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Marking behaviour and dominance in Suni antelope (*Neotragus moschatus*)

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Abstract

Studied the antorbital gland, pedal gland and elimination product marking in 3 groups of captive suni (*Neotragus moschatus*). Antorbital gland marking was performed almost exclusively by dominant (territorial) males and gas chromatograms of dominants marks differed from subordinates. Marking posts are short vertical twigs in open areas away from paths, with highly visible bulbs of deposit and arranged in concentric rings. Their unusual distribution may be associated with the suni's specialised forage. Based on site marking frequency, marks last 4 days. Strange secretions are recognised but not marked over. Pedal gland marking was assumed to be highest on paths, a characteristic feature of suni territories. Paths had a consistent density independent of enclosure size. Midden sites do not appear to serve a marking function. Strange elimination products are marked over by the dominant male. The findings are discussed in relation to the "scent matching" hypothesis.

Introduction

Suni (*Neotragus moschatus*) are one of the smallest of the antelopes with a mean shoulder height of 350 mm and a mean mass of 5 kg (SMITHERS 1983). The species has a patchy distribution throughout the eastern regions of Africa in areas where the preferred habitat – dense woody vegetation with a high stem density in the shrub layer and low ground cover – is present (LAWSON 1986). ANSELL (1971) recognises five subspecies. This study was conducted on the most southerly of the five, *N. m. zuluensis* (THOMAS 1898) which is distributed along the coastal area of Natal northwards to southern Mozambique and Zimbabwe (HEINICHEN 1972).

Very little is known about the behaviour of the suni, which is listed in the South African Red Data Book as being an endangered species. Its ecology in Natal-KwaZulu has been studied in detail by LAWSON (1986). However, owing to its small size and shy habits, detailed observations on various behaviour pattern complexes are either sparse or lacking, especially information on marking behaviour.

Suni possess at least three means of indicating their presence olfactorally. These are the secretions from the extremely large antorbital glands, secretions from the pedal glands and elimination products, which are usually deposited in middens. Antorbital glands differ widely in size, type and functional ability in Artiodactyls (see GOSLING 1985 for a review) but are conspicuous in all Neotraginae. These, together with the duikers (Cephalophinae), are classified by JARMAN (1974) as category A species and hold either individual or pair territories.

The use of olfactory cues to indicate spatial tenure is widespread amongst mammals (MÜLLER-SCHWARZE 1971; STODDART 1976; LEUTHOLD 1977; BROWN 1979; BROWN and MACDONALD 1985) and scent marking has been shown to be associated with dominance or intolerance of conspecifics in a number of species (see RALLS 1971 for a review). Suni are territorial with partial overlap between territories of male and female (LAWSON 1986). This

study investigates the olfactory means by which territory occupancy could be indicated. HEINICHEN (1972) was unable to observe marking behaviour in a free-living Kenyan suni population but hypothesised, on the basis of deposits found, that territorial males marked objects in their territories. LAWSON (1986) reports that, in captive groups, scent marking comprises 0.3 % of the male total activity patterns and 0.1 % of those of females in winter (July) but marking is infrequent (absent?) in summer (Dec.–Jan.). No further reference to marking in this species exists.

Material and methods

The study was conducted on 4 captive groups of suni held at De Wildt Cheetah Research and Breeding Station near Brits, Transvaal. The group size and composition was as follows (M = male, F = female): Group A – 1M, 2F; Group B – 1M, 2F; Group C – 4M; Group D – 3M. Heterosexual groups were held in enclosures of 290 m² while male bachelor groups had enclosures of 80 m². A covered shelter, bushes and trees were present in each enclosure and enclosures were separated from one another by a 2 m high wooden fence. Observations were conducted from a hide at one end of the enclosure. Apart from the natural forage present, the animals' diet was supplemented with lucerne and antelope pellets and water was available ad libitum.

Observations were conducted on 3 different groups (A, B, C) from mid-February to mid-September for a total of 101 hours, with observation periods being arranged to cover the entire timespan from 0630 to 1800 h. All instances of marking with the antorbital glands were recorded together with the duration, location, sequence of behaviour patterns performed and the individual performing them. Since marking with the pedal glands is considered to occur passively when the animals walk (GOSLING 1985), no quantitative data on marking frequency by this means could be obtained, although the paths used by the animals in the enclosure were mapped. Practically the entire enclosure was used, however, when the animals foraged.

To determine the responses of animals to foreign marks, two marking posts were moved from group C's enclosure to group A's on different occasions and the behaviour of the animals encountering the mark recorded for 1 h after introduction of the marking post.

