e) Loud whine (Fig.A2g): Steady tonal sound of high pitch and medium amplitude. *Fundamental frequency*=3.0kHz; *Syllable*=0,5-1,0s; *Bout*=1; *Context*: Emitted by an individual feeding very close to others, and can grade into giggling; *Response*: None visible, or as for 2c.

2f) Growl (Fig.A2h): Non-tonal rattling at medium pitch of variable amplitude and duration. *Syllable*=0,3-1,0s; *Bout*=1; *Context*: Emitted by one or both hyaenas squabbling over feeding position, while lightly biting or pushing each other; *Response*: Reciprocate, or laugh as at Fig.A2i.

3. Spacing Call (Fig.A3)

3a) Whoop (Fig.A3a-1): Very loud tonal "whoo" sound of variable pitch, comprising three or four phases (see Fig.A3a): beginning with deep lowing (phase 1) followed by a slow rise in pitch and in harmonic complexity (phase 2), and a sharp transition to a high howl (phase 3), sometimes followed by descending lowing (phase 4). For each phase, changes are evident in fundamental frequency and in the harmonic components, which can be as high as 8kHz (see Fig.A3l which was recorded from a distance of 3m). The first and last syllables are sometimes incomplete, with only one or two phases. *Syllable*=2-5s; *Intersyllable*=2-5s; *Bout*=2-20; *Context*: Distant contact call, often with territorial connotations; *Response*: Often no visible response, or reply with whooping or approach caller, sometimes showing an increase in excitement.

A high degree of variablity is evident between most individuals, but the various phases are usually distinct in character for each individual, which often make the caller recognizable to a human listner. Resident native males may change their whooping when becoming prospective immigrants as can be seen in the comparison of Fig.A3l (Rw in natal clan) with Fig.A3k (Rw as prospective immigrant) and in the comparison of Fig.A3j (Rz in natal clan) with Fig.A3i (Rz as prospective immigrant).

3b) Fast whoop (Fig.A3f): Short duration of each phase of a syllable in whooping, usually at high amplitude, and often in a lengthy bout. Comparison of Fig.A3f and Fig.A3g, and of Fig.A3b and Fig.A4b indicate that the character of each phase for whooping for an individual remains fairly constant, but the duration of each phase decreases, and the short squeal of the third phase is more pronounced. *Context*: Encounter with intruders or with lions (see 4b); *Response*: Immediate excitement and rallying of other clan members within hearing.

4. Interspecific Interactions (Fig.A4)

4a) Low (Fig.A4a): As for 2d. *Syllable*=1-2s; *Intersyllable*=1-2s; *Bout*=1-30; *Context*: When surrounding lions at a moderate distance (10-30m), often emitted by several hyaenas simultaneously, and could draw lions' attention to the presence of hyaenas; Lowing also accompanies more offensive activities when fast whooping and loud squealing; *Response*: None visible or lions look up at hyaenas.

4b) Fast whoop (Fig.A4b): As for 3b. *Context*: While standing close to lions; *Response*: Clan members gather.

4c) Loud squeal (Fig.A4c&d): Very loud screeching "eee" with a harsh quality, at medium pitch, rising and dropping abruptly, long syllables resembling wailing siren and short syllables resembling human maniacle cackling laughter; *Fundamental frequency*=1,5-2,0kHz; *Syllable*=0,1-1,5s; *Intersyllable*=0,1s or irregular; *Bout*=1-10; *Context*: Very aggressive and standing within 1-10m of lions with high tendency to attack or harrass lions, but often mixed with defensive threat or evasive attitudes, sometimes emitted by several hyaenas simultaneously to produce a cacophony while mobbing lions (see Fig.A4d, which was recorded while nine hyaenas drove lions off a kill); *Response*=Defensive threat, retreat or counter-attack by lions, sometimes showing signs of being confused.

4d) Yell (no sonogram): Short single loud squeal (see 4c). *Context*: Surprise encounter with lion, man, or other clan, followed by fleeing.

4e) Grunt-laugh (Fig.A2a): See 2a. *Context*: Alarm when close to lions, showing strong tendency to flee; *Response*: Conspecifics likewise become alert or disperse.

4f) Grunt (no sonogram): See 5b. *Context*: Posture indicating high degree of aggression when first sighting lions from a distance.

5. Encounter between Unfamiliar Hyaenas (Fig.A5)

5a) Snarl-Growl (Fig.A5a-j): Loud rasping growling containing many elements, which grade into each other. The principal sound, snarling, is a non-tonal deep rapid series of staccato grunts resembling the sound made by a band-saw, varying in pitch and rate, produced clearly when exhaling (Fig.A5d&g), or with airy quality as when inhaling while vocalizing (Fig.A5a). Between this snarling, elements of loud squealing (Fig.A5b&e; see 4c), growling (Fig.A5c; see 2f), mewing (Fig.A5f; see 1e), and modified whooping (Fig.A5h,i&j) are heard. *Duration*=1-30min; *Context*: Accompanied by postures indicating strong evasive tendency mixed with defensive threat, lying prone while being mobbed by conspecifics; *Response*: Difficult to separate from general activity of inhibited attack and biting to bruise but not kill.

