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Behavioural Responses to Scent Marks of Increasing Age in Klipspringer *Oreotragus oreotragus*

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Abstract

Klipspringers *Oreotragus oreotragus* are small antelopes which use scent marks to demarcate and defend their territory. The strength of behavioural response to the introduction of unfamiliar scent was measured in order to estimate the effective lifespan of scent secretion. The total number of scent marks deposited during the experiment was higher than control levels when fresh scent was introduced, but not when older scent was introduced. However, the proportion of marks deposited on introduced twigs remained higher than control levels until scent was aged at least 7 d. The probability of licking twigs immediately before scent-marking was much higher than control levels when scent aged up to 3 d was introduced, but not when scent was aged 7 d or more. These results indicate that preorbital gland scent retains at least some degree of efficacy for up to 7 d. The decreasing level of response to scent aged 0–7 d is most likely to be due to decay of the scent signal. However, in contrast to the total number of marks deposited and the probability of licking before scent-marking, which both consistently decreased in response to older scent, the proportion of marks deposited on scent aged 3 d was higher than over fresh scent. It is suggested that, in view of the role that scent-marking plays in territory defence, this difference in the timing of peak response between the three variables may represent an adaptive response to the perceived threat of encounter with an adversary, which is mediated by the age of the scent marks.

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Introduction

The efficacy of animal scent marks is not constant but varies with time after deposition (Alberts 1992). The two principal parameters of temporal variation are the rise time, which is the interval between deposition and achievement of maximal detectable radius, and the fade-out, or persistence time, which is the time between deposition and that when the mark can no longer be detected (Bossert & Wilson 1963; Sipos et al. 1993; Ferkin et al. 1995). For all scent signals and particularly for 'range marks' (Alberts 1992), which may advertise territory occupancy and ownership in the absence of the signaller (Gosling 1982, 1990; Roberts 1994, 1997; Roberts & Lowen 1997), temporal parameters are of great importance. First, for a range mark to be effective, signallers may require marks to persist for relatively long periods. Second, receivers may use the relative proportions of volatile sub-

components of the scent to estimate the age of the mark (Johnston & Schmidt 1979; Apps et al. 1989; Ferkin et al. 1995).

Information about the age of scent marks may allow receivers to modulate their response to scent encountered in proportion to the perceived likelihood of imminently encountering the signaller. For example, if the receiver is an intruder on a territory, it might withdraw if the scent is very fresh in order to avoid potentially costly conflict with the owner, but not take evasive action if the scent is older (Maynard Smith 1974; Clutton-Brock et al. 1979). Conversely, owners encountering foreign scent marks will react in opposite fashion. Melemis & Falls (1982) have termed the strength of response to territorial intrusion in relation to perceived threat as the 'defence function'.

Klipspringers (*Oreotragus oreotragus*) are small African antelopes in which adult pairs maintain exclusive territories and use scent-marking as a means of advertising ownership (Dunbar & Dunbar 1974; Norton 1980; Roberts 1997; Roberts & Lowen 1997). Scent from the preorbital glands is usually deposited on the ends of low twigs which are revisited on average once every 7 d, although revisit frequencies range between once every 2–20 d (Roberts 1994). Here, the time-course of klipspringer scent mark decay is estimated by measuring the defence function of a captive subject in response to an unfamiliar scent of increasing age.

Methods

Freshly marked twigs were collected at Sentinel Ranch in south-west Zimbabwe (about 60 km west of Beit Bridge, see Roberts (1994) for details) from the same wild klipspringer pair on their own territory over a period of 2 d. The klipspringers were observed through binoculars while they scent-marked; branches bearing freshly deposited secretion were broken off about 20 cm behind the mark, with care being taken not to touch the scent itself. Branches were included only if both members of the pair had marked at that site. Twigs were defoliated (to remove the potential confounding factor of food availability during the experiments), removed from the area and placed together in an open spot that received direct sunlight (there was no rain during this period). Three twigs were selected at random on each of days 0, 3, 7, 10, 15 and 20 after deposition, placed in labelled plastic bags and frozen at -10°C (those from day 0 were frozen within 3 h of collection). Freezing at this temperature preserves scent samples for several months (P. Apps, personal communication; Apps et al. 1989); in this study, samples were stored for between 17 and 50 d. In addition, three control twigs were collected on the same days from favoured tree species at a height of about 1.8 m (which ensured that they could not have been scent-marked), placed in a labelled bag and frozen on the day of collection.

