

Perspectives on over-marking: is it good to be on top?

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Abstract What we refer to as over-marking occurs when one individual places its scent mark on top of, touching, or adjacent to the scent mark of another individual, usually a conspecific. Over-marking frequently occurs among mammals that share common paths, trails, and runways. Despite its ubiquity among terrestrial mammals, we know little about how individuals respond to over-marks and the function(s) of over-marking. Studies on voles and golden hamsters indicate that after exploring an over-mark, individuals respond selectively to the mark of the top-scent donor relative to that of the bottom-scent donor. Thus, individuals may be able to focus their attention on a particular scent mark relevant at a particular time and in a particular context, neglecting other scent marks that are present. The function(s) of over-marking are examined within the framework of ten hypotheses. Several hypotheses are plausible. However, the bulk of the literature is consistent with hypotheses stating that over-marking serving a role in olfactory communication between opposite and same-sex conspecifics. Lastly, we postulate the costs and benefits that may be garnered by the top-scent donor of an over-mark.

Keywords Function · Olfactory communication · Over-marking · Top-scent donor

Over-marking: background

Imagine a small mammal, such as a rodent, in its home range or territory. It is surrounded by scent marks; some are its own scent marks and some are the scent marks of conspecifics (Thiessen and Rice 1976; Brown and Macdonald 1985; Gosling and Roberts 2001; McClintock 2002). A number of these scent marks are placed down at some distance away from the scent marks of conspecifics, whereas other scent marks are placed on top of or very close to the scent marks that were deposited previously by conspecifics (Ferkin 2001; Johnston 2001, 2003). We refer to the latter phenomenon as over-marking, which has a broader and more inclusive definition than has been suggested by others (Macdonald 1980; Hurst et al. 1990a; Johnston et al. 1994).

Scent over-marking appears to be ubiquitous among terrestrial mammals (Johnson 1973; Biben 1980; Macdonald 1980; Hurst 1990a; Johnston et al. 1994, 1997a; Heymann 1998; Sliwa and Richardson 1998; Brashares and Arcese 1999; Woodward et al. 2000; Lewis 2005). Johnston et al. (1994) outlined three scenarios for what might happen when scent over-marking occurs. The first scenario, scent blending, was proposed mainly for colonial species and occurs when the scent marks of two or more individuals mix forming a new scent. The new scent loses any individual-specific information but may be unique to the colony. The second scenario, the chemical bulletin board, was proposed mainly for wide-ranging species. In this scenario, animals place their scents in a centrally located area. The scents of each individual remain distinct from one another, and an animal can visit this central area to find out about its neighbors and to place its own scent marks. The third

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scenario, scent masking, was proposed for solitary and asocial species. The hypotheses of Johnston et al. (1994) focused principally on the physical attributes of overlapping scent marks, whether the scent marks became blended, whether they remained distinct, or whether the top-scent mark physically occluded the bottom scent. Johnston et al. (1994, 1995) and Ferkin et al. (1999) discovered that golden hamsters and meadow voles exposed to an over-mark later behaved as if they had a selective memory and preference for the odor of the top-scent mark relative to that of the bottom-scent donor. That is, they treated the top-scent mark as if it was somehow distinct, and of somewhat greater intrinsic value relative to the bottom-scent mark (Ferkin 2001; Johnston 2001, 2003).

