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Female meadow voles, *Microtus pennsylvanicus*, do not alter their over-marking in response to female conspecifics that were food deprived

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Abstract

Many terrestrial mammals will deposit scent marks and over-marks, the latter being the overlapping scent marks of two conspecifics. Studies have shown that male rodents that are exposed to the overlapping scent marks of two female conspecifics later spend more time investigating the mark of the top-scent female than that of the bottom-scent female. This suggests over-marking is a form of competition and that the top-scent female is more likely than the bottom-scent female to be chosen as a potential mate. Thus, females should over-mark the scents of neighboring females at a rate that will maximize their chances of attracting males. However, meadow voles live in areas that may contain patchy food availability, and residents may differ in their nutritional status. Females in a better nutritional state may be more likely than those in poorer nutritional states to indicate their presence in an area, signal possession of a territory, and to attract mates. Thus, we tested the prediction that female meadow voles, *Microtus pennsylvanicus*, that were not food deprived would deposit more over-marks than female voles that were food deprived for six hours. Food-deprived female voles and female voles that had continuous access to food deposited a similar number of scent marks and used a similar proportion of those marks as over-marks when they encountered the scent marks of female conspecifics. These findings suggest that the nutritional status of female voles does not affect their ability to signal their presence in an area marked by a female conspecific.

Keywords

Meadow vole; same-sex competition; over-mark; nutritional status; territoriality

Introduction

Many terrestrial mammals move along trails, paths, and runways that may contain the overlapping scent marks of two or more scent donors. These overlapping scent marks are a common feature for mammals that scent mark in runways and paths and on prominent objects in their habitat (Biben 1980; Hurst 1990; Johnston et al. 1994; Heymann 1998). Studies have shown that individuals spent similar amounts of time investigating the scent marks of two different conspecifics of similar quality if the scent marks did not overlap (Hurst and Beynon 2004; Ferkin et al. 2011). However, after exposure to the overlapping

scent marks of the same two donors, individuals later spent more time investigating the mark of the conspecific that provided the top-scent mark than that of the conspecific that provided the bottom-scent mark when the marks were offered separately and simultaneously (Johnston et al. 1994; Ferkin et al. 1999; Fisher et al. 2003; Ferkin et al. 2011). The scent marks of the top-scent donors were more attractive than bottom-scent donors to opposite-sex conspecifics, which may aid them in being chosen as a potential mate (Johnston et al. 1995; Ferkin et al. 2007). Thus, over-marking may be considered a form of competition between same-sex conspecifics because individuals that encounter them can use information about the donors that left them to assess possible mates and competitors (Rich and Hurst 1999; Johnston 2003; Ferkin and Pierce 2007).

Presumably, by placing their scent mark on top of that of a conspecific, the top-scent donor of an over-mark is signaling to investigating conspecifics its ownership of a territory, presence in the area, or social dominance over the bottom-scent donor of that over-mark (Rozenfeld et al. 1987; Hurst 1990; Johnston et al. 1995). In many species of small mammals, females compete for territories (Wolff 1993), and over-mark the scent marks of female conspecifics (Hurst 1990; Ferkin et al. 2004). For example, female meadow voles, *Microtus pennsylvanicus*, scent mark within their territories (Brown and Macdonald 1985) and presumably over-mark the scent marks of female conspecifics to signal their residency in that area (Ferkin et al. 2004; Ferkin and Pierce 2007). However, female voles occupy territories that vary in the quality and quantity of forage (Madison 1980; Batzli 1985; Bergeron and Jodoin 1989; Bergeron et al. 1990). The quality or quantity of their forage may affect the scent marking and over-marking behavior of female voles because scent marks are partially composed of digestive exudates (Albone 1984), and provide accurate information about a scent donor's condition (Pierce et al. 2005; Roberts 2007; Sabau and Ferkin 2012).

