The scent marking behaviour of the brown hyaena *Hyaena brunnea*

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The deposition onto grass stalks of two distinct, strong-smelling substances produced in the anal scent pouch, is the most common form of scent marking in the brown hyaena (*Hyaena brunnea*). It is called pasting. The behaviour associated with pasting is described, as is the related functional anatomy of the scent pouch. The dispersion pattern of pastings within a group territory and the rate of marking in different parts of the territory were ascertained by direct observations on radio collared hyaenas. The data were analysed by the computer programs SYMAP and SYMVU which graphically display the data as a three dimensional map. Brown hyaenas leave most pastings in those areas in which they spend most time. This is in the central part of the territory. When they visit the boundaries, however, the frequency of pasting increases. GLC analyses of the pastings from two known individuals show distinct differences in the relative concentrations of the many compounds in the pastings of each. Behavioural observations show that the hyaenas are able to recognize different individuals' pastings. Pasting could function to inform group members of each other's movements as well as to inform outsiders that the territory is occupied.

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Die deponering op grasstingels van twee afsonderlike, sterkruikende afskeidings wat in die anale ruiksak geproduseer is, is die algemeenste vorm van ruikmerking in die bruin hiëna (*Hyaena brunnea*). Dit word 'pasting' genoem. Die gedrag wat met 'pasting' verbonde is word hier beskryf sowel as die funksionele anatomie van die ruiksak. Die verspreidingspatroon van die afskeidings binne 'n groepterritorium en die tempo van merking in verskillende dele van die territorium is vasgestel deur direkte waarnemings op hiënas met radionekbande. Die data is deur die rekenaarprogramme SYMAP en SYMVU, wat grafies die data as 'n driedimensionele kaart vertoon, ontleed. Bruin hiënas deponeer die meeste van hulle afskeidings in die gebiede waar hulle die meeste tyd deurbring. Dit is in die sentrale deel van hulle territorium. Wanneer hulle egter die grense besoek, vermeerder die frekwensie van merking. GKV-ontledings van die afskeidings van twee bekende individue toon duidelike verskille in die relatiewe konsentrasies van die baie verbindings in die afskeidings van elkeen. Gedragswaarnemings toon dat die hiënas verskillende individue se afskeidings kan herken. 'Pasting' mag funksioneer om groepslede van mekaar se bewegings te vergewis, sowel as om buitestanders te laat weet dat die territorium beset is.

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The brown hyaena (*Hyaena brunnea*) is essentially a species of the south-west arid and adjacent drier parts of the southern savanna biotic zones (Von Richter 1972). In the southern Kalahari, where we have worked, brown hyaenas live in small groups which use a large home range of 250 – 540 km^2 (Mills 1976 and in prep.). The members of a group forage alone and at night, showing no co-operation in hunting and finding food. The home ranges of neighbouring groups overlap to a small extent (Fig. 1), but should hyaenas of the same sex from different groups meet they will fight in a ritualised manner (Fig. 2). For these reasons we consider the home range to be a territory.

In our study area the social group is a family group consisting of a varying number of breeding females and related, but non-breeding, males. The task of mating the females falls to far-ranging nomadic males who occasionally appear in the area (Mills in prep.).

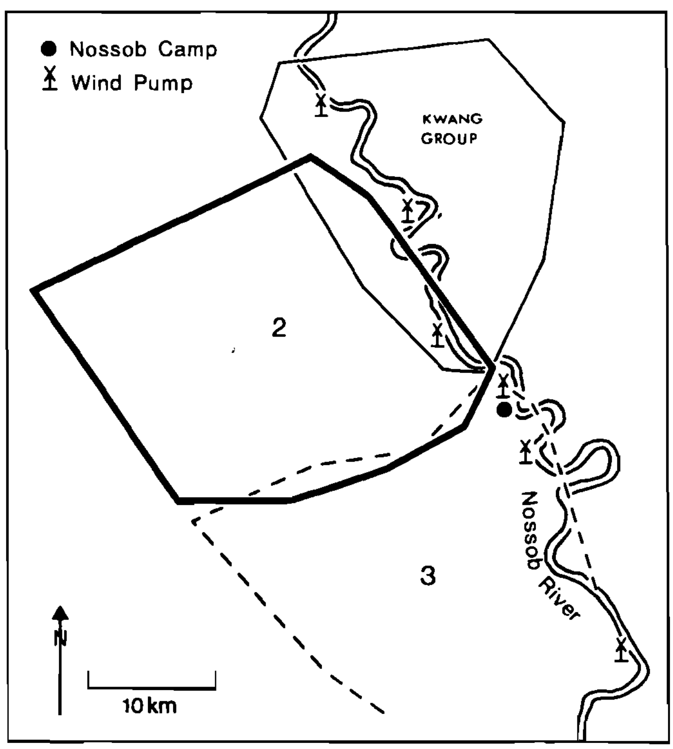

Fig. 1 Map of part of the Nossob river valley showing the territories of three brown hyaena social groups. The territory outlines are based on observations of known animals (from Mills 1976).

Fig. 2 A ritual fight between a territory owner (right) and an intruder (left). Note the depressed ears of the subordinate intruder.

Brown hyaenas can communicate with each other by postures and vocalisations but the most usual line of communication is by scent. Throughout a brown hyaena territory one finds latrines with accumulations of faeces (Mills in prep.) as well as grass stalks on which hyaenas have deposited a blob of strong-smelling white secretion and a smaller smear of black material (Fig. 3). Both of these secretions are products of the anal scent pouch (Fig. 4).