5b) Grunt-growl (no sonogram): Single tonal soft growl of very deep pitch, resembling the grunt-laugh (see 2a), but with no staccato qualities. *Syllable*=0,5-3,0s; *Bout*=1; *Context*: Alert and aggressive stance, facing intruder before approaching closer; *Response*: Conspecifics may reciprocate, apparently sizing each other up, or flee.

5c) Fast whoop (Fig.A3f & A4b): As for 3b. *Context*: When sighting non-immigrant intruders, preceding their eviction; *Response*: Intruders flee.

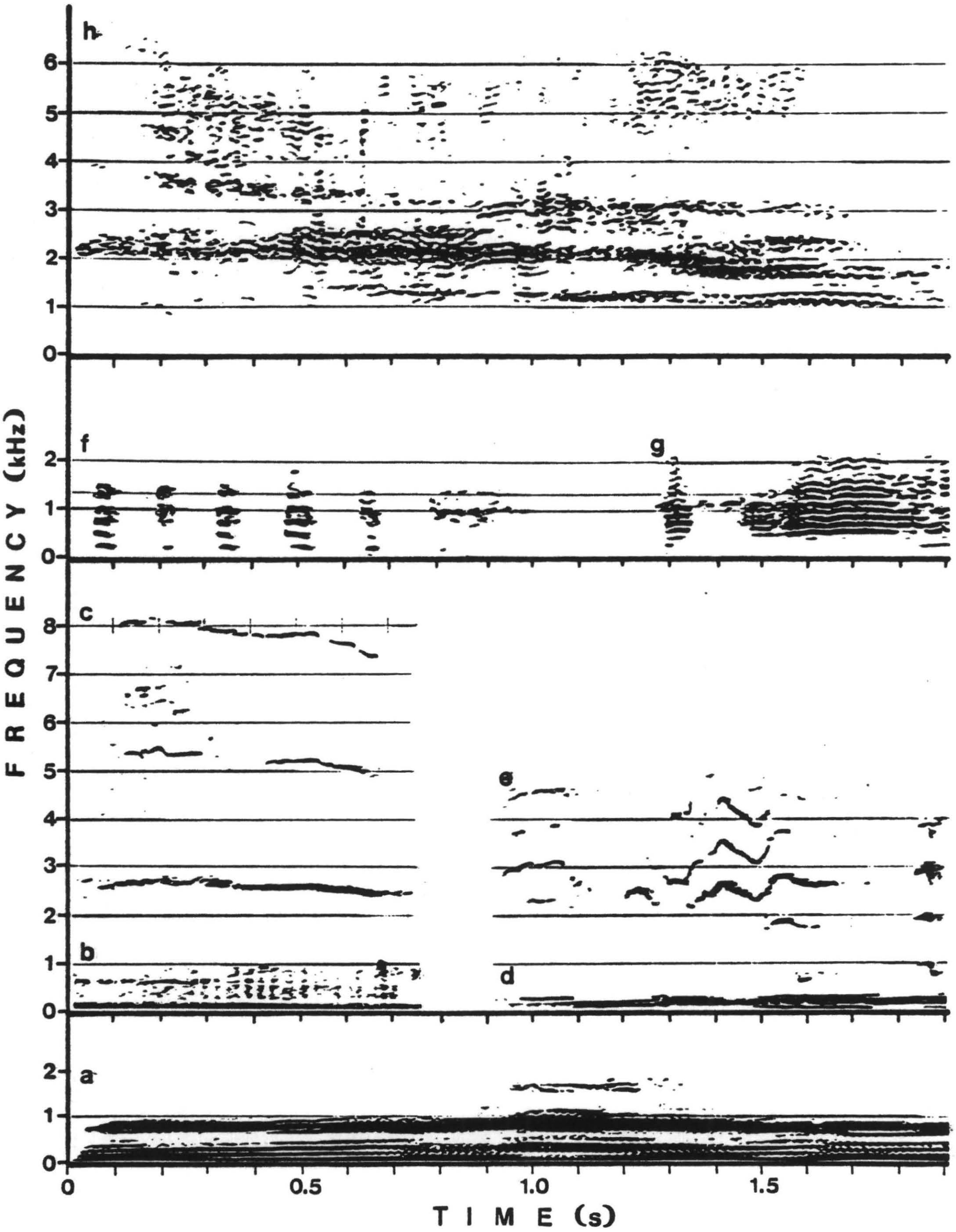


Figure A1: Sonograms of hyaena vocalizations at amicable encounters. a) groan; b) groan; c) soft cry; d) groan; e) soft whine; f) chuckle; g) mewing; h) mewing.