The fact that animals have the capacity to distinguish between the top-scent mark and the bottom-scent mark, and generally behave selectively towards donor of the top-scent mark, suggest that over-marking may serve a particular role in olfactory communication (Johnston et al. 1994). Yet, we know little about its function and how and if individuals can distinguish between the top- and bottom-scent donors of an over-mark. The function of over-marking has been discussed in countless studies of scent marking, usually as a speculation based on observations of its occurrence. Indeed, the literature is replete with observations of mammals over-marking the scent marks of conspecifics, and at least ten hypotheses have been attributed to its role in odor communication. Briefly, these hypotheses state that over-marking may be a form of competitive marking, a bulletin board, a form of self-advertisement, a territorial behavior, a form of mate attraction, a means to increase foraging efficiency, a guide for navigation, the formation of a group/colony scent, a threat behavior, a means to identify conspecifics, and an artifact of laboratory studies. Some of these hypotheses are not mutually exclusive. Moreover, some of the hypotheses that predict the function of over-marking have not been tested systematically or have been shown to occur under very special conditions. Thus, despite ubiquity among terrestrial mammals, we know very little about the function(s) of over-marking. We also know little about how animals respond to over-marks, how they distinguish between the top- and bottom-scent donors of such marks, and what kinds of information animals exposed to over-marks can glean about the top- and bottom-scent donors.

In this paper, we will focus on (1) the occurrence of over-marking, (2) hypotheses dealing with the function(s) of over-marking, (3) how animals respond to the top- and bottom-scent donors of an over-mark, and (4) the costs and benefits that may be garnered by the

top-scent donor of an over-mark. Where the literature exists, we will provide many examples of over-marking in a variety of mammals.

To over-mark or not to over-mark: that is the question

The literature is replete with observations and anecdotes of mammals depositing their scent marks on or near the scent marks of conspecifics (Johnson 1973; Biben 1980; Macdonald 1980; Hurst 1990a; Johnston et al. 1994, 1997a; Heymann 1998; Sliwa and Richardson 1998; Brashares and Arcese 1999; Woodward et al. 2000; Lewis 2005). These include reports of over-marking in rodents, insectivores, ungulates, carnivores, and primates. A review of the literature allowed us to formulate ten different hypotheses that deal at some level with the role of over-marking. These ten hypotheses are not mutually exclusive and some overlap considerably. We list and describe these hypotheses; the citations associated with each hypothesis indicate studies that presented the hypothesis and may have supported it. Please note that several studies support more than one hypothesis.

The first hypothesis pertains to counter-marking and competition and states that individuals over-mark because they gain some advantage over those individuals whose scent marks they overlap. The advantage may be as simple as physically masking the presence of the bottom-scent mark (Johnston et al. 1994) as a means to incite competition (Biben 1980; Macdonald 1980; Stralendorff 1986; Hurst 1990a, b; Johnston et al. 1995; Ferkin 1999a, b; Begg et al. 2003; Johnston 2003; Ferkin et al. 2004a; Lewis 2005), as an indication of social rank (Rich and Hurst 1998, 1999), or as a threat (Smith and Abbott 1999). This hypothesis would imply that the top-scent donor's mark is responded to more favorably than the bottom-scent donor's mark by individuals investigating the over-mark. Thus, a prediction of the competition hypothesis is that individuals will over-mark the scent marks of same-sex conspecifics more than those of opposite-sex conspecifics. Another prediction is that individuals over-mark the scent marks of same-sex competitors more than those of other same-sex conspecifics. For example, they may over-mark a greater proportion of scent marks of unfamiliar same-sex conspecifics than those of familiar siblings (Kohli and Ferkin 1999). Direct and indirect support for the competition hypothesis comes from studies on meadow voles, prairie voles, tree shrews, sifakas, golden hamsters, house mice, dogs, Mongolian gerbils, moustached tamarins, deer, bilbies, grey wolves, honey badgers, ring-tailed lemurs, bank voles,

and African antelopes (Johnson and Johnson 1983; Mertl-Millhollen et al. 1986; Rozenfeld et al. 1987; Hurst 1990a, b; Smith and Abbott 1999; Ferkin et al. 2004a; Palagi et al. 2004; Lewis 2005).

