

## Selection of scent-marking sites by klipspringers (*Oreotragus oreotragus*)

S. C. ROBERTS<sup>1</sup>

*Department of Anthropology, University College London, London WC1E 6BT, U.K.*

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(With 4 figures in the text)

Klipspringers deposit scent marks in the form of secretion from the preorbital glands on branches of low trees and shrubs within their territories. Local environmental factors which affect choice of scent-marking sites in a population of wild klipspringers in Zimbabwe are described. Scent marks were typically placed within a narrow vertical range at the end of upward-pointing twigs. Twigs were more likely to be selected if they were located above bare rock, particularly if the ground was raised above the immediately surrounding area or was close to a significant break in slope. A substantial proportion of sites were placed on dead wood. Marking sites may remain in use for a number of years, with turnover rates calculated at between 1 and 2% per annum. The species of tree on which marks were placed were recorded and compared with overall abundance in the habitat. Palatable tree species were found to be selected preferentially when compared to unpalatable ones. Several explanations for this are compared. It is concluded that, simply through preferential selection of certain local characteristics, klipspringers may enhance the visibility and predictability of their scent marks.

### Introduction

The economic approach to scent-marking (Gosling, 1981, 1985, 1986) predicts that animals should adopt a marking strategy which maximizes the difference between the costs and benefits of producing and positioning scent marks. In territorial species, the benefits of marking which accrue to the owner most likely relate to its success in retaining the territory or its resources and are directly proportional to the effectiveness of signal transmission to territorial intruders (Guilford & Dawkins, 1991).

Most interest in the past has focused on the ways in which animals position scent marks within their home range in order to maximize these benefits, and has been predominantly concerned with attempts to classify the observed spatial distribution as either 'perimeter-' or 'hinterland-marking' (see, for example: Kruuk, 1972; Roper *et al.*, 1986, 1993; Gorman, 1990; Richardson, 1990). Recently, however, Alberts (1992) reviewed various means by which the effectiveness of a scent mark, in terms of detection by intruders, can be maximized at the local scale. These include ways to maximize the active space of chemical components within the scent deposit, such as placing marks as high as possible or marking on dead branches to increase scent persistence times. Preferences for certain local characteristics also suggest that a certain degree of bimodality in signal type may be used in order to transmit information. For example, easily-localized visual cues may be used to direct receivers towards involatile olfactory signals (Alberts, 1992), as in scraping the ground around marking sites (pronghorn: Gilbert, 1973; steinbok: Estes, 1991, pers. obs.) and denuding bark from trees prior to marking by elk (Graf, 1956).

This paper describes the choice of scent-marking sites by wild klipspringers (*Oreotragus oreotragus*), a small (11–13 kg) African antelope in which monogamous pairs defend contiguous

<sup>1</sup> Present address: Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY

territories which are permanently occupied (Dunbar & Dunbar, 1974, 1980; Roberts, 1994). Klipspringers scent-mark using preorbital glands, which they rub against twigs to leave behind a small deposit of scent which is visible to human observers (Norton, 1980; Dunbar, 1985; Roberts, 1994; Roberts & Lowen, 1997).

For a klipspringer, there are essentially three decision levels involved in the choice of a marking site: (1) on which part of a tree to deposit the scent; (2) on which trees within a given region of the territory; and (3) in which regions of the available territory area. Regulation of site choice at each of these levels will have important implications for the success of signal transmission, but this paper deals with only the first two levels to investigate local environmental factors which might affect site choice. Regional scent-marking strategies by klipspringers are described elsewhere (Roberts & Lowen, 1997).

### Materials and methods

The study was carried out between September 1991 and February 1993 at Sentinel Ranch, a privately-owned 32,000 ha game ranch in southern Zimbabwe, approximately 60 km west of Beit Bridge. The study was confined to a 190-ha section of the ranch which centres on Siezi Spring (22° 09' N, 29° 27' E), immediately north of the Limpopo River and lying at about 500 m above sea level. This section of the Limpopo Valley is a semi-desert area and receives only 332 mm of rainfall per annum, falling mainly between November and February. The area consists almost entirely of horizontal and tilted beds of Karoo sandstone with localized areas of Karoo basaltic intrusions. The sandstone regions are typified by extensive areas of bare rock broken by small thickets along fault lines, comprising mainly *Combretum apiculatum* and *Acacia erubescens*, with some large *Terminalia sericea*, *Pappea capensis*, *Sclerocarya birrea* and *Lonchocarpus capassa*. Small crevices and nooks which have accumulated organic material support the low-lying *Euphorbia neopolycnemoides* and the spectacular *Euphorbia cooperi*. In the areas of nearly-bare rock, shrubs such as *Croton pseudopulchellus* and *Hexalobus monopetalus* are widespread, as well as the xerophytic *Adenia multispinosa*, *Aloe chabaudii* and *Ficus abutilifolia*. The basaltic areas particularly suit *Terminalia prunioides*, *Solanum kwebense* and several *Grewia* spp. Full details of the area are provided by Roberts (1994).

