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ORIGINAL PAPER

Scent communication by female Columbian ground squirrels, *Urocitellus columbianus*

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Abstract Scent-marking is a frequent behaviour of highly social ground squirrels and might play an important role in their social dynamics. Female Columbian ground squirrels exhibit considerable scent-marking during the reproductive period. We examined how gestating and lactating females responded to jugal gland scent-marks of same-sexed and opposite-sexed conspecifics with attention to genetic relatedness and the geographical location of the territory of individuals. We tested the dear-enemy, threat-level and kin-discrimination hypotheses to explain patterns of scent-marking. Females sniffed the scent of non-neighbouring males significantly longer than other types of scent categories and tended to over mark the scent of females more than the scent of males. Furthermore, females sniffed significantly longer at scents during gestation than during lactation. We concluded that scent-marking mainly functioned in the defence of female territories and for protection of pups against infanticidal females (threat-level hypothesis). Our results were also in accordance with the kin-discrimination hypothesis, because greater attention was paid to the marks of non-kin females. Kin females might not pose an infanticidal threat, perhaps explaining greater tolerance among related reproductive females. We concluded that scent-marking may be a relatively low-cost means of territorial defence, as well as a means of communication of aspects of individual identity.

Keywords Columbian ground squirrel · Scent-marking · Territoriality · Dear-enemy hypothesis · Threat-level hypothesis · Kin discrimination

Introduction

Many mammals communicate social information to conspecifics via the deposition of odoriferous secretions from specific glands, in urine and also in faeces (Brown 1979). These depositions can indicate the presence of an individual at particular locations (Roper et al. 1993; Jordan 2007), such as on the boundaries of a home range (Brashares and Arcese 1999) or in some cases directly on the body of conspecifics (Kruuk et al. 1984). A main advantage of this form of olfactory communication, called scent-marking, is that the signals emanating from scent-marks are perceived by putative receivers even in the absence of the scent bearers themselves (Eisenberg and Kleiman 1972). A variety of functions for scent-marking have been proposed, such as territorial marking (reviewed in Gosling 1982 and Ralls 1971), mate attraction (reviewed in Johnson 1973), self-advertisement (Wolff et al. 2002), status advertisement (reviewed in Roberts 2006), dominance reinforcement (e.g. Herrera and Macdonald 1994), and perhaps other functions (reviewed by Gosling 1990).

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Among the ground-dwelling squirrels *Urocitellus columbianus*, *Urocitellus undulatus*, *Urocitellus richardsonii*, *Ictidomys tridecemlineatus*, *Callospermophilus lateralis* and *Poliocitellus franklinii* (Helgen et al. 2009) scent-marking seems to occur more intensively in highly social species (e.g., colony living) than in asocial species (primarily solitary living) (Kivett et al. 1976). In the Columbian ground squirrel (*U. columbianus*), a highly social species (Hare and Murie 2006), females are philopatric (Murie and Harris 1984; Neuhaus 2006) and have home ranges that sometimes cluster into small kin groups (King 1989a; Viblanc et al. 2010). Steiner (1974) described four scent-marking-related behaviours: cheek-rubbing with oral glands, anal-dragging with anal glands, scratching with pedal glands (although the role of scratching in scent-marking is unclear, Halpin 1984), and the most elaborated marking behaviour, twist-marking with dorsal glands. Males scent-mark to the greatest extent during the mating period, that is, during the last week in April through the two first weeks in May (Kivett et al. 1976), when they are highly aggressive and territorial (Murie and Harris 1978; Manno and Dobson 2008). Females exhibit a peak in scent-marking during the gestation and lactation periods, when they are also most agonistic and highly territorial (Betts 1976; Festa-Bianchet and Boag 1982), and scent-mark less during the remainder of the active season. Thus scent-marking may serve a territorial function and as a consequence scent-marks may complement the agonistic interactions between females and other colony members during the reproductive period.