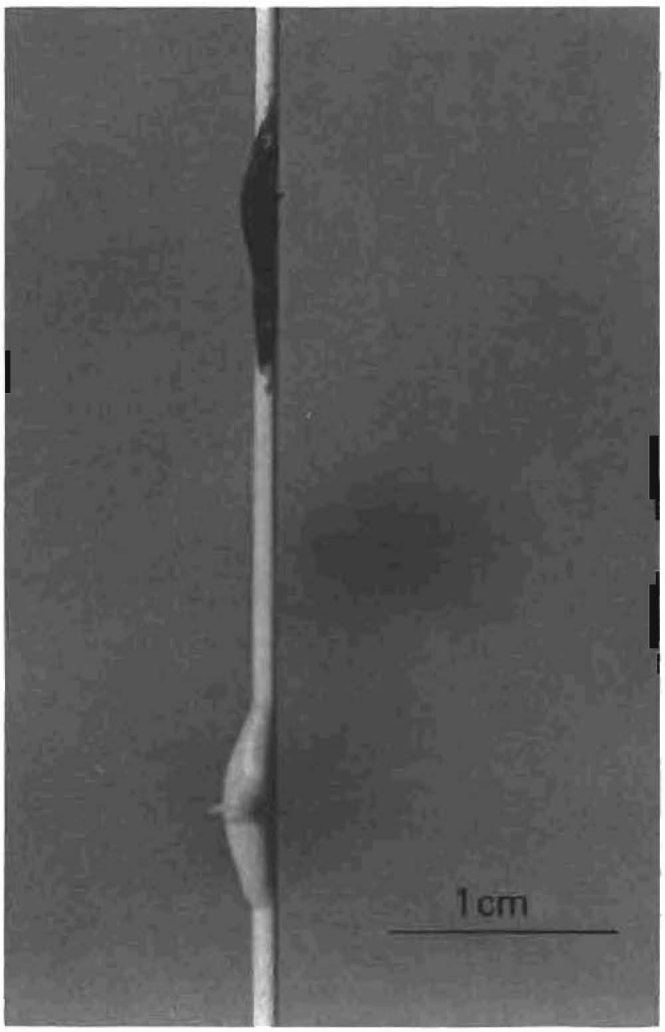

Fig. 3 A grass stalk marked by a brown hyaena with black and white pastes.

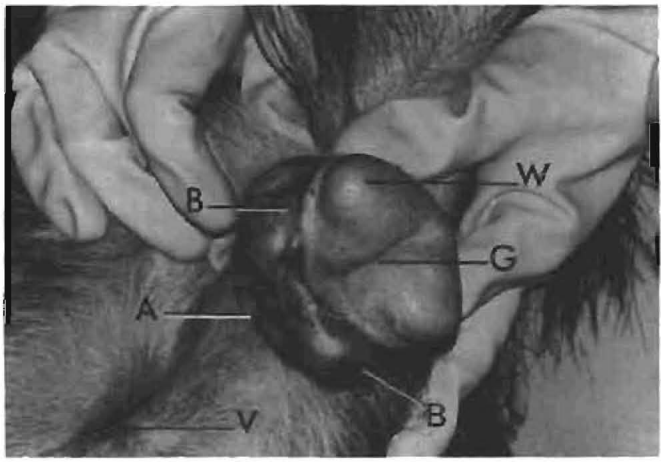

Fig. 4 The everted anal scent pouch of an anaesthetized female brown hyaena. A - Anus; B - Lateral area secreting the black paste, G - Groove running down the centre of the tissue producing the white paste; W - Large central area secreting white paste; V - Vagina.

In this paper we describe the behaviour associated with scent marking and the related functional anatomy of the scent pouch. The dispersion pattern of scent marks within a group territory and the rate of marking in different parts of the territory are also described, and preliminary chemical analyses of the black and white secretions are presented.

Materials and Methods

Study area

The study was carried out in a part of the Kalahari Gemsbok National Park, Republic of South Africa and the neighbouring Gemsbok National Park, Republic of Botswana (Mills 1978). The area is semi-desert with a mean annual rainfall of 220 mm and is largely covered with a layer of red sand, blown by the wind into a series of dunes. These dunes are broken by several pans and by the dry bed of the Nossob River. The dunes and river form quite different habitats, with the riverbed and vicinity providing a much higher density of hyaena food than the dunes (Mills in prep.). The riverbed is dominated by relatively large *Acacia erioloba* trees and supports both tall and short perennial grasses. In contrast the dunes support a very open scrub dominated by smaller trees; *Boscia albitrunca*, *A. erioloba* and *A. haematoxylin*, and by tall perennial grasses.

Behavioural

We made our behavioural observations by following seven hyaenas with a four-wheel-drive vehicle. Each of the hyaenas was fitted with a radio-collar to which were fixed two beta-lights (Saunders-Roe Development, England); sealed glass capsules filled with tritium gas which cause a phosphor coating to emit green light. With the radio it was possible to locate an animal and then with the help of the beta-lights to follow it for long distances. On dark, moonless nights we used a hand-held spotlight to observe details of behaviour.

The majority of our observations were made, between 1976 and 1978, on three males and two females which formed a single family group which we called the Kwang group (Fig. 1).