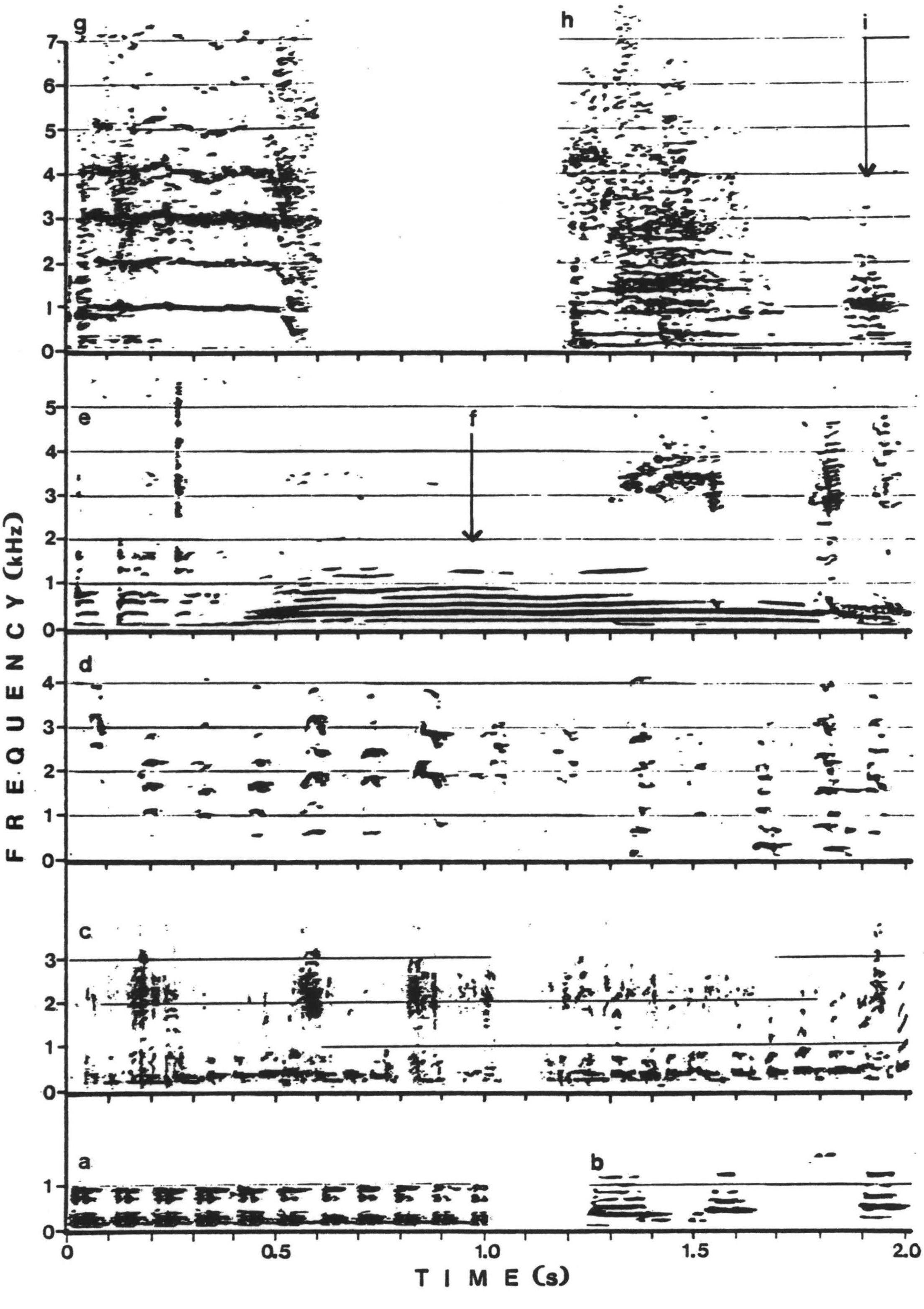
