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Authors: Blank, David A., Ruckstuhl, Kathreen, and Yang, Weikang

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Secretion marking with preorbital glands in goitered gazelle, *Gazella subgutturosa* (Artiodactyla: Bovidae)

David A. BLANK[1,2]*, Kathreen RUCKSTUHL[3] and Weikang YANG[1]

[1] *Key Laboratory of Biogeography and Bioresource in Arid Land, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi, China; e-mail: yangwk@ms.xjb.ac.cn*

[2] *Institute of Zoology, Kazakh Academy of Sciences, Alma-Ata, Kazakhstan; e-mail: blankdavid958@yahoo.com*

[3] *Department of Biological Sciences, University Calgary, Canada; e-mail: kruckstu@ucalgary.ca*

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Abstract. Scent marking is a widespread component of mammal communication and important in the maintenance of territories as a form of status signal advertising territorial ownership, and potential source of information on the quality and competitive ability of the signaller. Marking behaviour with preorbital glands is a common research topic for tropical antelopes, while such behaviour in goitered gazelles, until now, has been poorly understood. We investigated this behaviour in goitered gazelles and found that adult males marked with their preorbital glands all year round, but especially intensively during the rut and most often while patrolling their territories and chasing females; rarely did they mark during territorial conflicts. Adult males preferred to mark the most conspicuous eatable shrubs that reached close to the height of the male. With a few minor exceptions, goitered gazelle performed marking behaviours in a manner similar to other antelope species, and overall did not show any distinctive differences. Preorbital marking behaviour as an essential part of social organization demonstrated its conservatism, but environmental factors also had their impacts, which led to considerable quantitative seasonal fluctuations in marking behaviour.

Key words: Antilopinae species, individual territories, rutting period, scent communication

Introduction

All mammals are well equipped with odour-producing skin glands that exude secretions used for marking objects in their environment (Mykytowycz 1972, Sokolov & Chernova 2001). And scent marking is a very important and widespread component of mammal communication by means of chemical signals or pheromones (Johnson 1973, Brown & MacDonald 1985, Wyatt 2003). There are several hypotheses that have been proposed to explain the function of scent marking (Gosling & Roberts 2001), but in general scent marks are important in the maintenance of territories as a form of a reliable status signal, advertising territory ownership; scent marking also may provide condition-dependent signals as to the quality and competitive ability of the signaller, which might help to reduce the costs of territorial defence (Gosling 1982, Roberts & Gosling 2001). For the most part, olfactory marks do not prevent the intrusion of strangers into an individual territory, but they do serve as a direct advertisement of a male's ability to defend his territory from rivals (Gosling 1982, Brashares & Arcese 1999). Many bovids and some cervids are territorial animals and use a number of skin glands, especially the preorbital glands, for marking their territories (Owen-Smith 1977, Carranza et al. 1990). However, since these glands are opened widely in male gazelles when fighting with rivals and courting females, they release intense odours from the gland sacs, and in these situations the preorbital gland likely plays an additional functions for this species. Of course, this behaviour has nothing to do with object marking, but it does have strong effects on both rivals and females (Walther et al. 1983). The muskox (*Ovibos moschatus*) is a non-territorial ungulate and uses his preorbital markings for threat displays (Gray et al. 1988). In cervids too stags open their preorbital glands when fighting (Bartoš 1983) or roaring (Butzler 1974), while the preorbital secretions of females are used for establishing mother-offspring bonds (Hatlapa 1977). The opening of the preorbital glands in red deer calves is thought to function as a signal to their mothers that they are hungry (Bartoš et al. 2005).

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* *Corresponding Author*

Preorbital glands are paired exocrine organs, which are typical for all Antilopinae species. These glands consist of a black integumental thickening formed around an invaginated pocket of skin; an elongated slit, located below and in front of each eye, exudes black, tarry secretions which contain pheromones and other semiochemical compounds (Albone 1984, Kingswood & Blank 1996). Even though all gazelles and their relatives possess preorbital glands, in reality only some species actually use them (Walther et al. 1983). Males of goitered gazelle have large preorbital glands that stand out as prominent bulges on either side of the snout, the secretions of which are used very intensively in marking individual territories. Goitered gazelle females, on the other hand, like other Antilopinae, do not mark at all (Walther et al. 1983).