The second hypothesis is that scent marking is a bulletin board that allows individuals to place their mark along paths traversed by conspecifics or on a large feature in the area, such as a rock, tree, or mound. In this way, individuals may indicate their presence in an area. An inference of this hypothesis is that each scent mark is distinct and that the top-scent donor's mark and the bottom-scent mark are responded to in a similar manner by individuals investigating the over-mark. The bulletin board hypothesis is such that both the top- and bottom-scent donors of an over-mark can indicate their presence in an area, in which the top-scent donor may or may not have an advantage over that of the bottom-scent donor. In this way, the bulletin board would allow self-advertisement by the scent donors (Wolff et al. 2002). Direct and indirect evidence for this hypothesis can be drawn from studies on prairie voles, red-bellied tamarins, and marmosets (Lazaro-Perea et al. 1999; Thomas and Wolff 2002; Smith and Gordon 2002).

The third hypothesis is similar to the counter-marking/competition hypothesis in that a scent donor receives a benefit for being on top, but is more specific in that it applies to over-marking in one's territory. This hypothesis would predict that an individual over-marks the scent marks of intruders, but is less likely to do so when it is an intruder. Over-marking may take place inside the territory or along its borders or both (Rosell and Bjorkoyli 2002), and possibly function to facilitate scent matching (Gosling 1982; Gosling and Roberts 2001). Support for this hypothesis can be inferred from studies on hyena, Eurasian beavers, Ethiopian wolves, rabbits, Alpine marmots, aardwolves, and klipspringers (Sillero-Zubiri and Macdonald 1998; Sliwa and Richardson 1998; Bel et al. 1999; Roberts and Dunbar 2000; Rosell et al. 2000; Drea et al. 2002; Hayes et al. 2002).

The fourth hypothesis is that over-marking is a form of mate attraction (Ferkin 1999; Hurst and Rich 1999; Woodward et al. 2000). In this case, individuals would over-mark marks of opposite-sex conspecifics more than they would the scent marks of same-sex conspecifics (Heymann 1998; Kappeler 1998; Ferkin et al. 2004a; but see Smith and Gordon 2002). Another prediction of the mate attraction hypothesis is that individuals will over-mark the scent marks of sexually receptive opposite-sex conspecifics more than those of opposite-sex conspecifics that are not sexually receptive or less so. An assumption of the mate attraction

hypothesis is that over-marking of the opposite-sex conspecific would occur before coitus. In this way, the top-scent mark may serve as a greeting or invitation to the donor whose mark was over-marked, and facilitate interactions between the two scent donors. The mate attraction hypothesis has gained some support from studies on zebras, hyenas, wolves, meadow voles, ring-tailed lemurs, moustached tamarins, and mouse mice (Penzhorn 1984; Mertl-Millhollen et al. 1986; Hurst 1990c; Heymann 1998; Kappeler 1998; Drea et al. 2002; Ferkin et al. 2004a, b; but see Thomas 2002).

The fifth hypothesis is that over-marking the marks of an opposite-sex conspecific may be a form of mate guarding. This hypothesis predicts that by over-marking the bottom-scent mark, the top-scent donor is somehow devaluing the features of it to conspecifics (Woodward et al. 2000). That is, individuals that investigate such an over-mark would be able to determine that the top-scent donor may have an association with the bottom-scent donor. Thus, the bottom-scent donor may be no longer interested in mating, may have established a pair bond with the top-scent donor, or is indicating to investigating individuals that the top-scent donor is present. An assumption of this hypothesis is that over-marking the scent mark of an opposite-sex conspecific occurs after they engaged in coitus. Studies on hyena, prairie voles, wolves, klipspringers, antelope, moustached tamarins, and ring-tailed lemurs suggest direct and indirect support for the mate guarding hypotheses (Mertl-Millhollen et al. 1986; Heymann 1998; Brashares and Arcese 1999; Woodward et al. 1999, 2000; Roberts and Dunbar 2000; Drea et al. 2002; Ferkin et al. 2004a, b; Palagi et al. 2004).

The sixth hypothesis is related to navigation. The navigation hypothesis states that over-marking allows individuals to navigate in unfamiliar area (Peterson 1988), and allows them to return to familiar areas. Thus, an individual will over-mark the scent marks of conspecifics and use its own scent marks as navigational aids and possibly signposts in less familiar and unfamiliar areas that it may traverse. This hypothesis has not been tested directly. Thus, there is little data available that supports or refutes this hypothesis.

