Factors affecting the movement patterns of brown hyaenas, *Hyaena brunnea*, in the southern Kalahari

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Most brown hyaenas (*Hyaena brunnea*) in the southern Kalahari live in partially overlapping territories. The movement patterns of hyaenas from two territories are illustrated and use has been made of the computer programs SYMAP and SYMVU to graphically display the data as three-dimensional maps. These illustrate how the movement patterns of hyaenas from different territories vary, depending on the habitat composition of the territory and therefore on the dispersion pattern of the food. The local density of spotted hyaenas (*Crocuta crocuta*) may also affect the movement patterns of brown hyaenas, as spotted hyaenas are socially dominant to brown hyaenas and in high-density areas they may also deprive brown hyaenas of a significant amount of food.

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Die meeste bruinhiënas (*Hyeana brunnea)* in die suidelike Kalahari bly in gedeeltelike-oorvleulende terrotoriums. Die bewegingspatrone van hiënas van twee territoriums is geïllustreer en gebruik is gemaak van die rekenaarprogramme SYMAP en SYMVU, wat grafies die data as driedimensionele kaarte vertoon. Dié illustreer hoe die bewegingspatrone van hiënas van verskillende territoriums varieer, afhanklik van die habitatsamestelling van die territorium, en daarom van die verspreidingspatroon van die voedsel. Die lokale digtheid van gevlekte hiënas *(Crocuta crocuta)* mag ook die bewegingspatrone van bruinhiënas beïnvloed, want gevlekte hiënas is sosiaal dominant oor bruinhiënas en in hoëdigtheid-gebiede mag hulle ook bruinhiënas van 'n betekenisvolle hoeveelheid voedsel beroof.

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Introduction

The brown hyaena *Hyaena brunnea* in the southern Kalahari is predominantly a nocturnal, solitary forager. Scavenged mammal remains and to a lesser extent wild fruits make up the bulk of the brown hyaena's diet in this region (Mills 1978; Mills & Mills 1978). Approximately 64% of the population inhabit large territories ($\bar{X}$ = 330 km^2) which they share with a varying number of other brown hyaenas of both sexes. Cubs are raised at a den within the territory and are brought food by all the members of the group. The rest of the population comprises dispersing subadults of either sex or nomadic adult males (Mills 1982a and b).

Elsewhere, (Mills 1982b) it has been suggested that the size of a brown hyaena territory is affected by the distribution of the food in the territory. There was a significant positive correlation between territory size and the mean distance travelled by hyaenas in each territory between finding successive mammal food items. It was also suggested that the number of brown hyaenas inhabiting a territory depends on the 'quality' of the food in the territory.

In this paper we illustrate the movement patterns of brown hyaenas from two territories, one comprising mainly dunes habitat, the other containing a large slice of river habitat, and discuss the influence of food dispersion on brown hyaena movement patterns. Then we discuss what we believe to be the other important factor affecting their movement patterns, namely the influence of the larger, closely related, spotted hyaena (*Crocuta crocuta*).

The study area

The study was conducted in a 2 750 km^2 area in the southern Kalahari centred on Nossob Camp in 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 the mean annual rainfall at Nossob Camp between 1967 and 1981 being 253 mm.

The area is largely covered with a layer of red windblown sand piled into dunes. These dune areas are broken by a large dry river-bed, the Nossob, which runs roughly north to south through the middle of the study area (Figures 1 & 2). The dune areas are extremely open shrub or tree savannah, mainly *Boscia albitrunca*, with tall perennial