The purpose of our study was to test the behavioural responses of females to scent-marks of both same-sexed and opposite-sexed conspecifics. Harris and Murie (1982) tested the behavioural responses of males and females to the marks of unknown and known (neighbouring) males. They found that gestating and lactating females discriminate between the marks of unknown and neighbouring males. Thus, they suggested a “dear-enemy” phenomenon to explain the greater attention toward the marks of unknown males. In agonistic and territorial species such as the Columbian ground squirrels (Murie and Harris 1978, 1988; Festa-Bianchet and Boag 1982; Manno and Dobson 2008), scent-marking may reduce the cost of aggressive interactive defence against familiar/neighbouring conspecifics (Temeles 1994). Furthermore, unknown males may represent a threat to the survival of offspring via infanticide (Balfour 1983; Dobson 1990; Harris and Murie 1982; Waterman 1984). Nonetheless, lactating females are responsible for most infanticidal cases in Columbian ground squirrels (Stevens 1998), and reproductive females might be expected to pay closer attention to the marks of same-sexed rather than opposite-sexed individuals. Thus, scent-marking in this species may also fit with the “threat-level” hypothesis (Temeles 1994); that the response of residents may be stronger toward same-sexed conspecifics, especially when females are lactating.

The responses to the marks of same-sexed individuals may also be influenced by the familiarity and genetic relatedness of the receiver and the sender. In *U. columbianus*, females recognise littermate sisters and mother–offspring kinship via a familiarisation process that takes place in the natal nest burrow (Hare and Murie 1996). As females behave more amicably toward littermate sisters (King 1989b) and spacing behaviours in females are close-kin biassed (King 1989a; reviewed in McLean 1984), females may pay less attention to the marks of familiar kin. This hypothesis predicts that females discriminate kin scents and non-kin scents. If kin recognition were associated with a familiarisation process in Columbian ground squirrels (Hare and Murie 1996), however, the ability of females to discriminate the scents of familiar kin and neighbouring females might be masked. In other words, the sniffing duration between familiar female scents (neighbouring females and kin females) and unfamiliar female scents (non-neighbouring females) are expected to differ.

The descriptions of scent-marking by females (Kivett et al. 1976; Steiner 1974) and the great amount of information about the sociality of the Columbian ground squirrel (reviewed in Hare and Murie 2006) led us to evaluate three different, but not mutually exclusive, hypotheses to explain scent-marking. First, scent-marking may serve a territorial function through the dear-enemy hypothesis (Temeles 1994), from which we expected that the scent-marks of non-neighbouring individuals would draw the greatest attention from reproductive females. Second, the threat-level hypothesis (Temeles 1994), predicts that the marks of unrelated lactating females (neighbours or not) and non-neighbouring males should draw the greatest attention from reproductive females. Finally, the kin-discrimination hypothesis suggests that the marks of non-kin females should draw stronger responses than the marks of kin females. In order to better understand the role of scent-marks from the jugal glands during the reproductive period, and to evaluate these three hypotheses, we studied how females respond to jugal gland scent-marks of same-sexed and opposite-sexed conspecifics with attention to their genetic relatedness and their proximity to the territory of focal individuals.

Materials and methods

Animals and study area

All experiments were conducted from May to June in 2009 when females were gestating and lactating, at a colony of Columbian ground squirrels in Sheep River Provincial

Park, Alberta, Canada. This species emerges from winter hibernation during the last half of April (Dobson 1992). Each female mates on a single day during the last week in April through the two first weeks in May, and they give birth 24 days later during the later part of May or the first part of June (Dobson and Murie 1987). Litters emerge from natal burrows and young are weaned about 27 days later (Murie and Harris 1982). Our study colony had been monitored since 1992, and the matrilineal kinships (all mothers and sisters) were known from birth (roughly six generations). All scent donors and focal adult females came from our study colony. When they were first seen in the colony, all individuals were trapped and fitted with numbered metal fingerling eartags for long-term identification (National Band and Tag Co., Newport, KY, USA). At spring, emergence from hibernation and later at weaning, all individuals were dyed for visual identification with a unique black symbol on the dorsal pelage (Lady Clairol Hydrience, Black Pearl; Proctor and Gamble, Stamford, CT, USA).