Marking behaviours of many tropical antelopes and gazelles and the peculiarities of these behaviours have been studied quite well over time (Walther et al. 1983, Roberts 1998, Brashares & Arcese 1999). And even though the preorbital gland was described for goitered gazelles long ago (Pocock 1910), it was not until much later that there were investigations into the morphological and histological structure of these glands (Schaffer 1940, Sokolov 1982). During the 1950-1970s, the ecology of the goitered gazelle in its natural Central Asian environment was studied very intensively (Sludskiy 1956, Mambetzhumaev 1970, Zhevnerov 1984), but the researchers involved in these studies did not show any interest in the function of the preorbital glands or the gazelles' marking behaviours. It was not until a decade later that the first investigations of territorial behaviour in goitered gazelles, and the use of their preorbital glands for marking territorial borders, began (Blank 1985, Marmazinskaya 1996), but even then, these studies were mainly declarative in content. So the focus of this paper is to give a detailed quantitative description of the preorbital gland marking behaviour of the goitered gazelle, and to define differences and similarities of goitered gazelle of their behaviour with other antelope species.

Based on previous studies of scent marking by other gazelles and antelopes, we made several predictions for this behaviour in the goitered gazelle. The earlier studies established that adult males of antelopes and gazelles use their preorbital glands for marking their territories most intensively during the rutting period (Walther et al. 1983). So we thought that the same phenomenon would be true for goitered gazelles as well, and expected to find season, sex, age and social status differences in marking behaviours. Our first prediction: male goitered gazelles would perform preorbital gland marking most intensively during the rut in November and December (Blank 1998), less significantly during a "false" rut in April (Kingswood & Blank 1996), and least often in other months. In addition, since the physiological activity of preorbital glands depend on a male's hormone (testosterone) production (Rajagopal & Archunan 2011), we also thought that the duration of each act of preorbital marking would be longer during the rutting season than in other months.

Since secretion marking was connected mostly with rutting adult males which typically were alone in their individual territories (Blank 1998), we made our second prediction: marking activities would be observed more often for single males and considerably less for males in groups.

Walther (1984) found that preorbital glands started functioning in Thomson's gazelles at the age of 1 year, although yearlings rarely showed marking behaviour. In the few cases where they did show scent marking activity, the yearling males were imitating the actions of adult males rather than actually leaving their own scent marks. Moreover, females did not use their preorbital glands at all. We thought these findings would be true for goitered gazelles, so we proposed our third prediction: young males would mark considerably less often than adult males, while females would not mark at all.

If males scent marked to maintain priority access to receptive females in competition with other males (Gosling & Roberts 2001), then we had our fourth prediction: rutting males should mark more often while courting receptive females than during other activities.

During a study of territorial behaviours of oribis (*Ourebia ourebi* – Brashares & Arcese 1999) and klipspringers (*Oreotragus oreotragus* – Kruger et al. 2002), a territorial male was found to recognize neighbouring males as the greatest threat to his territorial ownership, especially if the neighbour has an additional one or two subordinate males in his territory. So during territorial conflicts, the territorial male marked his territory more intensively with his preorbital glands compared to when he encountered transient males. We supposed this also would be true for goitered gazelles, which became our fifth prediction: males would mark their territory more intensively during territorial conflicts with neighbours than with transient males.

When marking with the preorbital gland, males positioned their heads so that a suitable twig could be inserted directly into the widely opened gland and rubbed back and forth to deposit the secretions (Walther et al. 1983). Since dry grasses were rare during the rutting period in November and December and mostly dry bushes and saxaul trees were available for marking, we made our sixth prediction: thinner twigs of bushes would be used more often for marking than the larger saxaul branch tops.

And finally, Walther (1984) was convinced that all Antilopinae, including gazelle species, performed scent markings with the preorbital gland in a similar way. So, we posited our seventh prediction: goitered gazelles would demonstrate this behaviour in a similar manner to other gazelles and antelopes.