A series of experiments were performed to ascertain the role of middens as olfactory territorial marking sites (RASA 1973). To determine whether middens were site specific, the original midden site was thoroughly cleaned and covered with fresh sand in group A and group B's enclosures and the elimination products removed to a site 2 m away. To determine whether personal elimination products alone acted as attractive elements in the choice of elimination sites or whether faeces and urine of strange individuals were also attractive, the middens in the same 2 enclosures were thoroughly cleaned, as above, and the elimination products of another group placed at a different site, also 2 m away. In all cases, the behaviour of the animals was recorded for 1 h after manipulation. Each set of experiments was conducted once in each of the two enclosures to minimise disturbance effects. Faeces quantity at the sites was estimated visually at 24 h intervals for comparison of site usage. Since a large and variable number of small pellets are produced at each defaecation, the actual number of defaecations could not be measured.

Although suni are active throughout the 24 h period (LAWSON 1986), observations could only be conducted between 0630 and 1800 h, the hours of winter daylight. Quantitative data on marking frequencies are therefore probably biased towards low values since only the diurnal part of the activity cycle could be monitored.

To ascertain whether differences were present in the marking substances from the antorbital glands of dominant and subordinate animals, marking posts were collected for analysis of volatiles by the dynamic solvent effect (see APPS et al. 1987 for the chromatographical sampling techniques used). Posts were removed shortly after they had been actively marked and placed in closed test-tubes on crushed ice until analysed. Two samples were taken from the dominant male in group C, one from the dominant male in group D and two from two subordinate males in group D.

Statistical tests used are mentioned at appropriate points in the text.

Results

Marking behaviour

Antorbital gland marking consisted of a sequence of behaviour patterns with a mean duration of 7.5 sec (range 1.5–24 sec, $n = 111$). The four behaviour patterns involved were 1. olfactory monitoring of the marking post (sniffing), 2. insertion of the tip of the marking

post into one of the everted antorbital gland pouches and moving the head vertically with a short jerky motion (mean = 1.09 strokes, range = 1–4 for a mean duration of 2.2 sec, range = 1.5–8.5 sec) termed marking, 3. licking the marking post and 4. insertion of the tip of the tongue into the antorbital gland (licking gland).

Of the 141 observed contacts with marking posts, 21 % consisted of olfactory monitoring only. For the 111 cases of antorbital gland marking recorded, olfactory monitoring of the marking post preceded marking on 104 (93.7 %) of the occasions. By far the majority of contacts with marking posts consisted of olfactory monitoring followed by marking only (58.6 %). All 20 cases where animals were observed to lick their antorbital glands followed marking of the post. For the 9 records of licking the marking post, 4 occurred after marking and 5 took place between olfactory monitoring of the post and marking. The sequence in which marking behaviour patterns occur in suni therefore appears to be, highly stereotyped, only licking the marking post, a relatively uncommon behaviour, being variable in its sequential positioning. The basic sequence can, however, be repeated up to three times and fragmentation of the sequence can occur at any point during repetition.

During a single marking sequence, only one antorbital gland is used for marking. However, glands may be alternated in sequential marks. Of the 48 marks recorded for the territorial male in group A, 24 were performed with the left and 24 with the right gland. The male in group C, however, performed significantly more marks with the left gland than the right ($x_1 = 2$, $N = 14$, $p = 0.019$ Binomial Test). The frequency of left or right gland useage therefore appears to differ amongst individuals.

Self-anointing with the antorbital glands was not observed. Allomarking with these glands has been reported for several antelope species (RALLS 1974; LEUTHOLD 1977). It did not occur in the suni groups studied, although licking of the partner's antorbital gland occasionally took place.

Marking posts

Antorbital gland marks are confined to definite marking posts. These were all firm, sharp objects such as twigs, sprouts of wild asparagus (*Protasparagus* spp.) and grass stalks, which appeared to have been bitten off close to the ground with a mean height of 75 mm (range 15 to 280 mm, $n = 19$). The secretion dried to a hard, greyish-black, crystalline substance that, due to accretion, formed highly visible bulbs of deposit.

Each enclosure contained numerous marking posts. The two 290 m² enclosures contained 41 and 65 posts each, the 80 m² enclosure contained 14. This gave a mean density of 0.184 ± 0.043 posts/m² i.e. approximately one post/5 m².

Posts were sited both singly and in groups. Of the 120 posts recorded for the three enclosures, 54 were within 1 m of each other with a distance greater than 2 m between them and their nearest neighbour. Groups had a mean size of 3.18 ± 1.33 posts ($n = 17$, range = 2–7).