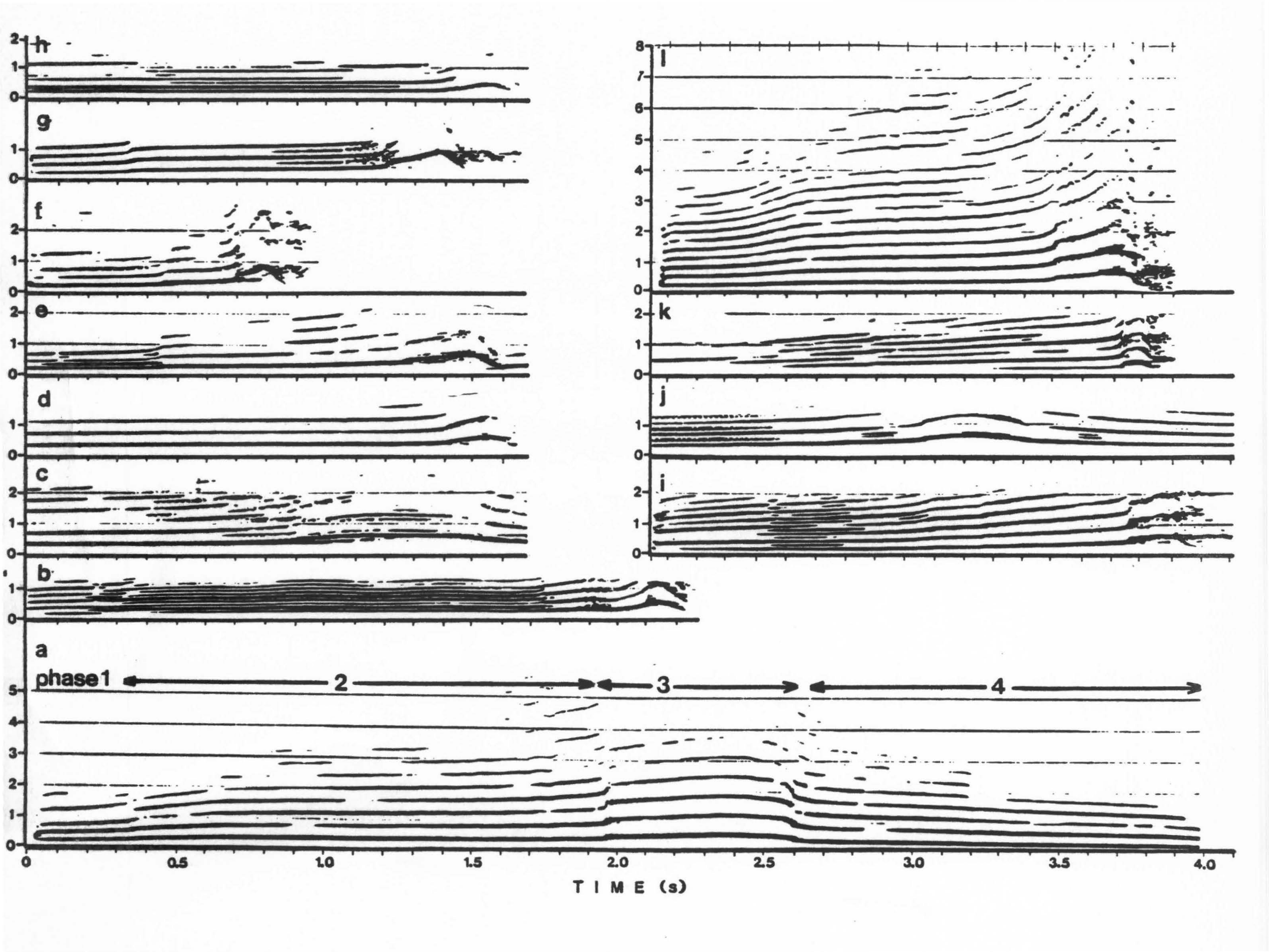