Several studies have shown that food availability affects the sexual behaviors of female animals. For example, 48 hours of food deprivation reduced the incidence of lordosis in female Syrian hamsters (*Mesocricetus auratus*) (Jones et al. 2002) and after 48 hours of food restriction, female musk shrews (*Suncus murinus*) and rats (*Rattus norvegicus*) no longer mated with a male conspecific if given the opportunity (Wade et al. 1996; Gill and Rissman 1997; Jones and Wade 2002; Temple and Rissman 2000). Similarly, male and female meadow voles spent more time investigating the scent mark of an opposite-sex conspecific that had continuous access to food compared to that of an opposite-sex conspecific that was food deprived for 6 hours (Pierce et al. 2005; Sabau and Ferkin 2012). Female voles that were food deprived for 6 hours were less likely to mate when compared to those that were not food deprived or restricted (Pierce et al. 2005; Sabau and Ferkin 2012). Collectively, these observations suggest that females that were food deprived may be weaker competitors or of lower quality relative to those that were not food deprived (Pierce and Ferkin 2005). If so, food availability would also affect the scent marking and over-marking of female voles when they encounter the scent marks of conspecific females.

In this study, we determined whether a female meadow vole's over-marking behavior is affected by her nutritional state or that of the female whose scent mark she over-marks. To do so, we compared the proportions of scent marks that food-deprived and ad lib-fed female

voles over-marked, and the proportion of their scent marks that they used as over-marks. We used female voles that had continuous access to food and those that had been food-deprived for 6 hours prior to testing as top-scent donors and bottom-scent donors of over-marks. We hypothesized that female meadow voles tailor their rates of scent marking and over-marking in areas containing the scent marks of a female conspecific to reflect their own current nutritional state or that of the female conspecific. Specifically, we predicted that female voles that were not food deprived (AL) would deposit more scent marks and over-marks, and use a greater proportion of their scent marks as over-marks than would those used by females that were previously food deprived for 6 hours (FD). By doing so, the former females would be the top-scent donor more often than the females that were food deprived.

Materials and methods

Scent donors

Female scent donors were randomly selected from our colony. Female meadow voles used as bottom-scent donors ($n = 76$) and top-scent donors ($n = 167$) were maintained from birth under a long photoperiod (14:10h L:D, lights on at 0700h CST), which simulates the day length prevalent in the summer breeding season. Meadow voles used in these experiments were descendants of free-living voles captured in central Pennsylvania and western New York, USA. We introduce free-living voles into the captive population every 24 months. At 18 days of age, voles were weaned and then housed with littermates in clear plastic cages ($26 \times 32 \times 31$ cm) with wood chip bedding until they were 40 days of age. At 40 days of age, the females were paired with a stud male and delivered a litter three to four weeks later. After weaning their litters, the dams were housed singly in clear plastic cages ($18 \times 12.5 \times 10$ cm) with wood chips as a substrate until the start of the experiment. Food (Harlan Teklad Rodent Diet, #8640, Madison, WI, USA), water, and cotton nesting material were provided *ad libitum*. Cotton was replaced every seven days. The female voles used as scent donors were housed singly for at least 6 weeks before being used in the experiments. All female scent donors were between 5–11 months. Paired scent donors were similar in body mass and unrelated and unfamiliar with one another. Female meadow voles do not undergo regular estrous cycles and are induced ovulators (Keller 1985). Sexually mature female voles reared under long photoperiod that are not pregnant or lactating are considered to be in behavioral estrus and will readily mate with male conspecifics (Milligan 1982; Meek and Lee 1993). None of the female voles were pregnant or lactating during the experiment. We followed Animal Care Protocol 0647, which was approved by the IACUC at The University of Memphis. We adhered to the 'Guidelines for the use of animals in research' as published in *Animal Behaviour* (1991, 41:183–186).

Nutritional Status

Female voles used as top- or bottom-scent donors were either provided with continuous access to food (AL, $n = 40$) or were food deprived (FD, $n = 36$). Six hours before testing, the food was removed from the cages of the FD voles but not the cages of the AL voles (Pierce et al. 2005). We chose 6 hours of food deprivation because such treatment reduced the attractiveness of the scent marks produced by female voles to males, the amount of time that

female voles spent investigating the scent marks of male conspecifics, and the willingness of females to mate (Pierce and Ferkin 2005; Pierce et al. 2005).