There was significant tendency in the larger enclosures containing heterosexual groups for posts to be located more than 1 m away from regularly used paths. In enclosure A, only 10 of the 41 posts (24.9 %) were located near paths (Binomial Test, $x_1 = 10$, $N = 41$, $p = 0.001$), in enclosure B, 18 of the 65 posts (27.7 %) were near paths (Binomial Test, $x_1 = 18$, $N = 65$, $p = 0.0003$). In contrast, in the bachelor group in enclosure C, all 14 posts were sited within 1 m of paths. This finding could, however, be influenced by the small enclosure size (8 × 10 m). The vegetation also influenced marking post distribution. In enclosure A, none of the posts were in grass-covered areas and in enclosure B, only 2 were on the fringes of grassy patches (3.1 %). There was no grass in enclosure C. Posts therefore appear to be restricted almost entirely to areas of open ground and, at least in heterosexual groups, only a small proportion of posts are located near the network of regularly used pathways.

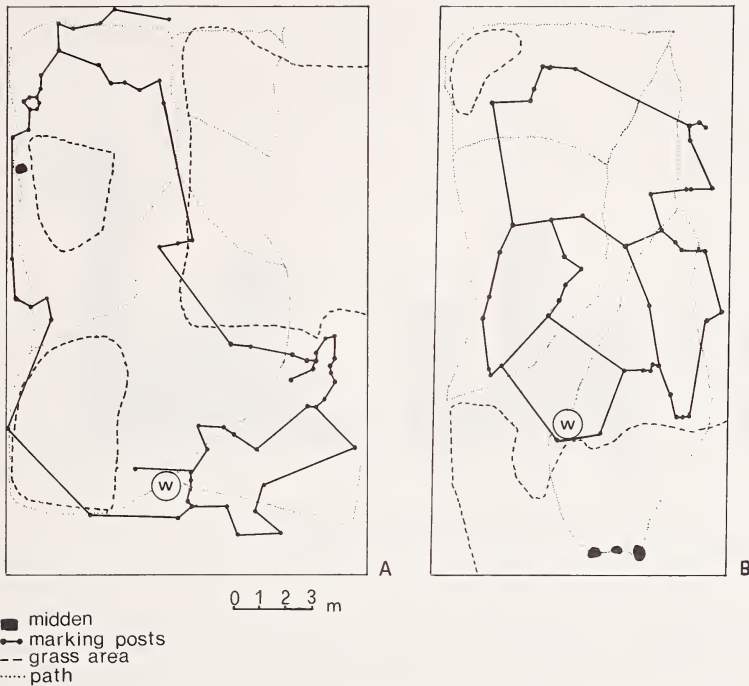


Fig. 1. Maps of enclosures A and B drawn to scale showing the pattern of marking posts, connected using the "nearest neighbour" method. These form concentric rings, especially obvious in enclosure B. No marking posts are present in grassy areas. The network of paths joining salient sites in the enclosures and the position of middens is illustrated. W = waterhole

Using the nearest neighbour method (GOŚLING 1981) to investigate the pattern of marking sites, a large ring of marking posts could be demonstrated in enclosures A and B (Fig. 1a and 1b). Since the animals were held in enclosures, the enclosure walls could be equated with the territory boundaries. The enclosure was, however, much smaller than the territory sizes mapped by LAWSON (1986) for free-living suni. In the Tembe Elephant Reserve these varied from 0.49 to 3.61 ha. A second circle within the boundary circle, but containing fewer marking posts can also be constructed for both territories with connections between the two circles. In both enclosures, neighbouring groups, which were not visible but which could be detected by sound and odour, were present adjoining the whole length of the north and south walls of the enclosures. There appeared to be no tendency for a higher aggregation of marks to occur along these boundaries. In enclosure A, only 5 of the 41 posts were within 1 m of the N and S boundary fences with none located on the east and west sides. For enclosure B, 6 of the 65 posts were within 1 m of the N and S fences and 4 were adjacent to the E and W ones.

Frequency of marking

The frequency of marking by various individuals in the three groups A, B and C was recorded. The 9 individuals involved (5 M, 4 F) marked a total of 73 times in 67 observation hours. Of these, 67 (91.2 %) marks were made by the dominant males in each of the groups. The subordinate male which was second in rank in bachelor group C was observed to mark twice (2.7 %). The lowest-ranking male in this group was never

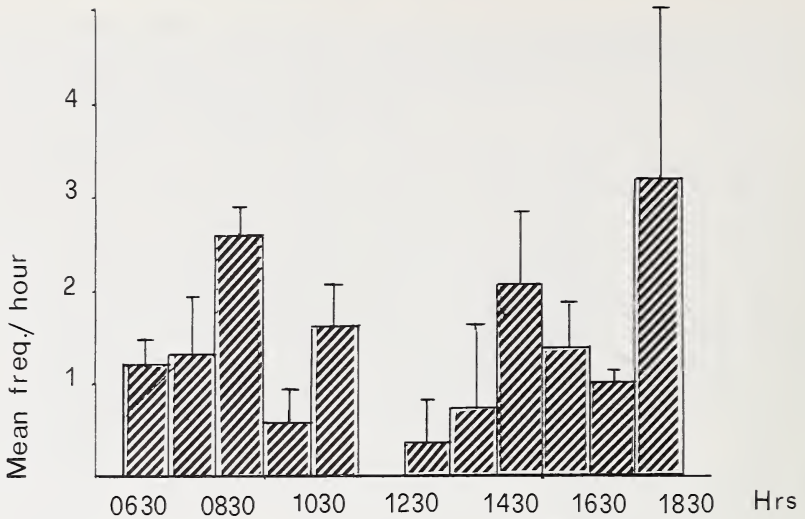


Fig. 2. Mean frequency of marking per hour, with standard deviations of the means, from sunrise to sunset during winter (February to September, 100 hours total)