Material and Methods

Our observations were conducted over a 6-year period from 1981 to 1986 in the Ili Depression (southeastern Kazakhstan). We collected our data during the goitered gazelles' rutting period in November-December, during their less significant "false" rut in April-May, as well as other months out of the rutting season (March, June-August, October) (Kingswood & Blank 1996, Blank 1998). However, since males were quite mobile during the months outside the rut, moving almost constantly in morning and evening hours (Blank 1990), the intensity of marking behaviour was very rarely observed; therefore some data were absent for this period, such as intervals between marking acts. In contrast, during the "false" and "real" ruts when males remained in their individual territories for several weeks (Blank 1998), marking acts were observed considerably more often, so that we collected more abundant information for preorbital marking during those times. Our main method of study was through continued focal observations over long periods of time (up to 9 h) using binoculars (magnification 8×) and a telescope (magnification 30 × 60 ×). We mostly did focal animal observations, concentrating on only one randomly selected group of gazelles (usually the closest one) at a time, observing separated individual and recording the preorbital marking acts. All of the behaviours were recorded in the order in which they occurred and each time they occurred (all occurrence method). Observation posts were usually established on elevations and in different parts of our study area to avoid pseudo-replication. We measured the frequency of markings, the time and duration of the acts, and the intervals between separate acts with a stopwatch (seconds counter), and noted the sex (male or female), age (adult, sub-adult and young) and status of the performer (territorial or non-territorial male). Territorial bucks are those that stop their everyday movements from their night grazing pastures to their daytime resting places, and establish their own territories in which they stay during the entire rutting period (both the "real" rut in November-December and the "false" rut in April-May). Non-territorial males do not establish territories or stay in one area and instead continued with their regular everyday movements (Blank 1998). For the entire 6-years of our study, we had a total 38 of focal observations in March, 181 hours in April, 470 hours in May, 374 hours in June, 173 hours in July, 59 hours in August, 63 hours in October, 224 hours in November and 148 hours in December.

We classified the sex and age of each gazelle according to the description provided by Zhevnerov (1984): adult males were older than 2 years of age with horns 1.5 times longer than the ears and the absence a black spot on the front of the muzzle; adult females were older than 2 years of age, without horns and absence of a black spot on the muzzle; sub-adult males were 1-2 years of age with horns equal to or shorter than the ears and a black spot on the muzzle; sub-adult females were 1-2 years of age without horns and a black spot on the muzzle; and young animals were up to 1 year old with a body size 2-3 times smaller than an adult and a black sport on the front of the muzzle.

In this paper, we will restrict the term "secretion marking" to cases where the animal deposited an odoriferous substance from the preorbital glands on an object in its environment by special or at least somewhat ritualized actions (Walther 1984). During focal observations it was very difficult in many cases to differentiate among species of dried, defoliated plants from a distance of several hundred meters, so we divided all plants into three categories – grasses, bushes and saxaul trees – and analyzed plants preferred by gazelles for marking according to these classifications.

For statistical data analyses, we used an ANOVA test for comparing of frequency distribution during daytime hours and over months, since according to Shapiro-Wilk and Kolmogorov-Smirnov tests the data distribution was normal. Other indexes, such as scent marking durations and intervals, had a not normal distribution, so we used the Mann-Whitney U test for comparing two variables and the Kruskal-Wallis test for comparing several variables. We also used the Log-linear model test for comparing portions of separate behavioural acts, as well as Spearman's correlation and Cross-tab test for checking the possible correlation between two variables. In cases of multiple comparisons of the same data set we Bonferroni-corrected the P-value to account for this.

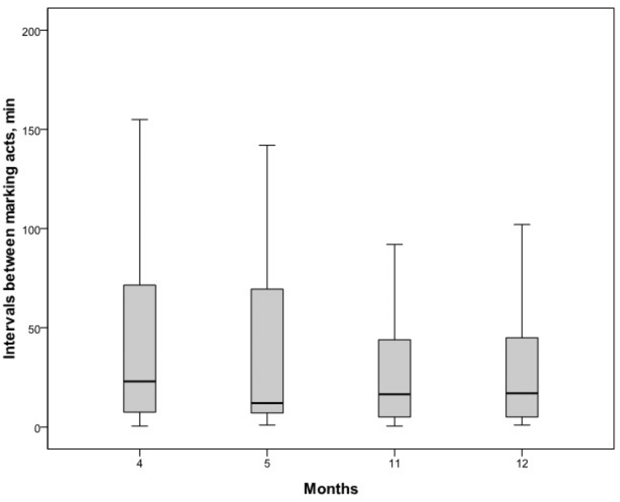

Fig. 1. Intervals between marking acts in male goitered gazelle in April-May (4-5) and November-December (11-12).