Placement of the bottom-scent marks

Scent marking took place in a T-shaped arena constructed of opaque green acrylic, which simulates an intersection of two vole runways (Ferkin et al. 2004; Hobbs and Ferkin 2011a). Arms and stem of the arena measured 25 cm long $\times$ 13 cm wide $\times$ 15 cm high. White photocopy paper was used as substrate, and was replaced after each testing run. Each of the arms of the T-shaped arena contained 16 scent marks from a female scent donor placed in two equidistant rows of 8 marks. An identical configuration has been used in previous studies of vole over-marking (Ferkin et al. 2004; Hobbs and Ferkin 2011a). This configuration allows the experimenter to control for the size and the number of marks placed by the bottom-scent donors. We simulated the deposition of scent marks by the bottom-scent female by gently rubbing a combination of fresh feces, urine, and anogenital area secretions from a selected female on a sheet of white copy paper that served as the substrate of the arena. Voles typically deposit feces, urine and anogenital area scent marks when they move along paths and runways (Ferkin et al. 2004). These sources of scent are sexually discriminable (Ferkin and Johnston 1995) and convey current and accurate information about the diet of the scent donor (Pierce et al. 2005; Hobbs and Ferkin 2011a; Ferkin and Sabau 2012). Each scent mark was similar in size, approximately 0.5cm (length) by 0.25 cm (width). In a control condition, we placed 16 distilled water drops in a configuration that was identical to that used for placement of the bottom-scent scent marks from vole donors. Five minutes after the last bottom-scent mark or water mark was placed in its respective arm of the arena, we outlined each of the bottom-scent marks with a #2 pencil (Ferkin et al. 2004; Hobbs and Ferkin 2011a). By doing so, we could distinguish these scent marks from those deposited by the top-scent female (see below). The experimenter wore disposable nitrile exam gloves to minimize the transfer of human scents when creating the bottom-scent marks, handling the white copy paper, and preparing the arena.

We placed either 16 scent marks of the bottom-scent donor or 16 water marks in each arm of the arena. Thus, an arena could have in its two arms the following five possible combinations of bottom-scent marks: 1) the scent marks of a food-deprived for 6 hours (FD) female in one arm and the scent marks of a female that had continuous access to food (AL) in the other arm; 2) the scent marks of an FD female in both arms; 3) the scent marks of an AL female in both arms; 4) the scent marks of an FD female in one arm and water marks in the other arm; 5) the scent marks of an AL female in one arm and water marks in the other arm (Table 1). The placement of bottom-scent marks or water marks in the right or left arm of the arena was alternated between tests. All testing took place between 10:00 and 15:00 CST to encompass periods of high activity by voles (Madison 1985).

Over-marking by the top-scent donors

Ten minutes after placement of the bottom-scent marks, top-scent female scent donors (AL, $n = 80$; FD, $n = 87$) were placed into the arena for 15 minutes during which time they were allowed to deposit their scent marks in the right and left arms. After 15 minutes, the top-scent donor was returned to its home cage. After 5 more minutes we used an ultraviolet lamp

(Blak-Ray Longwave UV lamp, UVP Model B100 AP, Upland CA, USA) in a darkened room to identify each scent mark deposited by the top-scent female in the left and right arm of the arena (Ferkin et al. 2004; Hobbs and Ferkin 2011a). We highlighted each of the top-scent donor's marks with blue ink to differentiate it from the marks of the bottom-scent donor. We used previously established criteria for evaluating over-marks (Ferkin et al. 2004; Hobbs and Ferkin 2011a); an over-mark is any scent mark deposited by a top-scent female that was overlapping, within 1 mm, or touching the scent mark of a bottom-scent donor. We counted the total number of scent marks deposited by the top-scent donor in the left and the right arms of the arena, calculated the proportion of the scent marks of the top-scent donor used to over-mark the scent marks of the bottom-scent donor, and the proportion of bottom-scent donor's marks that were over-marked by the top-scent donor. After each test, the arena was cleaned with 70% ethanol and allowed to air dry. We used four identical arenas in this study.

Statistics

We used a 2×2 multiple analysis of variance (MANOVA) with diet of the top-scent female donor (AL or FD) and nutritional status of the bottom-scent female donor (AL, FD, or water control) as main effects. We did so to determine whether statistically significant differences existed between the: 1) total number of scent marks deposited by the top-scent donor in each arm of the arena, 2) proportion of the top-scent donor's scent marks that over-marked the scent marks of the bottom-scent donor, and 3) proportion of bottom-scent donor's marks that were over-marked by the top-scent donor. All the proportional data were arcsine square-root transformed for statistical analysis (Sokal and Rohlf 1995). We used *a posteriori* multiple pairwise comparisons (Holm-Sidák method) to assess statistical differences across groups. Statistically different significance was accepted at $\alpha = 0.05$.

