

**Optimal patterns of scent marks in klipspringer
(*Oreotragus oreotragus*) territories**

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(With 5 figures in the text)

The distribution of preorbital gland scent marks and dung middens within three territories of wild klipspringers in Zimbabwe are described. Nearest-neighbour analyses revealed that scent marks were distributed non-randomly and in a rough ring some distance within the territory boundary. Marking densities were greatest at about half the territory radius. In two territories, marking densities were shown to be sensitive to intrusion pressure at the periphery, being higher along contested boundaries than where territories were not contiguous. Marks were placed on branches facing neighbouring territories, where they are more likely to be detected, along contested boundaries but not in other areas. An analytical model is developed which tests the efficacy of scent-marking strategies along the continuum between extreme hinterland and extreme perimeter marking. This shows that the optimal position for a ring of scent marks is at 0.78 of the territory radius and is the product of a trade-off between maximizing the probability of mark detection by intruders and minimizing the cost of intrusion.

Introduction

Scent-marking is a form of animal communication which has attracted much interest in the past. At least in territorial species, it is usually thought to advertise occupancy and ownership of the territory to conspecifics and may therefore serve to reduce the frequency of fighting to maintain territorial rights. Gosling (1982) and Gosling & McKay (1990) suggested that intruders may even match the scent that they find on the territory with that of any adversary in order to establish whether it is the owner of the territory. Others (e.g. Geist, 1965; Johnson, 1973; Richardson, 1993) contend that some inherent attribute of the scent signal intimidates intruders, usually resulting in their withdrawal from the territory. Whatever the actual mechanism involved, however, it is clear that scent marks should be placed in such a way that they are easily detected by the intended receiver so that the benefits of producing the scent mark are maximized.

Studies which have examined the distribution of scent marks within a territory have usually found that they are either clustered at the territory boundary or towards its centre. Perimeter marking has been described in several taxa, including hyenids (Kruuk, 1972) viverrids (Bearder & Randall, 1978), canids (Macdonald, 1979; White *et al.*, 1989), mustelids (Roper *et al.*, 1986, 1993; Pigozzi, 1990), felids (Smith, McDougal & Miquelle, 1989), and artiodactyls (Gilbert, 1973; Franklin, 1974; Walther,

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1978; Gosling, 1987). Dung middens, especially, are often placed at the perimeter (Hendrichs & Hendrichs, 1971; Dunbar & Dunbar, 1974; Ono *et al.*, 1988).

Hinterland marking (Mills, Gorman & Mills, 1980) is perhaps less striking and is reported less frequently than perimeter marking. It occurs in preorbital gland marking of dikdik (Hendrichs & Hendrichs, 1971; Ono *et al.*, 1988) and klipspringer in the Cape (Norton, 1980), but is best documented in studies of hyenids (e.g. Mills *et al.*, 1980; Mills, 1983; Mills & Gorman, 1987; Gorman, 1990; Richardson, 1991). Hyenas living in large clans with small territories mark along the perimeter, but in the Kalahari desert, where they live in small clans and very large territories, marks are clustered towards the centre of the territory. This occurs both within and across species and indicates that the marking strategy is not species-specific but dependent on ecological factors which dictate the optimal distribution of scent. In other words, the marking strategy is the outcome of a trade-off between the costs of producing and positioning scent marks and the benefits accruing to the owner in terms of territory defence (Gosling, 1981, 1985).

Klipspringers (*Oreotragus oreotragus*) are small African antelopes in which monogamous pairs defend contiguous territories which are permanently occupied (Dunbar & Dunbar, 1974, 1980; Norton, 1980; Roberts, 1994). They scent mark with a pair of preorbital glands, leaving a small deposit of secretion on suitable twigs or leaves (Roberts, 1994, 1997). Although Norton (1980) noted the locations within territories where he observed klipspringers scent-marking, no systematic search (see, for examples, Walther, 1978; Gosling, 1981) of a klipspringer territory has yet been reported. In this study, the distributions of scent marks on three territories in southern Zimbabwe are mapped and described in detail. In the light of the results, a simple analytical model is presented to compare the efficiency of perimeter and hinterland marking strategies in the context of marking economics.

Materials and methods

The fieldwork was carried out by SCR between September 1991 and February 1993 at Sentinel Ranch, a privately-owned game ranch in the Limpopo Valley, southern Zimbabwe. The area lies at 500 m above sea level and receives 332 mm of rainfall per annum. Fuller descriptions of the study area are given elsewhere (Roberts, 1994, 1997).

The core of the study area was partitioned in November–December 1991 in order to map territories in detail. A 0.25 ha grid system was superimposed over a 1 : 3875 aerial photograph of the area, the grid square intersections being marked on the ground using wooden stakes. Three contiguous territories (SZ, RH and BB) included within the gridded area were chosen for intensive mapping. The territory boundaries for these (and 3 other) klipspringer family groups had already been determined by plotting locations of sightings and movements of these groups, which could be distinguished by group size and composition and individual ear patterns or tears (Roberts, 1994).

