



Scent matching modulates space use and agonistic behaviour between male snow voles, *Chionomys nivalis*

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The 'scent-matching' hypothesis predicts that competitors could identify resource holders by investigating scent marks from a given area and matching these with the owner's odour when they meet. Previous studies on small rodents have supported the use of scent matching among males with mutually exclusive ranges. We designed an experiment to evaluate the potential role of scent matching in the snow vole, a species in which males have largely overlapping ranges but individually use specific locations within shared areas. Initial exploration of enclosures containing a choice between a scent-marked and an unmarked area established that males were more attracted to recently occupied areas. During a subsequent social encounter with either the donor of the scent marks present in the enclosure (matching opponent) or another male (nonmatching opponent), males were less aggressive towards matching than nonmatching opponents. Furthermore, during exploration of enclosures after encounters, males spent significantly less time at the scent-marked side after meeting a matching male but not after meeting another male. These results suggest that male snow voles may use scent matching to identify potential opponents and to respond differentially to occupied areas. By modifying their behaviour after assessing the identity of their opponents, males may be able to minimize current and prospective costly encounters with resource holders. Our findings show that the mechanism of scent matching is also compatible with spatial systems in which competing conspecifics possess overlapping ranges.

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Within social systems, access to limited resources such as territories or mates often generates a conflict between same-sex conspecifics, increasing the likelihood of agonistic interactions (Krebs & Davies 1993; Pusey & Packer 1997). Escalation of aggressive behaviours may result in serious injury, which can drastically reduce fitness (Huntingford & Turner 1987). In this context, evolutionary theory suggests that animals should adopt strategies to avoid or minimize the level of aggressive interactions, thereby reducing the associated costs (Maynard Smith & Parker 1976; Maynard Smith 1982). By assessing their potential opponents, individuals may be able to predict the probable outcome of social encounters and eventually decide whether to initiate aggression (Caldewell 1985; Rubenstein & Hack 1992). For example, holders of a particular territory are generally more likely than intruders to escalate aggression to defend it (e.g. Krebs

1982; Grafen 1987; Leuck 1995). Thus, to reduce costly agonistic encounters with resource holders, individuals should be able to identify them in advance (Dugatkin & Reeve 1998), which may be accomplished by using signals (Bradbury & Vehrencamp 1998).

Scent marking to signal occupancy of territories is common among many terrestrial vertebrates, including salamanders (e.g. Jaeger et al. 1986; Simons et al. 1994), reptiles (e.g. Carpenter & Duvall 1995; López et al. 1998) and mammals (Gorman 1984; Brown & Macdonald 1985). Because chemical signals persist in the environment after being emitted (Alberts 1992), conspecifics can use scent marks to obtain information about the scent donor even in its absence (e.g. Johnston 1990; Ferkin et al. 1997). In addition, individuals may be able to identify territory owners by directly comparing the scent of substrate marks with those of any conspecifics they encounter nearby, discriminating whether they match or not, a mechanism known as scent matching (Gosling 1982, 1990). A few studies support the existence of scent matching in small rodents, although the particular responses of individuals towards resource holders may vary between species (Gosling & McKay 1990; Hurst et al. 1996). For

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example, male house mice, *Mus domesticus*, may reduce their willingness to fight with a territory owner, but not with other males, only after they have matched its odour with that of the scent marks present in the vicinity (Gosling & McKay 1990). Among males of the aboriginal mouse, *M. spretus*, where access to high-quality locations is largely determined by relative dominance settled by direct fighting, encounters with matching territory owners result in considerable agonistic behaviour (Hurst et al. 1996)

Nevertheless, although the use of scent matching has been empirically documented in species in which males have mutually exclusive territories (Gosling & McKay 1990; Hurst et al. 1996, 1997), we do not know whether this mechanism also operates when males have overlapping home ranges. In many small rodents, males occupy home ranges that overlap extensively with each other (see reviews at Gipps 1985; Ostfeld 1990). However, within these areas of overlap use of space by competing individuals may generally differ, each male individually exploiting different locations to a greater extent than other males (Mares & Lacher 1987). In these cases, it might pay to recognize holders of particular locations to minimize costly agonistic encounters. In fact, given the spatial overlap between individuals, the chance of invading occupied locations may be even higher than in a strict territorial system (e.g. Aragón et al. 2000). Therefore, it is reasonable to suggest that scent matching could similarly contribute to modulate intrasexual aggression among males with nonexclusive home ranges.