Results

Fifty-seven of the 80 AL top-scent females deposited at least one scent mark into one arm of the apparatus. Sixty-seven of the 87 FD top-scent females deposited at least one scent mark into one arm of the apparatus. Females that did not scent mark in either arm of the arena were excluded from the data analysis. FD and AL fed top-scent females did not differ in the total number of scent marks they deposited in either arm of the T-shaped arena ($\lambda = 0.992$, $F_{2, 112} = 0.465$, $p = 0.629$). Similarly, the total number of scent marks the top-scent donors left in either arm of the arena was not affected by whether the bottom-scent donors were FD or AL fed, or if they were a water control ($\lambda = 0.884$, $F_{8, 224} = 1.784$, $p = 0.081$) (Figure 1a). There was no interaction between the diet of the top-scent donors (FD or AL) and that of the bottom-scent donors (FD, AL, or water control) in the total amount of scent marks the top-scent donors left in either arm of the arena during testing ($\lambda = 0.955$, $F_{8, 224} = 0.645$, $p = 0.739$). FD and AL top-scent females did not differ in the proportion of their scent marks they used to over-mark the scent marks of the bottom-scent donors ($\lambda = 0.995$, $F_{2, 110} = 0.259$, $p = 0.772$). Similarly, the proportion of their scent marks the top-scent donors used to over-mark the scent marks of the bottom-scent donors was not affected by whether the bottom-scent donors were FD or AL, or if they were a water control ($\lambda = 0.922$, $F_{8, 220} = 1.139$, $p = 0.338$) (Figure 1b). There was no interaction between the diet of the top-scent

donors (FD or AL) and that of the bottom-scent donors (FD, AL, or water control) in the proportion of their scent marks top-scent donors used to over-mark the marks of the bottom scent donors ($\lambda = 0.948$, $F_{8, 220} = 0.747$, $p = 0.650$). FD and AL top-scent females did not differ in the proportion of bottom-scent donor's marks they over-marked ($\lambda = 0.980$, $F_{2, 112} = 1.121$, $p = 0.330$). Similarly, the proportion of bottom-scent donor's marks the top-scent donors over-marked was not affected by whether the bottom-scent donors were FD or AL fed, or if they were a water control ($\lambda = 0.928$, $F_{8, 224} = 1.072$, $p = 0.384$) (Figure 1c). There was no interaction between the diet of the top-scent donors (FD or AL) and that of the bottom-scent donors (FD, AL, or water control) in the proportion of bottom-scent donor's marks that were over-marked ($\lambda = 0.949$, $F_{8, 224} = 0.745$, $p = 0.651$). Chi-squared tests indicated that top-scent donors did not mark one side of the apparatus more than the other ($\chi^2 = 0.196$, $df = 1$, $p = 0.901$).

Discussion

Our data did not support the prediction that females that had continuous access to food (AL) would deposit more scent marks and over-marks, and use a greater proportion of their scent marks as over-marks than would those used by females that were food deprived for 6 hours prior (FD). Instead, we found that food-deprived female voles and those that were not food deprived deposited a similar number of scent marks, used a similar proportion of their scent marks as over-marks, and over-marked a similar proportion of the scent marks of bottom-scent females independent of the dietary condition of both the top- and bottom-scent donors. Similarly, Hobbs and Ferkin (2011a) found that female and male voles fed an isocaloric diet containing varying amounts of protein over-marked and were over-marked by a similar proportion of male and female conspecifics, respectively. Together, these results suggest that female meadow voles do not alter their scent- and over-marking behaviors in response to relative differences in the nutritional status of male conspecifics (Hobbs et al. 2011a) as well as differences in food availability of female conspecifics (this study).

It is not clear why, female meadow voles did not tailor their rates of scent marking and over-marking in areas containing the scent marks of a female conspecific to reflect their own current nutritional state or that of the female conspecific. We offer three alternative explanations to account for our results. First, because food is distributed in patches and will vary in quality and availability in a female's territory throughout the breeding season (Batzli 1985; Bergeron and Jodoin 1987, 1989; Bergeron et al. 1990), many female voles that occupy a territory may experience changes in their nutritional status. Consequently, there may be little benefit or relatively high costs for females to adjust their rates of scent marking and over-marking to reflect such transient changes in their nutritional state. There is no direct support for this speculation. However, female voles that were food derived for 6 hours no longer displayed a preference for the top-scent mark donor of a male-male over-mark - a preference that was displayed by females that were not food deprived (Pierce et al. 2007). A second possibility is that female meadow voles cannot detect differences or choose not to respond to scent marks of female conspecifics that differ in their nutritional status. This possibility does not explain why female voles can distinguish between the scent marks of male conspecifics differ in their diet (Ferkin et al. 1997; Hobbs et al. 2008). Third, it is possible that 6 hours of food deprivation was not sufficient to induce changes in the rate of