Fourteen adult females were used as experimental subjects, and were exposed to scent from discrete types of individuals: neighbours (N), encompassing neighbouring females (Nf) and neighbouring males (Nm); and non-neighbours (Nn), encompassing non-neighbouring females (Nnf) and non-neighbouring males (Nnm). Nf and Nnf together formed the category of non-kin females (Nkf) were compared to kin females (Kf) to test for kin bias. Furthermore, we pooled Kf and Nf in the category of familiar females (Ff) to compare to Nnf. To compare female scents and male scents, we pooled Nm and Nnm in the category males (M) and Nf and Nnf in the category females (F) without the category Kf to avoid kin bias, except for the pairwise comparison of female scent cubes and control cubes. We considered females as neighbours when their nest burrows were less than 40 m apart. The distances between a subject's nest burrow and non-neighbouring females' nest burrows ($N=12$; mean=111.4±8.0 m) were significantly greater than the distances between a subject's nest burrow and neighbouring females' nest burrows ($N=13$; mean=25.3±2.9 m; two independent samples permutation test: $p<0.001$). We considered males as neighbours when their core areas, which were used more frequently than other areas (Samuel et al. 1985), included the location of the nest burrows of focal females.

Scent collection

Acrylic cubes (transparent cubes, 3.7 cm^3) were used to collect oral gland scents of individuals (methods after Harris and Murie 1982). Upon capturing a scent donor, we rubbed the squirrels' oral angles three times on each face of a cube. A clear greasy streak and a characteristic odour confirmed that cubes were marked. Scent cubes were kept in a container with ice packs until they were used in an experiment. The scent cubes were used on the day of the scent collection or the day after. If used the next day, the scent cubes were stored at −20°C overnight. After each trial, the cubes were washed in soap and water, rinsed in water and rinsed again in 90% ethanol and air dried.

Experimental procedure

Each test included five successive trials in which the five groups of scent donors (Nf; Nnf; Kf; Nm; Nnm) were presented to each subject. For each trial, two cubes were simultaneously placed at a distance of 30 cm from the entrance of the burrow in which the subject was last seen; and 30 cm separated the two cubes. One cube had a scent belonging to one of the five scent donor treatments. The second cube had no scent and was used as a control. The control simply measured any response to a novel object (the scent cube).

The trials were performed early in the morning (after 0800 hours) and lasted until late in the afternoon (1800 hours). For each test, the order of the presentation of the five scent donors was chosen randomly. For each trial, the two cubes (the control cube and the cube with a scent) were placed randomly on the left or right side of the burrow (left or right from the perspective of the observer). Each trial was separated from the next trial by at least 1 day. After the cubes (control and treatment) were set out, the observer sat about 20 m away on the ground or on a 2-m-high observation platform. Binoculars (7×50) and a digital voice recorder were used to collect all behavioural observations. A trial began as soon as the subject was observed in the area and each trial lasted 1 h. We recorded sniffing duration as the length of time when a focal individual's nose was 1 cm or less from the cube. We recorded the length of time the cubes were sniffed by speaking into a digital voice recorder and timing with a stopwatch afterwards (Harris and Murie 1982). Furthermore, we recorded the occurrence of all scent-marking-related behaviours on the cubes and on the ground (cheek-rubbing, twist-marking, anal-dragging) just after the subjects sniffed the cubes. If another squirrel marked one of the two cubes we ended the trial.

Statistical analyses

All the statistical analyses were carried out under StatXact software (Cytel Software Corporation, Cambridge, MA, U.S.A.). Results are presented as medians, quartiles (Figs. 1 and 2 from statistical package SPSS version 17.0), and percentages (%). We used nonparametric statistical analyses due to small sample sizes (<30). To compare the sniffing duration between female or male scent cubes and control cubes, we carried out Paired Sample Permutation Tests (exact procedure). We tested the association between the

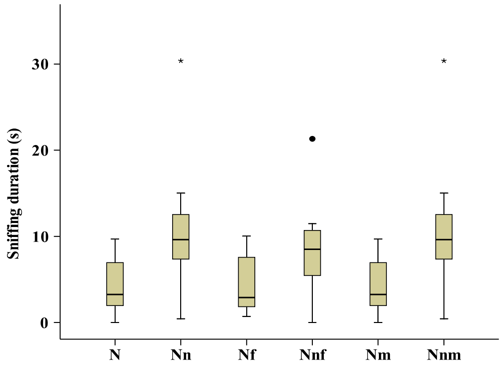

Fig. 1 Length of time that reproductive females sniffed acrylic cubes carrying the scent from the categories of scent donors neighbours (*N*), non-neighbours (*Nn*), neighbouring females (*Nf*), non-neighbouring females (*Nnf*), neighbouring males (*Nm*) and non-neighbouring males (*Nnm*). The median is indicated by the *horizontal bar inside the box*, the first and third quartile by the *box* itself, and the *horizontal bars outside the box* indicate the minimal values and the fourth quartile (except for the categories *Nn*, *Nnf* and *Nnm* with two individual outliers shown by a *black-filled circle* and a *black-filled star*)