Each grid square within these territories was subdivided into 4 cells using temporary markers; each cell was then systematically searched by 2 closely-spaced observers walking in straight lines across the quadrat until its entire surface had been covered. The location of every encountered dung midden and scent-marking site within the cell, and its host-tree species, were carefully recorded. During the mapping process, it was found that bushes often had numerous closely-positioned twigs which each bore separate scent deposits. For this reason, the following distinction was drawn in the definition of scent marks and scent-marking sites:

Scent mark: An individual, discrete deposit of secretion from the preorbital gland. Scent marks are most commonly positioned at twig termini, but are also occasionally placed on thorns, leaf margins and lateral branchlets (and perhaps rocks (cf. Smithers, 1983), although this was never observed in this study).

Scent-marking site: A discrete scent-marking location, which can be no less than one klipspringer bodylength from its nearest neighbour, and which may contain one or many scent marks.

Analysis of spatial distribution was carried out using nearest-neighbour analysis. The positions of scent-marked

trees within each of the 3 mapped territories were first digitized on to a 2.5×2.5 m matrix based on the 0.0625 ha grid used during the mapping process. The relative positions of each tree were then plotted using a FORTRAN program written specifically for this study. Centrality distances and nearest-neighbour distances were then calculated for each tree using this program. The centrality distance was defined as the straight-line distance between each tree and the territory centre (here defined as the arithmetic mean of all 0.0625 ha cells within the territory; cf. Peres, 1989).

Frequency distributions of nearest-neighbour distances between host trees were compared with expected distributions given random tree choice generated by the Poisson distribution of expected distances based on scent-mark density (using Cullen & Bulmer's expression in Patterson, 1965), in which:

$$T(X) = \exp[-\pi n/A](X - 0.5a)^2 - \exp[-\pi n/A](X + 0.5a)^2$$

where $T(X)$ is the number of trees occurring at a given distance, X , from its nearest neighbour, n is the number of host trees in the sampled area, A is the size of the sampled area and a is the size of the sampling unit (in this case, 2.5 m).

Two definitions of territory core and periphery were used. The first was adopted by Paton & Carpenter (1984) on hummingbird territories. They described the core as the area enclosed by a circle drawn around the territory centre which has a radius of half the longest radius of the territory ($0.5R_{\max}$). Because 2 of the territories in this study were distorted in one dimension, resulting in a large R_{\max} and hence a large core area, a smaller core was also produced by calculating a core area with a radius of $0.33R_{\max}$. The second definition is adapted from studies of hyenid territoriality (Mills *et al.*, 1980; Richardson, 1990, 1991). In these studies, the periphery is defined as the border cells of a matrix superimposed over the entire territory. Here, the outer two 0.0625 ha cells of the matrix were classed as peripheral cells, which meant that marks were at least 50 m in from the boundary before they were classed as occurring in the core. The size of the peripheral zone in this study is then of approximately the same proportion as that in the hyena studies: 53% of the territory was classed as periphery by Richardson (1990, original cells in his fig. 2), compared to 48, 54 and 58% for BB, RH and SZ territories, respectively.

Results

Spatial distribution of scent marks

Territories were thoroughly demarcated by a large number of closely-spaced scent marks, varying between 1619 on RH territory and 2398 on SZ territory. Total counts of host trees ranged from 238 (RH) through 411 (SZ) to 423 (BB), at respective densities of 10.7, 19.1 and 23.2 marked trees per hectare (see also Table I). The average distance between host trees was extremely small (means: RH = 10.52 m; BB = 7.75 m; SZ = 7.19 m) and smaller than would be expected if they were randomly distributed (RH: $\chi^2 = 65.7$, $d.f. = 6$, $P < 0.01$; BB: $\chi^2 = 26.6$, $d.f. = 4$, $P < 0.01$; SZ: $\chi^2 = 90.5$, $d.f. = 4$, $P < 0.01$).

The pattern of scent-marking sites within a territory can be visualized by the nearest-neighbour mapping technique used by Gosling (1981), and are presented for each territory in Fig. 1. These show that territories were demarcated with an inner ring of marked trees at some distance from the perimeter, from which a number of branches extended outwards towards the boundary. The rings were less clear, however, in BB and SZ territories than in RH territory or those previously shown in other species (Walther, 1978; Gosling, 1981); possible reasons for this are discussed later. None the less, a plot of the frequency distributions of host trees at increasing distances from the territory centre showed that, although host trees were placed throughout the territory, the number of host trees peaked in each territory at around 0.5 of the maximum radius (Fig. 2; RH: 0.45; BB: 0.45; SZ: 0.57).

Marking in the territory core and periphery

The division of host trees, scent-marking sites and total scent marks into core and peripheral regions

TABLE I
Binomial tests to test the marking densities in the territory core and periphery ($C = \text{core}$, $P = \text{periphery}$)