Table 1. Fluctuations in mean duration of preorbital gland marking (seconds) in adult males over various months.

Month	Mean duration	N	SD	Kruskal-Wallis test	
				Chi-square	P
April	7.4 ± 0.9	31	5.2	18.923 df = 4	0.001
May	5.0 ± 0.5	36	3.1		
July	4.8 ± 1.1	10	3.2		
November	6.0 ± 0.3	160	4.2		
December	7.3 ± 0.4	132	4.1		

Results

During the 1730 hours of our focal observations, we observed totally 528 cases of preorbital marking; the marking duration was measured in 369 cases from them (Table 1) and intervals between marking acts in 251 cases. We analyzed 501 cases of group size and 477 cases of other circumstances, in which preorbital marking was observed (Table 2); and we distinguished 489 cases of marked vegetation type (grass, bush or saxaul trees).

The frequency of preorbital markings significantly differed across months (One-way ANOVA, F = 176.474, d.f. = 7, P < 0.001), with maximal intensity observed in November and December (1.0-1.15 acts/hour, LSD Post-Hoc test, P < 0.001 for both), and considerably less in other months (0.03-0.29 acts/hour in March-July; LSD Post-Hoc test, P = 0.028). The mean interval between separate marking acts fluctuated between 43.7 ± 12.3 min, n = 16 and 59.6 ± 21.5 min, n = 20 in April and May, and 33.4 ± 4.0 min, n = 119 and 36.1 ± 4.8 min, n = 96 in November and December, though the median provided other proportions (23.0, 12.0, 16.5, 17.0, respectively) (Fig. 1) without statistical significance (Kruskal-Wallis test, Chi-square = 0.742, d.f. = 3, P > 0.05). The duration of each marking act was longer in April, November and December and shorter in May and July (Table 1); but a real statistical difference showed between April and May (Mann-Whitney U test, Z = –2.302, P = 0.021) and May and December (Mann-Whitney U test, Z = –3.416, P = 0.001). The intensity of the preorbital marking in males was different for males in different group sizes (Kruskal-Wallis test, Chi-square = 339.283, d.f. = 2, P < 0.001) and single males marked considerably more often than males in groups (Fig. 2; Mann-Whitney U test, Z = –3.820, P < 0.001). Furthermore, male marking activity negatively correlated with group size (Spearman's correlation = –0.760, P < 0.001).

We found that young males started secretion marking with the preorbital gland at the age of one year (in May), but only very rarely, with just 9 such cases (recorded in May-July) from all marking acts observed during our entire study, (1.7 %, n = 528; Chi-square goodness of fit test, Chi-square = 492.614, d.f. = 1, P < 0.001); just one female marked only once and females never showed any interest in male markings.

In addition, during the rut in November and December, goitered gazelle males marked with the preorbital gland secretions most often when patrolling their individual territories and when courting females, while during the "false" rut in April-May, they marked mostly while grazing (Table 2). Furthermore, at the beginning of the rut in November, males marked with their preorbital glands more often while patrolling

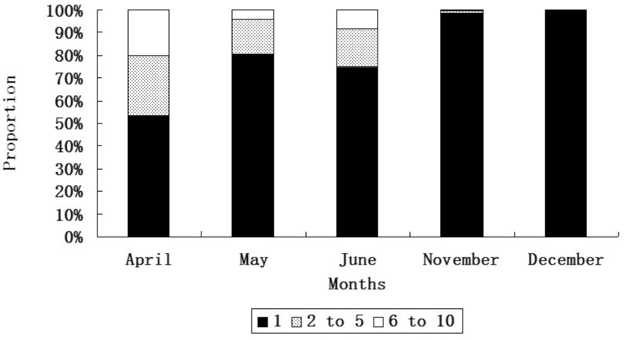

Fig. 2. Scent marking activity of single males (1 gazelle) and bucks in groups of intermediate (2-5 individuals) and large sizes (6-10 individuals) in different months. Totally, it was analyzed 501 cases. According to Blank et al. (2012) proportion of single males fluctuated around 40-50 % for the whole year, increasing up to 71 % only in November and decreasing up to 45 % in December.