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, 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. Each grid square within the territory 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 locations of every dung midden and scent-marking site within the cell, and its host-tree species, were carefully recorded. Once mapping was completed within a quadrat, it was searched a second time to enumerate the number of each species of tree or bush present which had at least one branch available for scent-marking (i.e. below a klipspringer's maximum reach, about 1 m).

This permitted calculation of Ivlev's electivity index (Krebs, 1989: 394) for each host species, obtained by:

$$E_i = \frac{r_i - n_i}{r_i + n_i}$$

where  $E_i$  is Ivlev's electivity measure for species  $i$ ,  $r_i$  is the percentage of species  $i$  which are scent-marked and  $n_i$  is the percentage of species  $i$  in the habitat. Electivity varies from  $-1.0$  to  $+1.0$ , with values between  $0$  and  $+1$  indicating preference and values between  $0$  and  $-1$  indicating avoidance.

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.

A total of 1883 sites were discovered (SZ 836; RH 403; BB 644). These were subsequently examined, noting:

- (a) the tree species on which the scent marks were placed;
- (b) the number of marks within the site;
- (c) the substratum with which the forefeet of a klipspringer are in contact while scent-marking at the site (i.e. bare sandstone, bare basalt, soil, sand);
- (d) whether or not a site was positioned above a break in slope, where a break in slope is defined as a change in elevation of 2 m or more within a 2 m horizontal distance;
- (e) the elevation of the site in relation to the immediately (within a 2 m radius) surrounding area, using 3 categories: i) 60 cm or more above the surroundings, iii) 60 cm or more below the surroundings and ii) elevation between i) and iii);
- (f) the presence or absence of available food within each site and on each scent-marked tree. This was done by recording presence of green or brown leaves within klipspringer reach. Those sites formed by dead branches, dead trees or fallen branches were noted. These data were recorded: i) at the end of the dry season in August\September 1992 and ii) after the rains in January 1993.

Expected figures for (c), (d) and (e) were obtained using 10 randomly drawn 200-m line transects across the mapped area, recording the substratum type, elevation category and whether it was near a break in slope at each stride-length.

A total of 310 sites were randomly chosen for closer examination. Within each site, every individual scent mark was measured, providing a sample of 1140 scent marks. The following were recorded for each:

- (g) Height above ground, measured by the minimum straight-line distance (to the nearest mm) between the underside of the scent-marked twig and the ground. In most cases, this was the vertical height, but in sites with an uneven or steeply-graded substratum the measured distance could be significantly non-vertical.
- (h) The narrowest diameter of the twig measured (to the nearest mm) immediately proximal to the scent deposit.
- (i) Twig inclination: whether it was upward-, downward- or level-pointing.
- (j) The leafiness of a branch proximal to a scent mark was measured at two levels of scale. The number of (green or brown) leaves occurring on the branch within 5 and 30 cm of the scent mark. Straight-line distances along the main branch were measured with a tape measure, and leaf counts included leaves on all side branches. Counting was discontinued on any one branch if it had more than 30 leaves within either of these measures; they were recorded as such. Whenever a marked branch was counted, the leafiness of the closest non-marked branch was also enumerated as a control.
- (k) Plant part on which the scent is deposited (twig terminus, thorn, leaf, twig 'elbow' or crook).

## Results

### *Local site selection*

Klipspringer scent marks were placed within a narrow vertical range (Fig. 1). The vertical distribution peaked between 55 and 62 cm, which is about the same height as the preorbital gland when an animal is standing at rest. However, marks were found as low as 13.2 cm and the distribution was negatively skewed towards lower-placed marks.