The snow vole is a little-known rock-dwelling microtine mainly found in high mountain areas (up to 4700 m), where it typically inhabits natural rocky formations (e.g. broken outcrops, scree, limestone bedrocks) on open slopes (Kropp 1982). Fresh accumulations of faeces and urine can often be detected underneath these rocky structures, indicating current use by snow voles (personal observations). Live trapping and radio-telemetry data on this species have revealed that although adult males possess broadly overlapping home ranges during the breeding season, every individual exclusively uses particular areas within the shared area (our unpublished data). In addition, we have observed that, like other microtines (e.g. Ostfeld 1985; Wolff 1985; Ferkin & Seamon 1987), breeding snow vole males are highly aggressive to one another (unpublished data). Males that are often engaged in aggressive interactions may incur energetic or survival costs (Huntingford & Turner 1987; Marler & Moore 1989), so it seems plausible that any mechanism of reducing the frequency of potentially risky encounters, for example with resource holders (Maynard Smith 1982), would be advantageous. For snow vole males, given the spatial overlap between competing animals and the aggressive nature of their interactions, recognition of holders of specific locations by scent matching might be particularly useful to individuals minimizing costly interactions.

We examined the response of snow vole males to areas occupied by other males and the potential role of scent matching in male–male competition. We suggest that males use scent matching to recognize resident

individuals from particular areas, which will affect both their aggressive response and subsequent use of these locations. More specifically, we predicted that: (1) after exploring a recently occupied (i.e. scent-marked) area, males should be less aggressive towards the donors of scent marks than other individuals, and (2) males should spend less time in scented areas after interacting with the donor of scent marks than after interacting with another male.

METHODS

Experimental Animals

We captured male snow voles during summer (June/August) 1999 in the Puerto de Navacerrada (40°46'N, 4°00'W; Guadarrama Mountains, central Spain), at an elevation of 2000 m. Voles were live-trapped with clean Sherman traps baited with fresh apples and carrots, which were also a good source of water, and provided with hydrophobous cotton as bedding material. Traps were set early in the morning and then checked every 4 h during 24-h periods. Although we generally removed animals from traps within minutes of capture, a soft Plexiglas cover fitted to the upper side of each trap was provided to protect them from the weather between checking periods. Trapping sites were localized on mountain slopes, which are characterized by a mosaic of extensive patches of large granite rocks and scree interspersed by juniper shrubs, *Juniperus communis* (Martín & Salvador 1992). Because previous contact between individuals may influence the outcome of social interactions (e.g. Ferkin 1988), we trapped snow voles at four different sites within the same population (≥ 900 m apart) to ensure that males were unfamiliar to each other. For instance, radiotracking data during the breeding season show that home ranges of adult males do not on average exceed 400 m in diameter (our unpublished data). Thus, the minimum separation between capture sites seems to be adequate to ensure unfamiliarity between individuals. We recorded trap coordinates, body weight, type of pelage (juvenile or adult) and reproductive condition for each vole captured. We used only sexually active adult males (i.e. showing scrotal testes). None of the trapped animals died in traps or afterwards, including other species that occasionally entered the traps (i.e. *Apodemus sylvaticus*, *Eliomys quercinus*, *Sorex minutus*, *S. granarius*), which, together with all snow voles that were not adult males (i.e. young of both sexes and adult females) were released immediately to the wild.

The males were transferred to a quiet animal room in El Ventorrillo Field Station (Navacerrada, Madrid Province, 4 km from capture sites) and individually housed in rodent cages (50 × 25 cm and 15 cm high; Panlab S.L., Barcelona, Spain) containing sawdust bedding substrate and hydrophobous cotton for nesting. Rodent chow (Panlab S.L.), lettuce, carrots, sunflower seeds, water and wooden sticks as chewing material were supplied daily. Ventilation and sunlight were provided by an open double window, which maintained the animal room under the natural photoperiod and ambient temperature.

At the end of the study, all animals were released to their respective capture sites. All voles maintained or increased their body weight and were healthy when released. Differences between capture and release body weights of individuals never exceeded $\pm 3\%$. All animals were captured with permission from the Consejería de Medio Ambiente y Desarrollo Regional (Comunidad de Madrid).