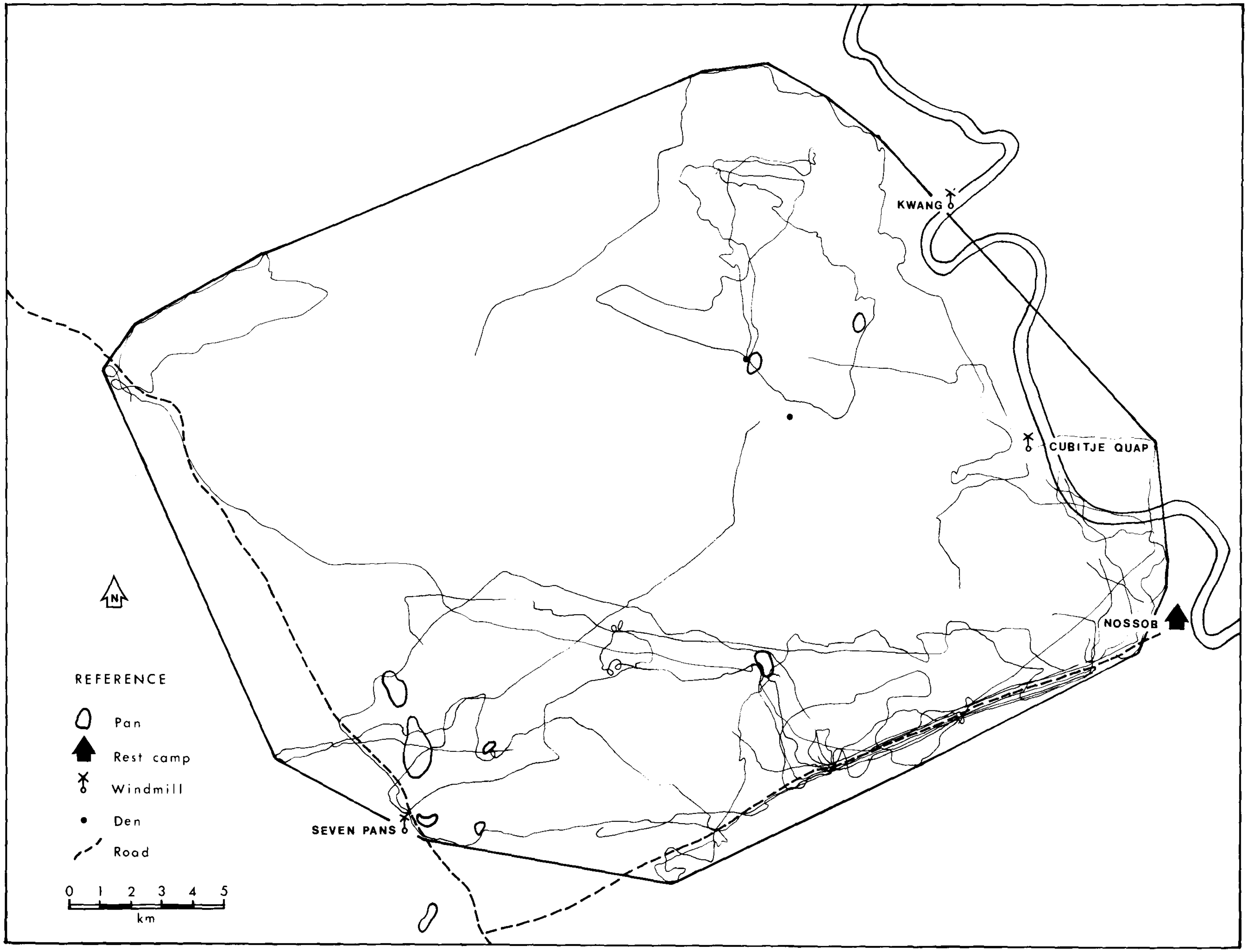

Figure 1 The observed movements of two female brown hyaenas from the Seven Pans group; January — September 1975.