A smaller number of marks were placed very high. In September 1992, six marked twigs at four different locations were discovered (which were not present, or possibly missed, during the mapping process), all of which turned out to be over 90 cm high (91.5, 94.0, 96.4, 97.8, 99.0, 101.6 cm). In addition, a female was once observed (at a separate site) rearing up on to her hindlegs four times in

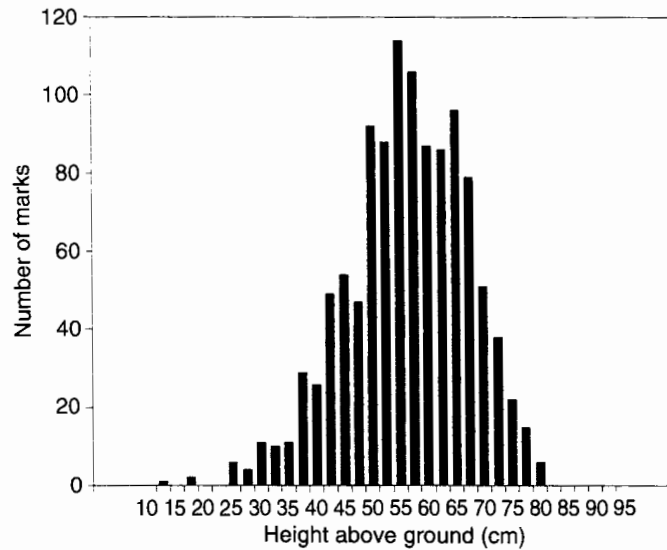


FIG. 1. Vertical distribution of scent marks.

quick succession, managing to deposit scent on twigs at least twice. These marks were subsequently measured at 102.1 and 103.5 cm from the ground.

Scent marks were almost entirely placed on twig termini (93% of 1140 surveyed twigs), but could also be deposited on hook-thorns (3.2%, usually *Acacia nigrescens*) or straight-thorns (0.9%, all *Acacia tortilis*), conveniently exposed crooks in branches (1.2%) or on leaf margins (1.8%). Upward-pointing branches were preferred over downward-pointing ones (upward = 56.6%, downward = 37.1%). Very thin twigs were preferred to thicker ones and over 90% of all marks were placed on twigs less than 0.5 cm in diameter at the terminus (Fig. 2).

Scent-marked branches had significantly fewer leaves immediately proximal to the terminus than non-marked branches of the same species. This was true within both the 5 cm ( $\chi^2 = 702.61$ ,  $d.f. = 11$ ,  $P < 0.001$ ) and 30 cm ( $\chi^2 = 924.14$ ,  $d.f. = 11$ ,  $P < 0.001$ ) categories measured.

Table I shows the availability of leaves within scent-marking sites, and on the host tree as a whole. In both the dry and wet seasons, there was a high proportion of sites which had no available leaves, even when leaves were present within reach elsewhere on the tree. There were also a substantial number of host trees, especially in the dry season, which had either green or brown leaves somewhere on the tree, but none within klipspringer reach. A very large proportion of sites (43.7% in January 1993) were composed of dead branches on living trees, or on dead trees (8.5%). A further 3.5% were formed by dead boughs lying on the ground with upward-pointing branches.

Klipspringers preferred to place scent marks above a bare rocky surface ( $\chi^2 = 1811.5$ ,  $d.f. = 3$ ,  $P < 0.001$ ; see Table II). Sandstone substrata were clearly selected to a greater degree than basaltic ones, even when the relative abundance of each rock type was considered, while sites were established on soil and sand less often than expected.

On a very local scale, areas which were slightly elevated above the immediate surroundings were also preferred scent-marking sites. Raised areas were used more often than expected, while relatively level areas supported slightly fewer sites than their availability would predict ( $\chi^2 = 5077.6$ ,  $d.f. = 2$ ,  $P < 0.001$ ). Similarly, although the proportion of total surface area above a significant break in slope was