observed marking. Only one of the 4 females, the dominant in group A, marked. This occurred 4 times (5.5 %) immediately after the original dominant male in the enclosure had been replaced by another adult male. (This exchange of breeding males is performed yearly to mitigate inbreeding effects.) These findings indicate that antorbital gland marking is performed almost exclusively by dominant males, although females do mark under exceptional circumstances.

An incidental observation which supports this is the change in marking frequency of the subordinate male in group C, mentioned above, after transfer to group D containing 3 young males. He assumed dominant status within 3 days and his marking frequency increased from 0.07 marks/h, observed in the original enclosure, to 8.57 marks/h in the new group.

To determine whether marking activity showed temporal patterning, data from all 4 groups were pooled and the mean frequency of marking/hour calculated for each hourly interval from 0630 to 1830 h. Marking showed two peaks of activity during the daylight hours (Fig. 2). The highest mean marking rate, however, occurred just prior to sunset and may indicate increased marking activity during the early evening. This section of the animals activity cycle could not, however, be monitored.

If, however, as LAWSON (1986) has shown, suni activity continues throughout the night also in captive groups, and assuming that marking shows the same relatively even temporal pattern found during daylight for the entire 24 hour cycle, then the frequency of marking for the territorial male in group A could be estimated at a mean of 24.88 marks/day (1.12 marks/h \times 24). Enclosure A contained 41 marking posts and enclosure B, 65 posts. Assuming that the males' marking was evenly distributed between posts, for which there is no contrary evidence from the daytime observations, then the male in group A could mark each site every 1.65 days and the group B male every 3.98 days.

Response to foreign marking posts

Two marking posts from enclosure C were introduced at different times into enclosure A and positioned in the same way as natural posts (i.e. vertical and approximately 8 cm above

ground level). On both occasions the dominant male in the group approached the strange post first and responded by sniffing and jerking its head back abruptly. This sequence was repeated 3 times, after which the post was ignored. The same behaviour patterns were recorded for the dominant female but here, the sniff/head-jerk was repeated only twice on both occasions. None of the animals marked over the marking post in the 1 hr observation period subsequent to its encounter. Similar behaviour was never observed in response to "own" marking posts. This behavioural difference suggests that the odour emanating from the introduced post was identified as being unfamiliar.

Antorbital gland activity

Dominant males appeared to have highly active antorbital glands, suggested by their "wet" appearance, with secretion extruding from the gland orifice. This was not the case for subordinate males, where the gland appeared "dry". The amount of secretion produced appears to correlate with gland useage. As previously stated, dominant males are responsible for 91.2 % of the total marking observed, subordinates for only 2.7 %. The earliest observed case of antorbital gland activity, inferred by active marking behaviour, was in an 11 month old male.

Pedal gland marking and pathways

Since pedal gland marking occurs passively while the animals walk, quantitative measures of marking intensity or frequency could not be conducted. However, particular routes within the enclosure were used with such regularity that obvious paths were formed. The assumption is that such paths, owing to disproportionately frequent useage in contrast to the rest of the enclosures, would have a greater concentration of pedal gland secretion present than areas which were infrequently traversed.

Paths were not distributed randomly throughout the enclosures but connected salient sites within it i.e. shelter, waterhole, artificial feeding site, midden and preferred resting sites. In enclosure A there were 83 m of paths, in enclosure B 93 m, and in the smaller enclosure C, 34 m. This gave a mean of 1 m of path/2.8 m² for enclosure A, 1 m/2.5 m² for enclosure B and 1 m/2.4 m² for enclosure C. The mean for all enclosures was 1 m of path/2.57 ± 0.21 m². The close agreement between the figures suggests that paths, at least in these captive groups, tend to show a rather typical density independent of enclosure size. This could not be attributed to the fact that the salient sites of enclosures A and B were similar and the animals had to adopt the same path patterns to reach them. As Figs. 1a and 1b show, the path networks in the two enclosures were very different. For enclosure C, the salient sites were arranged in a completely different pattern from those in the other two enclosures, yet the path length/m² was approximately the same.

Apart from pedal gland secretion, elimination products might also be used to passively mark paths, owing to the dominant male occasionally performing scraping motions with the forefeet in the contents of middens (see below).