trial dates and sniffing durations within the different groups of donors using Pearson's correlation tests. The sniffing durations among the different types of donors were compared pairwise via Wilcoxon signed-rank tests. Tests for dependent samples were performed, although it was unlikely that the scent of a given category (Nf; Nnf; Nm; Nnm; Kf) influenced the response of the subject in the next trial because a few days separated each trial. However, we performed these pairwise comparisons to avoid effects of inter-individual variability. Our sample size was not adequate for pairwise tests of the category Kf. Indeed some combinations of Kf and Nkf as well as Ff and Nnf were missing because of field conditions. That is, some subjects were tested with Kf scents but not Nkf and vice versa. We therefore performed two independent permutation tests (exact procedure). The occurrences of scent-marking were compared between different categories of scent donors using Fisher's exact tests. We pooled all the scent-marking-related behaviours occurring both on the cubes and the ground nearby the cubes in the same statistical analysis. The sample sizes of the different types of scent-marking (cheek-rubbing, twist-marking and anal-dragging) did not allow separation of statistical comparisons among the five groups of scent donors.

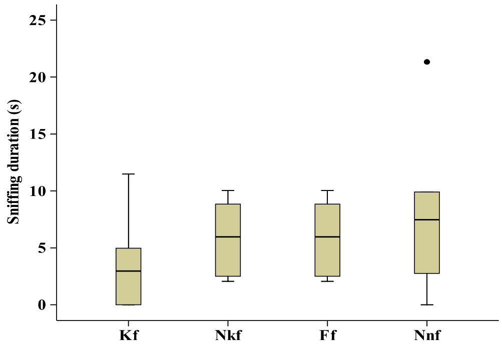

Fig. 2 Length of time that reproductive females sniffed acrylic cubes carrying the scent of kin females (*Kf*) and non-kin females (*Nkf*), familiar females (*Ff*) and non-neighbouring females (*Nnf*). The median is indicated by the *horizontal bar inside the box*, the first and third quartile by the *box* itself, and the *horizontal bars outside the box* indicate the minimal values and the fourth quartile (except for the category *Nnf* with one individual outlier shown by a black-filled circle)

Since the predictions from the dear-enemy and kin-discrimination hypotheses are directional (Murie and Harris 1982, Hare and Murie 1996), pairwise tests between N and Nn for both sexes and comparisons encompassing Kf were one-tailed. However pairwise tests between M, F and Pearson's correlation tests (threat-level hypothesis) were two-tailed. Significance was accepted at $\alpha \leq 0.05$ level (Sokal and Rohlf 1994).

Results

After eliminating eight trials in which neither of the two scent cubes were sniffed, 48 trials were analysed: ten trials with Nf scent, ten trials with Nnf scent, nine trials with Nm scent, 13 trials with Nnm scent and six trials with Kf scent. Scent-marking occurred most of the time on the ground nearby the cubes immediately after the subject sniffed the cubes (i.e. within a minute following investigation of the cubes). We observed only two scent-markings directly onto the cubes. One case was a twist-marking on a cube with a non-neighbouring male's scent immediately followed by a twist-marking on the ground near the scent cubes. The second case was a cheek-rubbing on a cube with a neighbouring female's scent, followed by scratching on the ground near the scent cubes.

Length of time the scent cubes were sniffed

Females spent significantly more time sniffing cubes that carried a male's scent, whether neighbouring males or non-neighbouring males (N=22; mean=8.18 s±1.59 s) than control cubes (mean=1.65±0.56 s; paired sample permutation test, p<0.001). In tests with female scent (both kin and non-kin females), however, subjects showed similar interest in the scent cubes (N=26; mean=6.01±0.96 s) and the control cubes (mean=7.71±4.77 s; paired sample permutation test, p=0.98). This was likely caused by three outlier females that spent most of their time investigating the control cube (data not shown). In these three cases, the scent donors were both neighbouring and non-neighbouring females.