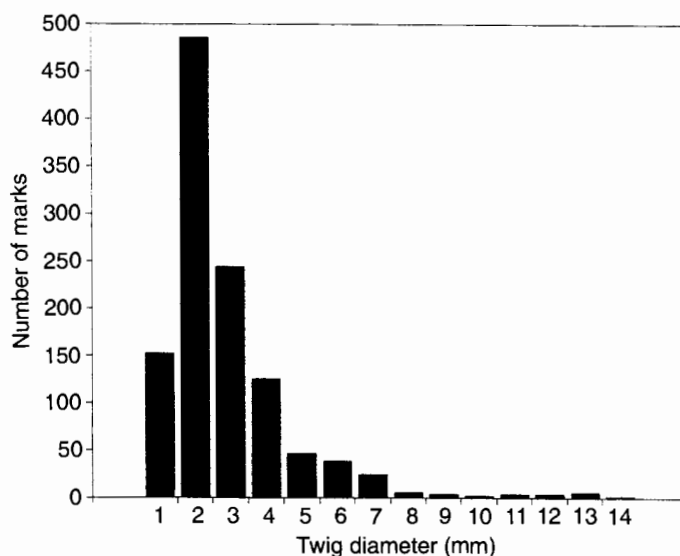


FIG. 2. Frequency distribution of the diameter of marked twigs.

small, the number of sites positioned above a break was significantly greater than expected ( $\chi^2 = 1956.6$ , *d.f.* = 1,  $P < 0.001$ ).

Approximately half of all the surveyed sites contained either one or two scent marks, but up to 22 different deposits were found to occur within a single site (Fig. 3).

A number of sites became defunct during the study as the host branch was broken by passing animals, or the tree was uprooted by elephants or strong wind. In all, 23 sites were damaged: 15 on SZ territory during 11 months and 8 on RH & BB territories during 8 months. This gives turnover rates of 1.96% and 1.15% per year in SZ and RH & BB territories, respectively.

TABLE I

Availability of leaves: (1) within sites and (2) on whole host trees. (Data are expressed as the percentage of the total number of surveyed sites)

Leaf availability	Dry season		Wet season	
	Site	Tree	Site	Tree
None; site is on fallen branch	3.5	3.5	3.6	3.6
None; on dead branch of a living tree	34.4	—	43.7	—
None; on a dead tree	7.4	7.4	8.5	8.5
None; on a live branch	31.0	18.4	2.2	0.2
Only dead leaves	9.7	22.8	0	0
Green leaves	13.8	26.0	41.1	68.6
Only dead leaves on tree; all out of reach	—	6.7	—	0
Green leaves on tree, but all out of reach	—	15.0	—	18.3
Site defunct <sup>a</sup>	0.1	—	0.8	0
Sample size	1896	1896	1896	1896

<sup>a</sup> Branches broken or entire tree destroyed (e.g. by elephant damage)

TABLE II  
The influence of substratum type and elevation on site choice

		Observed	Expected
Substratum	Soil	468	964.8
	Sand	135	395.2
	Sandstone	1119	387.7
	Basalt	161	135.2
		$\chi^2 = 1811.5, df = 3, P < 0.001$	
Elevation	1	782	97.4
	2	1059	1716.5
	3	42	69.1
		$\chi^2 = 5077.6, df = 2, P < 0.001$	
Slope break	Break	549	106.2
	No break	1334	1776.8
		$\chi^2 = 1956.6, df = 1, P < 0.001$	

#### Host-tree choice

Scent marks were recorded on a total of 71 different species, all of which are dicotyledons with the exception of *Sansevieria pearsonii*. Apart from *Peristrophe gillilandiorum* and *S. pearsonii*, all of these species were woody. No marks were recorded on grasses, which are commonly or almost exclusively marked by other antelope species such as oribi (Gosling, 1972), Cape grysbok (Novellie, Manson & Bigalke, 1984), Thomson's gazelle (Walther, 1978), topi (Gosling, 1987) and suni (Somers, Rasa & Apps, 1990). Many species had only a small number of marked individuals and only a handful of species contributed a substantial proportion of individual trees to the total. The most commonly

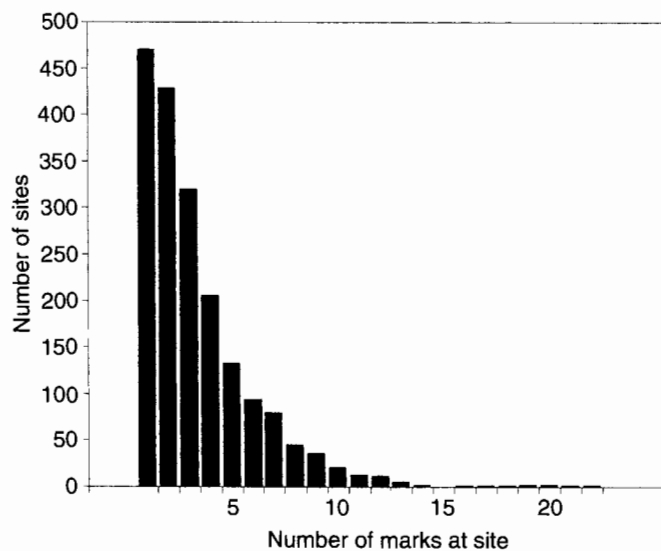


FIG. 3. Frequency distribution of the number of scent marks deposited at each marking site.