Our strategy was to locate a hyaena as soon after dusk as possible and then to follow it for as long as we could before it rested up for the day. In this way we hoped to build up a representative picture of how the group used the different parts of its territory. When following a hyaena we noted the direction in which it was moving by using the stars as reference. Whenever it stopped or changed direction we noted the distance it had travelled from the vehicle's odometer. In addition we noted the odometer reading everytime we passed a landmark whose position was accurately known, for example windmills, crossroads and large trees. Each time a hyaena stopped to scent mark (henceforth termed pasting) the odometer reading was again noted. At a later date all movements and pasting locations were plotted on a large scale map, an example of which is given in Fig. 5.

Detailed descriptions of pasting behaviour were based on numerous direct observations with the aid of a spotlight and on a 16 mm cine sequence owned by the British Broadcasting Corporation.

Histological

Two anal scent pouches were removed from freshly killed hyaenas, one male and one female, and quickly frozen. Later they were fixed in 10% buffered formal-saline. Representative pieces of tissue from the areas of the pouch producing the black and white secretions were dissected, washed, dehydrated in ethanol, cleared in methyl benzoate and embedded, under vacuum, in paraffin wax. Sections of 10 μm for general descriptive histology were stained in haematoxylin and eosin or in Mallory's trichrome stain. Paraffin sections and 20 μm frozen sections were subjected to the histo-chemical procedures listed in Table 1.

Chemical studies

We collected a series of grass stalks on which two known hyaenas (Charlie and Shimi) had just pasted. The pastes of each individual were collected at different times, but within a period of 72 h for each individual. The black and white secretions were separated and deep frozen approximately six hours after being collected and at a later date extracted in 1 ml redistilled dichloromethane. Later the extracts were centrifuged and the supernatant reduced to 250 μl under nitrogen.

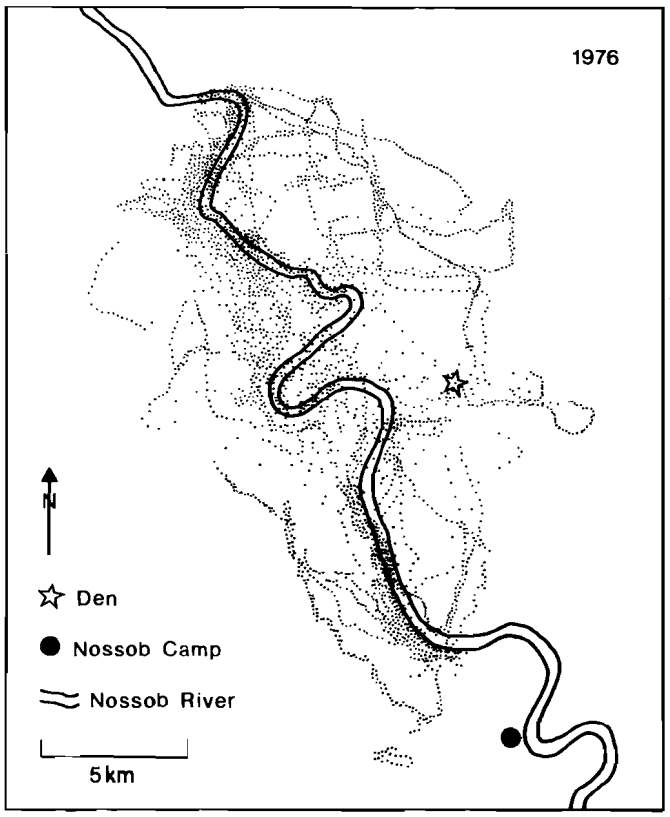

Fig. 5 Map of the locations at which the two members of the Kwang social group were seen to paste during 1976.

GLC separations were carried out on a Pye-Unicam 104 gas chromatograph equipped with a flame ionisation detector and using N_2 as carrier gas. The analyses were performed on a 25 m (I.D. 0,23 mm) WCOT column coated with a 0,21 μm film of methyl silicone gum (SE30). The injected samples were split 1:100 and passed through the column with nitrogen at 1,5 ml per minute. The analysis was temperature programmed from 100°C to 200°C at 4°C per minute. Injector and detector were maintained at 275°C. Peak areas were measured with an LDC308 computing integrator.

Table 1 The histochemical reaction of tissues from the brown hyaena anal pouch

Substance	Reaction (Pearse, 1968)	Section	Sebaceous gland	Apocrine gland
Free lipids	Oil Red	Frozen	+ + +	+
Polysaccharides	Periodic acid/Schiff	Paraffin	+	+ + +
Free aldehydes	Schiff	Paraffin	–	±
Acid muco-polysaccharides	Toluidine Blue	Paraffin	–	+ +
	Alcian Blue	Paraffin	–	+ +
	Methylation/Alcian Blue	Paraffin	–	–
Lipo-fuschin	Nile Blue & Schmorls Methods	Paraffin	–	+ + +
Iron	Perle's method	Paraffin	–	+ + + (pigment)

– no reaction
+ to + + + increasingly strong reaction.

Results

Pasting behaviour and the structure of the anal scent pouch

Brown hyaenas normally paste on long stalks of grass (if these are not available other objects such as bushes or rocks will be used), as do the other species of hyaena (Kruuk 1972, 1976; Kruuk & Sands 1972; Rieger 1977). The brown hyaena is unique among the hyaenas, however, in that it produces a scent-mark with two quite distinct pastes (Fig. 3).