Table 2. Different behavioral patterns of goitered gazelles, which triggered scent marking with preorbital glands during the rutting period (November-December) and "false" rut (April-May). Numerator is absolute frequency value and denominator is proportion of this frequency within a month (%).

Months	Feeding	Territory patrol	Territorial conflict	Chase males	Chase females	Walk, run
April	43/82.7	3/5.8	-	2/3.8	4/7.7	-
May	28/62.2	11/24.5	-	-	1/2.2	5/11.1
November	45/20.8	97/44.9	12/5.6	15/6.9	42/19.5	5/2.3
December	35/21.4	43/26.2	2/1.2	3/1.8	81/49.4	-
Log-linear model test	Z = 3.153, P = 0.002	Z = 3.422, P = 0.001	-	-	Z = 4.219, P = 0.000	-

their territories compared to when courting females, while at the end of the rut in December, they marked more often when courting females rather than when patrolling. Also throughout the rut, males very rarely made preorbital secretion markings during territorial conflicts (Table 2).

Male goitered gazelles usually marked shrubs that gazelles commonly ate, such as *Eurotia ceratoides*, *Salsola arbusculaeformes*, *Athraphaxis*, and *Calligonum*; among trees, they marked saxaul (*Haloxylon aphyllum*); and among grasses, *Phragmites*. They most often used the twigs of dry shrubs and semi-shrubs for secretion markings (91-98 % cases, N = 489), while marking the tops of tall grasses and branch tops of saxaul trees was observed considerably less often (1-6 % in different months; Log-linear model test, Z = 3.726, P < 0.001). This tendency was demonstrated especially clearly during the rutting period (96-98 % in November and December, N = 379) and slightly less often (albeit not significantly) in other months (91-94 %, N = 120); this ratio showed an insignificant change (Log-linear model test, Z = 0.081 – 0.299, P > 0.05).

For a goitered gazelle, the ritualized act of marking with its preorbital glands rarely began with sniffing the plant stem or twig (less than 4 %). Instead, the goitered gazelle male opened both preorbital glands and carefully lowered the preorbital region toward the plant stem, bringing the stem's tip or twig into the widely opened gland. With quivering movements of the gland's margin, he deposited some secretions which soon hardened in the open air. To position himself for scent marking, the male typically stretched his head upward to get his preorbital gland as high as possible, although he never raised his body to stand on just his hind legs for this purpose. During the marking procedure, the male's ears stayed slightly apart with the ear holes oriented forward.

The most often used marking technique was when a male turned his head slightly sideways toward the shrub branch to be marked (87.5-94.7 %, N = 410), while he rarely (5.3-12.5 %) turned his head in a position parallel to the ground (Log-linear model test, Z = 6.654, P < 0.001). Goitered gazelle males also at times opened their mouths widely when marking with their preorbital glands, apparently causing an even greater widening of the gland entrance hole. This pattern was observed rarely (1.1-3.7 %), and fluctuated insignificantly over most months (Log-linear model test, Z = 0.864 and –0.210, P > 0.05) with the exception of April, when the maximum of mouth openings for the year were observed (12.5 %, N = 64; Log-linear model test, Z = 2.464, P = 0.014). These cases when the males turned their heads parallel to the ground and opened their mouths while scent marking were found in April-May and November-December, and not noted at all in other months (June-October). Similarly they occasionally sniffed branches before or after marking (less than 4 %), and sometimes marked a particular branch several times in succession and/or changed from one side of the head to the other (3-16 %); these changes from one gland to the other fluctuated insignificantly over months (Log-linear model test, Z = 0.392 – 0.724, P > 0.05). In most cases, males marked only once (66-91 %; Log-linear model test, Z = 4.785, P < 0.001), less often twice (6-24 %; Log-linear model test, Z = 2.731, P = 0.006) and very rarely (2-11 %, N = 435) several times (up to 5) in a row, but these fluctuated insignificantly over months (Log-linear model test, P > 0.05). Proportions of these behaviours were the same across all months (Log-linear model test, Z = –0.673, P > 0.05).