The use of middens as marking sites

Suni urinate and defaecate almost exclusively at certain places in the enclosure, termed middens. These are used by all group members. Enclosure B contained only a single midden, enclosure A had 3 adjacent ones and enclosure C, 3 widely separated ones. All middens were sited at the periphery of enclosures. Animals urinated and then defaecated on the sites but did not scrape middens with their forefeet during normal elimination.

To determine whether middens were sited so as to function in olfactory demarcation of the territory, or whether the choice of elimination site was arbitrary and dependent on the presence of the elimination products themselves, the experiments described in the

Table 1. Response of groups A and B to manipulation of the midden site in their enclosures

	Group A		Group B	
	24 h	48 h	24 h	48 h
I. Own faeces				
Old site	0	0	75	0
New site	100	100	25	100
II. Strange faeces				
Old site	0	0	50	0
New site	100	100	50	100

In experiment I, own elimination products were placed approximately 2 m away from the old, cleaned site. This was termed the new site. The same procedure was followed in experiment II but using elimination products from a strange group of animals. Midden usage was estimated by the approximated percentage of faeces deposited at the two sites during the two subsequent 24 hour intervals

“Methods” section were conducted. The hypothesis tested was that if the site of the midden was important in territory boundary demarcation, animals would continue to defaecate on the original site rather than change to a new site. The results are shown in Table 1.

The findings indicate that elimination products, whether familiar or unfamiliar, act as attractants for subsequent urination and defaecation. In no case was fidelity to the previously used site observable after 24 hours. Group A changed midden sites immediately. In the case of group B, the original midden site was large and well established. The 24 h delay before the new site was used exclusively could have been dependent on elimination product odour (especially urine) remaining at the old site.

Animals in experiment I showed no behavioural change except transfer of their

elimination behaviour to the new site. In experiment II, however, there was a marked behavioural response to the strange elimination products. In group A, only the dominant male approached the site within the first hour following introduction of the strange elimination products. His response was intense olfactory monitoring followed by urination and defaecation on the site. Subsequent to this, the site was scraped repeatedly with the forefeet with olfactory monitoring occurring between scraping bouts. The entire sequence was repeated twice within the first 20 min after which the male ignored the site. In group B the dominant male's response was more intense and the above behaviour patterns, especially scraping with the forefeet, were performed almost continuously for 18 min. During this period, the male urinated on the site 4 times. These observations indicate that strange elimination products are recognised as such but that the dominant male superimposes his own faeces and urine on them, the frequent scraping with the forefeet probably serving to mix his own and the strange elimination products as well as cover the latter. The midden is then adopted for future use rather than the site being avoided.

Chromatographic profiles of dominant and subordinate males' marks

The volatile components of antorbital gland secretion deposited on marking posts by dominant and subordinate males and analysed by the dynamic solvent effect, were qualitatively and quantitatively different. The gas chromatograms of the dominant males in groups A and D are shown in Fig. 3a and 3b and those of the two subordinate males in group D in Fig. 3c and 3d. The antorbital secretions of dominant males contained greater numbers and larger quantities of highly volatile substances than those of subordinate males. The components concerned, however, have not yet been chemically identified. Dominant and subordinate animals therefore differ in the chemical composition of their antorbital gland secretions.

Discussion

The study has shown that suni territories are liberally provided with olfactory cues indicating occupancy. Male suni mark posts in their territories with secretions from the

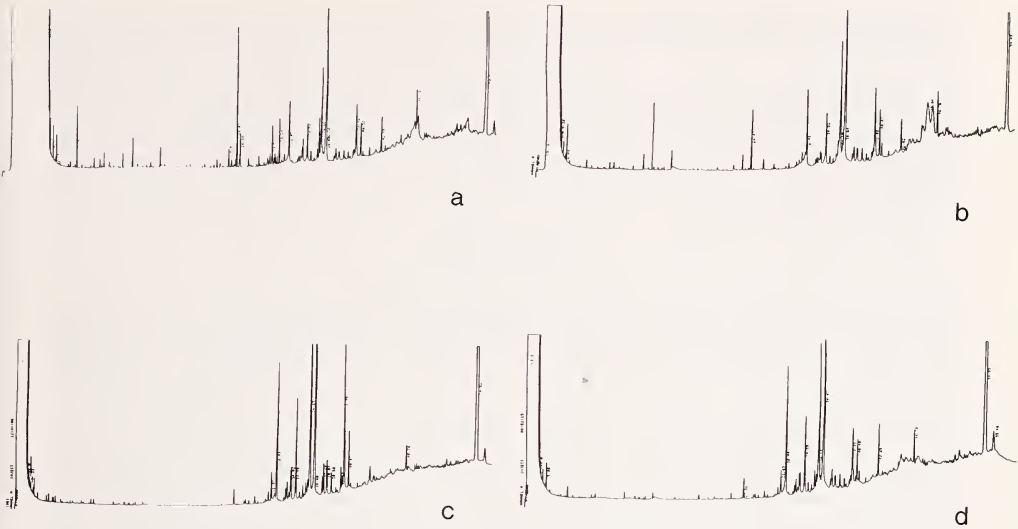


Fig. 3. Gas chromatograms of the antorbital secretions of 2 dominant (a, b) and two subordinate (c, d) suni males, obtained using the dynamic solvent method. Chromatograms of dominants show qualitative and quantitative differences from those of subordinates