The seventh hypothesis is related to increasing foraging efficiency and states that over-marking the scent marks of conspecifics increases foraging efficiency by the individual and/or family members for locating food sources. Thus, individuals will over-mark the scent marks of conspecifics and their own scent marks to create a path that allows them to locate a food source, and may be akin to trail marking in ants. The foraging efficiency hypothesis has gained indirect support from

studies on honey badgers and wild otters (Kruuk 1995; Begg et al. 2003).

The eighth hypothesis is directed at mammals that live in groups. It states that over-marking allows scent marks to mix, thereby providing group members with a unique group scent. A group scent may provide cohesion among group members and allow individuals the means to distinguish between group and non-group members. Indirect support for this hypothesis can be inferred by studies on marmosets (Lazaro-Perea et al. 1999) and Ethiopian wolves (Sillero-Zubiri and Macdonald 1998).

The ninth hypothesis states that over-marking serves no function. This is essentially a null hypothesis, which is based on reports of some mammals that rarely over-mark or over-mark a very small proportion of the scent marks of conspecifics (Thomas 2002; Rostain et al. 2004; but see Rozenfeld and Rasmont 1991; Ferkin et al. 2004a, b). Some of these researchers argue that over-marking is an artifact of scent marking studies in animals that are in captivity, or a by product of captive individuals scent marking in small areas (Wolff 2003). Let us address the issues raised by this hypothesis. First, we know little about the proportion of scent marks that need to be over-marked for over-marking to serve a function. Perhaps only a few over-marks are needed for an individual to be considered the top-scent donor in an area by conspecifics. Second, it is not too surprising that observations of over-marking can be affected by the condition or context in which an animal finds itself. Many terrestrial mammals, including those reported not to over-mark, rarely (Thomas 2002) do over-mark the scent marks of other animals when tested under different conditions and in different apparatus (Ferkin et al. 2004a, b). Such a finding suggests that over-marking is not an artifact of an experiment or a coincidence of two or more individuals scent marking in the same area. Although this hypothesis raises some interesting issues with regard to how and where some over-marking studies are conducted, there is little empirical evidence that shows that over-marking serves no function. The fact that most of the available literature suggests that mammals over-mark the scent marks of conspecifics (Johnson 1973; Biben 1980; Macdonald 1980; Hurst 1990a; Johnston et al. 1994, 1997a; Heymann 1998; Sliwa and Richardson 1998; Brashares and Arcese 1999; Woodward et al. 2000; Lewis 2005), differ in the proportion of scent marks of particular conspecifics that they over-mark (Ferkin et al. 2004a, b), and respond differently to the donors of the top- and bottom-scent marks of an over-mark (Johnston et al. 1994), suggest that it likely a specialized form of olfactory communication that is

inherently different from, or requires special explanation additional to, that for scent marking.

The tenth hypothesis states that over-marking serves multiple functions depending on the identity of the top- and the bottom-scent donors as well as that of the identity of the individual investigating the over-mark. That is, it can serve as a form of competition, mate attraction, indicator of a territorial border, a bulletin board, etc. While it is tempting to assign all such tasks to over-marking, it may be premature to suggest over-marking is an all-purpose type of scent marking. The manner in which individuals respond to scent marks and whether they over-mark the scent marks of conspecifics may be context dependent. Differences in over-marking behavior may be concomitant with changes in their life history patterns, season, space use and social tolerance, reproductive condition, social status, age, etc. Nevertheless, it is hard to imagine that over-marking has only one or a small number of functions. A test of the multiple functions hypothesis may entail measuring and determining rates of over-marking, and the sex and identity of the top- and bottom-scent donor's of mammals that display seasonal shifts in sexual behavior, space use, diet choice, and social biology of animals.