Response intensity experiments to these twigs were carried out at Chipangali Wildlife Orphanage, near Bulawayo in Zimbabwe. The experimental twig was removed from cold storage 2 h before the experiment began. At the beginning of the experiment it was tied firmly to the enclosure fence with a length of new string, taking care not to touch the secretion. Observation began 1 min after the twig was

introduced, or when the subject approached the twig for the first time if this was after the 1-min interval (this happened only twice — the subject usually attempted to investigate the twig while it was being tied to the fence) and continued for the next 40 min. Every scent mark deposited, whether it was placed on the introduced twig (overmarking) or on existing marking sites within the enclosure, and every instance of licking of scent marks immediately before or after marking were recorded. Differences in the number of marks deposited during exposure to experimental or control twigs were compared using t-tests, while measures of response based on proportions (the proportion of overmarks and probability of licking twigs before marking) were analysed using general linear models; all tests are two-tailed.

In order to remove individual variation in response intensity to introduced twigs, the experiment was performed using the same individual male klipspringer. This male was housed in an open enclosure of $\approx 500 \text{ m}^2$ and was paired with an adult female. In this experiment, scent was introduced as though it had been deposited by an intruder on the subject's territory, even though it originated from a pair resident on their own territory. It is assumed that the composition of the preorbital gland scent secretion does not vary whether the marker is on its own or another's territory; in any case, all samples were collected under the same conditions (while the pair was resident on its own territory) and the experiment was primarily concerned with the time-course of the response, rather than its absolute value.

To prevent habituation effects and observer bias, respectively, the order in which twigs were to be presented was determined using a random number table and the experiments were carried out 'blind' (Martin & Bateson 1986). A retrospective analysis showed that there was no detectable habituation to the procedure during the course of the experiment, nor was there any relationship between the strength of response and length of time for which scent was frozen (Pearson correlations, all nonsignificant). Up to two experiments were run each day, either in early morning (0800 h) or late evening (1700 h) and were completed in a period of 16 d. Data were recorded using a stopwatch and portable Dictaphone and were transcribed at the end of the experiment.

Results

The total number of scent marks deposited by the subject within 40 min of the introduction of the twigs is shown in Fig. 1. More marks were deposited after experimental twigs carrying fresh scent were introduced than when control twigs were offered (0 d: $t = -3.45$; $df = 4$; $p < 0.05$). There was no difference between the response to control twigs and those carrying scent aged 3 d or older.

Of those marks deposited, the proportion that were placed on the introduced twig (as opposed to previously existing marking sites) is shown in Fig. 2. As with the total number of marks deposited, overmarking proportions on experimental twigs were higher than on unmarked control twigs (0 d, $F = 55.0$, $df = 1,4$, $p = 0.002$, 3 d, $F = 462.7$, $df = 1,4$, $p < 0.001$). However, the shape of the curve differed from that in Fig. 1, in that the proportion of marks placed on the introduced

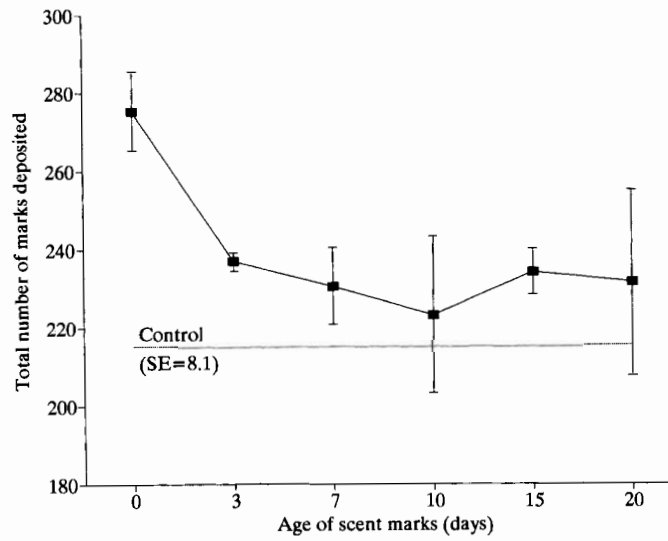


Fig. 1: Number of marks deposited in the 40-min period following introduction of experimental twigs carrying scent of varying age ($\bar{X} \pm SE$)