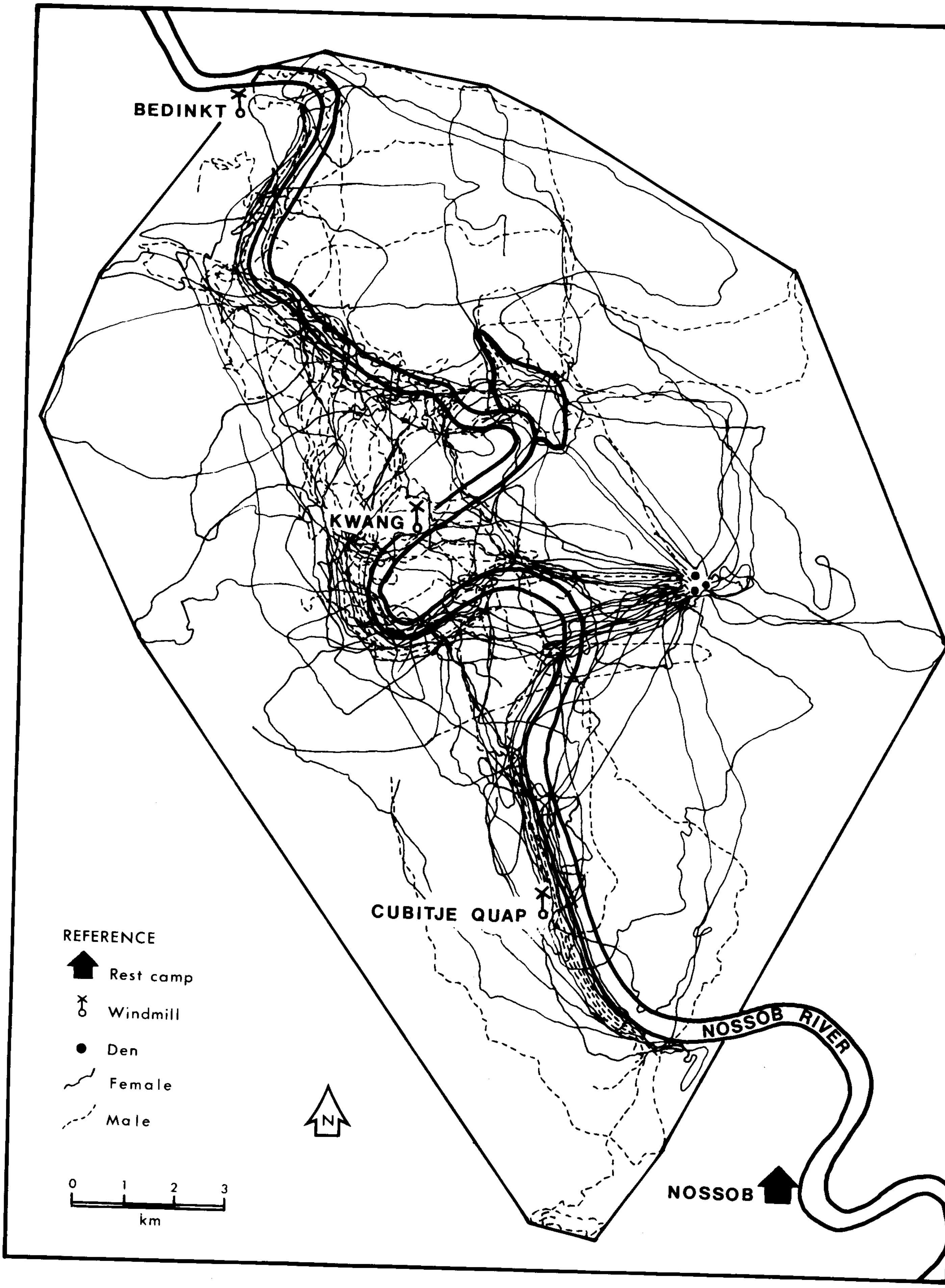

Figure 2 The observed movements of a male and female brown hyaena from the Kwang group; January — July 1976.

grasses. The river-bed has numerous tall *Acacia erioloba* trees, and generally shorter grasses. Adjoining the river-bed are large limestone flats up to 4 km wide covered with the low shrub *Rhigozum trichotomum* and the short perennial grass *Stipagrostis obtusa* (Leistner 1967).

The river-bed and environs supported far higher densities of all ungulates, except steenbok (*Raphicerus campestris*), than the dunes did throughout the study (Table 1). Other important mammalian food items for brown hyaenas such as small canids, Cape hares (*Lepus capensis*) and springhares *(Pedetes capensis)* (Mills and Mills 1978) tended to be more evenly distributed in both habitats, but at far lower densities than the large ungulates along the river-beds (Mills 1981). The important wild fruits in the brown hyaena's diet, the tsama *(Citrullus lanatus)* and the gemsbok cucumber *(Acanthosicyos naudianus)*, were almost exclusively confined to the dunes. In 30 strip counts of 100 x 10 m carried out in river habitat only 29 tsamas and no gemsbok cucumbers were counted, whereas in 90 equal sized strip counts carried out in the dunes 2 807 tsamas and 2 070 cucumbers were counted. Both fruits were patchily distributed in the dunes and their densities fluctuated markedly from year to year (Mills 1981; 1982b).

Table 1 The mean number and standard error, of ungulates counted per 100 km driven annually in river and dunes habitats between 1974 and 1980 (from Mills 1982b).