Discriminating the top-scent mark from the bottom-scent mark

So far we have postulated on the responses and functions of individuals when they encounter the scent marks of conspecifics and whether they should over-mark these marks. If we extend the Johnston et al. (1994) hypotheses about over-marking, we can develop four testable hypotheses about how animals may behave when they encounter an over-mark and later encounter the marks of the top-scent donor and the bottom-scent donor separately. The first hypothesis states that over-marking produces a blended scent mark that is somehow different from the individual scent marks that comprise it. This hypothesis has two predictions: (1) after exploring an over-mark, animals would spend similar amounts of time investigating the marks of the top-scent donor and the bottom-scent donor of the over-mark; and (2) after exploring an over-mark, individuals would spend more amounts of time investigating the blended scent mark than either the scent mark of the top donor or that of the bottom donor. We may expect this type of situation to occur in mammals that form groups where membership is rather fixed. The second hypothesis is that over-marking produces a chemical bulletin board in which the two

scent marks remain distinct as the top- and bottom-scent marks; this hypothesis does not mention whether the top- and bottom-scent marks differ in intrinsic value to investigating individuals. This hypothesis predicts that, after exploring an over-mark, individuals would spend similar amounts of time investigating the marks of its top-scent donor and bottom-scent donor. We may expect this situation to occur in individuals that form groups where membership is fluid, or among small groups, pairs, or family units. The third hypothesis, the competition hypothesis, states that, by over-marking, the top-scent donor lowers the intrinsic value of the bottom-scent mark relative to that of the top-scent mark. The competition hypothesis predicts that, after exploring an over-mark, individuals would spend more time investigating the marks of the top-scent donor than those of the bottom-scent donor. We may expect solitary and asocial mammals and those that form dominance hierarchies to behave in such a manner. The fourth hypothesis is an extension of the bulletin board hypothesis proposed by Johnston et al. (1994). This hypothesis, termed the modified bulletin board, states that over-marking produces a modified chemical bulletin board in which the top- and bottom-scent donor's marks are distinct, but the investigating animal assigns an intrinsic value to each. This hypothesis predicts that, after exploring an over-mark, individuals would spend greater amounts of time investigating the marks of the particular donor that is of greater selective value to that animal, independently of whether it was the mark of the top-scent donor or the bottom-scent donor. An assumption of the modified bulletin hypothesis is that over-marking is a cheat-proof signal (*sensu* Gosling 1982; Gosling and Roberts 2001). That is, there is a cost to over-marking and therefore dominant individuals, adults, and reproductively active individuals are more likely to over-mark the scent marks of conspecifics than are subordinate individuals, juveniles, and reproductively quiescent individuals.

How mammals respond to over-marks and distinguish between the top- and bottom-scent donors' of an over-mark has been limited to studies on golden hamsters (Johnston et al. 1994, 1995; Wilcox and Johnston 1995; Johnston and Borhade 1998; Cohen et al. 2001) and voles, *Microtus* spp. (Johnston et al. 1997a, b; Ferkin 1999a, b; Ferkin et al. 2001a, b, 2004a, b). A common finding is that, after being exposed to an over-mark, these animals behaved selectively towards the donor of the top-scent mark as compared to the donor of the bottom-scent mark. This finding led to several inferences. First, the top-scent donor would be more likely than the bottom-scent donor to convey its

chemical message to conspecifics (Johnston et al. 1994; Ferkin et al. 1999; Johnston 2003). Second, in some cases, investigating animals later behaved as if the bottom-scent mark was not present (Johnston et al. 1995; Ferkin et al. 1999). Third, in other cases, animals behaved as if the bottom-scent mark was present, but it was less salient relative to the top-scent mark (Woodward et al. 1999, 2000). These findings provide no support for the scent-blending hypothesis or the chemical bulletin board hypotheses, but do support the competition hypothesis as the rodents responded selectively toward the top-scent mark. The data did not rule out the possibility that the modified bulletin board hypothesis could explain the findings.

