Ethology 88, 223—235 (1991)

ISSN 0179-1613

Mammal Research Institute, University of Pretoria, Pretoria

Territorial Behaviour by a Clan of Spotted Hyaenas *Crocuta crocuta*

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HENSCHEL, J. R. & SKINNER, J. D. 1991: Territorial behaviour by a clan of spotted hyaenas *Crocuta crocuta*. Ethology 88, 223—235.

Abstract

Territorial behaviour of a clan of spotted hyaenas, *Crocuta crocuta*, was investigated in the Kruger National Park over a period of 27 months. These hyaenas were highly territorial, spending ⅓ of their total activities on territory patrol by scent-marking intensively and monitoring 64 marking posts, particularly in border regions. Females, the more philopatric sex, were most active in territory defence. Local intensity of territorial activities by residents within their 130-km^2 territory was directly proportional to intrusion pressure by neighbours. When clan size was reduced, the ability to defend disputed land declined and larger neighbouring clans appropriated parts of the territory. We propose a relationship between resource distribution, intrusion pressure and territory defence.

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Introduction

An animal's home range must satisfy all of its energetic needs (GITTLEMAN & HARVEY 1982). Within this home range, territories may be established in specific areas where residents dominate and limit access of non-resident conspecifics to resources (KAUFMANN 1983). For carnivores, food distribution and richness have often been identified as independent determinants of territory size and group size, respectively (MACDONALD 1983). In some cases, however, territory size may be affected by the relative group sizes of adjacent territory holders; larger groups can muster more strength to establish larger territories with more resources (KRUUK & MACDONALD 1985).

Spotted hyaenas (*Crocuta crocuta*) live in social units, or clans, whose members have established social relationships, i.e. they frequently engage in interactions that express mutual tolerance. Clans of 4—80 individuals occupy ranges of 13—1500 km^2 (KRUUK 1972; BEARDER 1977; WHATELEY & BROOKS 1978; WHATELEY 1981; TILSON & HENSCHEL 1986; FRANK 1986; HENSCHEL & SKINNER 1987; GASAWAY et al. 1989; MILLS 1990). Variations in clan and range

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sizes have been attributed to the nature of their food or water resources. In addition, the land tenure system of spotted hyaenas can vary. On one extreme are clearly delimited territories that are contiguous with those of adjacent clans (e.g. Ngorongoro; KRUUK 1972); on the other extreme temporary groups of hyaenas appear to have large overlapping ranges that encompass migration routes of their prey (KRUUK 1972); an intermediate condition is represented by defended core areas separated by wide areas of undefended terrain (TILSON & HENSCHEL 1986; FRANK 1986; GASAWAY et al. 1989). Typically, territorial behaviour in spotted hyaenas involves scent-marking and monitoring of the presence or odours of other hyaenas, or, rarely, active defense by fighting (KRUUK 1972; MILLS & GORMAN 1987; MILLS 1990). The type and intensity of territorial activities is, however, very variable.

Questions arise as to how the use and defence of space is affected by the extent to which neighbouring clans seek access into common areas. Furthermore, do sex and social status affect participation by an individual in the defence of space?

To analyze these questions, we studied a spotted hyaena clan in the Kruger National Park, South Africa, where hyaenas are highly territorial (BEARDER 1977; HENSCHEL & SKINNER 1987). After defining the clan's territory, we characterized its use, quality, advertisement and defence by individuals and for the clan as a social unit. Some space-related activities of territoriality are compared to those of foraging as the other major reason for hyaenas to traverse the area. Towards the end of our study period, natural changes in the size of this clan provided an opportunity to investigate consequences this may have had on adjacent territory holders.

Methods

The study focused on one group of spotted hyaenas, the Mavumbye clan, living in the upper catchment area of the Mavumbye river (24°20'S; 31°45'E), 5—15 km north of Satara in the Central District of Kruger National Park (Fig. 1). One of us (HENSCHEL) visited this area on 456 occasions (mean duration per visit 6.7 h; 72 % at night) between Jun. 1982 and Sep. 1984.

Of 18 ungulate species occurring in the area, buffalo (*Syncerus caffer*), zebra (*Equus burchelli*), wildebeest (*Connochaetes taurinus*), kudu (*Tragelaphus strepsiceros*) and impala (*Aepycerus melampus*) were the most important hyaena prey species (HENSCHEL & SKINNER 1990). Abundance of ungulates (20—1000 kg) in the region was determined by biennial aerial censuses (National Parks Board, unpubl.) and by monthly ground censuses (HENSCHEL 1986). The Mavumbye territory contained a mean density of 11.6 ungulates/km^2 (SE = 0.9; range = 5.5—14.3).