antorbital glands while such marking in females is rare. This tendency for male Artiodactyls to be most active in territorial marking has been reported for oribi *Ourebia ourebia* (GOSLING 1972), pronghorn antelope *Antilocapra americana* (KITCHEN 1974), Coke's hartebeest *Alcelaphus buselaphus cokei* (GOSLING 1974), impala *Aepyceros melampus* (JARMAN 1979), blackbuck *Antilope cervicapra* (HEDIGER 1949), Grant's gazelle *Gazella granti* (WALTHER 1965) and Thompson's gazelle *Gazella thomsoni* (GOSLING 1985), amongst others. Only dominant male suni show high rates of antorbital gland marking. As RALLS (1971) indicated, high marking frequency is associated with intolerance of conspecific rivals and LAWSON (1986) has shown that the territories of male suni are almost mutually exclusive.

Although the majority of sightings of free-living suni indicate that the species is probably pair-living, male and female territories do not show the degree of coincidence found in the dik-dik *Madoqua kirki* (HENDRICHS 1975) and a single male may show territorial overlap with two or more females. Even groups of a single male and up to 4 females have occasionally been sighted (LAWSON 1986). Mutual exclusivity is thus not typical of female ranges and may be associated with low marking frequency in females.

Marking appears to be suppressed in subordinate animals of both sexes. No subordinate female was ever observed marking and the subordinate male in bachelor group C marked rarely until he became the dominant male in group D. Other subordinate males did not mark or only at very low frequencies. The gas chromatograms of antorbital gland secretions from dominant and subordinate males show clear differences in their volatile components. This suggests that status related physiological differences exist between territorial and non-territorial males and that these changes can occur rapidly, in the abovementioned case, within 3 days. Dominance is therefore not only reflected in the constituents of the antorbital marking secretion but also in marking frequency.

The sequence of behaviour patterns in suni antorbital gland marking was found to be highly stereotyped and marking was almost always preceded by olfactory monitoring of the marking site. Vertical up and down movements of the head during marking have been reported for most antelope species which mark with antorbital glands (GOSLING 1985).

Compared with other Artiodactyls (WALTHER 1979), however, suni are unusual in that typically only one of the glands is used during any one mark and the majority of marks consist of a single stroke only, rather than a repeated nodding movement of the head. The actual performance of marking does not appear to have a signal value, as has been reported for hartebeest (GOSLING 1984), impala (JARMAN 1979) or chital *Axis axis* (SCHALLER 1967) probably owing to its brevity and relative inconspicuousness. Licking of the gland after marking has not been reported for other species to date.

Marking posts

Marking posts appear to be manufactured by biting off the plant just above ground level, although this was not actually observed. All the plants used as marking sites are normally at least 0.5 m high and *Protasparagus* and grasses are not forage plants. It is therefore unlikely that the short stumps used were the byproducts of normal feeding. Manufacture of marking sites has been recorded for oribi (GOSLING 1972), pronghorn antelope (KITCHEN 1974) and chevrotains (DUBOST 1975). Only 2 marking sites were on twigs of overhanging branches and by far the majority of posts were 7 cm or lower. GOSLING'S (1981) maximum mark detection hypothesis states that marking posts should be sited so as to maximise the chances of encounter. Gerenuk and oribi place their antorbital gland marks at head-height for detection by a walking intruder (GOSLING 1972, 1981). For suni, however, this would be approximately 30 cm, yet marking posts are practically at ground level. It is during foraging that the head would be carried low, suggesting that the posts are "aimed" at intruding foragers.

A further corollary of GOSLING'S "maximum detection" hypothesis is that marks should be located near routes regularly used by potential territorial invaders i.e. pathways and game trails. This has been demonstrated for pronghorn antelope (GILBERT 1973), gerenuk (GOSLING 1981) and dik-dik (GOSLING 1985). In suni there was a significant tendency for marks to be sited in open areas away from regularly used pathways. The differences between the findings for the bush-savannah/open grassland living species and suni may be associated with their differing food sources. Oribo, gerenuk and dik-dik are either browsers or grazers on short grass swards. Suni live in woodlands and are specialist feeders, foraging mainly on fallen leaves (especially *Ficus* spp.), flowers and fruit (LAWSON 1986). As GOSLING (1985) points out, territory owners would be expected to mark near objects that are likely to attract other animals. Since the suni's preferred food items are patchy resources, in contrast to bushes and grass, and tropical woodland trees are rarely synchronised in their flowering and fruiting cycles (FRANKIE et al. 1974), a tree which is either dropping its leaves, flowers or fruit would be a relatively isolated food patch. This would serve as a strong attractant for other animals. A territory owner should thus mark where encounter rate by an exploiting invader would be highest i.e. near ground level and in the open around or under such trees.