Sniffing duration to the scents of males and females were not significantly different (Wilcoxon signed-rank test, N=18; T=−1.1; p=0.3). Females sniffed significantly longer at the scents of donors that were non-neighbours than neighbours (Wilcoxon signed-rank test, $N=17$; $Z=2.3$; $p=0.009$; Fig. 1). This phenomenon occurred for male scents (Wilcoxon signed-rank test, $N=9$; $Z=-1.6$; $p=0.06$) and for female scents (Wilcoxon signed-rank test, $N=8$; $Z=-1.7$; $p=0.05$). The scents of non-kin females triggered, though not significantly, higher sniffing durations than the scents of kin females (Kf ($N=6$) vs. Nkf ($N=20$); two independent samples permutation test, $p=0.09$; Fig. 2). The scents of non-neighbouring females were sniffed longer than those of familiar females (Ff ($N=16$) vs. Nnf ($N=10$); two independent samples permutation test, $p=0.045$).

At the beginning of the test period, all females were gestating, while at the end of this period, most of the females were lactating. Females sniffed longer at any marks during the beginning of the test period (Pearson's correlation test, $N=48$; $r=-0.321$; $p=0.03$; Fig. 3). A similar effect of the testing dates was revealed for the marks of non-neighbouring males (Pearson's correlation test: $N=13$; $r=-0.618$; $p=0.03$). There were also negative correlations between the testing dates and the length of time the cubes were sniffed for the marks of the neighbouring males and females and the marks of non-neighbouring females, but these effects were not significant (Pearson's correlation test: Nf, $N=10$; $r=-0.282$; $p=0.42$; Nnf, $N=10$; $r=-.397$; $p=0.26$; Nm, $N=9$; $r=-0.228$; $p=0.58$). Females sniffed, though not significantly, longer at the marks of kin females at the end of the test period (Pearson's correlation test: $N=6$; $r=0.701$; $p=0.14$).

Occurrences of scent-marking after the first contact with the scent cubes

For each category of scent donors, we recorded the occurrences and the types of scent-marking after the first contact with the scent cubes (Table 1). Females marked, though not significantly, three times more often after they sniffed female scents than male scents (Fisher's exact test, $p=0.08$). This was not observed for neighbouring scents versus non-neighbouring scents (Fisher's exact test, $p=0.80$). The scents of non-neighbouring males were not marked significantly more often than the scents of neighbouring males (Fisher's exact test, $p=0.66$). Females marked the scents of neighbouring and non-neighbouring females at a similar frequency (Fisher's exact test, $p=0.675$). No scent-marking occurred after the females sniffed the scent cubes from the kin females (Fisher's exact test, $p=0.08$).

Discussion

Our results are in agreement with the results of Harris and Murie (1982). They suggested a role of scent-marks in relation to the dear-enemy phenomenon (Temeles 1994) because females sniffed cubes with the scents of stranger males significantly longer than those with scents of neighbouring males. We found that females sniffed the scents of non-neighbours longer than the scents of neighbours for both sexes. Our findings suggest that the neighbouring marks are more familiar to the territorial females than the non-neighbouring marks and consequently fit well with the dear-enemy phenomenon (Temeles 1994; Rosell and Bjorkoyli 2002). Rosell and Bjorkoyli (2002) concluded that European beaver (*Castor fiber*) display the dear-enemy phenomenon because they showed strongly aggressive behaviours (overmarking and pawing) toward artificial and experimental scent mounds from unknown adult conspecifics. In our study, the display of scent-marking was similar after the females sniffed the marks of both neighbouring and non-neighbouring males and females, so this result did not give further support for a dear-enemy interpretation. Females may have paid more