Core definition	Territory	Area		Proportion of total area		Tree density (ha^{-1})		Site density (ha^{-1})		Mark density (ha^{-1})	
		C	P	C	P	C	P	C	P	C	P
$0.33R_{\text{max}}$	BB	5.45	12.80	0.30	0.70	20.7	24.2	36.3	34.8	129.0	132.4
						NS		NS		NS	
	RH	5.79	16.46	0.26	0.74	13.0	9.9	20.2	17.3	85.8	68.2
						NS		NS		$P < 0.001$	
	SZ	3.04	18.46	0.14	0.86	27.3	17.7	57.9	35.7	173.7	99.6
						$P < 0.001$		$P < 0.001$		$P < 0.001$	
$0.5R_{\text{max}}$	BB	12.25	6.00	0.67	0.33	21.9	25.8	34.2	37.5	129.8	134.7
						NS		NS		NS	
	RH	13.05	9.20	0.59	0.41	10.8	10.5	17.6	18.9	75.9	68.8
						NS		NS		NS	
	SZ	6.84	14.66	0.32	0.68	28.8	14.6	62.2	28.0	172.6	81.0
						$P < 0.001$		$P < 0.001$		$P < 0.001$	
Inner cells	BB	9.5	8.75	0.52	0.48	20.7	25.8	35.2	35.4	134.3	118.1
						$P < 0.05$		NS		NS	
	RH	10.25	12.00	0.46	0.54	10.6	10.8	16.3	19.7	74.2	71.8
						NS		NS		NS	
	SZ	9.0	12.50	0.42	0.58	27.2	13.3	57.4	25.5	157.6	76.2
						$P < 0.001$		$P < 0.001$		$P < 0.001$	

of the territories are shown in Table I. Although there was no clear consistent trend towards core or periphery marking across the three territories, on all but one occasion when a significant difference in marking density between the regions was revealed (Table I), the difference was in the direction of greater densities at the territory core. This was true for tree, site and mark densities on SZ territory at both core sizes, and for the density of marks on RH territory when the core was defined as $0.33R_{\text{max}}$. However, the 'inner cells' core definition indicated that there were more marked trees in the periphery on BB territory.

The trend towards core or periphery marking was better resolved on SZ territory than on either RH or BB. This could be due to differences in the proportions of the territory which constitute the core, which are affected by territory shape and the degree of deviation from having isometric boundaries. The shape of the SZ territory was the least distorted from a regular circle. However, the 'core proportion' of total territory area was about the same on SZ territory at $0.5R_{\text{max}}$ (32%) as on RH and BB territories at $0.33R_{\text{max}}$ (30 and 26%, respectively), and the core proportions of all three territories were very similar with the inner-cells method (42, 46 and 52%). This suggests that the differences between territories were not caused by discrepancies in core proportions, although distorted territory shapes may still have caused some loss of resolution of marking strategy. There was little qualitative difference in the results across the three definitions of core areas, but the inner-cells method produced the least inter-territory variation in core proportions, and is used for the remaining analyses.

Effects of intruder pressure

A large proportion of the boundaries of each territory bordered an adjacent territory and could be described as 'contested' boundaries. However, a smaller fraction of the boundary formed a 'hard

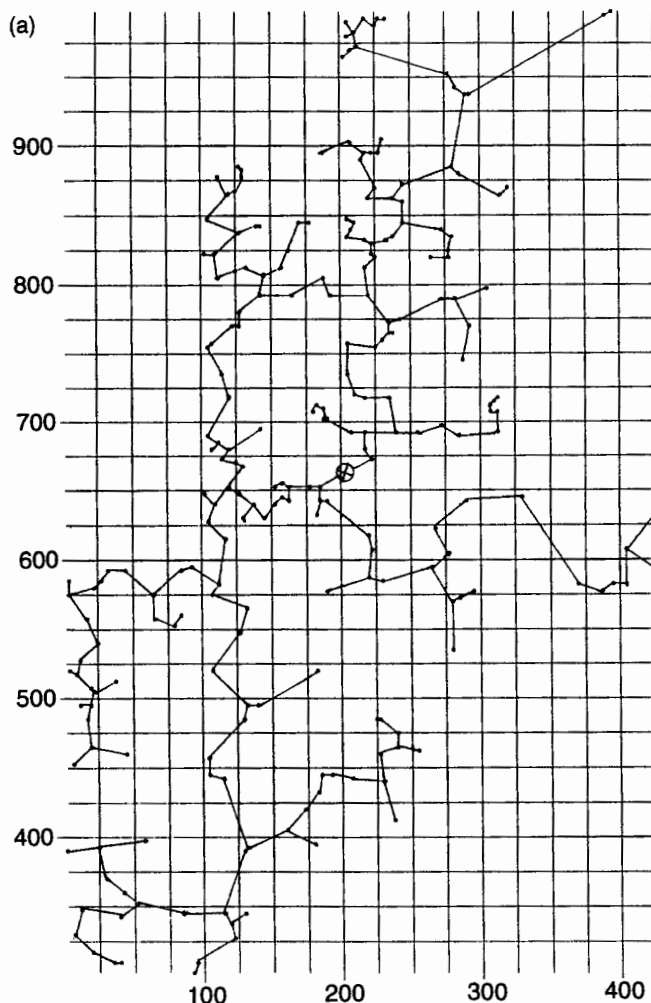


FIG. 1 Spatial patterns of host trees as revealed by nearest-neighbour mapping: (a) RH, (b) BB and (c) SZ territories. The cross marks the gap which remains when the process is complete.

edge', from which there appeared to be little or no threat of intrusion by conspecifics. These usually occurred around the foot of a rocky outcrop beyond which there was no suitable habitat for other klipspringers, at least for a considerable distance. The south-facing slopes which give way to the ancient Limpopo floodplain were good examples from within the study area. Taking into consideration only peripheral cells, more peripherally-positioned marks were deposited in contested border cells than in non-contested cells, at least in SZ and BB territories (Table II; BB: $\chi^2 = 120.5$; SZ: $\chi^2 = 39.3$, both $d.f. = 1$, $P < 0.01$; RH: $\chi^2 = 1.31$, NS).