The high visibility of suni marking sites also suggests that their function is in forage resource demarcation. All marking sites except two were on open ground and away from grassy areas which would obscure the large blackish-grey bulb of secretion. A relationship between marking site and preferred food has been demonstrated for gerenuk (GOSLING 1981) and the evidence presented for suni suggests strongly that a similar relationship is present in this species.

The spatial patterning of marking posts agrees well with GOSLING'S (1981) economic marking hypothesis. This states that, if the pattern of marks is adapted to intercept animals entering the territory, marks should be concentrated at the territory boundary and should it be to the owner's advantage that more than one mark be encountered, then concentric circles should be formed. The pattern of marking sites revealed by the mapping of "nearest neighbour" marks shows that suni mark predominantly along the territory boundary and

that smaller concentric circles may be present. Similar patterning of antorbital gland marking sites has been demonstrated for gerenuk (GOSLING 1981) and Thompson's gazelle (GOSLING 1985 redrawn from WALTHER 1978a).

GOSLING (1985) hypothesises that territorial animals should concentrate their marking sites in areas where the likelihood of encounters with neighbouring males would be high. Enclosures containing territorial males adjoined the N and S sides of enclosures A and B. Although these adjacent groups were not visible, owing to the fence, their presence was known, as evidenced by the "butting" fights directed at the fence by neighbouring males. However, there was no tendency for marking sites to be concentrated at these boundaries.

In gerenuk, marking sites tended to occur close together more frequently than if they were randomly distributed (GOSLING 1981). In this study, approximately half the total number of suni marking posts occurred in groups with a mean of 3 posts within 1 m of one another. The significance of this clumping of marking sites is unknown, but may aid in forage site defence.

From the frequency of marking per site calculated from the observed marking frequency/hr during daylight, the known activity cycle of suni and the number of marking posts present, the male in group A could mark each site every 1.65 days and the group B male every 3.98 days. These values compare well with those found for other Artiodactyls (4.5 days/site for gerenuk [LEUTHOLD 1978], 2.8 days/site for Thompson's gazelle [WALTHER 1978a, b, in GOSLING 1985]). The intervals between site marking given above suggest that there is an upper time limit beyond which a mark loses its effectiveness and that this is relatively short and consistent for the species studied to date, ranging between 1.6 and 4.5 days. Whether these are maximum or minimum times between mark deposition and loss of effectiveness is unknown.

Pedal gland marking

All enclosures had a network of paths connecting salient sites within them. These paths are a recognised feature of suni territories (HEINICHEN 1972). In the captive animals, paths showed a consistent density independent of enclosure size, path pattern and salient site distribution. If pedal gland secretion is present in higher concentrations on such paths than on the surrounding areas, then consistent path density may indicate that paths have a marking function. No quantitative data are available, however, for free-living suni.

On paths, marks from both males and females would be present, in contrast to the male antorbital gland marking sites. In addition, paths would also indicate the intensity of range useage (GOSLING 1985). They are unlikely to reflect the presence of preferred forage, a function of pedal gland secretion suggested for grassland Artiodactyls such as Coke's hartebeest (GOSLING 1974) and reindeer (MÜLLER-SCHWARZE et al. 1978), since the majority of suni forage is sited away from paths. A combination of pedal gland secretion on paths and antorbital gland marks away from paths would thus almost completely olfactorally delineate the range occupied but by different means.

Middens

With one exception, enclosures contained more than one midden. Their positioning, however, appeared to bear no relationship to the presence of neighbouring groups. The natural siting of middens does not suggest their role as territory markers, as has been found for dik-dik (HENDRICHS 1975). This is supported by the results of the experiments conducted. Where the midden is sited appears to be unimportant, since animals changed their elimination sites completely within 48 h of the site being artificially changed. The presence of elimination products themselves appeared to determine where further elimination occurred and there was no fidelity to the previous site even after long-term useage.

However, the response of the territorial males to elimination products from a strange suni group placed in the enclosure indicates that they do carry olfactory cues associated with identity. Strange elimination products evoked attempts, at least on the part of the male, to cover the odour with his own. After this, they were used as the focus of a new midden. Similar findings have been recorded for a carnivore, the dwarf mongoose *Helogale undulata rufula* (RASA 1973). These experiments contrasted with those where strange antorbital gland secretions were introduced into the territory. Although these marks were identified by both male and female as being unfamiliar, no attempt was made to mark over them and they were avoided or ignored.