Figure A2: Sonograms of hyaena vocalizations during intraspecific interactions at food. a) grunt-laugh; b) laugh; c) giggle; d) giggle; e) giggle; f) low; g) loud whine; h) growl; i) laugh.



<u>Figure A3</u>: Sonograms of whooping by nine different Mavumbye hyaenas: a) Cb, indicating the phases of a normal whoop syllable; b) Fm; c) Po; d) Pk; e) Rf; f) Jp, fast whoop; g) Jp, normal whoop; h) Fl; i) Rz, in 1984; j) Rz, in 1983; k) Rw, in 1984; l) Rw, in 1983, showing many harmonics at close range.

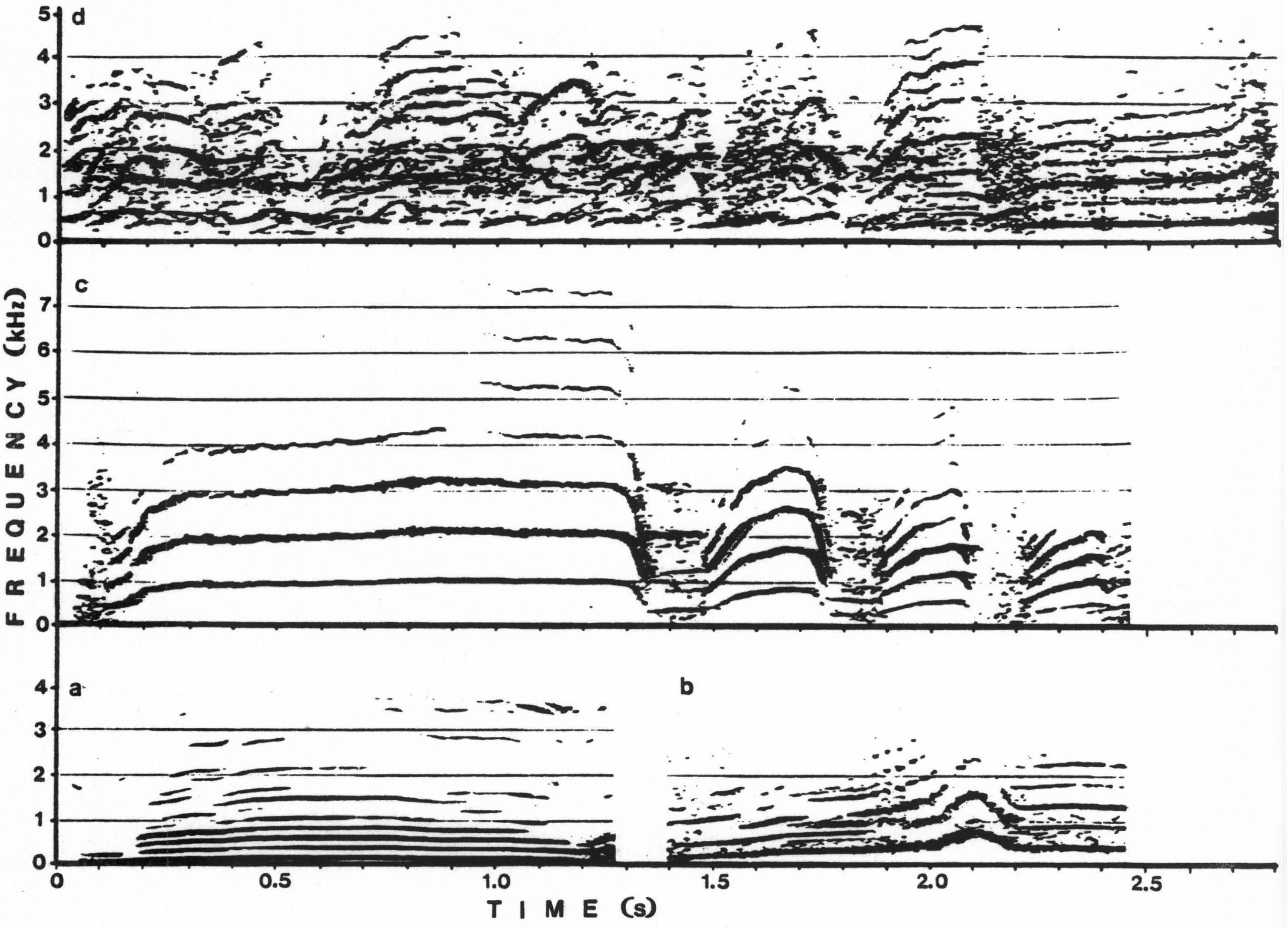


Figure A4: Sonograms of hyaena vocalizations uttered at interspecific interactions. a) low; b) Fm, fast whoop; c) loud squeal accompanied by low; d) loud squeal and low by nine hyaenas.