If marks are placed in such a way as to maximize the probability of detection by intruders, the position of marks on trees should be biased towards branches of the tree which faces the closest boundary, especially in zones where intrusions occur more frequently. Of all peripheral sites, the number positioned parallel to ($\chi^2 = 4.50$, $d.f. = 2$) and facing ($\chi^2 = 4.41$, $d.f. = 2$) the closest boundary

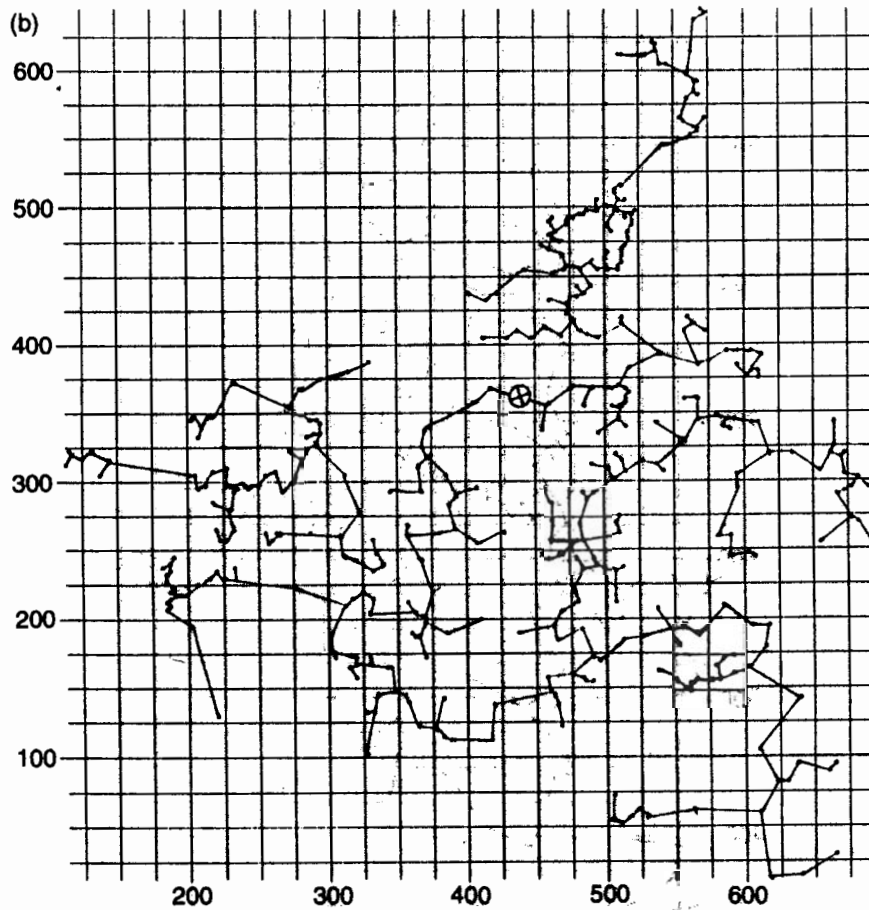


FIG. 1. (cont.)

were not significantly different from that predicted if the sites were positioned randomly, but fewer sites were placed facing towards the territory centre than expected ($\chi^2 = 7.74$, $d.f. = 2$, $P < 0.05$; see Table III). However, when peripheral cells were subdivided, sites in contested cells were significantly more likely to face the closest boundary ($\chi^2 = 13.95$) and less likely to face the territory centre ($\chi^2 = 15.83$; both $d.f. = 2$, $P < 0.01$) than expected. Conversely, in non-contested cells, sites were more

TABLE II
Comparisons of marking site densities in contested and non-contested peripheral areas

Territory	Area of contested periphery (ha)	Area of non-contested periphery (ha)	No. of sites in contested periphery		No. of sites in non-contested periphery		χ^2	P
			Obs	Exp	Obs	Exp		
BB	4.50	4.25	256	158.4	54	150.6	120.5	<0.01
RH	8.00	4.00	149	157.3	87	78.7	1.31	NS
SZ	9.50	3.00	280	123.7	99	83.3	99.3	<0.01