To determine whether the competition hypothesis or the modified bulletin board hypothesis could explain the responses of voles and hamsters to over-marks, several additional studies were carried out. Essentially, these studies determined if the scent marks of the bottom-scent donor were actually masked by the top-scent donor or if they were distinct. In one study, Ferkin et al. (1999) first exposed meadow voles to an over-mark in which the top-scent mark overlapped about 5% of the bottom-scent mark, and then during the test phase exposed them to the top- and bottom-scent marks separately. After the exposure to the over-mark, meadow voles spent more time investigating the top-scent donor's mark as compared to that to the bottom-scent donor's. Similar findings were reported for golden hamsters, suggesting that they too had a better memory for the top-scent mark (Cohen et al. 2001). Such a finding suggests voles and hamsters may be "aware" of the presence of the bottom-scent mark, but they behaved as if it was not salient. Interestingly, the top-scent mark and the bottom-scent mark had to overlap for meadow voles, but not for golden hamsters, for them to respond selectively toward the top-scent mark (Ferkin et al. 1999; Cohen et al. 2001), suggesting that meadow voles and hamsters may behave in a similar manner to the top- and bottom-scent marks, but the way that they perceive such marks is different.

Further experiments were undertaken to disentangle the competition and modified bulletin board hypotheses. In one study, male and female meadow voles and prairie voles were exposed to a mixed-sex over-mark; an over-mark containing a male and a female scent donor. The results of the study were quite interesting and demonstrated that species differences exist in the manner in which meadow voles and prairie voles respond to the top- and bottom-scent donors of an over-mark. Both meadow voles and prairie voles displayed a preference for the odor of the top-scent donor over the bottom-scent donor if the top-scent donor was an

opposite-sex conspecific and the bottom-scent donor was a same-sex conspecific. If, however, the mark of the opposite-sex conspecific was on the bottom of a mixed-sex over-mark, meadow voles later spent more time investigating it relative to the donor of the top-scent mark (Woodward et al. 2000). Prairie voles, on the other hand, did not respond preferentially to the opposite-sex donor of mixed sex over-marks if it was on the bottom of an over-mark (Woodward et al. 2000). Taken together, the data suggest that the modified bulletin board hypothesis may best explain the responses of meadow voles while the competition hypothesis may best explain the responses of prairie voles.

The modified bulletin board hypothesis and the competition hypothesis were also tested in experiments that examined the response of male meadow voles to over-marks in which the two donors differed in their circulating gonadal hormone titers. In that study, Leonard et al. (2001) found that the response of male and female meadow voles to over-marks depends on the gonadal hormone titers of the two donors. That is, male meadow voles appear to base their response on the estradiol titer of the female, preferring the scent mark of a female with higher circulating titers of estradiol as compared to the scent mark of a female with low circulating titers of estradiol, independently of the position of the two scent marks in the over-mark. In contrast, female meadow voles appear to use both the position of the male's scent mark in an over-mark and the male's testosterone titer for the basis of their preference. That is, females preferred a male donor if he was both the top-scent male and had a higher testosterone titer compared to the bottom-scent male (Leonard et al. 2001). The results provide further support for meadow voles placing a higher value on a particular scent donor, and not simply responding selectively to the donor of the top-scent as compared to that of the bottom-scent mark.

Is it better to be on top than on the bottom of an over-mark?

Our knowledge about over-marking and the responses of individuals to over-marks will grow. In the meantime, we need to test and develop alternative hypotheses before one can assess whether over-marking is an artifact (Wolff 2003) or whether over-marking affects the tactics and strategy individuals employ to secure mates and resources (Johnson 1973; Daly 1977; Kappler 1998; Ferkin et al. 2001a, 2004a). Much of the current literature supports the view that individuals