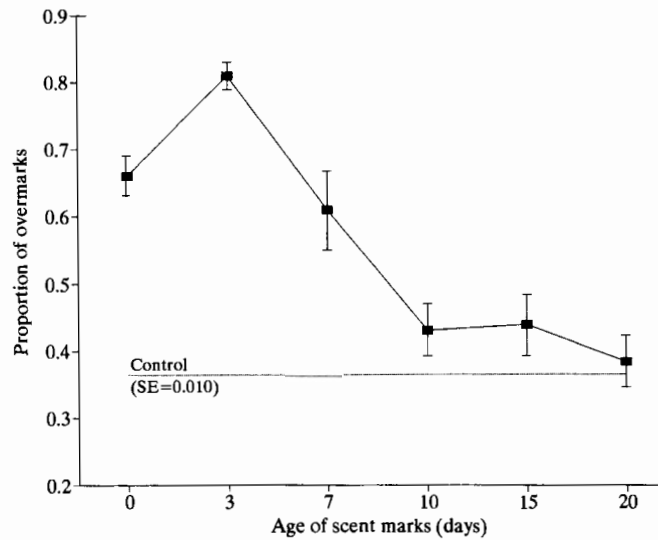


Fig. 2: Probability of overmarking introduced scent: the proportion of all scent marks deposited during trials which were placed on the introduced twig ($\bar{X} \pm SE$)

twig was higher on 3 d twigs than on freshly marked ones. Scent aged 7 d elicited a response which was almost as strong as to freshly deposited scent and which was

greater than control levels ($F = 12.2$, $df = 1,4$, $p = 0.005$), but response intensity had reached an asymptote when marks were aged 10 d or more.

Klipspringers frequently lick and bite the tip of scent-marked twigs (Gosling 1972; Norton 1980) during marking bouts. The proportion of cases where scent-marking was immediately preceded or followed by licking, on both introduced twigs and on existing marking sites, are shown in Fig. 3. Introduced twigs, carrying a strange scent, were licked more than control twigs when scent was fresh ($F = 12.3$, $df = 1,4$, $p = 0.025$) or aged 3 d ($F = 10.2$, $df = 1,4$, $p = 0.033$) but there was no significant difference between experimental and control twigs when scent was aged 7 d or more. The probability of licking existing scent marks (on bushes already within the enclosure, which contained the resident's scent only) was significantly higher than control levels when fresh scent was introduced ($F = 17.0$, $df = 1,4$, $p = 0.015$) but there was no such difference in response to older scent. Licking scent was more common on introduced twigs than on existing scent marks when experimental scent was aged up to 3 d (0 d, $F = 74.8$, $df = 1,4$, $p = 0.001$; 3 d, $F = 67.1$, $df = 1,4$, $p = 0.001$); when scent was aged 7 d or more, there was no significant difference between introduced twigs and existing marks.

Discussion

Scent-marking rates were very much higher than control levels after the introduction of twigs bearing freshly deposited strange scent, but this difference was not evident in scent aged 3 d. Differences in the likelihood of licking scent followed

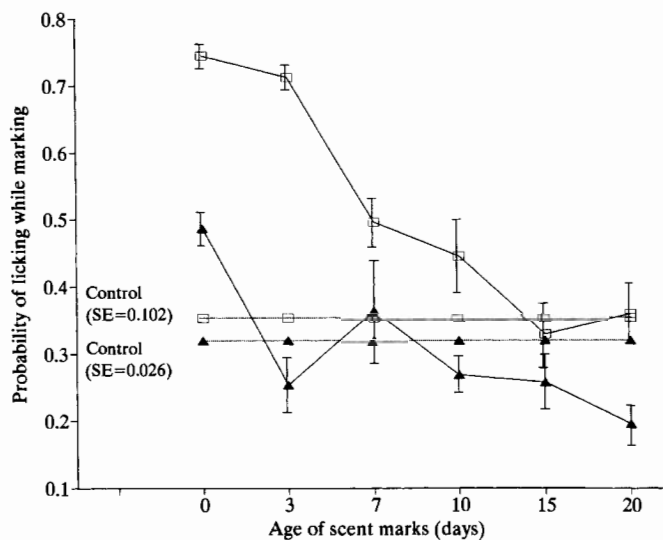


Fig. 3: Probability of licking twigs before scent-marking: comparison between introduced twigs (boxes) and existing twigs (triangles) carrying only the resident's scent ($\bar{X} \pm SE$)

a similar time course but overmarking experimental twigs remained greater than on controls until scent was at least 7 d old. For each variable measured, the level of response decreased with increasing age of secretion. These findings indicate that klipspringers can recognize strange scent and modulate their response in relation to age of scent, thus reacting in a way which enables measurement of the intensity of response (Melemis & Falls 1982).