The functional significance of marking

Several hypotheses have been put forward as to the functional significance of territorial marking in Artiodactyls, ranging from threats (RALLS 1971) and deterrents (HEDIGER 1949) to "increased self confidence" (RICHTER 1972) and as an "aid in self orientation" (WALTHER 1978a). GOSLING (1985) suggests that Artiodactyl territorial marking functions in "scent-matching", allowing a territory owner to be identified and "assessed" by an opponent, thus reducing the time and energy spent in territorial defence. According to this hypothesis, only intruders intending to compete for territory ownership would then engage in a possibly costly fight. The four predictions which arise from this hypothesis are a. the territory owner will mark the area in a way that maximises mark detection; b. will mark himself with the same marking substances; c. remove or replace marks that do not match his own; d. make himself available for scent-matching.

The first prediction holds true only when antorbital gland marking is taken in conjunction with pedal gland marking. Then, both paths and areas between paths are marked, the latter in concentric rings, suggesting boundary marking. However, suni do not actively anoint themselves with their antorbital glands which, however, are large and under muscular control. It is likely that the secretion exuding from the "wet" glands of territorial males is sufficient to provide the necessary odour cues. As far as prediction c. goes, suni show no tendency to remove or replace strange antorbital gland marks but rather to avoid or ignore them. This was not the case for elimination products, however. Whether territorial male suni make themselves available for scent-matching in agonistic encounters is speculative. Owing to the captive conditions under which the animals were held, open encounters were not possible, although fights between territorial males occurred through the fences. The observation that suni occasionally lick each others' antorbital glands and also lick marking posts may indicate that scent-matching behaviour may form part of an assessment process, although in the observed cases, this licking was probably affiliative rather than agonistic, occurring between pair partners. Similar behaviour, pressing of the antorbital glands of partners against one another, is recorded in Maxwell's duiker (RALLS 1974).

Fights only occurred between territorial males, even though the opponents were not clearly visible to each other, suggesting that there is some mechanism of olfactory recognition of dominant/territorial status. The gas chromatograms of antorbital gland secretions from dominant and subordinates differed qualitatively and quantitatively in volatile content. It is likely that these volatiles indicate status, identifying potential competitors. Further experiments are necessary to determine the existence of individual scent-matching. For a territorial male, there would be no advantage in attacking all intruders, since this strategy is energy consuming and would also exclude females. Competing males, however, should be rapidly identified as such and excluded. The volatile components of the antorbital gland secretions could serve as the means by which this rapid identification could be achieved.

In summary, marking behaviour in suni fulfills the predictions of GOSLING's "scent-

matching and assessment" hypothesis only if all means of marking are taken into account. The hypothesis does not hold for antorbital gland marking alone since prediction c) is not fulfilled, but does if it is considered in conjunction with marking with elimination products at middens, where prediction a. does not hold. Prediction d. can, at present, only be related to status and not to individuals and prediction b. may not apply to this species, owing to the size of the antorbital glands in relation to body mass. The use of different modes of olfactory communication to construct a single "message" has been demonstrated for dwarf mongooses (RASA 1973) and may be a more widespread phenomenon than hitherto recorded.

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Zusammenfassung

Markierungsverhalten und Dominanz bei der Suni-Antilope (Neotragus moschatus)

Untersucht wurde Markieren durch Voraugendrüsen, Interdigitaldrüsen und Ausscheidungsprodukte bei 3 gefangengehaltenen Suni-Gruppen (*Neotragus moschatus*). Voraugendrüsenmarkierung findet fast ausschließlich bei dominanten (territorialen) Männchen statt, und Gaschromatogramme der Sekrete von dominanten und subdominanten Männchen zeigen Unterschiede. Markierungsstellen sind kurze, senkrecht stehende Zweige, in offenen Gebieten zu konzentrischen Kreisen angeordnet. Die außergewöhnliche Anordnung der Markierungsstellen könnte mit den spezialisierten Futterquellen der Suni zusammenhängen. Die Wirkung des Markierungssekretes hält ungefähr 4 Tage an. „Fremde“ Sekrete werden identifiziert, aber nicht übermarkiert. Es wird angenommen, daß die höchste Konzentration des Sekretes der Interdigitaldrüsen auf Pfaden vorkommt, die typisch für Suni-Territorien sind. Pfade haben eine fast konstante Dichte, unabhängig von der Gehegegröße. Kotplazierung scheint keine Markierungsrolle zu spielen. Fremde Ausscheidungsprodukte werden von dominanten Männchen jedoch übermarkiert. Die Befunde werden in bezug auf die „Geruchsschätzungs“-Hypothese diskutiert.

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