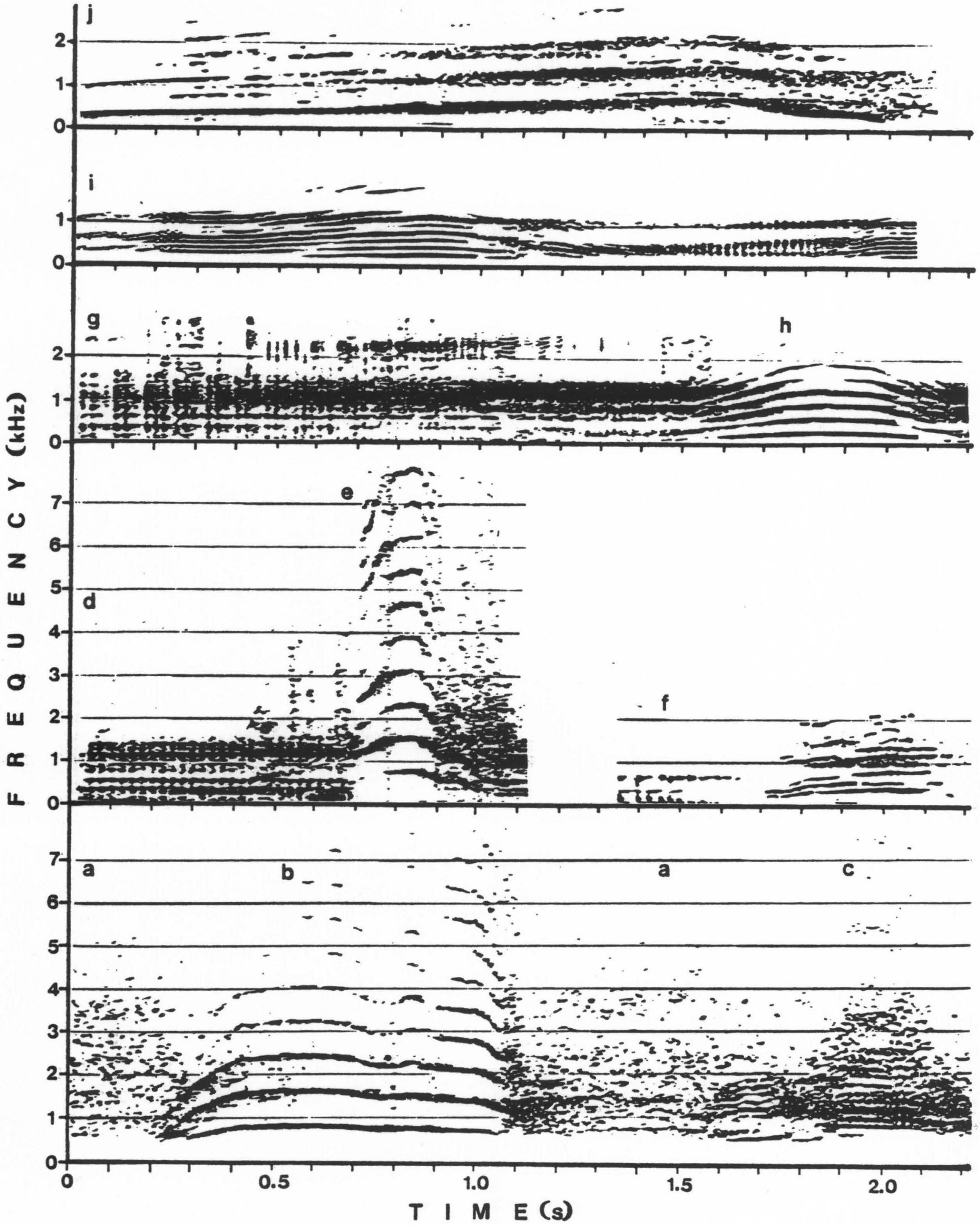


Figure A5: Sonograms of various elements of snarl-growling uttered by immigrant males while being attacked by resident clan members. a) snarl with airy quality; b) squeal; c) growl; d) rasping snarl; e) squeal; f) mewing; g) rasping snarl; h & i) Po, fast whoop; j) Po, modified whoop.

DISCUSSION

The present study is in agreement with descriptions of vocalizations by Kruuk (1972), but four additional sounds were recognized (Table A3). Within wide limits of variablity, the repertoire comprises 16 different vocalizations. Three changes in terminology from Kruuk's (1972) categories were made to match my interpretation of tonal qualities and the resemblance of sounds on sonograms.

The present description of loud squeals was made for a great variety of sounds, which differed especially in amplitude and duration, different varieties of which could be produced by several hyaenas simultaneously, but had uniform tonal structures on sonograms (Fig.A4). This complexity and possible regional differences may explain the apparent disparity of the loud squeal with the "loud grunt-laugh" (Table A3), which was produced under identical circumstances (mass attack) according to Kruuk (1972).

Table A3: Comparison of spotted hyaena vocalizations described in the present study with previous terminology given by Kruuk (1972) and with brown hyaena vocalizations (Mills 1981), which were compared with sonograms.

SPOTTED HYAENA		BROWN HYAENA
Sound	Kruuk (1972)	Mills (1981)
Groan	Groan	Soft Growl
Soft Whine	Soft Squeal	-
Soft Cry	-	-
Chuckle	-	Hoot ?
Mewing	Whine	Harsh Whine
Grunt-Laugh	Soft Grunt-Laugh	-
Giggle	Giggle	-
Low	Low	-
Loud Whine	-	-
Growl	Growl	Loud Growl
Whoop	Whoop	-
Fast Whoop	Fast Whoop	-
Loud Squeal	Loud Grunt-Laugh ?	-
Yell	Yell	Yell
Grunt	Grunt	Short Deep Growl
Snarl-Growl	-	-
-	-	Soft Whine

From a preliminary comparison of sonograms, it is suggested that most of the vocalizations produced by brown hyaenas (Mills 1981) appear to have counter-parts in the spotted hyaena repertoire (Table A3). A more detailed comparative analysis could therefore reveal some common patterns that underly the vocalizations of these two species.