Hyaenas of the Mavumbye clan and adjacent clans were identified on the basis of body characteristics, especially spot patterns and ear shape noted on profile charts. Sex of 6 female and 8 male clan members was determined by palpation during immobilization. Three other Mavumbye males and adult members of other clans were sexed visually: males have descended testes in protruding scrotal sacs, small nipples and a slim waistline in contrast to the female condition (MATTHEWS 1939; FRANK et al. 1990).

In 1982 and 1983, the Mavumbye clan size was 11, but at various times 17 clan members immigrated, emigrated or died. After Nov. 1983 the Mavumbye clan decreased as all females died until only four Mavumbye males remained in mid-1984. Data for the periods before and after Nov. 1983 are therefore often treated separately. As males immigrated or emigrated, they were regarded as clan members if they were frequently resighted in the clan territory for 2 months or more and if they were tolerated by other members. Foreign hyaenas that appeared in the territory for one night only were regarded as intruders unless they were solitary prospective immigrant males that engaged in submissive interactions with residents without fleeing and often attempted to stay for longer periods (HENSCHEL & SKINNER 1987). Intruders could sometimes only be identified and sexed reliably upon repeated sightings and by following them to their territory of origin.

11 Mavumbye hyaenas were fitted with radio collars. To conduct focal animal observations, one of us (HENSCHEL) located individuals by radio-tracking, sighted them with a red-filter spotlight and followed them by vehicle at distances of 30—100 m, often for their full activity period. Observations of the Mavumbye clan involved 1578 sightings on 328 nights and focal observations over 3678 h and 3317 km, 66 % before Nov. 1983. Intruders were observed 38 times for a total duration of 28 h. 8 Mavumbye hyaenas were observed for more than 198 h each, but each of the remaining 9 for less than 70 h (HENSCHEL 1986). On 55 occasions, focal observations were carried out over continuous 24-h periods. Calculations of activity rates are based on observations made prior to the decline of the clan after 1983, unless stated otherwise.

Behaviour was recorded onto tape recorder and later transcribed to computer. Hyaena territorial behaviour involved deposition or monitoring of scent-marks, agonistic interactions between clans, and, possibly, whooping calls (KRUUK 1972; MILLS 1990). Hyaenas scent-marked by pasting with anal gland secretions, scratching with their paws to deposit interdigital gland secretions or by defecating. Accumulations of scent-marks at latrines and pasting sites (with and without faeces respectively; MILLS 1990) were not analyzed separately. These sites are here collectively termed marking posts, defined as places to which hyaenas frequently returned to scent-mark over periods exceeding 3 months. An estimate of the concentration of scent-marks at any one time in the territory was calculated using MILLS' (1990) formula (Concentration = $N \times M \times D \times E$; where N = number of adults in clan; M = mean rate of marking per individual; D = mean distance each individual moved in the area per night; E = 30, the number of days marks are assumed to remain effective).

A hyaena's movement was plotted on a 1 : 50000 Universal Mercator 1-km gridded map by noting its initial location relative to a known point and recording the distance by vehicle odometer and the direction of movement determined by compass. Distance (accurate to 0.1 km) travelled by vehicle behind a hyaena was calculated for each 1-km^2 grid cell. Time spent in each grid cell was calculated by multiplying the proportion of distance travelled in the grid cell to the total distance between known points by the total time taken to travel between the points. Food obtained in each grid cell was calculated by summing up the amounts obtained by each hyaena at each feeding bout relative to a meal to satiation (HENSCHEL & SKINNER 1990).

For 9 individuals (4 females, 3 natal males, 2 immigrant males) there were sufficient data to examine ranges in detail. Ranges were computed by the minimum area vs. probability method: MAP (0.95) and MAP (0.50) (FORD & KRUMME 1979; ANDERSON 1982). Degree of similarity of the utilization distribution of any two hyaenas was calculated using Spearman's correlation coefficient on probabilities of occurrence in grid squares.

Results are often presented as $\bar{x} \pm SE$; confidence limits were 95 % except where otherwise indicated.

Results

Territory Boundaries

The boundaries of the Mavumbye territory were defined by locations of the clan's peripheral marking posts. Boundaries of the Mavumbye territory were confirmed by the outcome of 18 encounters between clans (Fig. 1) during which territory holders evicted intruders.