	Habitat	
Animal	River	Dunes
Springbok	1655 ± 234	2 ± 2
Gemsbok	83 ± 19	34 ± 10
Hartebeest	152 ± 25	10 ± 3
Wildebeest	308 ± 63	9 ± 9
Steenbok	2 ± 1	14 ± 3

Methods

Data on movements of brown hyaenas were obtained from direct observations of animals fitted with radio collars and green-glowing beta lights or from tracking known individuals' spoor (Mills 1978, 1982b). When an animal was first located the vehicle's odometer reading was noted and, if possible, its position relative to a known fixed point was established. The direction in which the animal was moving was ascertained by using the sun, moon and certain constellations of stars, particularly the Southern Cross, Orion and the Scorpion as reference points, and by dividing the points of the compass into 16 divisions; N, NNE, NE, ENE, E, etc. Whenever the hyaena made a direction change and maintained the new direction for more than 50 m, the new direction and the odometer reading at the point of change were noted. Whenever the hyaena passed a known fixed point the odometer reading was also noted.

At the termination of the observation period the odometer reading was noted and the vehicle was driven on a fixed compass reading until a known point was reached, when the odometer reading was again noted. At a later date each movement was plotted on a 1: 10 000 map. The composite maps of the movement patterns of hyaenas from two of the territories were subjected to the computer programs SYMAP and SYMVU (Laboratory for computer graphics, Harvard University, U.S.A.) (M. Gorman pers. comm. 1981).

In order to perform these analyses, a grid matrix was overlayed on each hyaena territory, each grid covering an area of 2,5 × 2,5 km (Figures 3 & 5). The total distance moved within each grid square in each territory was measured, and the distances per square were analysed by the SYMAP program. This produced a contour map of movement densities over the surface area of the hyaena territory. The SYMAP program grouped the movement density values into 10 class intervals of equal size covering the range 0 — 27 km per square in the Seven Pans territory and 0 — 88 km per square in the Kwang territory. The contour matrix generated by the SYMAP was then used to compute the three-dimensional SYMVU plots (Figures 4 & 6).

Observations of interactions between brown and spotted hyaenas were carried out whilst following members of either species, or at carcasses of herbivores which we either opportunistically discovered or specifically put out for this purpose.

Results

The influence of the dispersion of food

The observed movement patterns of brown hyaenas from two territories are illustrated in Figures 1 and 2. Figure 1 shows the movement patterns of two brown hyaenas from the Seven Pans group in 1975 from 539 km of following and Figure 2 shows the movement patterns of two hyaenas from the Kwang group in 1976 from 1 235 km of following. The Seven Pans territory comprised 95% dunes habitat and 5% river habitat, whereas the Kwang territory comprised 38% dunes habitat and 62% river habitat (Mills 1982b). The movements of the Seven Pans animals tend to be randomly distributed throughout their territory, whereas those of the Kwang animals tend to be clumped along the Nossob river-bed. Data from other territories also show that movements in dune territories tend to be random whereas those in mainly river habitat territories tend to be clumped along the river-bed (Mills 1981).

In order to illustrate these differences in movement patterns more clearly, use has been made of the computer programs SYMAP and SYMVU (Figures 4 & 6). These programs graphically display spatially distributed quantitative data, first as a two-dimensional contour map and then as a three-dimensional map. In the present study the first two dimensions represent the surface area of a hyaena territory and the third (vertical) dimension reflects the density of movements within each part of the territory.

These maps are displayed as if seen from the south-east at an altitude of 35° above the horizontal. Figures 3 and 5 show maps of both territories viewed from this angle in order to orientate the reader. In the three-dimensional SYMVU plots, therefore, the peaks represent areas of the territory in which high movement densities were observed.