During pasting a brown hyaena bends a grass stalk forward by walking over it, often lifting a fore-leg and turning slightly as it does so. The hyaena continues to move forward until the base of the grass comes to lie between its hind legs and the stalk runs forward under its belly. Then the hyaena, with its tail curved up over its back and its back legs slightly bent, extrudes its anal pouch (Fig. 6).

Fig. 6 A pasting brown hyaena. Note that the grass already supports a pasting. The notches in the animal's ear are identification marks.

The anal pouch, which lies between the rectum and the base of the tail, consists of two distinct regions (Fig. 4). The large central area, which is normally covered in an accumulation of white secretion, has a distinct, deep groove running vertically from top to bottom. Lying, one to each side of the central area, and separated from it by non-secretory epithelium, are two circular areas which produce the black secretion (Figs. 4 and 6).

Having extruded its pouch the hyaena now feels for the grass stalk, sometimes for several seconds, and eventually succeeds in locating it in the groove running down the white central area. The hyaena then moves forward, pulling the anal pouch along the grass stalk and at the same time retracting it. The first effect of this action is to smear a thick, creamy blob of white paste on to the grass stem. Then, as the pouch continues to retract, the non-secretory portions of the pouch and the black secretory areas, collapse in turn on to the stem. In this way a thin smear of the black secretion is deposited some distance above the blob of white paste. The dimensions of these paste marks are given in Table 2.

Hyaenas usually paste clean grass stems but under certain circumstances (see below) they will paste on top of existing pastes (Fig. 6). The freshly deposited secretions have a strong odour, the white being different from the black. The smell of the white paste can still be detected by the human nose 30 days after deposition. By this stage it has turned black. The smell of the black paste is not as long lasting as that of the white paste.

Table 2 The dimensions of 50 brown hyaena pastings

	Mean (mm)	Standard error
Length of black secretion	11,9	0,5
Distance between black and white secretions	12,4	0,5
Length of white secretion	12,7	0,1
Height above the ground, to bottom of white secretion	687,2	21,9

Note: The mean shoulder height of 20 adult brown hyaenas is 787,0 ± 81,0 mm

At a histological level, the central area of the pouch which produces the white paste is composed of numerous, enlarged sebaceous glands (Fig. 7). This tissue, and the white paste produced by it, are rich in lipid (Table 1).

In contrast the circular areas responsible for producing the black secretion consist almost entirely of apocrine, sudoriferous tissue (Fig. 7). The black colour of the paste is due to accumulations of lipo-fuchsin, a common metabolite of apocrine tissue (Table 1). In contrast to the white paste the black material contains little lipid.

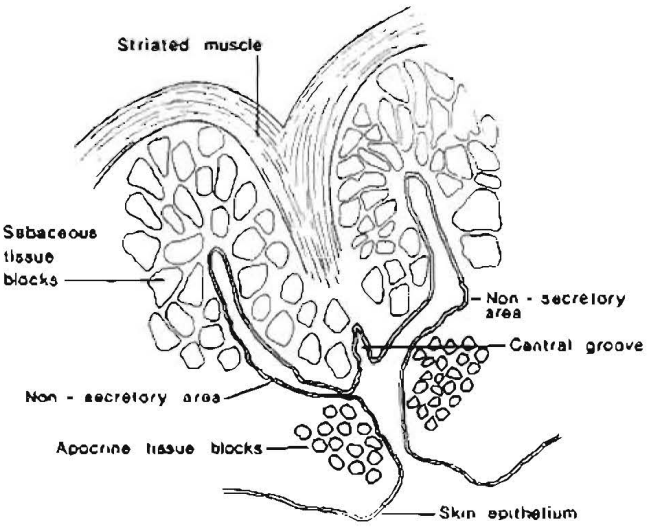

Fig. 7 Drawing of a horizontal section through the centre of the retracted anal scent pouch of a brown hyaena. The central sebaceous area with its vertical groove, and the two lateral apocrine areas can be clearly seen. The complex musculature terminating near the central groove consists of voluntary muscle blocks and functions to retract the pouch.

Dispersion pattern of pastings within the territory

Because the territory of the Kwang group changed slightly between 1976 and 1978 we have analysed our data separately for the periods 1976 and 1977–78.

During 1976 we radio-tracked an adult female and an adult male. At this time they were the only two adults in the group. From July 1977 to September 1978 we again followed these two hyaenas and in addition a young adult

female and two young adult males. The distances for which we followed these animals, together with the number of pastings we saw them deposit are shown in Table 3. Since we followed these hyaenas for long periods of time, often for two or more complete nights at a time, we are confident that our observations comprise a representative sample of the total movements made by the hyaenas, and of the dispersion pattern of their pasting points. Figure 5 shows the positions of all the pastings we saw deposited by the hyaenas we followed during 1976. It is clear that the pastings are scattered throughout the territory, but not uniformly so. We have similar data describing the pastings deposited in 1977 – 78.

Table 3 Distances for which the members of the Kwang group were followed in 1976 and 1977 – 78 together with the number of pastings observed to be deposited

Year	Age	Sex	Distance (km)	Pastings	Pastings/km
1976	Young adult[a]	F	767	1760	2,29
1976	Old adult[b]	M	353	1218	3,45
1977 – 1978	Middle aged[a]	F	154	296	1,92
1977 – 1978	Old adult[b]	M	28	56	2,00
1977 – 1978	Young adult	F	188	578	3,07
1977 – 1978	Young adult[c]	M	341	908	2,66
1977 – 1978	Young adult[c]	M	116	328	2,82
	Total		1947	5144	2,60

[a] and [b] The same individuals.
[c] The hyaenas whose pastes were analysed.