Space Use

Mavumbye hyaenas spent most of their time in only a small area of their 130-km^2 territory (Figs. 2, 3a); MAP(0.50) ranges of individuals were only 9—16 km^2. Most meals (82 %) were obtained in only ⅓ of the territory (Fig. 3b). The MAP(0.95) ranges of any two clan members (51—104 km^2) overlapped by at least 65 %. The utilization distributions within the territory correlated better among

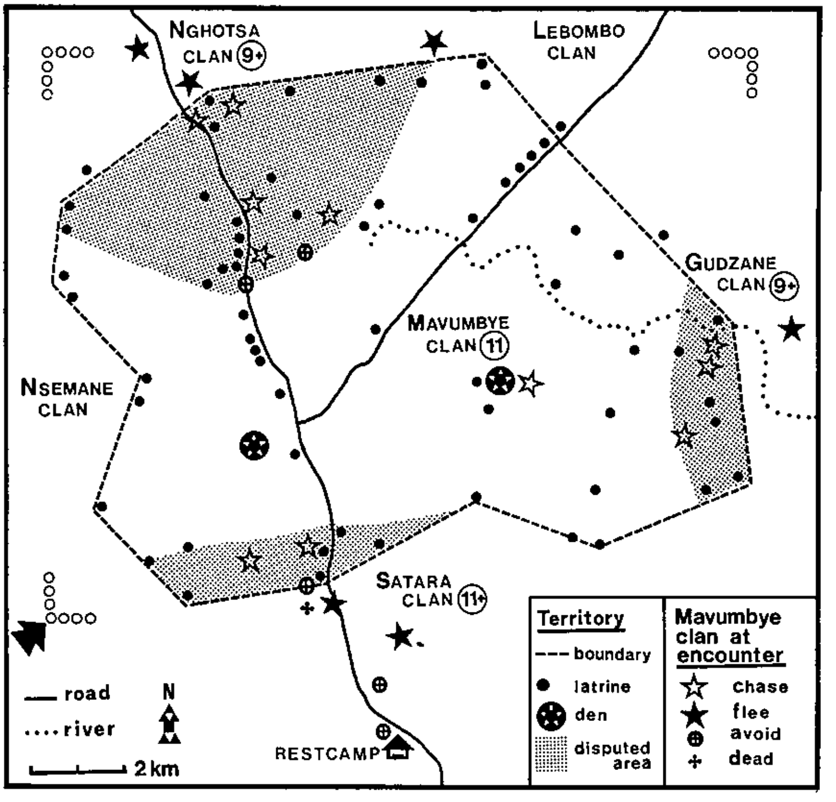

Fig. 1: Mavumbye clan-territory configuration compared to the location of den sites, marking posts, the disputed northwestern, southern and southeastern sectors (shaded areas) and places of interclan encounters (except by prospective immigrants). Activity of Mavumbye clan members at encounters is indicated. Figures in circles: actual or minimum clan sizes; arrow in the lower left: viewing angle for three-dimensional graphs (Fig. 3) which cover the area between stippled corners

resident natal members (females and natal males; $r_s = 0.51—0.75$) than this group did to immigrant or emigrating males ($r_s = 0.28—0.44$).

Not every clan member was seen at all extremities of the Mavumbye territory, but the 106—232 km^2 total range of each individual usually extended outside the clan's territory (Fig. 2). Total areas covered by three natal males as prospective emigrants (178 ± 33 km^2) were much larger than those covered by four resident females and their consort, the central immigrant male (128 ± 8 km^2; Mann-Whitney $U_{3,5} = 15$; $p < 0.05$). Four peripheral immigrant males sometimes wandered far (> 10 km) from the Mavumbye territory and associated with other clans. A crippled Mavumbye female (Fa) often scavenged from a human refuse dump 6 km into an adjacent territory without interacting with resident hyaenas that she encountered there (Fig. 2).

Territorial Behaviour

Territory patrolling was characterized by hyaenas visiting several marking posts in succession with fewer deviations and much higher rates of scent-marking than during foraging (Table 1). During continuous observations over 24-h periods (n = 55), hyaenas patrolled for 17 % of their total activity period and 22 % of the distance travelled per night (Table 1). While patrolling or foraging, individuals seldom whooped (Table 1) in comparison to the rate during all other activities (0.5 whoops/h).