It is tentatively suggested that the spotted hyaena repertoire comprises six families of sounds, which are distinct in sonographic representations. These are the following (with related or intermediate sounds listed in brackets):- a) groan; b) soft whine (soft cry, loud whine, loud squeal, yell); c) growl (mewing); d) grunt-laugh (grunt, grunt-growl, snarl-growl); e) low (whoop, fast whoop); f) giggling (chuckle, laugh). From the appearance of sonograms, and descriptions of sounds, it appears that five of these families of sounds are also present in brown hyaenas (Mills 1981).

According to this interpretation, lowing and whooping appears to be a unique feature of spotted hyaenas, besides the more complex development of the other five sound families. This stems from differences in territory advertisement, which is based on olfactory signals in brown hyaenas (Mills *et al* 1980), but relies much more on loud spacing calls with clear individual characteristics in the spotted hyaena. The latter, therefore, appears to parallel the pattern of territory advertisement seen in wolves (Harrington & Mech 1978a,b; 1979; 1983; Pilsworth 1979; Zimen 1981). These differences in the complexity of signals are also apparent in other aspects of hyaena communication, which form part of their social and interspecific relationships.

APPENDIX B: PARTURITION

INTRODUCTION

Previous descriptions of the reproduction of *Crocuta crocuta* have concentrated on litter size, gestation and lactation periods, cub growth, litter interval, the mating system, and the endocrinological basis of reproduction (Grimpe 1916; Schneider 1926; Matthews 1939a; Pournelle 1965; Golding 1969; Van Lawick 1970; Kruuk 1972; Lindeque 1981; Frank 1983; Chapter 4). However, to date no detailed description of behaviour associated with parturition and the initial integration of new-born cubs into the clan have been published. Such information could lead to a better understanding of the consequences of the unusual morphology of *Crucuta* female external genitalia (Matthews 1939a; Neaves, Griffin & Wilson 1980), the significance of social relationships among adults and subadults (Chapter 3) and the development of sociality in cubs.

METHODS

Between 5 December and 19 December 1982, 186h of observations were carried out on a radio-collared female, Fm, the dominant female of the Mavumbye clan (Chapter 3). After she gave birth on 6 December, continuous observations (except for a few hours about noon) were carried out for a week. The observer's vehicle was parked 30m from the den, except when following Fm on excursions. Most of the area around the den was visible in a 30m radius, except for a site covered by a dense shrub 2m from the den entrance, where Fm usually reclined, precluding detailed observations of nursing behaviour.

RESULTS

Parturition

Events that occurred shortly before and after parturition are described in detail. After having explored several dens during the preceding night, Fm was found alone at an earthen den situated near the territory centre at a secluded position in dense bush (*Acacia nigrescens* - *Grewia bicolor* - *Terminalia pruniodes* - *Combretum apiculatum* Brushveld) on the banks of a dry riverbed. Between 20h40 and 23h45, she repeatedly entered the den and excavated large quantities of soil. At 21h05 she lay down at the den entrance for 5min, adopting an unusual posture: Flat on the back with all legs stretched forwards, before resuming digging and occasionally exploring the vicinity. Eventually the den was large enough for Fm to turn around in.

Parturition occurred 15m from the observer. At 23h45 Fm sat down 30m from the den and licked her vulva intensively. She stood upright and adopted a squatting posture at 23h48, periodically turning her head to continue licking. By 23h51 her tail was red with blood and a very high-pitched cry was heard. Remaining in the squatting posture, Fm slowly walked 15m at 23h53, revealing a cub, which had partially emerged from the vulva in a forward direction and cried in a high-pitched whimper. Fm continued licking her vulva until 23h57, when she picked up the cub with her mouth and carried it into the den. Again whimpering cries were heard. Fm re-emerged from the den at 00h08 and licked the places occupied during parturition. During that night, Fm could only have given birth to the second cub at 00h13, when she disappeared out of sight down the river bank for 9min. For the remainder of the night, Fm remained inside the den and only thrice peered out briefly.

The Cubs

During the first three nights, the cubs remained inside the den, except for very brief appearances at its entrance, when their precocial development was evident. However, during the four nights that followed, they suckled outside or explored the den entrance for a total of 3,7h. Every night, they repeatedly emitted long bouts of soft cries (Appendix A.1c) for about 14% of the time, especially when Fm was in the vicinity but not with them.

The Dam

While Fm was alone with the cubs during the first three nights, she was inside the den for 15,4h, otherwise resting at its entrance or occasionally moving about the vicinity. She seldom entered the den from the fourth night onwards. During the first week, Fm left the den in the third (1,8h), fourth (1,6h) and seventh night (3,5h), when she each time drank water and scavenged bones from an old buffalo carcass, but obtained little to eat. She obtained her first larger meal during the seventh night, when her 15-month old daughter, Jp, brought a whole freshly-killed African civet to the den, dropped this at Fm's feet and paid no more attention to the carcass, which was consumed by Fm.