over-marking and scent marking in by female voles. However, 6 hours of food deprivation was sufficient to reduce estradiol titers, the amount of time that female voles investigated the scent marks of male conspecifics, and the number of females that mated relative to those of female voles that had continuous access to food (Pierce and Ferkin 2005, 2007; Pierce et al. 2005). Perhaps, the behaviors that surround sexual reproduction and interactions with opposite-sex conspecifics but not those that encompass social interactions between same-sex conspecifics are affected by differences in food availability among female voles.

Also of interest is the functional significance of our results. One interpretation of our findings is that both food-deprived female voles and female voles gain benefits in the transfer of olfactory information by having their scent marks in the top-scent position of that over-mark (Johnston et al. 1994, 1995, 1997a, b; Woodward et al. 1999; Ferkin and Pierce 2007). For example, in species that use over-marks to communicate, individuals may gain benefits in the transfer of olfactory information by having their scent marks in the top-scent position of that over-mark (Johnston et al. 1994, 1995, 1997a, b; Woodward et al. 1999; Ferkin and Pierce 2007). Over-marks demarcate territorial borders and to indicate to conspecifics that a territory is occupied (Johnston 2003; Hurst and Beynon 2004; Ferkin et al. 2004). Thus, both FD and AL female voles whose scent mark was in the top-scent position of an over-mark would be more likely than the bottom-scent female to indicate her possession of a territory. Possession of a territory increases the fitness and survival of female voles and other small female mammals (Wolff 1993). By over-marking the scent marks of other females at relatively high and similar rates, FD and AL females could signal their residency in a territory and thereby reduce intrusions by neighboring females and costly encounters with wandering female conspecifics (Ferkin and Seamon 1987; Vlautin and Ferkin 2013). Another interpretation is that by over-marking the scent marks of other females, the top-scent FD and AL females may be more likely to indicate to nearby conspecifics that this territory is occupied (Johnston 2003; Hurst and Beynon 2004; Ferkin et al. 2004). In this way, both FD and AL female voles may also benefit from having similar rates of scent marking and over-marking to attract nearby males as mates. Female and male meadow voles, like many other terrestrial small mammals, mate multiply (Boonstra et al. 1993; Birkhead 2000). The fact that FD females do not lower their rates of scent marking and over-marking relative to those of AL females suggests that they are not sacrificing opportunities to solicit mates despite facing food deprivation (Hobbs and Ferkin 2011a). However, males voles respond preferentially to the scent marks of AL females compared to those of FD females (Pierce and Ferkin 2005; Pierce et al. 2005; Hobbs and Ferkin 2011b). Thus, males may be less interested in seeking out a FD female and mating with her if he also encounters the scent mark of an AL female in the same area.

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Figure 1.

The total number of scent marks deposited by the top-scent donors in the left and the right arms of the arena, b) the proportion of scent marks the top-scent donors used to over-mark the scent marks of the bottom-scent donors, and c) the proportion of the scent marks of the bottom-scent donor's marks over-marked by the top-scent donors when placed in an arena containing the following combinations of over-marks: FD/AL, H₂O/AL, H₂O/FD, FD/FD, and AL/AL. Significant differences were not found at $\alpha = 0.05$

Table 1

Number of scent marks top-scent donor females placed on top of existing bottom-scent marks in each arm of the testing arena. Possible combinations of bottom-scent marks included: 1) the scent marks of an female that was food deprived for 6 hours (FD) in one arm and the scent marks of a female that had continuous access to food (AL) in the other arm; 2) the scent marks of an FD female in both arms; 3) the scent marks of an AL female in both arms; 4) the scent marks of an FD female in one arm and water marks in the other arm; 5) the scent marks of an AL female in one arm and water marks in the other arm. The position of the scents was randomized between arm 1 and arm 2 across each test.

Treatment	n = AL top-scent	n = FD top-scent	Scent in arm 1	Scent in arm 2
1	13	14	FD	FD
2	10	12	Water	FD
3	12	14	Water	AL
4	9	14	FD	AL
5	13	13	AL	AL