The spatial distribution of patrolling and scent-marking activities differed from that of most other activities (Fig. 3a—d). Patrolling hyaenas kept to game trails, dry riverbeds or roads more often (32 % of occasions) than foraging hyaenas (11 %; $\chi^2 = 13.70$; df = 1; $p < 0.05$); 78 % of 64 marking posts used by the Mavumbye clan were located along such routes (Fig. 1). Hyaenas scent-

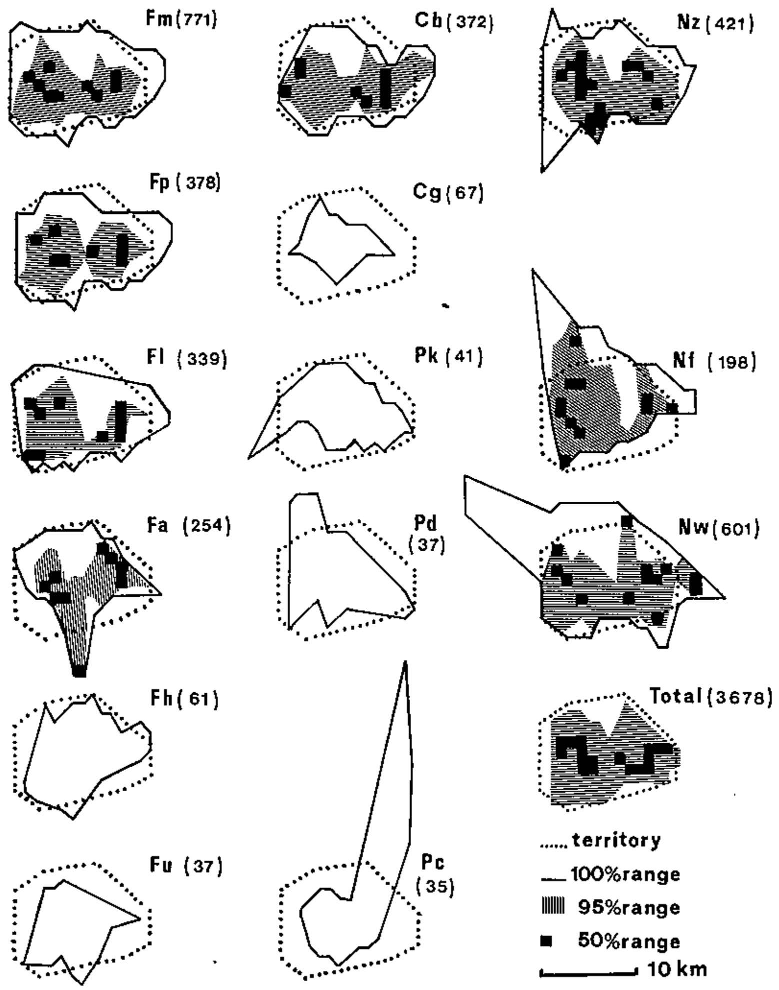

Fig. 2: Areas in which individual Mavumbye clan members spent 100 %, 95 % and 50 % of their time in relation to location of the Mavumbye territory. First letter of codes: F = female; N = natal male; C = consorting immigrant male; P = peripheral immigrant male; second letter: individual identity; brackets: duration (h) of focal observations