We have further analysed these data on the dispersion of pasting sites by means of the computer programs SYMAP and SYMVU (Laboratory for computer graphics, Harvard University, U.S.A.). These programs display graphically, spatially distributed quantitative data, first as a two-dimensional contour map and then as a three dimensional map in which the third, vertical dimension reflects the value of the quantitative data, in our case the density of pasting points. To facilitate such an analysis we superimposed on the 1976 and 1977 – 78 movement maps a matrix of 2,5 by 2,5 km squares covering the hyaena territory and surrounding terrain (Figs. 8 and 9). We then counted for each square, the total number of pastings deposited in 1976 and in 1977 – 78. The density values were then analysed by the SYMAP program using ten class intervals of equal size, covering the range 0 – 190 pastings per square in 1976 and 0 – 204 in 1977 – 78. The contour matrix generated by SYMAP was then used to compute the three dimensional SYMVU plots (Figs. 11 and 12). These maps, where the vertical dimension represents the pasting density, are plotted as if seen from the south-east at an altitude of 35° above the horizontal. The 1976 map of the area is shown in Fig. 10 as seen from this position in order to orientate the reader.

The SYMVU maps show clearly that the highest densities of pastings are to be found near the centre of the group territory with a progressive decrease in density

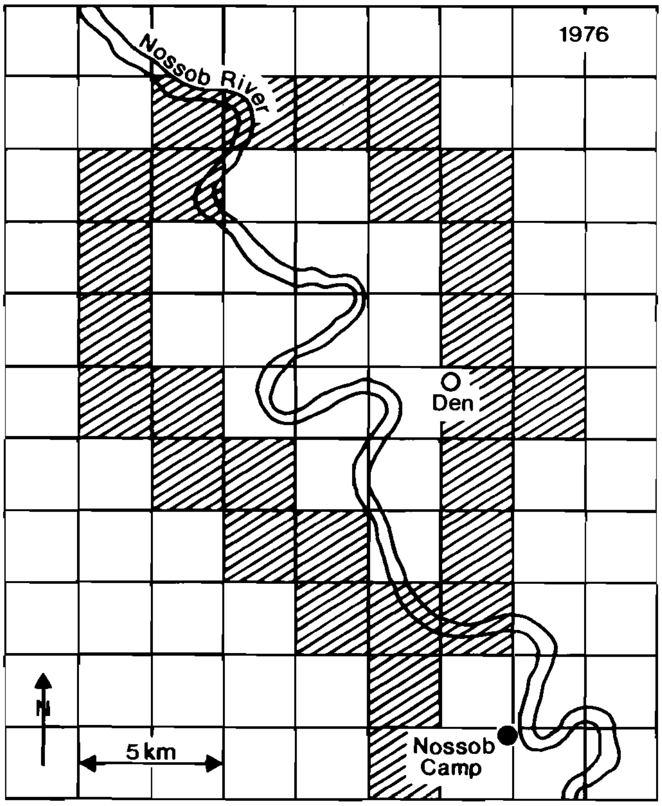

Fig. 8 Map of the Kwang group territory in 1976 with a superimposed 2,5 km grid. The hatched squares are those containing the outermost movements and are termed border squares. The inner ones are called internal squares.

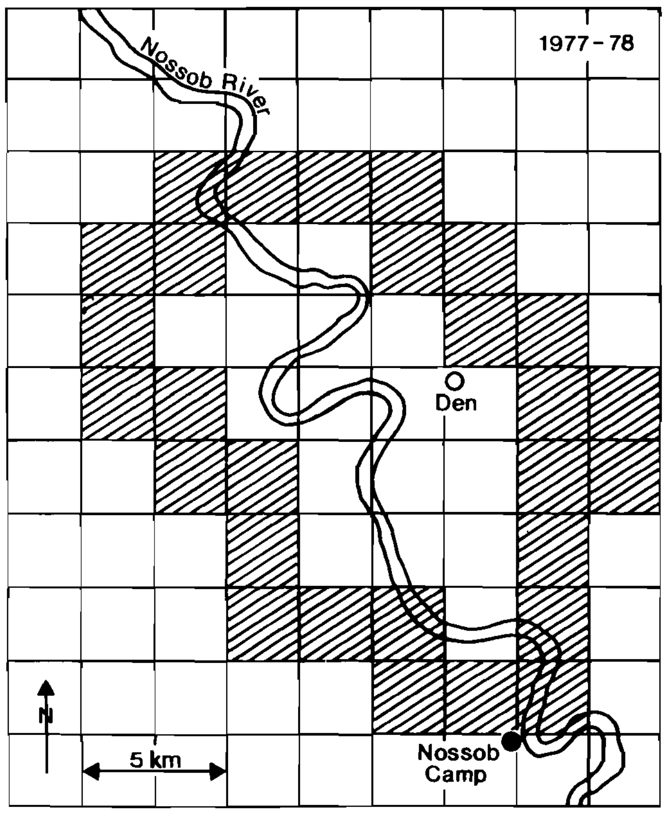

Fig. 9 Map of the Kwang group territory in 1977 – 78. Other details as in Figure 8.