display selective attention and selective memory to the top-scent mark of an over-mark, which may be of great importance to olfactory communication. If scent marks are “read” only selectively, we would have to adjust our thinking about olfactory communication to include as part of the process selective detection and selective perception. Such a change in thinking would suggest that individuals may be able to direct their attention on a particular scent mark relevant at a particular time and in a particular context, while ignoring other scent marks that are present. This would be especially important to individuals that need to assess relationships between two scent donors that may not be together in time and space (Gosling 1982). For example, the top-scent donor may be present, whereas the bottom-scent donor may no longer be present in that area. However, situations in which the top-scent donor's and bottom-scent donor's marks are static are probably rare in free-living populations. It is not too difficult to imagine that even a vigilant individual may have his scent mark over-marked by a same-sex conspecific. Whether the over-marker is a neighbor or a transient, such a situation may lead to several individuals depositing their scent marks in the same area and to frequent changes in the identity of the top-scent donor. Recent work has shown that voles rely on relative numerosity, distinguishing more from less, to identify donors whose marks were on top more than they were on the bottom of an over-mark (Ferkin et al. 2005). Thus, individuals whose scent marks are on top more often than they are on the bottom may be viewed by conspecifics as the most recent resident in that area. In this case, individuals should attempt to monitor areas that contain their own scent marks and insure that their marks remain on top of those of same-sex conspecifics, over-mark the scent marks of previous or potential mates, and be cognizant of over-marks of other conspecifics to assess relationships between particular conspecifics (Ferkin et al. 2004a, b, 2005).

Over-marking may be akin to a snap-shot of an interaction between two conspecifics, in this case the top- and bottom-scent donor (Ferkin 2001). Thus, a question that needs to be addressed is whether over-marking has some biological significance for individuals that do so. Based on the selective response of individuals for the top-scent donor of an over-mark, it is not too much of a stretch to imagine that a top-scent donor would be more likely to gain priority in conveying its chemical message to conspecifics investigating an over-mark. The relationship may be between a dominant and subordinate animal, a conspecific and its mate, and/or a resident and intruder. For example, over-marking may be important in situations in which

there is intense competition for mates, territories or other defendable resources (Johnston et al. 1995; Rich and Hurst 1999; Ferkin 2001; Gosling and Roberts 2001; Thom and Hurst 2004). Female mice respond selectively to males that over-mark the scent marks of other males (Rich and Hurst 1998, 1999; Humphries et al. 1999). Over-marking the scent marks of other males is generally performed by dominant males and not by subordinate males in rodents, ungulates, and primates (Rozenfeld and Rasmont 1991; Heymann 1998; Rich and Hurst 1998, 1999; Brashares and Arceese 1999; Nevison et al. 2000). Indirect evidence supports the view that dominant individuals may be more likely than subordinate individuals to maintain their position as the top-scent donor of an over-mark (Rozenfeld et al. 1987; Rozenfeld and Rasmont 1991; Rich and Hurst 1999) and it is likely that the former are monitoring areas containing their scent marks. If over-marking is adaptive and an evolutionary stable strategy for individuals to play, it must provide advantages to the top-scent donor, so individuals should attempt to monitor areas that contain their own scent marks and insure that their marks or a proportion of their marks remain on top of those of conspecifics. That is, an individual should over-mark the scent marks of conspecifics if the benefits of doing so (i.e., competition with same-sex conspecifics, eavesdropping, and predation) are greater than the costs to the top-scent donor in announcing its presence in an area.

Another question that begs to be answered is whether the manner that mammals over-mark and respond to over-marks is associated with aspects of their life history. For example, do the reproductive state and motivation, and the identity, condition, and reproductive state of the scent donors, affect over-marking behavior or responses to over-marks in species other than meadow voles (Leonard et al. 2001; Ferkin et al. 2004a, b)? Does the behavioral biology (mating and social system) of the individual, its ecology, or the habitat in which it lives, affect the proportion of scent marks it over-marks and its responses to over-marks? We also do not know if species differences in responses to over-marks are associated with social and mating systems. If so, are members of a pair bond, in species in which individuals are social, cognizant of the position of their own scent marks in an over-mark in their territories, and do they over-mark the scent marks of their mates and those of same-sex intruders? Failure to do so may indicate that the association between the members of the pair bond no longer exists. If, on the other hand, individuals do not form pair bonds and the association between particular opposite-sex conspecifics is ephemeral, do

males and females over-mark the scent marks of previous mates more than they would those of novel mates? Or, do they make any distinction in over-marking the marks of previous or novel mates?