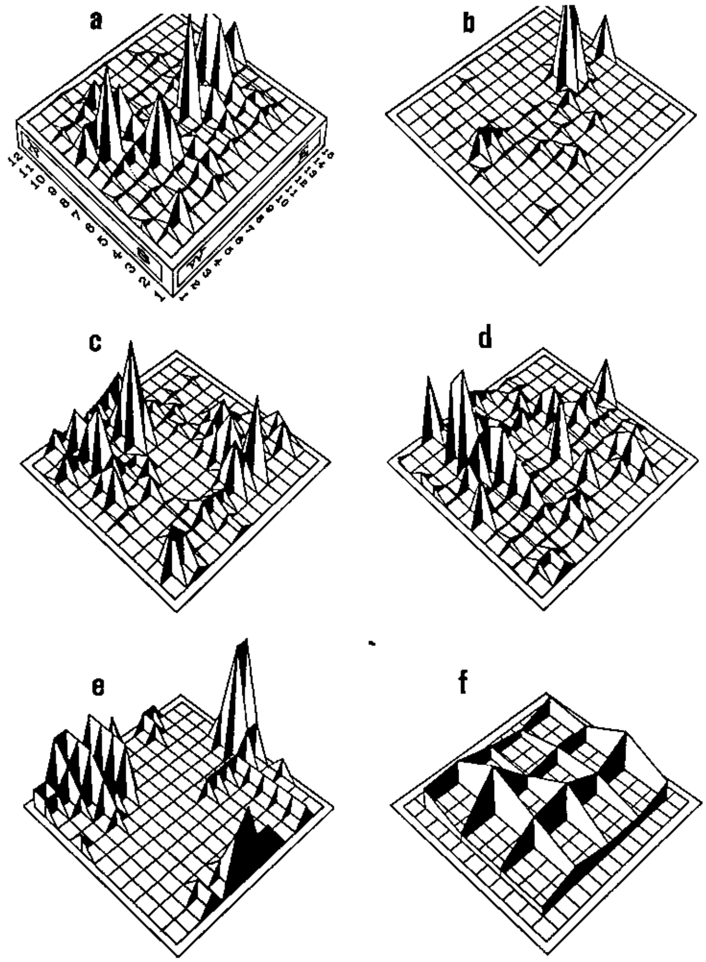

Fig. 3: Three-dimensional representation of the Mavumbye area (12 km S—N × 15 W—E km) showing: a) total duration Mavumbye hyaenas spent in 1-km² areas; b) quantity of food obtained by them; c) duration they spent on territory patrol; d) scent-marks deposited by them; e) frequency of intrusion by females from neighbouring clans; f) abundance of ungulates. Viewing angle is from south-west (Fig. 1)

marked on 58 % of 700 visits to marking posts, but only sniffed intensively without scent-marking on the remainder. Each hyaena marked an average of 2.2 times per visit to a marking post, more frequently by pasting (51 %) than by scratching (35 %) and defecating (14 %). Pasting was also the most frequent form of scent-marking (61 %) away from marking posts (n = 365). We calculated that at any time the territory contained about 2145 active marks.

Females generally displayed more territorial activities than males (Table 2). These differences can not be explained by dissimilarities in social rank between sexes (Table 2). Females scent-marked more frequently than males, although an

Table 1: Behaviour of Mavumbye hyaenas during territory patrol (n = 113; 192 h) compared to foraging (n = 881; 582 h). Duration and distance were determined during 24-h samples (n = 55) and other data during all observations of active hyaenas (1365 h). Rates are expressed per active individual of either sex

Behaviour	Patrol	Foraging	Total activity
Duration/night (h)	1.1 ± 0.2	3.7 ± 0.3	6.6 ± 0.4
Distance/night (km)	4.1 ± 1.0	13.2 ± 1.2	18.7 ± 1.4
Walking speed (km/h)	3.8	3.9	—
Scent-marks/h	9.1	0.6	0.9
Scent-marks/km	2.4	0.2	0.4
Whooping/h	0.21	0.12	0.30
Group size	2.6	1.5	1.6
Occasions solitary (%)	27.4	68.8	64.1

Table 2: Mavumbye clan members (excluding one female and four immigrant males for which insufficient data were gathered) and their social rank, total observed period of activity, rate of scent-marking while active, proportion of total activity time spent patrolling and the frequency of encounters with foreigners (members of adjacent clans) inside and outside the Mavumbye territory. Hyaena codes: F = female; N = natal male; C = consorting immigrant male; P = peripheral immigrant male

Hyaena	Rank	Observed active (h)	Scent-mark (/h)	Scent-mark (/km)	Patrol (%)	Meet foreigners inside (/100 h)	Meet foreigners outside (/100 h)
Fm	1	256.8	1.20	0.49	16.7	3.5	1.2
Fl	2	100.7	1.75	0.71	27.7	4.0	1.0
Fa[1])	3	61.5	0.44	0.19	8.5	1.6	9.8
Fp	5	152.2	1.02	0.54	14.1	2.6	0.0
Fh	6	65.1	0.76	0.38	13.9	3.0	0.0
Female			1.18	0.53	17.2		
Nz	4	195.3	0.55	0.23	9.3	3.1	1.0
Nf[2])	7	78.8	2.08	0.65	19.4	2.5	6.4
Nw	8	209.9	0.46	0.20	8.2	3.3	2.9
Cb	9	145.0	0.98	0.40	17.0	3.4	0.7
P[3])	10	72.5	0.39	0.09	15.1	1.4	5.5
Male			0.60	0.23	11.4		
U[4])			15	15	11		
τ[5])			−0.57	−0.50	−0.14		

[1]) Crippled female excluded from calculations;
[2]) Emigrating male excluded from calculations;
[3]) Combined data for three individuals;
[4]) Mann-Whitney U test of females vs. males (critical value = 15);
[5]) Kendall's τ correlation of social rank vs. variable (critical value = 0.64)

emigrating male marked at the highest rate of all (Table 2). During 24-h periods ($n = 55$) females patrolled for longer mean durations than males (1.4 ± 0.4 vs. 0.9 ± 0.3 h; $p > 0.2$). Despite differences in duration, both sexes were equally likely to participate in patrolling parties (mean sex ratio of each group size was 1 : 1).