The subject male responded to a strange scent by increasing, by a large degree, his marking rate to fresh scent but this response was very much reduced when scent was aged 3 d or more and was similar to that elicited by control twigs. In contrast, overmarking rates were higher on scent aged 3 d than on fresh scent, and remained high until at least 7 d after deposition. This suggests that scent is active for at least as long as 7 d, which is almost exactly the average return rate to marking sites in the wild. Although return rates are slightly longer in klipspringer than in other bovids studied to date (gerenuk 3.6–4.5 d, Gosling 1981; Thomson's gazelle 2.8 d, Gosling 1985; suni 1.6–4 d, Somers et al. 1990), scent in other taxa can remain active for much longer than this: up to 10 d in dwarf mongoose *Helogale parvula* (Rasa 1973), 25 d in meadow voles *Microtus pennsylvanicus* (Ferkin et al. 1995), at least 30 d in brown hyaenas *Hyena brunnea* (Gorman 1990) and up to 100 d in hamsters *Mesocricetus auratus* (Johnston & Schmidt 1979).

During scent-marking, experimental twigs were licked more than existing or control twigs when scent aged 3 d was introduced. Norton (1987:14) observed a tame klipspringer scent-marking a tap, and noted that 'if the tap was touched with wet hands, the scent was activated and the sickly sweet smell would hang around for hours'. He suggested that licking might release soluble scent, causing signal rise to coincide with investigation by the receiver (Alberts 1992). A further possibility is that licking may enable more precise sampling of the scent by the vomeronasal organ (Estes 1972). Somers et al. (1990) found that licking could occur just after marking, or between preliminary sniffing and marking in captive suni antelopes *Neotragus moschatus*. In these experiments, repeated licking during extended overmarking of introduced twigs may represent investigation of the branch in order to ascertain whether the strange scent has yet been smothered.

The difference between the shape of the curves in Figs 1 and 2 requires further explanation. If strange scent elicits elevated rates of both scent-marking and overmarking by the resident, why do residents increase absolute scent-marking rates only in response to fresh scent but sustain higher overmarking rates for several days? One possibility is that fresh scent contains information that is different from that of older scent. For example, persistence times of anogenital scent in meadow voles (Ferkin et al. 1995) and urinary signals in mice (Drickamer 1986) vary between males and females and may have different functions. Because the scent marks used in the experiment contained both male and female preorbital scent this effect could not be tested. However, owing to the large size and exclusivity of klipspringer territories, it would appear that even if there are gender differences in persistence times, the scent of both sexes will be relatively long-lasting in order to be functional.

A more likely explanation in this case may be an effect of the perception of

encounter probability with the intruders, mediated by the age of the scent. A notable characteristic of scent-marking as a form of signalling territory ownership is that it can continue to do so even in the absence of the signaller. One consequence of this is that, when meeting intruders, the owner should allow intruders to compare its odour with that of the scent marks on the territory. Intruders can thus match the odours of owner and territory as a means of assessing the status of their opponent and hence the likelihood that the encounter will be escalated (Gosling 1982; Gosling & McKay 1990).

If an owner encounters strange scent which is very fresh on its territory (or at the territory border), it is more likely that the animal which deposited the scent is still in the immediate area than if the scent is older. In view of this, in response to the fresh scent, the owner should increase its marking rate in order to cover the area with its own scent marks, so as to maximize the probability of scent-matching and emphasize its willingness to defend the territory should the two animals meet (Gosling 1982; Gosling & McKay 1990). For example, Ralls (1974) observed blue duiker *Cephalophus maxwelli* males increase marking rates before and during fights. In the same way, the owner should overmark the intruder's scent in order to reduce any advantage accruing to the intruder from the presence of its own scent and minimize the possibility of signal ambiguity to additional intruders. Conversely, when the owner encounters scent which is not fresh (i.e. after one or more days), the probability that the intruder is still in the area, and consequently the threat of an imminent encounter, are much lower; hence, residents should respond by overmarking to reduce ambiguity, but not necessarily with higher marking rates.