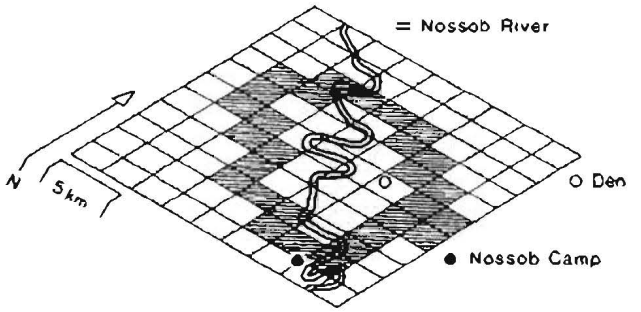

Fig. 10 The 1977–78 Kwang group territory map as seen from the South-East and from an altitude of 35° above the horizontal.

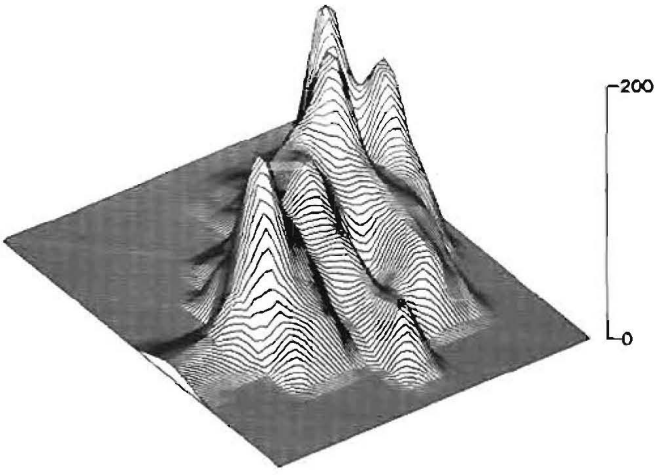

Fig. 11 A three-dimensional map, generated by SYMVU, of the density of pastings in the 1976 Kwang group territory. The scale represents the number of pastings per 2,5 km square. The area covered by the map and the orientation are as in Figure 10.

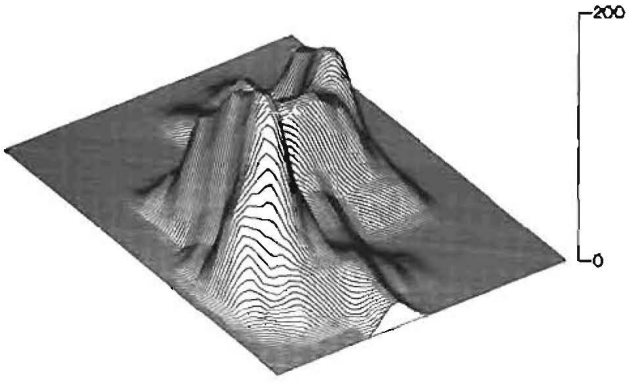

Fig. 12 As Figure 11 except that the data are from 1977–78.

towards the borders. In order to test statistically this difference in density between border and interior, we have designated those squares on the periphery of the territory as border squares and the others as internal squares (Figs. 8 and 9). The mean density of pastings was significantly lower in border squares than in interior ones both in 1976 and 1977–78 (Table 4).

Table 4 The mean number of pastings deposited in internal and border squares

Year	Mean number of pastes/square	
	Border squares	Internal squares
1976[a]	57,7	90,0
1977–78[b]	42,0	67,0

[a] $t = 4,18$ $p < 0,001$
[b] $t = 1,91$ $p < 0,05$

The difference in the density of pastings between border and internal squares is due to the fact that the number of pastings deposited in a square is related to the distance travelled in that square by the hyaenas (Fig. 13). The greater the distance the more pastings are deposited. Since hyaenas use the interior of their territory more than the periphery (Table 5) it follows that most pastings will be deposited in the interior squares.

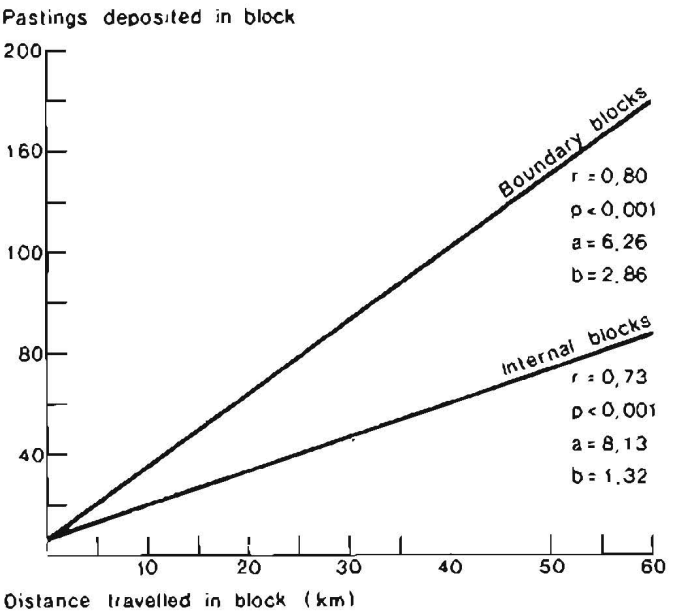

Fig. 13 The relationship between the distance moved by a brown hyaena in a particular 2,5 × 2,5 km square and the number of pastings deposited in it. All animals and both time periods combined.