In general (62-91 %, N = 528), marking with preorbital glands was performed as a single separate act, but occasionally, it was linked to other marking types, such as alternating markings preorbital glands with urination-defecation acts (4-28 % cases, Log-linear model test, Z = 5.413, P < 0.001) and/or acts of object-horning (4-10 % cases, Log-linear model test, Z = 2.877, P = 0.004). In addition, the proportion of combined markings fluctuated over seasons from a minimum of 8.7 % in the summer months (June-August) up to a maximum of 30.9 % and 37.5 % in November and December respectively, though without statistical significance (Log-linear model test, Z = –0.068 – 1.302, P > 0.05 in different months).

Discussion

Our data supported the first hypothesis that males' preorbital gland marking intensity would be significantly higher during the rutting season in November and December compared to other months. Additionally, the duration of each marking act was longer during the rut compared to the rest of the year. An explanation for the higher development of preorbital gland secretions (increase in size and density of sebaceous and apocrine cells of the gland) in territorial males during the rut – or even non-territorial males in rut – compared to other months may depend on a male's hormone (testosterone) production (Rajagopal & Archunan 2011) that may lead to an increase in the physiological excretion function of these glands (Marmazinskaya 1996). The preorbital glands swell during the rut, with the swelling so prominent that it could be seen from a distance along with the pitch-like substance that exuded from them (Habibi et al. 1993). We also clearly observed these rut related preorbital gland secretions that were intensively excreted from the opened foramen of the glands and flowed down towards the mouth; yet out of the rutting season, these stripes of wet secretions from the eyes to the mouth were not visible at all (Blank 1992). The preorbital glands in muskox excreted their secretion most intensively during the rut (Gray et al. 1988), and in small African antelopes, such as klipspringer (Dunbar & Dunbar 1974, Roberts & Dunbar 2000), grysbok (*Raphicerus melanotis* – Novellie et al. 1984), and dik-dik (*Madoqua* – Kranz 1991), a similar increase in the rate of scent marking also was observed for both sexes during periods when females were receptive to mating. Apparently, the adrenalin, which was available during agonistic situation during the rut, provoked the intensification of preorbital secretion (Gray et al. 1988).

In addition to observations during the autumn (real rut), our results demonstrated an increase in the males' preorbital marking activity during April (to the same degree as seen within the rutting season – Table 1), which was the goitered gazelles' second or "false" rutting period and a time when an increase in testicle activity was also observed (Tsapluk 1972). During this spring "false" rut males established individual territories, marked their borders, courted females and chased intruders. In short, they performed all behaviours, just as in the real autumn rut, only at this time of year young usually were not produced (Blank & Fedosenko 1983, Zhevnerov 1984, Marmazinskaya 1996).

The mean size of male groups in goitered gazelle are quite stable with the proportion of single males fluctuating around 50 % over the whole year, increasing up to 70 % only in November then decreasing again to 45 % in December (Blank et al. 2012). Our data supporting the second hypothesis demonstrated that single males use preorbital gland markings considerably more often than males in groups, especially during the rutting period; and correspondingly, males in larger groups marked less often than males in smaller groups. Goitered gazelle males established individual territories only during the rut, most often in autumn but also to a lesser extent in spring (Blank & Fedosenko 1983). During these periods, males stayed alone in their individual territories most of the time (Blank et al. 2012), and marked their areas with their preorbital glands more intensively than in any other periods; bachelor males without territories marked less often (Marmazinskaya 1996). Outside of the rut, many adult males gathered into groups, having lower hormone production (testosterone) and as a consequence lower agonistic and marking activity (Rajagopal & Archunan 2011). Even though they still scent-mark it was done very rarely (see also Blank et al. 2012). This clearly explains why single males marked more intensively than males in groups, though we observed kind of parity in April, which was difficult to explain. This difference in single versus group males was found to be true in territorial Thomson's gazelle (*Eudorcas thomsoni*) males as well: males that stayed alone in their individual territories, marked with their preorbital glands more often than non-territorial and migrating males, which often gathered in groups (Walther 1978a). In addition, after examining the bodies of dead bachelor males, Walther (1978a) observed secretions inside the preorbital glands, but not as abundant as in territorial males.