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Literature Cited

- Alberts, A. C. 1992: Constraints on the design of chemical communication systems in terrestrial vertebrates. *Am. Nat.* **139**, S62—S89.
- Apps, P., Viljoen, H. W., Richardson, P. R. K. & Pretorius, V. 1989: Volatile components of the anal gland secretion of the aardwolf (*Proteles cristatus*). *J. Chem. Ecol.* **15**, 1681—1688.
- Bossert, W. H. & Wilson, E. O. 1963: The analysis of olfactory communication among animals. *J. Theor. Biol.* **5**, 443—469.
- Clutton-Brock, T. H., Albon, S. D., Gibson, R. M. & Guinness, F. E. 1979: The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). *Anim. Behav.* **27**, 211—225.
- Drickamer, L. C. 1986: Acceleration and delay of puberty in female mice via urinary chemosignals: age of the urine stimulus. *Dev. Psychobiol.* **19**, 155—161.
- Dunbar, R. I. M. & Dunbar, E. P. 1974: Social organization and ecology of the klipspringer (*Oreotragus oreotragus*) in Ethiopia. *Z. Tierpsychol.* **35**, 481—493.
- Estes, R. D. 1972: The role of the vomeronasal organ in mammalian reproduction. *Mammalia* **36**, 315—341.
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- Ferkin, M. H., Burda, J., O'Connor, M. P. & Lee, C. J. 1995: Persistence of the attractiveness of two sex-specific scents in meadow voles, *Microtus pennsylvanicus*. *Ethology* **101**, 228–238.
- Gorman, M. L. 1990: Scent marking strategies in mammals. *Rev. Suisse Zool.* **97**, 3–29.
- Gosling, L. M. 1972: The construction of antorbital gland marking sites by male oribi (*Ourebia ourebia*, Zimmermann 1783). *Z. Tierpsychol.* **30**, 271–276.
- 1981: Demarcation in a gerenuk territory: an economic approach. *Z. Tierpsychol.* **56**, 305–322.
- 1982: A reassessment of the function of scent marking in territories. *Z. Tierpsychol.* **60**, 89–118.
- 1985: The even-toed ungulates: order Artiodactyla. In: *Social Odours in Mammals*, Vol. 2. (Brown, R. E. & MacDonald, D. W., eds). Oxford Univ. Press, Oxford. pp. 550–618.
- 1990: Scent marking by resource holders: alternative mechanisms for advertising the costs of competition. In: *Chemical signals in vertebrates*, V. (MacDonald, D. W., Muller-Schwarze, D. & Natynczuk, S. E., eds). Oxford Univ. Press, Oxford. pp. 315–328.
- & McKay, H. V. 1990: Competitor assessment by scent matching: an experimental test. *Behav. Ecol. Sociobiol.* **26**, 415–420.
- Johnston, R. E. & Schmidt, T. 1979: Responses of hamsters to scent marks of different ages. *Behav. Neural Biol.* **26**, 64–75.
- Martin, P. & Bateson, P. 1986: *Measuring behaviour*. Cambridge Univ. Press, Cambridge.
- Maynard Smith, J. 1974: The theory of games and the evolution of animal conflicts. *J. Theor. Biol.* **47**, 209–221.
- Melemis, S. M. & Falls, J. B. 1982: The defence function: a measure of territorial behaviour. *Can. J. Zool.* **60**, 495–501.
- Norton, P. M. 1980: The habitat and feeding ecology of the klipspringer *Oreotragus oreotragus* (Zimmermann 1783) in two areas of the Cape Province. MSc thesis, Univ. of Pretoria, South Africa.
- 1987: The klipspringer — Dainty mountain antelope. *African Wildl.* **41**, 12–15.
- Ralls, K. 1974: Scent marking in captive Maxwell's duikers. In: *The Behaviour of Ungulates and its Relation to Management*. (Geist, V. & Walther, F. R., eds). IUCN Publ. New Ser. **24**, Morges. pp. 114–132.
- Rasa, O. A. E. 1973: Marking behaviour and its significance in the African dwarf mongoose, *Helogale undulata rufula*. *Z. Tierpsychol.* **32**, 449–488.
- Roberts, S. C. 1994: Mechanics and function of territorial behaviour in klipspringer. PhD thesis, Univ. of London, London.
- 1997: Selection of scent-marking sites by klipspringers (*Oreotragus oreotragus*). *J. Zool. (Lond.)* **243**, 555–564.
- & Lowen, C. 1997: Optimal patterns of scent marks in klipspringer (*Oreotragus oreotragus*) territories. *J. Zool. (Lond.)* **243**, 565–578.
- Sipos, M. L., Nyby, J. G. & Serran, M. F. 1993: An ephemeral sex pheromone of female house mice (*Mus domesticus*): pheromone fade-out time. *Physiol. Behav.* **54**, 171–174.
- Somers, M., Rasa, O. A. E. & Apps, P. J. 1990: Marking behaviour and dominance in suni antelope (*Neotragus moschatus*) *Z. Säugetierkunde* **55**, 340–352.

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