marked species were *Terminalia prunioides* and *Combretum apiculatum*, both important food species.

For 58 of these 71 species, the density of individuals within the study area had been determined during the mapping process, enabling calculation of their electivity index which measures preferences for host-tree species relative to their density in the habitat. Species indices ranged from  $-0.92$  for *Abutilon pycnodon* to  $+0.87$  for *Terminalia sericea*. This high degree of variation suggests that host-tree choice is not simply based on random encounter rates with individuals of different species. In fact, rarer trees appeared to be preferred, as electivity indices were negatively related to species density (Fig. 4: Pearson  $r = -0.720$ ,  $d.f. = 56$ ,  $P < 0.01$ ). Electivity indices were also positively correlated with the number of sites at each tree ( $r = 0.390$ ,  $d.f. = 56$ ,  $P < 0.02$ ), but not with the number of marks at each site ( $r = 0.054$ ,  $d.f. = 56$ , NS).

To test further whether tree selection was non-random, the relative density of each host species was compared with the relative contribution each species made to the total number of host trees. Using relative values casts the data for each variable into a directly comparable format, with the resulting null hypothesis that the proportion of host trees contributed by each species is the same as its proportional representation in the total tree population. The null hypothesis was rejected as the two sets of proportions were found to be significantly different (Wilcoxon matched-pairs signed-ranks test,  $z = 2.164$ ,  $P = 0.0305$ ).

Of the 58 species for which electivity indices and densities were available, the foliage of 27 were known to be eaten by klipspringers, while 17 were thought not to be eaten. To test whether food and non-food trees were marked differently in relation to their relative densities, the signs from the matched test above (where the signs indicate that a species accounts for a greater or lesser proportion of total host trees than its relative density would predict) were compared (Table III). This showed that food trees were marked more often than non-food trees ( $\chi^2 = 7.28$ ,  $d.f. = 1$ ,  $P < 0.01$ ). Electivity indices for food trees were also larger than for non-food species (Wilcoxon test,  $z = 1.96$ ,  $P = 0.05$ ).

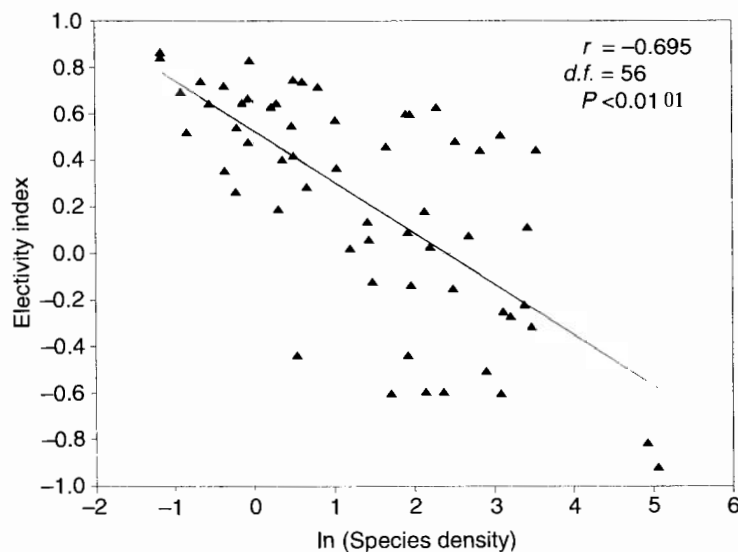


FIG. 4. The relationship between species density and electivity index for host-tree species.