Experimental Design

We carried out experiments between July and August 1999, corresponding with the reproductive period in the original natural population (unpublished data). Males were harmlessly marked by a dorsal fur clipping code for individual recognition and not tested before 48 h after capture. On the evening before the trials, the experimental enclosure (100 \times 50 cm and 50 cm high) was provided with a clean filter paper substrate and divided in half (50 \times 50 \times 50 cm) by a double Perspex partition. We then randomly introduced a male snow vole (i.e. scent donor) with its own nest into one half and left it overnight (18–20 h). The half sheltering males was provided with a bowl of food (lettuce, carrots and sunflower seeds) and a water bottle. Five minutes before the experiment, we gently returned the donor individual to its own cage and verified the presence of scent marks in the enclosure with ultraviolet light (Kohli & Ferkin 1999). Halves of enclosures sheltering donor males were impregnated with their odour after only a few hours and scent marks were always relatively abundant including faeces, urine and other glandular scents. Food and water sources were also removed before the start of trials.

The experimental procedure consisted of three consecutive tests. First, a randomly chosen experimental male was allowed 10 min to explore the experimental enclosure containing a choice between a recently scent-marked area with a soiled nest (i.e. occupied zone) and a clean area with an identical but clean nest (i.e. unoccupied zone). Immediately after exploration, we staged a social encounter lasting 5 min between the experimental male and either the donor of the scent marks present in the enclosure (matching treatment) or another male (nonmatching treatment). Finally, the experimental male was allowed another 10 min to explore the experimental enclosure containing both the scent-marked and clean areas with their respective nests. In all cases the donors of scent marks and opponents were previously unfamiliar to the experimental animal.

We conducted staged encounters in a neutral (clean) arena (50 \times 40 cm and 40 cm high) adjacent to the experimental enclosure to eliminate the effect that surrounding odours might have on the behaviour of animals (Mykytowycz et al. 1976; Hurst et al. 1996). Before encounters, the arena was divided in half (25 \times 40 \times 40 cm) by an opaque Perspex partition and the experimental male and its opponent were randomly transferred each to one half of the arena and allowed 5 min to acclimate before we removed the partition. Although we were not physically present during filming, the encounters were always monitored continuously from a contiguous room so that we could stop any

interaction showing high levels of aggression. However, this was not necessary and none of the individuals suffered physical injuries or showed physical stress during or after the trials. Once back in their cages, all animals ate and behaved normally after the experiments. Between each experimental sequence, we washed enclosures, arenas, nests and Perspex partitions with a nonodorous detergent and ethanol (70%) and thoroughly rinsed them.

We used 16 adult males of similar body weight ($\bar{X} \pm SE = 52.0 \pm 0.9$ g) as both experimental subjects and donors of scent. Each male underwent two experimental sequences: one in which the opponent of the staged encounter was the male whose scent matched the marks in the experimental enclosure (matching treatment) and another in which the opponent was a male with no relation to the marks (nonmatching treatment); males faced the matching and nonmatching experimental sequence on different days, with 3 days between treatments, and in a random order. To eliminate any effect of the opponent's body size between treatments, for each male we used matching and nonmatching opponents of similar body weight (matching treatment: $\bar{X} \pm SE = 50.3 \pm 0.8$ g; nonmatching treatment: 50.8 ± 0.6 g; Wilcoxon signed-ranks test: $Z = 0.56$, $N = 16$, NS). All the experiments were carried out between 2100 and 2300 hours and filmed under dim red light with a hidden video camera (Panasonic G100 NV-6100) 60 cm in front of the enclosure.

During exploration of enclosures we noted the frequency and duration of visits made by experimental males to each area, time invested in investigative and locomotive behaviours and frequency of visits and time spent inside nests. We also noted whether males made a final choice of area, if they remained for at least the last 60 s of the trial in one of the two areas (clean or scent-marked). During staged encounters we recorded the behaviour of the experimental male, including frequency and duration of investigative behaviours (nasal-nasal and naso-anal contacts, as well as sniffing any other part of the opponent's body) and agonistic behaviours, which we classified as aggressive (directed attack, counterattack, chase, boxing and fight) or avoidance behaviours (contact-avoidance postures, pushing away (shove off) opponent and fleeing). Male pairs did not show any amicable behaviours in any of the social encounters. It might be argued that males housed in isolation would be less tolerant towards conspecifics (e.g. Goldsmith et al. 1976); however, there is evidence that encounters between recently captured snow vole males are characterized by high levels of social intolerance (unpublished data). Nevertheless, they generally show very ritualized displays during staged interactions and biting or other aggressive behaviours are infrequent.