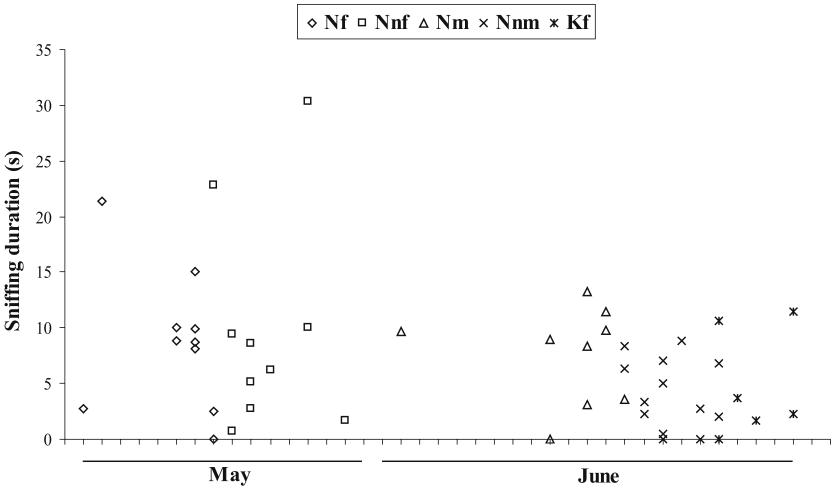

Fig. 3 Effect of the testing date on the length of time each scent cube was sniffed within each category of scent donors from May 21 to June 23: neighbouring females (*Nf*), non-neighbouring females (*Nnf*), neighbouring males (*Nm*), non-neighbouring males (*Nnm*) and kin females (*Kf*)

Table 1 Proportions of occurrences of scent-marking (marked vs. not marked) among the different groups of scent donors and the types of marking (i.e. twist-marking, cheek-rubbing, anal-dragging) within each category

Categories of scent donors (sample size)	F (n=26; %)	M, (n=22; %)	N, (n=19; %)	Nn, (n=23; %)	Nm, (n=9; %)	Nnm, (n=13; %)	Nf, (n=10; %)	Nnf, (n=10; %)	Kf, (n=6; %)	Nkf, (n=20; %)
Marked	30.8	9.1	26.3	21.7	11.1	7.7	40.0	40.0	0.0	40.0
Not marked	69.2	90.9	73.7	73.7	88.9	92.3	60.0	60.0	100.0	60.0
Twist-marking	37.5	100.0	80.0	20.0	100.0	100.0	75.0	0.0	0.0	37.5
Cheek-rubbing	50.0	0.0	20.0	60.0	0.0	0.0	25.0	75.0	0.0	50.0
Anal-dragging	12.5	0.0	0.0	20.0	0.0	0.0	0.0	25.0	0.0	12.5

See text for significance of comparisons

F females, *M* males, *N* neighbouring, *Nn* non-neighbouring, *Nm* neighbouring males, *Nnm* non-neighbouring males, *Nf* neighbouring females, *Nnf* non-neighbouring females, *Kf* kin females and *Nnf* non-kin females

attention to scents of non-neighbouring males (Harris and Murie 1982; the present study) because such males may represent a more deterable threat for the survival of the offspring via infanticide (Balfour 1983; Dobson 1990; Waterman 1984). Nevertheless, females paid greater attention to the scent of non-neighbouring males when they were gestating than when they were lactating. If males represented a threat, reproductive females would be expected to pay more attention to the marks of non-neighbouring males during the lactating period. Also, this finding does not fit with the threat-level hypothesis. On the other hand, the danger of unfamiliar males could be greatest near the time of parturition or lactating females may have less time to exhibit aggressive behaviours, because of the energetic demands of lactation. Additionally, the greater attention to the marks of non-neighbour males might be due to the need for more time to identify them.

Females more frequently marked over the marks of other females compared to the marks of males, whether they were neighbours or not. Females thus showed greater attention to the marks of other adult females than to the marks of adult males within the colony. Infanticide occurs in this species (Balfour 1983; Dobson 1990; Harris and Murie 1982; Waterman 1984), and most often lactating females are the perpetrators (Stevens 1998). A counter-strategy against infanticide is to become territorial in order to keep infanticidal individuals away from the juveniles (reviewed by Agrell et al. 1998). Aggressiveness and territoriality are two main behavioural characteristics of gestating and lactating females (Betts 1976; Festa-Bianchet and Boag 1982; Murie and Harris 1988). We found that gestating and lactating females paid attention to the scent-marks of other females. Thus, scent-marking appeared to play a role in the defence of female territories through the threat-level hypothesis, that is, against infanticidal females. As in other species, that rate of scent-marking declined during lactation (e.g. Wolff et al. 2002), a phenomenon that again may have reflected increasing energetic costs of reproduction. Thus, scent-marking may contribute to the defence of the territory by reproductive females, resulting in the protection of the litter. Such marks probably do not form a boundary, since intruders usually enter the territories of strangers (Halpin 1984; personal observation). However, scent-marks may render invaders more nervous, as females vigorously chase individuals out of their territories, except close kin (littermate sisters and mothers) that occupy nearby territories (King and Murie 1985).