TABLE III

*A comparison of food and non-food tree species as preferred hosts for scent-mark sites. (a '+' or '-' indicates that a species accounts for a greater or lesser proportion of total host trees than its relative density would predict; see text for analysis)*

Sign	Food species	Non-food species	Totals
+	23	8	31
-	4	9	13
Totals	27	17	44

## Discussion

### *Preference for food trees*

The study revealed that food trees are selected at levels above that predicted by their abundance in the habitat, and at greater levels than non-food species. There are four possible explanations for this observation: (1) *convenience*: that animals scent-mark close to where they feed, resulting in a high proportion of sites occurring on feeding trees; (2) *feeding tree defence*, where marking may reduce poaching of food trees by intruders; (3) "*book-keeping*" (Henry, 1977; Harrington, 1981), where animals mark in order to minimize wasted foraging time on recently visited trees; and (4) *maximizing detection probability*, either by residents or intruders (Gosling, 1981).

There is good evidence from this and other studies of small antelopes to reject the first three of these hypotheses. First, most marking visits to host trees are not accompanied by feeding on the same bush and often are part of an extended bout of uninterrupted marking (accounts of boundary marking patrols: Hendrichs & Hendrichs, 1971; Tilson & Tilson, 1986; Roberts, 1994). Second, this study demonstrates that klipspringers choose to mark on a very wide variety of tree species, which includes both food and non-food species. In addition, a very high proportion of marking sites were on dead trees or dead branches on live trees. This was also true in Gosling's (1981) study, but while he suggested that many of these sites had creepers and vines present, this was certainly not the case at Sentinel. These results indicate that scent-marking in this species is not directly related to defence of individual host plants. Third, mean return rates to marking sites vary between once every 5–7 days on different territories (Roberts, 1994; inferred return rates in other bovid species, as calculated by multiplying observed marking rates and the number of sites, are equally high: Thomson's gazelle: Walther, 1978; gerenuk: Gosling, 1981). This suggests that animals persistently revisited recently-marked sites; nor did they avoid remarking them, which is a characteristic feature of 'book-keeping' marking by canids (Harrington, 1981). A further difference between the two taxa is that selective browsers (e.g. klipspringer, gerenuk) do not usually exhaust feeding sites in the same way as wolves and foxes deplete food caches.

On the other hand, there is much supporting evidence and theoretical reasoning (e.g. Gosling, 1981; Gorman, 1990; Guilford & Dawkins, 1991; Roberts & Lowen, 1997) to expect marking animals to ensure maximum detection probability of scent marks in which they invest much time and energy. Assuming that intruding conspecifics feed while they are on the territory, marking on palatable tree species will substantially increase the probability of scent-mark detection.

### *Site choice and search images*

In common with gerenuk (Gosling, 1981) and hyenas (Gorman & Mills, 1984), klipspringer scent



marks are placed within a narrow vertical range. However, my observations show that adult klipspringers may also rear up on hindlegs in order to deposit scent on otherwise unreachable twigs. This is similar to Rasa's (1973) description of mongoose handstands which is thought to increase the scent's active field. When such a high scent mark was found, there were always other nearby branches within reach, suggesting that this wasn't a result of a lack of suitable branches in the vicinity. Selection of sites on elevated ground and above a break in slope will also effectively increase the active field of the scent mark, as well as making the site more visible.

Another possible way to control the efficacy of each scent mark is to select the surface type on to which the mark is deposited (Alberts, 1992). Like klipspringers, both gerenuk (Gosling, 1981) and wombats (Wells, 1978) scent mark on dead wood. Over 10% of sites were either on fallen branches or dead trees and more than a third of sites were on dead branches of living trees. It would seem that this bears advantages either through increased visibility or persistence time of scent marks. Given the last statistic, it is also possible that scent-marking is harmful in the long term to the host tree, whether it be through constant defoliation or the secretion itself.

Marking sites were found to be highly stylized, such that scent-mark presence or absence could be reliably predicted in a given area even by human observers. Most sites conform to a 'standard site description' so that in almost all cases where there is a raised area with a rocky substratum, a tree with branches available to a klipspringer will be marked. The use of 'standard sites' may operate along lines similar to 'search images' and so maximize the visual localization of deposited marks by territorial intruders. This may benefit owners by allowing a reduction in the volatile component of preorbital secretion, thereby prolonging the fade-out time of the non-volatile signal component (Alberts, 1992) and permitting more widely-spaced scent marks without substantially reducing detection probability. The results suggest that, at least in this species, the visual aspects governing scent-marking site choice may be an important component of long-term rangeland olfactory communication.

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