Territory Intrusions

During 1982 and 1983 intruders appeared frequently in three peripheral sectors of the Mavumbye territory and rarely elsewhere (Figs. 1, 3e; Table 3). They were silent, monitored Mavumbye marking posts, scent-marked frequently (4.9 marks/h), appeared to avoid residents and gained little or no food.

A northwestern sector (Fig. 1), into which groups of Nghotsa hyaenas intruded 18 times, contained a higher density of ungulates than the Nghotsa territory (Fig. 3f; Table 3). Nghotsa hyaenas usually intruded in groups (Table 3); only four intrusions were by solitary hyaenas. At least one of two identified Nghotsa females was present in 89 % of the intrusions. None of the Nghotsa intruders was observed to obtain any food in the Mavumbye territory before 1984.

Solitary hyaenas or small groups from the Satara and Gudzane clans often intruded into the southern and southeastern Mavumbye sectors respectively (Fig. 1; Table 3). Identified females participated in at least 71 % of these intrusions. Ungulates were less dense in these sectors than in the Satara and Gudzane territories except for a small, rich patch on the southeast boundary (24.7/km^2; Fig. 3f). Intruders thrice scavenged in these sectors during 1982 and 1983.

Table 3: Number of patrols and group size of the Mavumbye clan compared to intruding adjacent clans in the northwestern (NW), the south and southeastern peripheral (SE) and central sectors of the Mavumbye territory during 1982 and 1983. Mean densities of ungulates in each sector and in the adjacent territories are indicated

Variable	Mavumbye Territory Sector NW	SE	Central	Total
Mavumbye clan				
Number of patrols[1])	37	27	35	99
Patrolling group size	3.1 ± 0.3	3.2 ± 0.4	1.9 ± 0.1	2.6 ± 0.2
Solitary (% in sector)	24	22	40	27
Neighbouring clans				
Number of intrusions	18	17	3	38
Intruder group size	4.2 ± 0.6	2.3 ± 0.6	1.3 ± 0.3	3.2 ± 0.4
Solitary (% in sector)	22	64	67	45
Ungulate density				
Mavumbye sector	16.9	10.1	9.7	11.7
Neighbouring territories	7.4	18.7	—	—

[1]) Excluding presence in sector when not patrolling

Response to Intruders

Intrusion into three peripheral sectors evidently affected the behaviour and group size of residents in these areas (Tables 3, 4). Upon encountering intruders ($n = 18$), the resident clan furnished an equal or larger group in all but four cases (1.2 ± 0.3 more residents than intruders; Wilcoxon signs test $p < 0.005$) and dominated intruders. In all but one encounter physical contact was avoided. A single hyaena could evict a lone intruder ($n = 3$). Intruding groups usually withdrew when confronted by a group of residents ($n = 11$), but did not retreat from single residents until these had rallied other clan members with fast whooping ($n = 4$). To facilitate rapid response towards intruders, patrolling residents were seldom alone (Table 1) and were in significantly larger groups than when foraging ($\chi^2 = 108$; $df = 7$; $p < 0.001$).

The Mavumbye hyaenas obtained little food (Table 4) but were dominant in the disputed northwest sector. They usually patrolled this area in groups (Table 3) and scent-marked intensively (9.1 marks/h). During all movements, marks were deposited at a higher rate (0.58/km) than elsewhere in the territory (0.27/km), resulting in a higher calculated instantaneous concentration of marks ($34/km^2$ vs. $12/km^2$).

The situation was different in the southern and southeastern sectors. Mavumbye hyaenas spent a lot of time there and procured a disproportionately high amount of food. Although they frequently monitored the border by patrolling in groups, they did not scent-mark at a higher rate than elsewhere and seldom whooped (Table 4).

Territorial defense by males at encounters with intruding females apparently depended on the presence of resident females. On three occasions when solitary natal Mavumbye males encountered intruding females, they showed submissive approach behaviour and only challenged the intruders when resident females arrived.

Table 4: Proportion (%) of various activities performed by Mavumbye hyaenas in the northwestern (NW) and the south and southeastern (SE) peripheral sectors (each 26 km^2) compared to the central sector (C: 78 km^2) of the Mavumbye territory

Variable	Mavumbye Territory Sector NW	SE	C	Total
Territory portion	20	20	60	130 km^2
Time	14	28	58	3310 h
Distance	25	22	53	2660 km
Distance on patrol	42	31	27	150 km
Observed scent-marking	41 >	19 ns	40	916 marks
Counts on marking posts	46 >	30 >	24	1606 marks
Whooping	22 ns	8 <	69	330 calls
Full meals	5 <	37 >	58	185 meals
Ungulates (< 1 ton)	30 >	18 ns	52	1460 animals

χ^2 test on 2 × 2 contingency table of the total frequency in each peripheral vs. central sector against number of grid cells; > = more in peripheral sector than expected $p < 0.05$; < = less in peripheral sector than expected $p < 0.05$.