Table 5 The observed total distances hyaenas were seen to travel in border and internal squares. The expected distances are the distances they would have travelled had they used the different parts of their range in proportion to their areas

Year	Distance travelled (km)	
	Border squares	Internal squares
1976		
Observed	374	743
Expected	701	415
	62,8% of area	37,2% of area
1977–78		
Observed	256	546
Expected	499	303
	62,2% of area	37,8% of area

Rate of pasting

The difference in slope between the two regression lines relating the numbers of pastings deposited to the distances travelled in border and internal squares indicates that hyaenas paste at a higher frequency when they are in border squares than when in internal ones (Fig. 13). By combining the data for all hyaenas it is possible to show statistically that the frequency of pasting, expressed as pastings per km travelled, was significantly higher for border blocks than for internal ones in both 1976 and 1977–78 (Table 6).

Table 6 Overall pasting frequencies, all hyaenas and movements combined

	Mean frequency of pasting (pastings/km)		Mann-Whitney U Test		
Year	Border squares	Internal squares	*U*	*Z*	*p*
1976	4,54	2,46	335	−3,5	<0,0002
1977–78	4,37	2,16	796	−5,57	<0,00003

During the course of the study three hyaenas made excursions into areas we judged to be outside the group territory. During these excursions the rate of pasting dropped markedly to 0,4 per km. During one particularly long excursion one of them did not paste once in 17 km.

Within the territory there are differences between pasting frequencies of males and females. In the case of internal squares, males marked at a higher frequency than did females in both 1976 (Mann-Whitney *U* Test; $U = 153$; $z = -2{,}05$; $p = 0{,}02$) and 1977–78 ($U = 338$; $z = 1{,}99$; $p = 0{,}02$). When in border squares males pasted at much the same frequencies as females in 1976 but in 1977–78 the females pasted at a significantly higher frequency ($U = 36$; $p = 0{,}025$).

Reaction of hyaenas to existing pastings that they encounter

Sometimes, before pasting, a hyaena will sniff and lick at a grass stem. At other times it will sniff and lick the stem and then not paste on it, although it may then paste close by. Almost invariably, grass stems that are sniffed in this way already have a pasting on them. The response of a hyaena to a pasting investigated in this way depends largely upon where in the territory the pasting is encountered (Table 7). Hyaenas are much more likely to react to a pasting by over-pasting if they find the pasting in a border square rather than in an internal one (Table 7).

Table 7 The behaviour of hyaenas after sniffing pastings in different parts of the home range[a]

	Number of occasions	
Reaction	Border squares	Internal squares
Pasted on top of paste or close by	65	26
Did not paste	23	61

[a] $\chi^2 = 34{,}3$; $p < 0{,}001$

A pasting encountered in a border square has a higher chance of having been left by a hyaena from another social group than does one found in an internal square. This may account for the difference in response of the hyaenas; they may paste on top of foreign pastes but not on top of those deposited by animals from their own group. The few data we have on the response of hyaenas to pastings of known origin support this possibility (Table 8).

Table 8 The reaction of hyaenas to pastings from their own group and from foreign groups[a]

	Number of occasions	
Response	Pasting from own group	Pasting from foreign group
Approached within 1 m but did not sniff or paste	6	0
Approached within 1 m and then sniffed and/or pasted	6	11

[a] Fishers exact probability = 0,0092

On 23 occasions, all in internal squares, we have seen hyaenas come upon a fresh pasting whose author we know. In nine of these cases we had taken a pasted grass from another territory and had placed it in the Kwang group territory. On the other 14 occasions we had seen one hyaena paste and later another individual come up to the pasting. Twelve of the total of 23 cases involved pastings made by members of the Kwang group and 11 were made by animals from other groups. From these few data there are clear indications that hyaenas can distinguish between pastings belonging to their own group and those deposited by foreigners (Table 8). Hyaenas are more likely to investigate closely, and paste on top of, the pastings left by animals from other groups than pastings made by their own group.

Chemical analysis of the pastings

GLC analyses were performed on fresh uncontaminated pastings. In all we examined 11 white pastes, five from one hyaena (Charlie) and six from another (Shimi), and 15 black pastes, eight from Charlie and seven from Shimi. Typical chromatograms for the white and black pastes are shown in Figs. 14 and 15 respectively. The chemical composition of each is clearly complex and the two are distinctly different; work is continuing on identifying the major chemical constituents.

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

In order to detect any such differences in the relative concentrations of the compounds making up the black and white pastes, we have expressed the areas under selected peaks as a percentage of the total area under all of those peaks. We have then calculated for each individual, the mean percentage for each peak, together

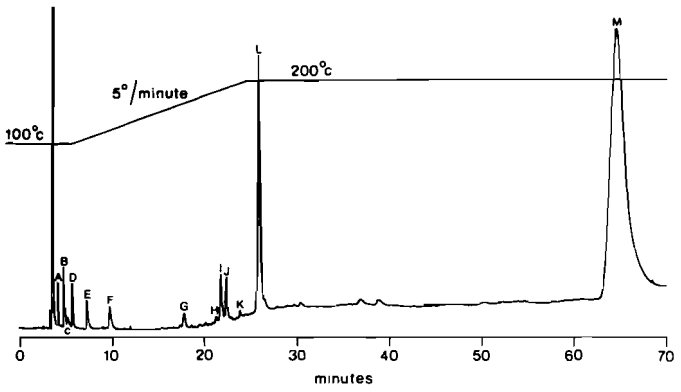

Fig. 14 A typical gas-liquid chromatograph of the white paste from a brown hyaena. The temperature programme used in the analysis is shown on the figure. The letters indicate the peaks used in the analysis of individual differences.