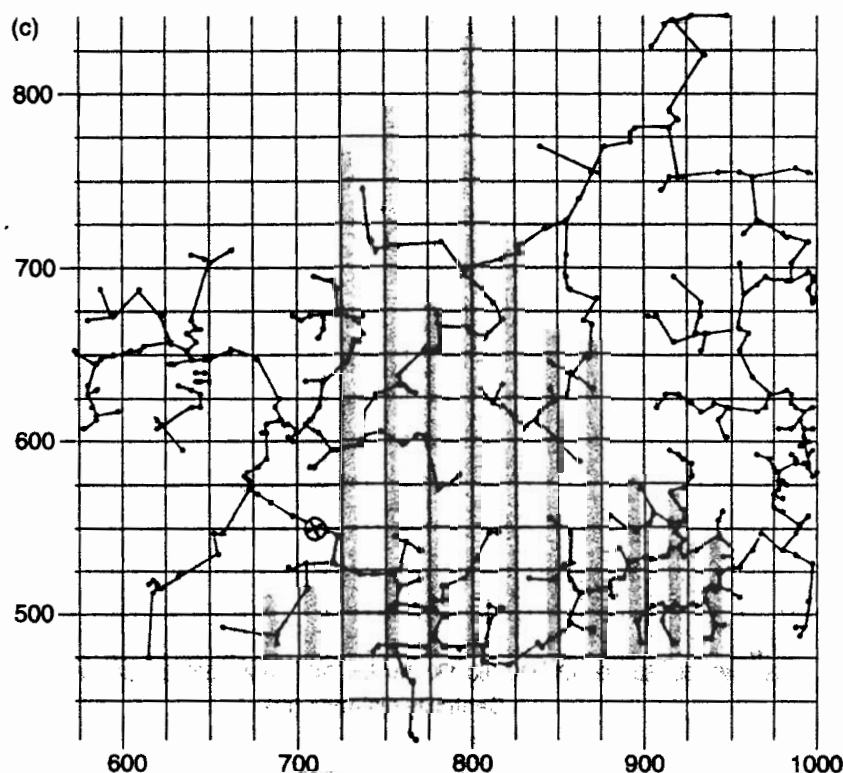


FIG. 1. (cont.)

often found to be positioned towards the territory centre ($\chi^2=9.14$, $d.f.=2$, $P<0.02$) and less often towards the nearest boundary ($\chi^2=28.11$, $d.f.=2$, $P<0.01$) than expected.

Host-tree availability as a potential constraint

It is possible that the variations in marking between different regions of the territory were determined to a greater extent by the availability of suitable host trees than by strategic marking as an adaptive response to economic constraints or variations in competitor pressure. To test whether this was so, the total number of available trees was compared between core and peripheral cells and between contested and non-contested cells of the periphery. There were no significant differences between core and periphery tree availability in either territory (Wilcoxon tests; BB: $W_x=1658.5$, $m=42$, $n=38$ cells, $z=0.40$; RH: $W_x=1801.5$, $m=42$, $n=41$ cells, $z=0.34$; SZ: $W_x=5342$, $m=68$, $n=99$ cells, $z=1.21$; all NS). Differences between contested and non-contested peripheral regions were inconsistent: there were fewer trees in contested cells of BB territory ($W_x=435.5$, $m=25$, $n=17$, $z=3.06$, $P=0.0022$) but more in SZ territory ($W_x=258$, $m=48$, $n=20$, $z=7.37$, $P<0.00006$), while no difference was found in RH ($W_x=322$, $m=27$, $n=15$, $z=0.01$, NS). Furthermore, if tree availability was an important constraint on marking patterns, one would expect that, where trees are in short supply, most of those that are available will be used. In other words, one would predict that the proportion of trees in a given area which are marked would be inversely related to the total number

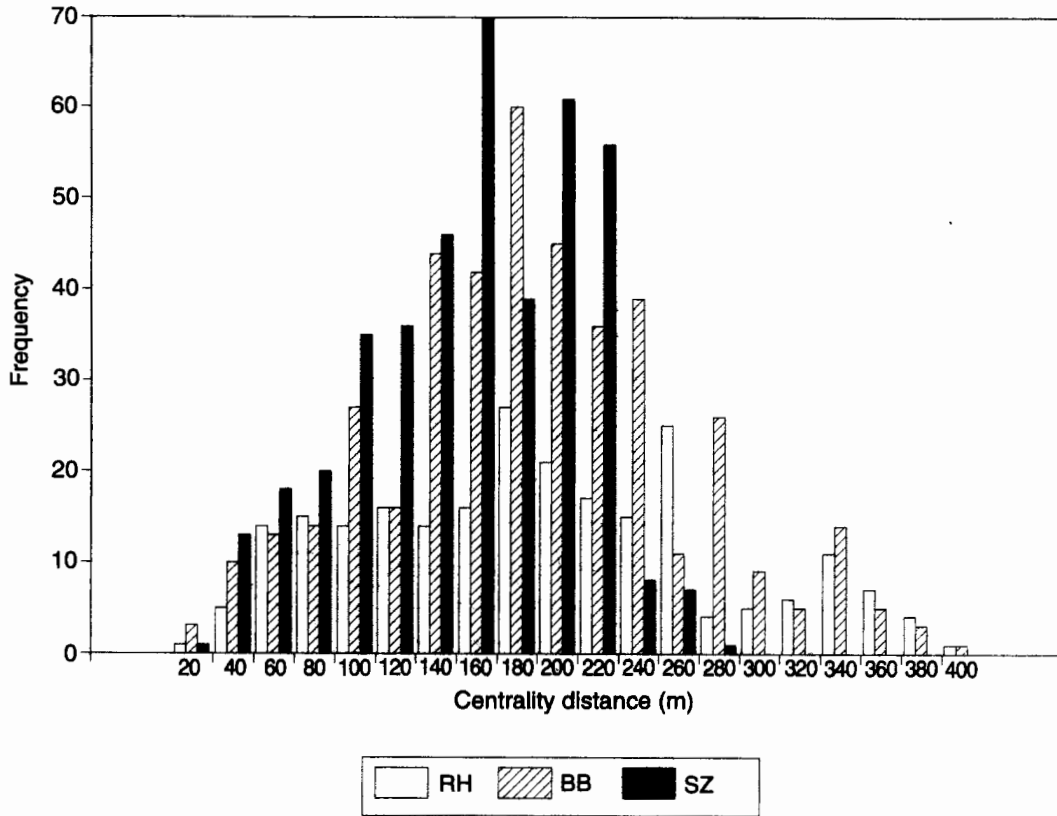


FIG. 2. Frequency distributions of centrality distances for host trees.