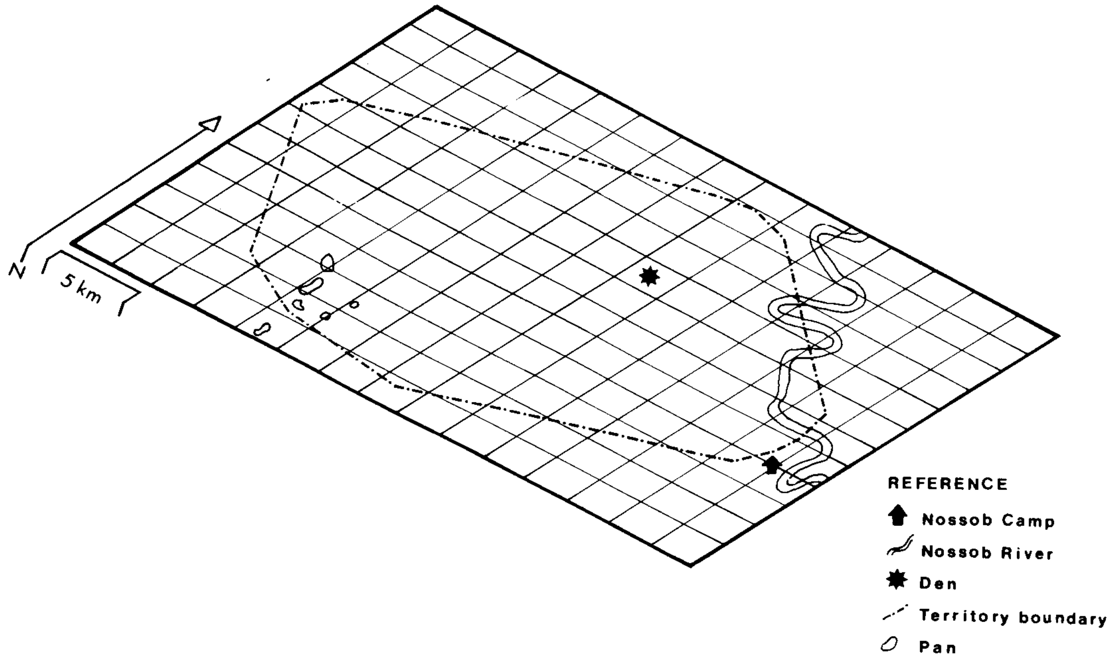

Figure 3 A map of the Seven Pans territory with a 2,5 x 2,5 km grid overlay as seen from the south-east and from an altitude of 35° above the horizontal.

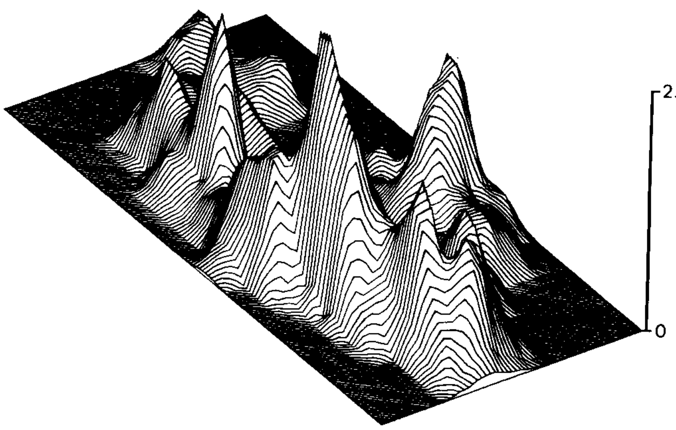

Figure 4 A three-dimensional map, generated by SYMVU, of the movement patterns of the Seven Pans group. The scale represents the distance that the hyaenas were followed per 2,5 × 2,5 km square. The area covered by the map and the orientation are as in Figure 3.

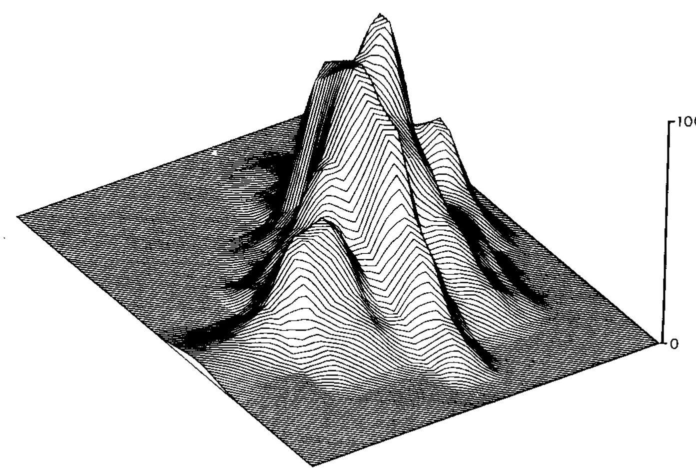

Figure 6 A three-dimensional map, generated by SYMVU, of the movement patterns of the Kwang group. The scale represents the distance that the hyaenas were followed per 2,5 × 2,5 km square. The area covered by the map and the orientation are as in Figure 5.