We have previously observed that the snow vole is a highly vocalizing species when threatened and that the intensity of vocalizations of pairs during interactions could be used as an additional measure of the agonistic nature of encounters (unpublished data). We therefore also recorded the total duration of vocalizations of male dyads during interactions.

Table 1. Male response to scent-marked areas during exploration of enclosures before and after meeting the owner of marks (matching treatment) or another individual (nonmatching treatment)

	Matching			Nonmatching		
	Before	After	<i>P</i>	Before	After	<i>P</i>
Total time (s)	480±29	233±58	**	425±32	352±63	NS
Relative time (%)						
Moving	17.8±3.3	36.1±7.8	*	20.1±4.1	18.7±5.6	NS
Investigating	10.5±2.8	13.5±3.9	NS	10.9±1.8	10.7±4.0	NS
Inside nest	70.9±6.6	41.9±10.4	*	67.4±5.3	52.3±10.5	NS
Number of visits to nest	6±1	3±1	*	7±1	3±0	**

Wilcoxon signed-ranks test for matching and nonmatching treatments; * $P < 0.05$; ** $P < 0.005$.

Data Analyses

We used two-tailed Wilcoxon signed-ranks tests to assess variation in the response of snow vole males to scent-marked areas before and after meeting the competitor male, and to compare the behaviour of males towards their opponents in staged encounters in the two treatments (Siegel & Castellan 1988). In addition, we conducted Spearman rank correlations to analyse the relationship between agonistic vocalizations of male dyads and frequency of agonistic interactions during staged encounters (Sokal & Rohlf 1995). Chi-square tests were used to evaluate differences between type of area (clean or scent-marked) in which males finished exploring before and after the social encounter (Siegel & Castellan 1988).

RESULTS

During initial exploration of enclosures, males spent most of their time in the scent-marked area (matching treatment: 80.0%; nonmatching treatment: 70.8%). Throughout this time, they used the occupied nest in both matching and nonmatching treatments (70.9 and 67.4% of time in scented areas was inside nest, respectively). However, during the exploration that followed the social encounter, use of scent-marked areas clearly varied with the treatment (Table 1). In comparison with their initial response, males spent less time in scent-marked areas after meeting the matching male (Wilcoxon signed-ranks test: $Z = 3.10$, $N = 16$, $P < 0.005$), whereas use of scent-marked areas by males after meeting a nonmatching male did not differ significantly from initial exploration ($Z = 0.85$, $N = 16$, NS; Table 1).

During exploration, males did not significantly vary the relative amount of time spent investigating scented areas after meeting an opponent male, either in the matching ($Z = 0.62$, $N = 16$, NS) or nonmatching treatment ($Z = 0.90$, $N = 16$, NS; Table 1). Nevertheless, males significantly increased locomotor activity in the scent-marked area after encountering the matching male ($Z = 1.96$, $N = 16$, $P < 0.05$), but not with a nonmatching male ($Z = 0.41$, $N = 16$, NS; Table 1). Males also spent relatively less time inside occupied nests after meeting the matching male ($Z = 2.32$, $N = 16$, $P < 0.05$), but not after meeting a

nonmatching male ($Z = 1.24$, $N = 16$, NS; Table 1). However, the number of visits to the occupied nest after encountering competitors decreased in both matching ($Z = 1.99$, $N = 16$, $P < 0.05$) and nonmatching treatments ($Z = 3.29$, $N = 16$, $P < 0.005$; Table 1).

Males remained in one half of the enclosure for the last 60 s in all exploratory trials. During initial exploration, the majority of males concluded trials in the scent-marked area in the two experimental treatments (matching: 13 out of 16; nonmatching: 14 out of 16). However, in the exploration subsequent to the staged encounter, fewer males ended in the scent-marked area in the matching treatment (6 out of 16; chi-square test: $\chi^2_1 = 13.06$, $P < 0.001$) but not in the nonmatching treatment (11 out of 16; $\chi^2_1 = 2.61$, NS).