TABLE III

Orientation of marking sites with respect to the territory centre^a on host trees in contested and non-contested peripheral cells

Territory		Contested cells			Non-contested cells		
		Towards	Away	Parallel	Towards	Away	Parallel
BB	Obs	75	116	44	37	5	12
	Exp	88.13	88.13	58.75	20.25	20.25	13.5
H	Obs	57	59	28	37	17	30
	Exp	54	54	36	31.5	31.5	21
SZ	Obs	64	123	83	24	12	2
	Exp	101.25	101.25	67.5	14.25	14.25	9.5

^aA site was judged to be oriented towards or away from the territory centre if it was within the appropriate 90° quadrant of the host tree with respect to the territory centre and main stem.

of trees in that area. However, no such relationship was found (SZ: $r^2 = 0.008$, $d.f. = 172$, NS; RH and BB: $r^2 = 1.06 \times 10^{-5}$, $d.f. = 169$, NS).

Dung midden distribution

A total of 65 dung middens were discovered on the three territories (RH = 18; BB = 18; SZ = 29). The observed distributions on RH and BB territories were not significantly different from those expected if middens are spaced at random within the territory (using three distance categories defined as <30, 31–50, and >50 m; RH, $\chi^2 = 2.76$; BB, $\chi^2 = 2.30$; both $d.f. = 2$, NS), but middens were more closely distributed than expected on SZ territory ($\chi^2 = 30.97$, $d.f. = 2$, $P < 0.01$).

A model to test the efficacy of marking strategies

In common with some other antelopes (e.g. Gosling, 1981; Ono *et al.*, 1988), klipspringers position scent marks in a roughly concentric circle within the territory boundary, and therefore appear to adopt a strategy which falls between the extremes of absolute perimeter and hinterland marking patterns. An analytical model was developed to investigate the relative successes of these strategies as determined by the probability of territorial intruders detecting scent marks as they entered the territory.

The model tests the efficiency of the scent-marking pattern *per se*, and does not consider movements of the owner in any way. While it is true that owner positioning is crucially important to successful territory defence if defence operates through scent-matching, which implicitly requires an intruder to encounter both scent signals and the producer of the signal before it will retreat, the scent-matching hypothesis none the less predicts a system of maximally detectable marks and the model therefore remains directly relevant. The model is also equally relevant to the intimidation hypothesis of scent-marking in which requirements for owner presence are far less stringent.

The model makes the following general assumptions regarding scent-marking:

- a) scent-marking behaviour constitutes a form of territorial signalling to advertise occupancy;
- b) marks are placed in a way that maximizes their transmission to intended receivers;
- c) scent secretion and marking time are finite resources.

It also makes more specific assumptions relating to its operation:

- d) owners use a circular range of radius R_0 , which is termed the territory;
- e) owners place scent marks along the circumference of a circle with radius R , such that $R \leq R_0$, which encloses a circular range referred to as the 'demarcated area';
- f) owners use their entire available scent volume to position and maintain n marks of equal volume;
- g) the ability of an intruder to detect a scent mark is a function of the distance between the intruder and the mark, such that mark detection always occurs at a distance of less than (or equal to) a_0 and never occurs at distances greater than a_0 .

The model examines intrusion costs to territory residents. It proposes that intrusion costs, C , are directly proportional to the area available to an intruder before it detects a scent mark. This definition avoids specification of the defended resource but the intrusion cost can be translated into a measure of the appropriate resource if it is known.

As stated above, the owner has a circular territory of radius R_0 . It places n marks of equal volume