Our third prediction was also supported as young males started to mark with their preorbital glands in May at the age of one year, although marking was done very rarely. Marmazinskaya (1996) found that for a semi-captive population in Uzbekistan, young males started to mark at the age of 14-16 months (July-August), but only males older than 2-2.5 years were able to make actual, effective preorbital gland markings (Marmazinskaya 1996). Our data also supported the assertion made by Walther et al. (1983) that females do not scent-mark with their preorbital glands. We observed only one case during our study, when a female marked a shrub in this way; Marmazinskaya (1996) had only two documented cases from her observations in Uzbekistan of females marking with their preorbital glands in her semi-captive population.

Furthermore, we found that at the beginning of the rut in November, adult goitered gazelle males made their preorbital markings most often while patrolling their individual territories, indicating that this is mostly a maintenance function to renew previous markings. During almost the entire rutting period, goitered gazelle males spent a special time each day patrolling and demarcation their territories, which reached 23.9 % of their daytime budgets, while during the "false" rut in April they devoted only 5.5 % of their daily time budget (Blank 1990). In contrast, during the "false" rut in April-May they marked mostly while grazing, spending most of their time in pastures (57 %); during the rut in November-December territorial males spent less time eating (21.2 % of their daily budget), devoting more time for patrolling their territories (Blank 1990). In general, the lifespan of scent marks is limited so that marks need to be periodically refreshed (Alberts 1992). The potency for scent secretions of a klipspringer was found to be no longer than 7 days, and since each klipspringer territory can contain over 1500 preorbital scent marks (Roberts & Lowen 1997), these marks needed constant over-marking for continuous effectiveness (Roberts 1998). The scent markings of other antelopes had even shorter potency times, such as only 3.6-4.5 days for the gerenuk (*Litocranius walleri*) (Gosling 1981), 2.8 days for the Thomson's gazelle (Gosling 1985), and 1.6-4 days for the suni (*Neotragus moschatus*) (Somers et al. 1990). It has been suggested that a scent-mark's potency limitation is perhaps the main reason the gerenuk and Thomson's gazelle have considerably smaller territories (Roberts & Lowen 1997) with fewer marks – 121 for the gerenuk (Gosling 1981) and 110 for Thomson's gazelle (Walther 1978b).

During the whole of the rut, females just crossed through the males' territories, staying with a male for no more than 15-20 min. By the end of the rut in December, however, the males' marking preferences changed, and they marked with their preorbital gland secretions most often while courting females, which when in estrous spent more time (up to 3 days) with the rutting males (Blank 1998). Thus, our data supported our fourth prediction that territorial males would mark most often during while courting receptive females than during other activities. Marmazinskaya (1996) also found that adult males in captivity started to mark more intensively after the appearance of an estrous female in the enclosure; and Habibi et al. (1993) observed that in captivity when male sand gazelles (*Gazella subgutturosa marica*) courted a female, their preorbital glands became dilated and a streak of black secretions flowed over the skin under their eyes. And klipspringer males (Roberts & Dunbar 2000) and Kirk's dik-dik (*Madoqua kirkii* – Brotherton et al. 1997) marked more intensively when they followed a marking female in estrous.

Because territorial males demonstrated only a negligible amount of preorbital marking during territorial conflicts (mostly threat displays), our fifth prediction was found to be untrue. On the other hand, our study did find that markings with urine-feces and horning (fighting against plants) increased during conflicts between neighbours (Blank & Yang 2014). Unlike our goitered gazelles, Habibi et al. (1993) found that the preorbital glands were dilated while a male sand gazelle showed aggressive behaviour, and Walther et al. (1983) recorded that the Thomson's gazelle (Walther et al. 1983) and small African antelopes, such as the oribi (Brashares & Arcese 1999) and blue duiker (*Cephalophus maxwelli* – Ralls 1974), increased the intensity of their preorbital gland marking during territorial conflicts; the klipspringer intensified its marking rate when it found the marks of other males (Roberts 1998). Small African antelopes have a different social structure compared to goitered gazelles, and live continuously in pairs or small mixed-sex groups with up to several males and females inside their territories all year round (Jarman 1974, Rowe-Rowe et al. 1992). They also use mostly urination-defecation and secretion markings, and not horning of plants, which is a very typical behaviour for gazelles during conflicts (Walther et al. 1983).