During social encounters there were significant differences between treatments. There were more social behaviours with the matching male ($\bar{X} \pm SE = 25 \pm 2$) than with the nonmatching male (18 ± 2 ; Wilcoxon signed-ranks test: $Z = 1.99$, $N = 16$, $P < 0.05$). In both situations, experimental males showed a similar percentage of agonistic behaviours (matching: $\bar{X} \pm SE = 54.1 \pm 7.3\%$; nonmatching: $46.6 \pm 7.1\%$; $Z = 0.95$, $N = 16$, NS). However, of all agonistic behaviours displayed during encounters, fewer were directed at matching males ($\bar{X} \pm SE = 41.3 \pm 10.0\%$) than nonmatching males ($65.2 \pm 7.4\%$; $Z = 2.04$, $N = 16$, $P < 0.05$; Fig. 1). Avoidance behaviours were more frequent in matching encounters ($\bar{X} \pm SE = 58.7 \pm 10.0\%$) than in nonmatching encounters ($34.8 \pm 7.4\%$; $Z = 2.04$, $N = 16$, $P < 0.05$; Fig. 1).

Time spent in agonistic vocalizations by male dyads did not differ significantly between matching ($\bar{X} \pm SE = 78 \pm 15$ s) and nonmatching encounters (77 ± 16 s; $Z = 0.10$, $N = 16$, NS). However, time spent vocalizing in nonmatching encounters increased with the frequency of agonistic interactions (Spearman: $r_s = 0.79$, $N = 16$, $P < 0.001$), whereas we did not find a significant relationship in matching encounters ($r_s = 0.45$, $N = 16$, NS).

DISCUSSION

Our results show that, during initial exploration of enclosures, snow vole males spent more of their time in the side scent-marked by another male than in the clean side. Similarly, males used soiled nests heavily while in the

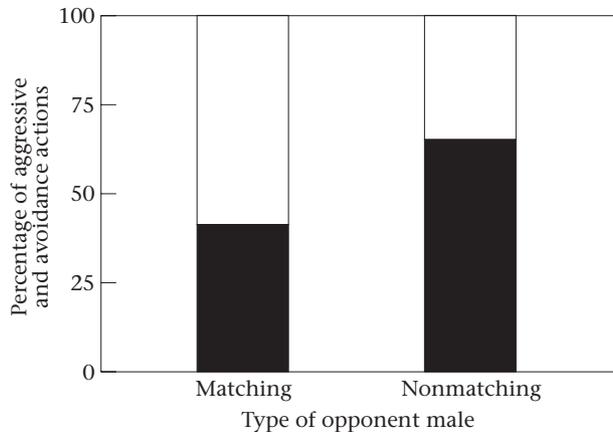


Figure 1. Percentage of agonistic behaviours involving avoidance (□) and aggressive actions (■) by male snow voles in encounters with either the odour donor (matching male) or another individual (nonmatching male) after exploration of a scent-marked area.

scent-marked areas, suggesting a preference for occupied locations. Previous studies on lizards and mice indicate that, besides advertising recent occupancy, the presence of fresh odour cues from conspecifics may alternatively indicate the suitability of a place to be used (Stamps 1987; Gosling 1990; Hurst 1990; Gosling et al. 1996a, b). Furthermore, a clean site close to one containing a conspecific's odours could indicate a place judged inappropriate by conspecifics already using the area (Hurst et al. 1996). It is then possible that scented substrates might represent zones of relatively higher quality than unmarked substrates to snow vole males. Predominant use of marked areas further suggests that the potential benefit of intruding into an occupied site may compensate for the risks incurred (e.g. being discovered by the owner). The costs of encountering the owner of the marks, however, may also be determined by the competitive ability of individuals and, thus, be dependent on their body size (van Zegeren 1980; van Oortmerssen 1985). For instance, male house mice of low body weight generally avoid scent-marked areas more often than heavier males since they would be more likely to be defeated or even injured by resource holders, which are generally also high-status individuals (Gosling et al. 1996a). In the present study, all snow vole males were large individuals, which may explain their willingness to intrude into scent-marked areas (Gosling et al. 1996a, b).