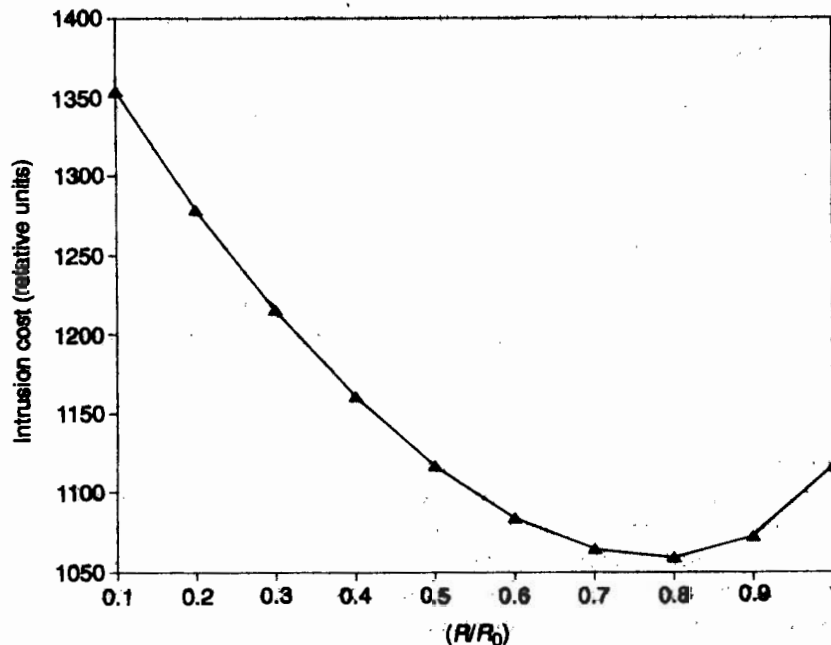


FIG. 4. Intrusion cost as a function of scent-marking radius. (The plot corresponds to an owner depositing 350 marks of radius 1.0 m in a 20 ha territory.)

when marks are placed at $0.78R_0$ (the optimum R , R_{opt}). The intrusion cost function is qualitatively similar and robust for other values of these parameters, including very large and very small territories.

The mechanism which leads to this result is quite simple. Although scent marks placed close to the territory boundary minimize intrusion cost provided they are detected, the probability of detection decreases as marks are placed further from the territory centre. Consequently, owners can minimize intrusion costs without placing scent marks along the boundary.

Discussion

This study has shown that scent-marking is a central feature of klipspringer behaviour. Resident pairs demarcate territories profusely, both with dung middens and particularly with preorbital secretion. In total, each territory contained over 1500 preorbital scent marks, compared with 121 in gerenuk (Gosling, 1981) and 110 in Thomson's gazelle (Walther, 1978). To a certain extent, the number of marks may be directly related to territory size: the marking densities between the Thomson's gazelle territory and those of the klipspringers are very similar, although they are both far higher than in gerenuk.

Scent marks were positioned non-randomly and appeared to be placed in a ring with radiating arms. These are similar patterns to those found in other bovid territories (e.g. gerenuk: Gosling, 1981; dikdik: Ono *et al.*, 1988; Thomson's gazelle: Gosling, 1985), although the number and degree of intricacy of the extensions appears to be greater in these klipspringer territories, presumably as a consequence of the greater number of marks. As Gosling (1981) suggested, this pattern is likely to maximize detection of marks by other klipspringers crossing the territory. At least in BB and SZ territories, marks were

and effective radius a_0 along the circumference of a circular area of radius R (concentric with the territory boundary).

The cross-sectional width of a single mark is $2a_0$, and the total length of n such marks is $2na_0$. Thus, as an intruder crosses the territory, the probability of collision with a mark as it crosses into the defended area is simply $(2na_0/2\pi R)$. (The model requires that marks are non-overlapping and that $2\pi R > 2na_0$). The probability of crossing into the defended area without detecting a mark is therefore $[1 - (2na_0/2\pi R)]$.

The size of the area (and hence the resource base) available to an intruder is dependent on likelihood of mark detection. If no scent marks are detected, the entire territory is potentially available to an intruder. If a mark is detected, only the territory area outside the defended area is available ($\pi R_0^2 - \pi R^2$). Considering only straight-line intruder trajectories which begin at a certain point along the territory boundary and terminate at any other boundary point, but which do not pass through the defended area, the available area given mark detection (A_d) is shown in Fig. 3a. For simplicity, A_d can be approximated to the area in Fig. 3b, which is expressed as:

$$\begin{aligned} A_d &= (4\theta/2\pi)(\pi R_0^2 - \pi R^2) \\ &= 2\theta(R_0^2 - R^2) \\ &= 2(\cos^{-1}[R/R_0])(R_0^2 - R^2) \end{aligned}$$

The expected cost of intrusion is then:

$$C = b(1 - na_0/\pi R)\pi R_0^2 + 2(na_0/\pi R)(R_0^2 - R^2)(\cos^{-1}[R/R_0])$$

where b is a constant.

In Fig. 4, the intrusion cost, C , is plotted as a function of R for various values of R_0 . The plot corresponds to an average Sentinel klipspringer who can deposit $n = 350$ marks of radius 1.0 m in a territory of 20 ha. It demonstrates that the owner can decrease intrusion costs by placing scent marks in a concentric ring well within the territory boundary. With these parameters, intrusion costs are minimized