The dam was aggressive towards other clan members that approached the den. Although Fm tolerated Jp continuously at the den from the fourth night onwards, she chased her thirteen times and bit her six times in the three nights that followed, once inflicting a skin wound. During the first week, only two other individuals, a subadult male (Rw) and a young adult female (Fh), were allowed to approach upto the den entrance for 9min and 7min respectively.

On night 14, when a hyaena of another clan arrived at the den, where Fm was alone with her young cubs, Fm gave vigorous chase until this intruder had left the territory. Upon her return to the den, she entered it and intensively explored the area before leaving, not to return. Close examination of the den a week later confirmed the loss of the litter, which probably occurred suddenly of unknown causes at the same time as the above-mentioned interclan interaction.

<u>Other Hyaenas</u>

During the first three nights after Jp's first arrival at the den, she remained there for a total of 21,1h, during which she showed restless behaviour, frequently scent-marked by pasting at the den entrance (2,1 marks/h), groaned (Appendix A.1a) for 22% of the time, sometimes in long bouts (>30min), while maintaining an erection for equally long periods for 17% of the total time. After having been chased from the den by Fm (see above), Jp followed this up with amicable greeting interactions with Fm (head, body and genital sniffing) on nine occasions.

When a young adult female, Fh, was prevented from approaching the den closely, she moved about within 30m of it for 3,4h and was five times chased by Fm. At the sixth aggressive approach of Fm, Fh presented an erection and Fm reciprocated with the greeting ceremony. After that, Fh followed Fm to the den, where Fh sniffed the cubs and pasted, before leaving. Similarly, a subadult male, Rw, was only permitted to approach the den for the first time after performing the greeting ceremony with Fm. None of the other six clan members came closer than 100m to the den during the observation period.

Other Species

During the first night, while Fm was inside the den, a porcupine walked up to the den entrance before fleeing. An aardvark approached the entrance twice during the second night, explored the vicinity and departed rapidly. These events suggest that both species could have been previous occupants of the den. An aardvark later reoccupied the den after it was abandoned by hyaenas.

DISCUSSION

In a comparison of observations of parturition in the spotted hyaena and captive striped hyaena (Shulov 1958), several similarities are evident. These include the time (9 cf. 12min), the direction of cub emergence head first (the spotted hyaena cub began vocalizing while not yet free of the vagina), and the posture of the dam, standing upright on her feet outside the den. The slow walking of Fm during parturition could have caused movements of the vulva to facilitate birth, but otherwise no behavioural peculiarities were evident that could be ascribed to the unusual morphology of the clitoris and vulva (Matthews 1939a; Neaves *et al* 1980).

One of the functions of the prominent display of a penis or clitoris was evident by its frequent use at the den, where this display appeared to appease the aggressive behaviour of the dam towards other clan members. This signal, which was reinforced by groaning sounds, can be interpreted as indicating amicable intentions. It is suggested that in this context, it bears similarity with the function of the greeting ceremony (Chapter 3), but is more strongly expressed.

Although paternity of this litter was uncertain, it should be noted that a central immigrant male (CIM) had died three months before this time. Although at the time, no male in the clan had CIM status, a male, that eventually gained this status appeared in the clan some two weeks later. In contrast to the present observations, when no adult male appeared, this male maintained closest attendance to new-born cubs of later litters.

Three further points are noteworthy:-

a) The dam remained alone at the den, often inside it, and did not feed for the first three nights, although it was apparent that other hyaenas were aware of her whereabouts. When the cubs began moving about independantly, she seldom entered the den and other clan members were allowed to approach the den. Van Lawick-Goodall (1970) and Kruuk (1972) had also noted that spotted hyaena dams kept very young cubs secluded, and only moved them to communal dens some time after parturition. The precocial state and rapid development of the cubs, which is unusual for carnivores, may be neccessary for the rapid integration of cubs into communal life.

b) The observation of the 15-month old cub provisioning her mother with food is only the second record of provisioning in spotted hyaenas. A previous record involved a dam provisioning her cubs (Hill 1980). However, because provisioning was not observed more regularly, the significance of this behaviour is unknown.

c) The den tunnel, which was excavated by the dam, could not provide adequate protection to the cubs in the event of an attack while the dam was absent (Chapter 4). This may explain the sudden loss of cubs during the period when the dam evicted an intruder from the territory. It has been suggested (Chapter 4) that the existence of a communal den could have affected the protection of cubs against predation, and could have alleviated the need for almost continuous vigilance, as observed in the present study.