Our data did support our sixth hypothesis, with males preferring to mark thin twigs of shrubs and semi-shrubs that were similar to their own height, while large, tall bushes (*Tamarix*) and saxaul trees, and small grasses with short, thin stems were used considerably less often; the klipspringer demonstrated similar behaviour, preferring thin twigs to thick ones (Roberts 1997). Signallers put their marks in places where they would be easily and quickly detected by territory intruders (Gosling 1981), and in our study area, goitered gazelle males marked the most edible shrubs, such as *Eurotia*, *Athrapahaxis*, *Salsola*.

Marmazinskaya (1996) also found that branches after browsing were marked considerably more often than those not eaten. Analogous behaviour was found for the gerenuk and oribi, both of which bit off the tips of vegetation at head height prior to scent marking (Gosling 1972, 1981).

Preorbital marks were often placed within a narrow vertical distribution, in spite of the fact that alternative marking sites were available (Gosling 1981, Roberts 1997). This was true for the goitered gazelles in our study, where shrubs and semi-shrubs close to the male's head height were marked, while lower grasses and higher saxaul trees were not. In areas with few apposite plants available for marking, marked plants were rarely found, if at all, even when the population density of goitered gazelles was high (Marmazinskaya 1996). The Thomson's gazelle (Walther et al. 1983), gerenuk (Gosling 1981), blackbuck (*Antilope cervicapra* – Dubost & Feer 1981) and klipspringer antelope (Roberts 1997) also preferred to scent-mark within a narrow vertical range at a height they could reach while standing on all four feet.

When marking with preorbital glands, goitered gazelle males rejected plants with fragile, unstable stems and shrubs with numerous small branches at the tops, but readily marked the tops of hard, stable branches (Marmazinskaya 1996). In addition, signallers advertised these scent mark locations so that their marks will be more likely detected (Roberts & Gosling 2001), therefore goitered gazelles likely rejected the common grasses and choose the more conspicuous branches (dry, broken or highest) instead (Marmazinskaya 1996). The gerenuk (Gosling 1981) and klipspringer (Roberts 1997) preferred to mark distinctive dead trees or dry branches, as well.

The marking procedure for Thomson's gazelles described by Walther et al. (1983) is similar to the marking procedure observed for goitered gazelles, but with a few notable exceptions. First, our goitered gazelles rarely sniffed objects before and after marking and never nose-touched, licked and nibbled at them. Second, goitered gazelle males turned their heads toward the shrub branch like the Thomson's gazelle, but rarely directed their cheeks to the ground. In contrast to Thomson's gazelles, which live in the short, grassy steppes of the African savannah (Estes 1967), goitered gazelles inhabit deserts with a predominance of shrubs. As the height of the shrubs is close to the height of a male gazelle's head, the goitered gazelle male did not need to turn his cheeks to the ground when marking (Blank 1992). Marmazinskaya (1996) also found that goitered gazelle males in Uzbekistan did not mark plants that were lower than 40 cm. Third, goitered gazelle males occasionally opened their mouths widely when marking, but this was not noted for other gazelle species (Walther et al. 1983).

Links between preorbital marking and marking through urination-defecation and object-horning, which we observed for goitered gazelles, were also found in several other antelope species, particularly in encounters between territorial neighbours (Walther 1984). Territorial pronghorn bucks (*Antilocapra americana*), for instance, were noted to alternatively mark an object with their subauricular glands and then butt it their "prongs"; and Topi (*Damaliscus korrigum*) and blesbucks (*D. pygargus*) have been observed to alternate object-horning with preorbital marking (Walther 1984).

To summarize, male goitered gazelles demonstrated marking behaviours that were very similar to marking behaviours of other gazelle species, but with exceptions related to seasonality and environmental diversity. But in spite of these variations, the goitered gazelles in our study area generally demonstrated the same patterns of preorbital marking behaviours as other gazelle species, together with many tropical antelopes. This, then, satisfied our seventh prediction.

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