Changes in Clan Size

Between Jul. 1982 and Nov. 1983, the size of the Mavumbye clan remained constant at 11, with immigration balancing emigration and mortality. Of 6 females, two died during this period (confirmed and suspected lion kills). In Nov. 1983, the largest (mass 81.0 kg; shoulder height 84.5 cm), sub-dominant female died in a fight between the Mavumbye and Satara clans. This fight between several members of each clan was initiated at a wildebeest carcass in Mavumbye territory and continued into Satara territory where the female was killed (Fig. 1). A change of conditions was evident in the subsequent period. New immigrant males no longer appeared. The remaining three females had close encounters with lions at food at twice the rate as before (rate of encounter per female hyaena per 100 h of activity: 8.8 before vs. 18.1 after; n = 341 h before, 122 h after). Evidently as a result of intensified interactions with lions and other clans, a crippled female was deprived of scavengable food and starved to death, and the dominant female and her daughter were killed by lions. The remaining four Mavumbye males occasionally left the area and survived.

Changes in Territory Size

A decline in territory size by ¼ was evident shortly before the clan's demise. During eight encounters between the Nghotsa and Mavumbye clans in the northwest sector during 1982 and 1983, Mavumbye hyaenas evicted the intruders. At that time each clan had 5—6 females. After Nov. 1983, however, the remaining three Mavumbye females never entered this sector. Instead we saw Nghotsa hyaenas four times in this area scent-marking frequently. At two encounters the Mavumbye females no longer challenged the Nghotsa hyaenas that had appropriated this 26-km^2 area. In the same period the Satara clan deposited new marking posts 1.1 km into the Mavumbye territory and appropriated at least 8 km^2 in the south following a fight between the two clans. By contrast, the Gudzane clan did not gain dominance over the southeast sector until the clan's demise. After all Mavumbye females had died by mid-1984, the four remaining males no longer maintained the former territory and tolerated females and males of the Gudzane and Satara clans in the Mavumbye area.

Discussion

Some local sources of variation underlying the expression of territoriality in spotted hyaenas were evident in the present study. These include the potential value of food resources in an area as perceived by residents and their neighbours and the nature of relationships of the resident clan towards neighbouring clans.

We suggest that Mavumbye hyaenas were strongly territorial because of high intrusion pressure into their range. These hyaenas spent ⅕ of their total activity period and distance on territory patrol. During this activity, their rate of scent-marking was 16-fold that during foraging. Easy access to marking posts was facilitated by positioning them along open ground or paths, which also maximized their potential for detection by intruders (BEARDER & RANDALL 1978).

By concentrating their marking activities during patrols, Mavumbye hyaenas emphasized certain territory sectors independent of the degree to which they utilized them for other purposes. Local intensity of patrol was apparently determined by degree of intrusion pressure. Of five clans neighbouring onto the Mavumbye clan (Fig. 1), two rarely intruded; hyaenas seldom patrolled the ill-defined boundaries between these clans. In contrast, the boundaries towards three other clans that intruded frequently were patrolled intensively and were clearly defined.

Degree of utilization by residents of resources in various boundary sectors appeared to affect the principal method of defence. The difference between the northwest and the south and southeast Mavumbye sectors illustrates this. Intrusion pressure was high in all of these sectors, but the resident clan's relationship to the resources differed. They did not exploit the full potential of high prey concentrations in the northwest, but resisted a neighbouring clan from gaining access to this resource by intensively signalling ownership with scent-marks. In contrast, Mavumbye hyaenas spent much time and obtained much food in the south and southeast sectors. Intruders may primarily have been held at bay in these areas by the physical presence of vigilant residents.

Residents differed in their degree of participation in territory advertisement and defence; adult females were more active in this respect. Furthermore, resident males on their own failed to evict intruding females and sometimes followed them as prospective mates into the other clan (HENSCHEL & SKINNER 1987). Defense by females of their key resource, food (HENSCHEL 1986), would explain their relatively strong expression of territorial behaviour.