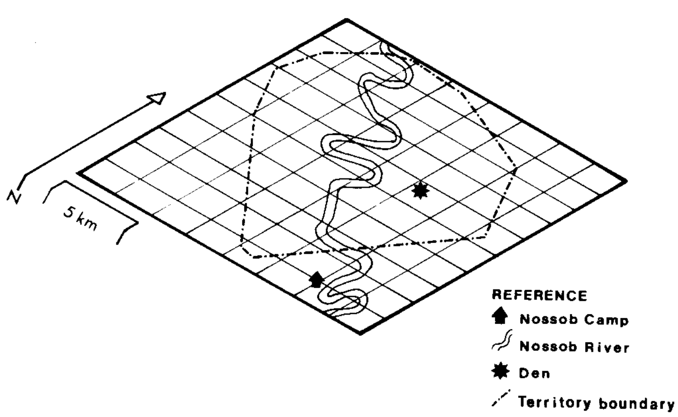

Figure 5 A map of the Kwang territory with a 2,5 × 2,5 km grid overlay as seen from the south-east and from an altitude of 35° above the horizontal.

The movements of individuals from the Seven Pans group (Figure 4) show a scattering of peaks throughout their territory, i.e. a random distribution, whereas the movements of individuals from the Kwang group (Figure 6) show a continuous peak along the Nossob river-bed and out to the den, i.e. a clumped distribution. These differences in the movement patterns are believed to be mainly due to differences in the distribution of the hyaenas food. Hyaenas with a large amount of river habitat in their territories tended to forage extensively in this habitat as this is where food was frequently to be found. The ungulates were concentrated there (Table 1) and relatively many of them became available to the hyaenas, either through being killed by other predators, or through non-violent mortality (Mills 1982b). Hyeanas which lived mainly in the dunes, however, were faced with a far lower density and a more even distribution of food, as there were no ungulate concentration areas in the dunes (Table 1.) They were, therefore, forced to forage more randomly over their territories.

The influence of spotted hyaenas

The local density of spotted hyaenas may also influence the movement patterns of brown hyaenas. Although the spotted hyaena density in the southern Kalahari is low, approximately 0,6/100 km^2, as opposed to a brown hyaena density of approximately 1,8/100 km^2 during the present study (Mills 1981), there was evidence that brown hyaenas avoided areas well frequented by spotted hyaenas. To test this the numbers of both hyaena species that were observed whilst driving at night and searching with a spotlight along two different regions of the Nossob river-bed, between July 1979 and December 1980, were recorded. The first region was between Nossob Camp and Bedinkt windmill (the Kwang area) (Figure 2), and the second was between Bedinkt and Leijersdraai windmill to the north (the Kousant area). Both regions were of similar size and habitat. Table 2 shows that the frequency with which these two hyaena species occurred in the two areas differed significantly, with brown hyaenas being encountered more frequently in the Kwang area than in the Kousant area.

Two possible reasons why brown hyaenas avoided the comparatively high spotted hyaena density area around Kousant windmill are: Firstly, direct antagonism at or away from food was frequently exhibited by spotted hyaenas towards brown hyaenas, and secondly, the spotted hyaenas appeared to have a negative influence on the brown hyaena's food supply in this area.

Table 3 clearly shows the social dominance of spotted hyaenas over brown hyaenas, even when no food is involved. Table 4 shows a significant difference in the proportion with which brown and spotted hyaenas were observed to feed on carcasses in the two areas, with the inference that in the Kousant area spotted hyaenas were depriving brown hyaenas of a significant amount of food. The low number of observations in the Kousant area is a result of the paucity of observations made in this area and not a result of there being fewer carcasses there. Even if brown hyaenas found a carcass first they could easily be dislodged by spotted hyaenas (Mills 1981).