Our data for staged encounters suggest that snow vole males may indeed use scent matching to identify and respond differentially to potential opponents. Although social intolerance characterized all interactions, males were less aggressive towards owners of recently investigated marks than to other individuals. In addition, time spent in agonistic vocalizations by male pairs in matching encounters did not depend on the frequency of agonistic interactions, underlining a more intolerant context in contrast to nonmatching encounters. Fights with resource holders are likely to be costly since they are generally prepared to escalate encounters to defend their resources (Maynard Smith 1982). Under field conditions,

albeit with a wide overlap between individual home ranges, snow vole males make restricted use of particular locations (our unpublished data), which may be interpreted as a form of partial or site-specific territoriality (e.g. Mares & Lacher 1987; Ostfeld 1990). Thus, meeting the odour donor soon after encountering its marks would probably indicate the presence of the resource holder (Hurst et al. 1996), which may induce males to become less aggressive and thereby reduce the costs of a potentially risky encounter (Gosling 1982, 1990). The fact that a male's behaviour depended only on whether its opponent matched the previously invaded marked substrate suggests that scent matching was relatively more important than other possible mechanisms of assessment, such as the use of intrinsic properties of scent marks (agreeing with Gosling & McKay 1990). If scent information was the principal cue used by males, the immediate response to a potential competitor would not depend on whether it matched the scents of the substrate. Nevertheless, this does not mean that snow voles could not obtain intrinsic information from the opponent's scents (i.e. androgen and other hormone levels; e.g. Sawyer 1980) or that other behavioural cues, such as fighting ability, are not also involved in competitor assessment under natural circumstances.

Use of scent matching is known in males of strictly territorial mice *Mus* sp. (Gosling & McKay 1990; Hurst et al. 1996, 1997). However, while in house mice intruders are more reluctant to direct aggression towards territory owners than towards other individuals (e.g. Gosling & McKay 1990), encounters with owners among males of aboriginal house mice are aggressive interactions, determined principally by differences in body size (Hurst et al. 1996, 1997). In our study, all males were large individuals (i.e. expected to show territorial behaviour linked to a particular location) and body weight of opponents did not differ between matching and nonmatching encounters, which may rule out the effect of relative size in explaining the divergence of the responses between situations. Therefore, it seems that among similar-sized individuals prior residency might play an important role in determining intrasexual interactions between adult snow vole males (e.g. López & Martín 2001). However, even when scent matching is used it constitutes just one part of the assessment process (Rich & Hurst 1999) and individuals may also seek further information about the behaviour or fighting ability of signallers. In this framework, investigations addressing the effects of body size, and, thus, of dominance relationships among competing males of this species are needed.

After the social encounters, the use of marked areas by males depended on the identity of their recent opponent. Compared with their initial response, males spent less time on the scent-marked side and inside scented nests after meeting a matching male but not after meeting another male (Gosling 1982, 1990). These results suggest that the response of males towards scent-marked areas might have been triggered by the nature of their recent experience. For instance, by reducing the use of an occupied zone immediately after encountering the presumed occupant, individuals might lower the chance of a risky

further attack. In contrast, the nearby presence of a male that is not the occupant might suggest a relatively lower threat since it may be less likely to escalate aggression (Maynard Smith 1982; Dugatkin & Reeve 1998). A learnt association between scent marks and the identity of individuals found close by seems to be the mechanism snow vole males use to modulate their postinteraction response towards occupied areas (Gosling 1990).

The males' behaviour after social encounters was also different in matching and nonmatching treatments. Although the number of visits to the soiled nest after encounters decreased in both cases, duration of nest use decreased only after matching encounters. Nevertheless, males increased their locomotor activity subsequent to matching encounters, which may indicate their unwillingness to remain in the area. Males spent the same amount of time investigating before and after social encounters in both treatments. To the experimental animals, a recent encounter with another male might have indicated possible modifications of the scent by this individual in the previously investigated marked areas (e.g. occurrence of new marking or countermarking events). Among small mammals, quantitative and/or structural relationships between scent marks of conspecifics constitute an important source of information about competitive relationships (e.g. Ferkin 1999) so males would benefit from being continually aware of any alteration in the odour milieu (Johnston 1999; Rich & Hurst 1999).

In conclusion, our results seem to indicate that snow vole males use scent matching to assess both their response towards other males and further use of occupied areas. More importantly, we have shown that the mechanism of scent matching is compatible with spatial systems in which competing conspecifics possess overlapping ranges. Indeed, spatial overlap cannot always be interpreted as evidence against territoriality as individuals may experience differential success in using and defending particular parts of their ranges (see Mares & Lacher 1987). The fact that snow vole males make exclusive use of certain areas within largely overlapping ranges indicates a partially nonterritorial system in which it may pay to avoid costly encounters with residents of these locations. Thus, the ability of males to discriminate and respond differentially to these individuals by using scent marks would be advantageous, independent of the degree of overlap between their ranges.

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