Data from studies on meadow voles and prairie voles suggest that species differences exist in their respective over-marking behavior. An obvious explanation for this difference may be related to the fact that prairie voles may be socially monogamous, form opposite-sex pair bonds, with males and females sharing a nest and territory (Carter et al. 1993; Getz et al. 1996). It is possible that, for prairie voles, the top-scent mark may have a greater value as compared to that of the bottom-scent mark of a same-sex over-mark. Among prairie voles, the male partner may need to over-mark in order to devalue any novel male's scent marks that he encounters within his territory. Over-marking may be especially important to male and female prairie voles in that prairie voles appear to have a selective memory for the top-scent donor that lasts for less than 12 h (Ferkin et al. 2001b). This suggests that prairie voles must over-mark the scent marks of same-sex conspecifics in order to signal their presence in the territory to their mates. Indeed, recent work has demonstrated that resident prairie voles are attentive to the scent marks of same-sex intruders by over-marking a majority of the intruder's scent marks (Ferkin et al. 2004a). Thus, as long as both residents are present and the pair bond is intact, there should be few changes in the identity of the top-scent donors. If the resident's scent marks are over-marked by a same-sex conspecific, it may indicate the ownership of the territory is in question and the pair bond is no longer intact (Woodward et al. 2000; Ferkin et al. 2004a, b). In contrast, meadow voles are promiscuous, males and females do not pair bond and do not share a nest and territory, and may have little interaction with opposite-sex conspecifics outside of copulation (Madison 1980; Dewsbury 1990; Boonstra et al. 1993). Male and female meadow voles should be attentive to the marks of sexually receptive opposite-sex conspecifics and same-sex conspecifics that may be viewed as a nearby serious competitor and less so to the marks of other conspecifics. Given that the top-scent donor of an over-mark is likely to be the most recent visitor to an area, the top-scent mark may have a much greater value to the investigating individuals relative to that of the bottom-scent mark; the bottom-scent donor may have moved on to another area. At present, it is not known if there are widespread species differences in responses to the top- and bottom-scent donors of an over-mark or whether such differences would be associated with differences in the social biology of species.

A critical question that remains unanswered is whether an association exists between over-marking and fitness. That is, individuals that over-mark the scent marks of conspecifics gain an advantage in fitness relative to individuals that have their scent marks over-marked. While this hypothesis has not been tested directly, indirect tests of this hypothesis have provided conflicting results. Huck et al. (1985) found that female golden hamsters mated more often with males that deposited more scent marks than with males that deposited fewer scent marks. In contrast, Thomas (2002) and Wolff et al. (2002) reported that female prairie voles do not differentially mate with the top- and bottom-scent male donors of an over-mark, concluding that scent marking and over-marking do not have an association with mating and reproductive success. However, the findings of these studies must be viewed with caution. First, the researchers did not measure reproductive success of the top- and bottom-scent donors of the over-mark. Second, Thomas (2002) and Wolff et al. (2002) examined only the mating behavior of females exposed to the over-marks of males, but did not examine the mating behavior of males exposed to the over-marks of females. Third, in the study involving prairie voles, the identity of the top- and bottom-scent male donors was arbitrary. Given that female prairie voles form pair bonds with their mates (Carter and Getz 1993), it is likely that, if the mate was present in the territory, his marks would be more likely to be on top of those of male intruders (Ferkin et al. 2004b). Fourth, Thomas (2002) examined the response of females to tethered male prairie voles, a situation that does not resemble the mating behavior of voles in free-living populations (Carter and Getz 1993; Getz and Carter 1996). Thus, it is probable that being tethered is not likely adaptive to voles and may be stressful, and that being tethered may have affected the behavior and responses of voles during mating and scent marking tests (Wolff 2003). At present, we need to test whether scent marking and over-marking affect the reproductive success of the top- and bottom-scent donors and the individuals that mate with them.

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