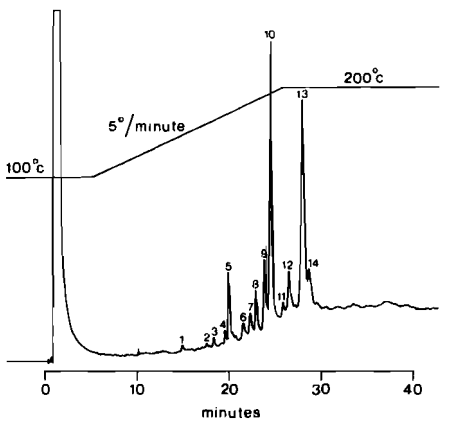

Fig. 15 As figure 14 but for a sample of black paste.

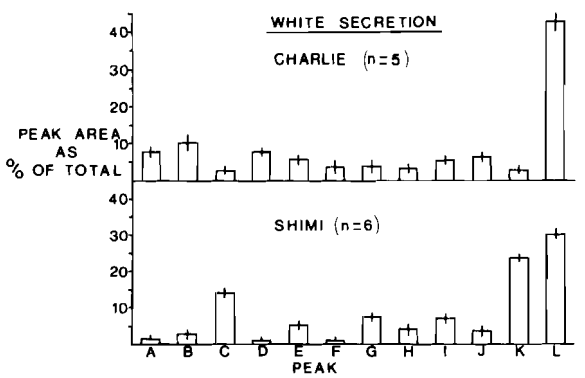

Fig. 16 Individual differences in the white pastes of two brown hyaenas (Charlie and Shimi). The number of samples analysed is given by n and the histograms represent the mean area of each peak measured as a percent of the total area of all the peaks. The vertical lines represent one standard deviation each side of the mean. The pastes of each individual were collected over a 72 h period.

with its standard deviation, using the data from the different pastes we have analysed (Figs. 16 and 17). Such an analysis reveals clear differences between Shimi and Charlie. For example, in the case of the white paste peaks C and K are relatively major components for Shimi but minor ones for Charlie. Again peaks A and B are relatively large in Charlie's paste but small in Shimi's (Fig. 16).

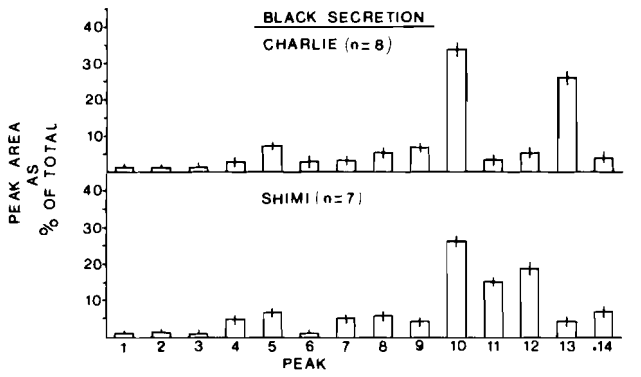

Fig. 17 As figure 16 but for black pastes.

Equally clear differences between the two hyaenas can be seen in the black paste (Fig. 17). Furthermore the small standard deviations in Figs. 16 and 17 suggest that the pastes deposited by an individual are similar to each other, at least over the 72 h periods during which we collected the samples.

Discussion

Brown hyaenas in the southern Kalahari paste throughout their territory but mostly in the central, heavily utilised areas (Figs. 11 and 12). However, when they are moving near the border of their territory they increase their rate of pasting (Table 6).

In this way the whole territory becomes saturated with the smell of the resident hyaenas. We estimate that during the 12 months of observations in 1977–78, the five hyaenas in the Kwang group deposited some 145 000 pastings in their territory. Each pasting is detectable by the human nose for at least one month and by a hyaena for probably much longer.

The biological function of scent-marking in carnivores is little understood. In the brown hyaena pasting behaviour could fulfil at least two functions. Firstly, it could be used to convey information within the social group. Brown hyaenas always forage alone and often feed on items that suffice to satisfy one hyaena only (Mills 1978, Mills & Mills 1978). It is therefore important for them to know where other hyaenas are foraging, or have foraged in the recent past, so that they can avoid areas which are likely to be unproductive. The series of pastings left by hyaenas may fulfil such a role. As the black paste loses its smell relatively quickly, it may transmit information on the length of time that has elapsed since a hyaena passed that way. A similar hypothesis for scent marking in the red fox (*Vulpes vulpes*) has been proposed by Henry (1977). Here urine marking is seen to be used as a signal showing that, although there might be a food odour at a particular place, the food has been eaten.

In addition to this intra-group function pasting may also serve to pass information between social groups. Saturation of the territory with scent by brown hyaenas could function to ward off intruders *i.e.* to show that the territory is occupied, and thus to save time and energy in ritualised combat. This information is likely to be transmitted by the longer lasting white paste.

Both of these possible functions demand that the hyaena can distinguish between the pastings of different individuals. In other words that the smell left by a hyaena should at least contain information on the identity of its author. This has been found to be the case with the small Indian mongoose (*Herpestes auropunctatus*) (Gorman 1976). We have both behavioural and chemical evidence for individual smells in the brown hyaena (Figs. 14 and 15, Tables 7 and 8). The different reactions of hyaenas to pastes deposited by fellow group members and those deposited by others indicate clearly that they can be told apart (Table 8). The differences in the chemical profiles of pastes from different individuals provide a chemical basis for such behavioural discrimination.

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