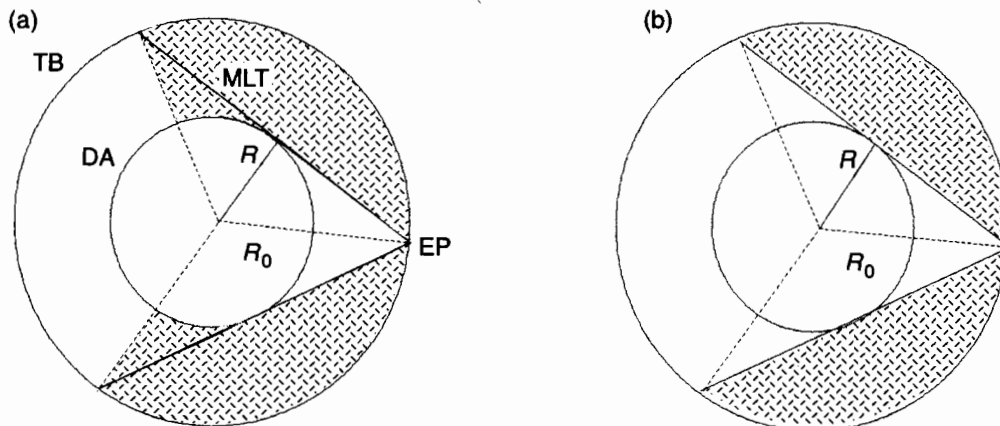


FIG. 3. Territory area used for enumeration of intrusion cost: (a) territory area potentially available to an intruder assuming mark detection (A_d); (b) approximation of A_d adopted for mathematical simplicity. (TB = Territory boundary; DA = Demarcated area boundary; EP = Intruder entry point; MLT = Maximum length trajectory; R = Radius of demarcated area; R_0 = Radius of territory.)

particularly densely distributed in areas where intrusion pressure was likely to be highest (along contested borders) and on branches which faced the direction from which intruders would originate.

Whether or not dung middens play some role in territory demarcation is unclear, although this has been claimed previously (*Oreotragus*: Dunbar & Dunbar, 1974; Norton, 1980; dikdik: Tinley, 1969). Middens were distributed non-randomly on SZ, but randomly on RH and BB territories. This suggests that if they are important in demarcation, they are less so than preorbital marks, which were more closely spaced than expected on all three territories.

The model demonstrates that minimization of 'intrusion costs' can lead owners to scent-mark along boundaries that enclose only a fraction of the territory. Since this is a simple model, few of the many other marking patterns observed in reality are explained (e.g. radiating arms: Gosling, 1981, this study). However, it demonstrates that in simple economic terms, the marking patterns established by the territorial owner may represent the outcome of a trade-off between maximizing the probability of detection of scent marks by intruders and minimizing the mean intrusion distance before mark detection occurs.

This trade-off will apply to scent-marking patterns irrespective of whether the exact function of the scent signal is to intimidate intruders or to advertize ownership through scent-matching. In addition, the model is relevant where territories are maintained for different reasons. The surrogate currency used by the model is the territory area accessible to an intruder before it encounters a scent mark, but the real currency may be any correlate of this measure. In most cases, for example, territories are defended to ensure exclusive access to valuable food resources (either for the owner's consumption or for attraction of mates as in resource-defence polygyny: Emlen & Oring, 1977). Assuming reasonably uniform food density throughout the territory, the feeding cost of intrusion, C_F , is the product of the resource depletion rate of the intruder multiplied by the area of intrusion. However, if territories are defended to safeguard a different resource, such as mates (e.g. Dunbar, 1988), the area available to an

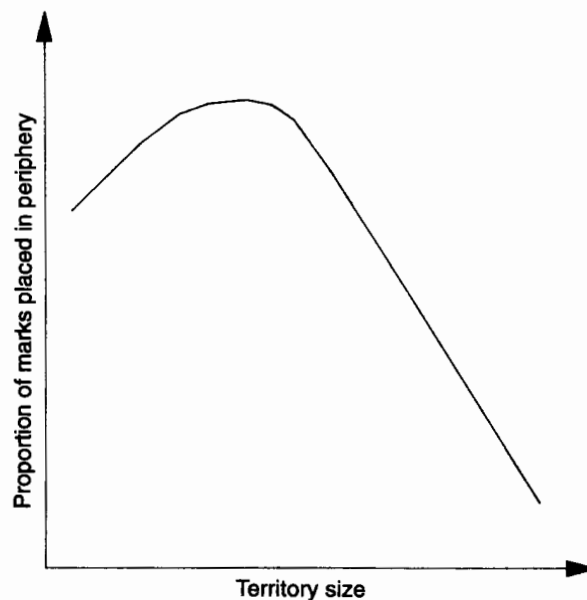


FIG. 5. Predicted relationship between the proportion of peripherally-positioned marks and territory size.

intruder is also proportional to the probability of encountering females, assuming again that they travel uniformly across all parts of the territory.

In previous studies of hyena (Gorman & Mills, 1984; Mills & Gorman, 1987; Gorman, 1990) and aardwolf (Richardson, 1991) territories under differing ecological regimes, the proportion of peripherally-placed marks is inversely related to territory size. Indeed, the marking pattern at Sentinel (approximately 20 ha territories) appears to be intermediate to that in the Cape (49 ha: Norton, 1980) and East Africa (2 ha: Dunbar, 1984) where peripheral marks are, respectively, uncommon and predominant. It would therefore appear that marks surplus to those required for the ring at 0.8R are generally added towards the periphery in small territories and towards the core with increasing territory size.

Although, as a general rule, the proportion of peripheral marks is inversely related to territory size, this may not always hold true. At very small territory sizes, it is possible that the effectiveness of marking at $R = R_0$ is sufficient to allow owners to construct one or a series of additional concentric rings, thereby decreasing the peripheral contribution to the total proportion of marks. The resulting predicted curve would then be similar to that in Fig. 5. However, the positive slope of this curve may be less common than expected, as additional hinterland marking over and above a certain effectiveness may only be selected for if the benefits from doing so outweigh the costs of abstention; for example, if there were high intruder pressure.

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