In all but one of the observed encounters between intruding groups and territory holders intruders deferred without fighting. In the exceptional case an adult female was killed outside her territory, reflecting the risks of not heeding signals of land ownership. Similarly, KRUUK (1972) reported occasional mortal combat between Ngorongoro clans, usually avoided by marking and displaying.

Surprisingly, the normal whoop, a loud, repetitive vocalization that has been suggested to have the potential for territory advertisement (MILLS 1990), was seldom emitted by the Mavumbye clan on patrol or while in the peripheral sectors. Instead, the normal whoop may be a territory-independent spacing mechanism that emphasizes space use rather than the defence of conventional boundaries, as has been suggested for wolves (HARRINGTON & MECH 1983).

Patrols were usually conducted in groups that could be quickly augmented by the rallying call, fast whooping. This evidently facilitated swift and effective expulsion of intruders. That intruding neighbours may be sensitive to the maximum group size a clan can muster is suggested by the loss of parts of the Mavumbye territory following a reduction in their clan size.

Relative size of neighbouring clans may influence the ability of a clan to change or resist change in territory size when disputes over resource patches arise. In his study of seven Ngorongoro clans, KRUUK (1972, p. 44) conceded that "one can see a likely relationship between the two — the larger the clan, the larger the range". This hypothesis would imply a correlation between clan size and territory size within a region (KRUUK & MACDONALD 1985), but remains, as yet, untested for hyaenas.

The present study suggests, however, that larger clans can gain access to new food patches at the expense of smaller clans. The Mavumbye clan lost parts of its territory while it still had three females left. Their demise soon after this indicates that the reductions in territory size may have been detrimental.

The foraging behaviour observed for Mavumbye hyaenas before the decline (HENSCHEL 1986) indicated that the territory originally encompassed several rich food patches that were frequently visited by residents. This suggests that resource dispersion may have been ultimately responsible for determining the size of a viable territory, in agreement with previous authors (MACDONALD 1983; KRUUK & MACDONALD 1985; TILSON & HENSCHEL 1986; MILLS 1990). Conversely, the reduced territory may have contained too few food patches. We suggest that as a result of the reduction of alternative food patches, contests with lions over food escalated, killing or starving the remaining females.

Our study outlines the consequences of clans attempting and finally succeeding to expand their territories into those of neighbours. We could demonstrate some of the costs for residents to resist such changes, but know relatively little of the actual costs of offence. Changing demands on local food resources may underlie the reason for intrusion.

In comparing various studies of spotted hyaenas, there indeed appears to be a relationship between the degree of intrusion pressure, the intensity of direct and indirect defence of territories and the scale of resource fluctuations. Where resident prey is relatively abundant, such as at Mavumbye and Ngorongoro (KRUUK 1972), intruding and resident hyaenas compete for predictable, rich resource patches. This gives rise to strong territoriality. In contrast, where most prey is highly mobile and concentrated, as in Serengeti (KRUUK 1972), hyaenas tend to follow prey migrations to some extent. With such high intrusion pressure, the potential costs of territory defence may be so high that it is little expressed. Where resident hyaenas depend on a succession of migrating prey passing through their territory, as at Mara (FRANK 1986) and Etosha (GASAWAY et al. 1989), intrusions (by non-immigrants) and territorial activities were reported to be rare. Intermediately mobile prey was so widely dispersed in the Namib (TILSON & HENSCHEL 1986) and Kalahari (MILLS 1990) that territories were vast, the chances of detecting intruders in the periphery was slim, and only the territory centre was advertised strongly.

In conclusion, we suggest that for spotted hyaenas the degree and place of exhibiting territorial behaviour — the exertion of or resistance against intrusion pressure — is ultimately affected by changing demands on resource patches by neighbouring social units and the potential costs of offence and defence.

Acknowledgements

We thank: National Parks Board of Trustees for permission to work in the Kruger National Park; J. BOTHA, V. DE VOS, I. ESPIE, I. A. HENSCHEL, S. C. J. JOUBERT, J. SCHOEMAN and A. S. VAN JAARSVELD for assistance; M. M. ENDERS, J. KOMEN, Y. D. LUBIN, J. W. MCNUTT, M. K. SEELY and D. M. WARD for helpful discussion; W. J. HAMILTON III, J. MENDELSOHN, A. P. MØLLER and two referees for suggestions; JURGENS Caravans for sponsorship. One of us (HENSCHEL) received a bursary from the Foundation for Research Development and the Charles Astley Maberley Memorial Scholarship of the Wildlife Society of southern Africa.

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Received: May 22, 1990

Accepted: May 3, 1991 (W. Wickler)