Spotted hyaenas and also probably lions (*Panthera leo*) may also influence the movement patterns of brown hyaenas in another way. Brown hyaenas show a marked tendency to den in the dunes, 93% of the 40 dens found in the present study being in the dunes. As 69% of 26 dens of spotted hyaenas found were in river habitat, the absence of brown hyaena dens from river habitat does not seem to be merely because there are few suitable dens there. Brown hyaena dens frequently have strong smelling carcasses scattered around them. This is the result of adults bringing food to the cubs and means that the dens may act as a strong attraction to potential enemies. Both spotted hyaenas and lions were twice each observed investigating brown hyaena dens, the spotted hyaenas scavenging from the den once and attacking a cub (without harmful effects) on the other occasion. Brown hyaenas may, therefore, locate their dens in the dunes in order to keep away from the river-bed which is the main activity area of the other large carnivores (unpublished observations) and therefore reduce the chances of being disturbed by them. This will accordingly affect their movement patterns in the territory.

Table 2 Number of brown hyaenas and spotted hyaenas counted at night in two different parts of the Nossob river-bed; July 1979 — December 1980.

Observation	Area: Kwang	Kousant	χ^2	p
Kilometres driven	1 053	1 166		
Brown hyaenas counted	20	6	26,40	<0,001
Spotted hyaenas counted	10	50		

Discussion

Group-living brown hyaenas in the southern Kalahari employ a land tenure system of large, partially overlapp-

Table 3 Outcome of interactions between a brown hyaena and spotted hyaenas away from food.

Behaviour	Observations: Number	Per cent	Number of spotted hyaenas involved: 1	2	3	4	5	6	7	?
Spotted hyaenas chase brown hyaena	14	74								
Spotted hyaenas catch up with and harass brown hyaena	9	–	4	4	0	0	0	0	1	0
Spotted hyaenas fail to catch up with brown hyaena	5	–	2	2	0	1	0	0	0	0
Brown hyaena avoids spotted hyaenas	4	21	1	2	0	1	0	0	0	0
Spotted hyaenas kill brown hyaena[a]	1	5	0	0	0	0	0	0	0	1
Total	19	100	7	8	0	2	0	0	1	1

[a]Discerned from spoor

Table 4 Number of times brown hyaenas and spotted hyaenas were observed feeding from carcasses in two different areas in the southern Kalahari

	Area		
	Kwang	Kousant	p[a]
Brown hyaena	20	0	0,003
Spotted hyaena	6	5	

[a]Fisher exact probability test; one tailed

ing territories, the sizes of which are chiefly related to the dispersion pattern of the food in the territory (Mills 1982b). In addition to territory size being affected by the dispersion pattern of food, so we suggest, are the movement patterns of brown hyaenas within their territories. The movement patterns varied in relation to the type of habitat available, which during the study strongly influenced the dispersion pattern of ungulates, the hyaenas' most important food. Hyaenas whose territories contained mainly river habitat spent much time foraging in this habitat because of the larger concentration of ungulate carcasses there. Animals with mainly dunes habitat in their territories had to search through their territories more randomly, as there were few concentrations of food sources.

No matter how high the density of ungulates along the river-bed, all brown hyaenas territories comprised some dunes habitat (Mills 1982b) in which the hyaenas also foraged (see, for example Figure 2). Apart from the fact that some important food items, notably the easily obtainable (when present) wild fruits, were almost exclusively found in the dunes, there is also the point that an exclusive river habitat territory would become so stretched out and the distance from the den to much of the territory so great, that it would impose heavy burdens on group members when carrying food back to the cubs. A stage would probably be reached when the shape of the territory would become uneconomical to forage in in terms of energy balance. In addition, as pointed out by Kruuk (1978), the ratio of border to surface area of a greatly elongated territory would make it more difficult to defend. Furthermore the preferred denning areas of brown hyaenas are in the dunes, most probably in order to avoid the main activity areas of spotted hyaenas and lions. Dunes habitat therefore, is probably an essential component of all brown hyaena territories in the southern Kalahari.

Brown hyaena movement patterns are also affected by the local density of spotted hyaenas. Areas well frequented by spotted hyaenas may well be avoided by brown hyaenas irrespective of the potential availiability of food. This may necessitate an adjustment to the foraging patterns of brown hyaenas in a particular territory. Several other studies on closely related sympatric carnivores have also suggested that the smaller species tend to avoid areas well frequented by the larger ones (Schaller 1967; Kruuk 1976; Seidensticker 1976; Berg & Chessness 1978; Skinner & Van Aarde 1981). In the southern Kalahari the influence of spotted hyaenas on the brown hyaena's movement patterns and ultimately on its population is small, because of the low density of spotted hyaenas there. In areas of high spotted hyaena density, however, they may well have a detrimental effect on the brown hyaena population.

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