Philopatric females might disperse short distances to share abutting territories with kin females and cooperate to cope with same-sexed competitors (Hamilton 1964; Harris and Murie 1984; Viblanc et al. 2010). In Columbian ground squirrels, females are more tolerant of the presence of kin than the presence of non-kin females within their territories (King 1989a; J.O. Murie, personal communication). Since kin are less of a threat for reproductive females, there is no need to overmark the scent of kin. However, this requires that females discriminate marks that belong to their kin. Regarding sniffing duration, our results suggested that neighbouring female scents as well as kin female scents were familiar to the subjects, although the marks of non-kin females stimulated, though not significantly, stronger responses than marks of kin females. However, females did not mark over any marks belong to their kin. Thus our results are in agreement with the prediction that females pay less attention to the marks of their kin, and as a consequence they likely discriminate kin females via scent-marks (Hare and Murie 1996).

Scent-marking is thought to advertise idiosyncratic characteristics of the signaller toward competitors (Roberts 2006), such as social status (e.g., Herrera and Macdonald 1994) and resource holdings (e.g., Luque-Larena et al. 2001). Thus, what kind of information do the marks provide and how do they help females to defend their territories? Twist-marking was most often observed after females sniffed the marks of neighbouring than non-neighbouring females. Cheek-rubbing, on the contrary, was more directed toward the marks of non-neighbouring females. The jugal and dorsal glands may both convey the identity of the scent bearers. Mateo (2006) found that Belding ground squirrels can use both oral and jugal gland odours to discriminate among conspecifics. Nevertheless, marking with the dorsal glands (i.e., twist-marking) involves a more complex behavioural pattern than marking with the jugal glands (i.e., cheek-rubbing; Steiner 1974). The differential responses toward the marks of neighbouring and non-neighbouring females may reflect the motivational states of the females (Halpin 1984). Similar interpretations have been reported for cotton-top tamarins, *Saguinus oedipus*. Females responded differentially to conspecifics and non-conspecifics intruders via supraoptic but not anogenital scent-marking (French and Snowdon 1981), and the latter was associated with sexual communication (French and Cleveland, 1984). In Columbian ground squirrels, females may mark to communicate their presence within the territory and the visual display of twist-marking may reflect their aggressive intentions. Thus, the display of marking may act as a complex signal involving different sensory modalities (Hebets & Papaj 2005) and increasing the probability that competitors perceive it (Johnstone 1996).

A scent matching mechanism has been proposed to explain the role of scent-marks in the defence of territory in house mice, *Mus domesticus*, and snow voles, *Chionomys nivalis* (Gosling and McKay 1990; Luque-Larena et al. 2001). Intruders spent less time in an area with the marks of the owners after they had experienced an agonistic interaction with the owner than if they had an agonistic interaction with another individual. In *U. columbianus*, intruders often stay in a stranger's territory until the owner chased them out (personal observations). We do not know if intruders modulate their spacing behaviours after an interaction with the owner of a given territory. Nevertheless, it is probable that marks communicate both the identity (Harris and Murie 1982, unpublished data) of the scent bearers and the cost of entering their territories (reviewed in Gosling 1990) toward same-sexed competitors, especially if intruders spend less time within these territories after they have been chased out by residents. Both female and male Columbian ground squirrels may spend considerable time and energy in chasing intruders from their territories. Thus, this cost may be reduced if their scent-marks influence the decision of the intruders to flee when confronted or to remain for shorter periods (Gosling 1990).

Living in colonies provides advantages to Columbian ground squirrel via a group-size effect of vigilance against predators (Fairbanks and Dobson 2007; 2010). This advantage of group-living may offset the disadvantage of attraction of predators. In the same way, coping with many neighbours is a likely social cost of group-living (e.g. Müller and Manser 2007). Our results suggest that females may invest in scent-marking to defend their territory against same-sexed competitors and especially unrelated neighbours. Scent-marking may be a less costly form of defence than direct aggression and constant patrolling of territory and its boundaries. Observation of whether females mark to a lower extent when they do not have to cope with as many neighbours, and whether greater fitness ensues for females that use scent-marking extensively, could test the evolutionary importance of scent-marking as a defensive tactic. Experimental studies in situ testing of whether scent-marks influence social interactions (e.g. scent-matching hypothesis, see the paragraph above) in living-colony species, like Columbian ground squirrels, will provide greater insights into the interaction of scent-marking and sociality..

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