



Female prairie voles do not choose males based on their frequency of scent marking

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Abstract

We conducted an experiment to test three alternative hypotheses for the function of frequency of scent marking in male prairie voles, *Microtus ochrogaster*: (1) sexual attraction (to advertise male quality for mating); (2) reproductive competition; and (3) self-advertisement or individual identity. In laboratory experiments, males deposited scent on all areas of a bare substrate, and more in an area next to a stimulus animal than other areas, regardless of the stimulus animal's sex. Females did not choose mates based on their frequency of scent marking and scent marking did not antagonize or stimulate aggression between males. The frequency of scent marking by males supports the individual identity hypothesis, and is less consistent with the sexual attraction or reproductive competition hypotheses. Mate choice is likely based on a complex suite of characters, but at least in prairie voles, the frequency of scent marking by males does not appear to be one of them.

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1. Introduction

Scent marking in mammals is a form of olfactory communication that can be used to establish dominance or mark territories (e.g. Brown, 1979; Gosling, 1982; Johnston, 1983), as a sexual attractant (e.g. Johnston et al., 1993; Rich and Hurst, 1999) and for individual identity (Thomas and Wolff, 2002). Numerous studies have addressed these various functions for scent marking in mammals; however, none has attempted to discern among the alternative hypothe-

ses for why male rodents scent mark (but see Hurst, 1990a,b; Thomas and Wolff, 2002).

Scent marking has been correlated with dominance in several species of rodents such as house mice, *Mus domesticus* (Desjardins et al., 1973), hamsters, *Mesocricetus auratus* (Ferris et al., 1987), cotton rats, *Sigmodon hispidus* (Gregory and Cameron, 1989), and gerbils, *Meriones unguiculatus* (Nyby et al., 1970; Yahr, 1977). In addition, mate choice has been associated with dominance (e.g. Shapiro and Dewsbury, 1986; Hurst, 1990b; Rich and Hurst, 1999; Horne and Ylönen, 1996). In at least two species of rodents, prairie voles, *Microtus ochrogaster*, and meadow voles, *Microtus pennsylvanicus*, females have been shown to spend more time investigating the scent of high than low quality males (Ferkin et al., 1997)

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and/or those that over mark a potential competitor (Johnston et al., 1997a,b; Ferkin, 1999a,b; Woodward et al., 1999, 2000). If females can use scent to assess male condition or status, scent marking by males also might function as a sexual advertisement to attract females (reviewed in Johnston, 1983). However, the one study conducted to test directly whether females mated more often with males that scent marked more than a competitor found no relationship between mate preference and frequency of scent marking (Thomas, 2002). Alternatively, Thomas (2002) and Thomas and Wolff (2002) concluded that scent marking functioned primarily to advertise individual identity. However, these two previous studies were not designed to test whether males might also use scent directly in male competition in the presence of a female, which would in turn be attractive to females.

A large number of studies have been conducted on scent marking using proximate indicators of mate choice such as time females spent in contact with a given male's odor (e.g. Johnston et al., 1997a,b; Ferkin et al., 1997; Ferkin, 1999b; Woodward et al., 1999, 2000; Rich and Hurst, 1998, 1999). In this study we test if the frequency of scent marking by males is directly related to their mating success. The first objective of our study was to determine if the frequency of scent marking by males was directed toward other male competitors or toward females. Secondly, we examined whether scent marking by males elicited aggression between males and/or was used to establish a hierarchical relationship. Third, we tested whether the frequency of scent marking in the presence of a female was a predictor of mate choice by females leading to male mating success. In meeting these objectives, we designed a series of experiments to discern among the three main hypotheses that have been proposed for the frequency of scent marking in males: to advertise male "quality" or status to females, to convey dominance in male–male interactions, or as a self-advertisement for individual identity. Male quality or status refers to those traits that females use directly in mate choice that would presumably contribute to genetic quality of offspring; dominance refers to some traits of a male that allows him to displace an opponent, and self-advertisement simply refers to an individual's identity, i.e. to identify an individual (sex, age, and individual characteristics) and his presence in an area.

We conducted a series of experiments with prairie voles in which we documented the frequency of scent marking by males in the presence of a competitor male and a female and a male competitor. We allowed males who marked in the presence of the female to directly interact and then gave the female the opportunity to choose between them. If males use the frequency of scent marking to attract mates, then they should mark disproportionately more in the presence of females than conspecific males, and females should mate with males who scent mark the most. Alternatively, if scent marking is used primarily for male–male competition, then males should mark disproportionately more in the presence of a male competitor than a female and act antagonistically toward one another in the presence of a female. Finally, if scent marking is used for individual identification, then individuals should scent mark throughout their territory and equally in the presence of a male or female. Scent marking typically has been considered to have three inclusive functions, sexual attraction, intrasexual competition, and individual identity. These three hypotheses might not be mutually exclusive or test for the ultimate origin of scent marking, but at least two previous studies have been able to discriminate among these alternative hypotheses (Thomas and Wolff, 2002; Thomas, 2002; Wolff et al., 2002). In this paper, we continue the line of reasoning of these three previous works and attempt to show further that hypotheses for the frequency of scent marking can be differentiated and tested experimentally. Although scent deposition may, in some cases, have non-social functions, its predominate functions seem to be reflected by these three hypotheses (reviewed in Eisenberg and Kleiman, 1972; Brown, 1979; Johnston, 1983).

2. General methods

Prairie voles used in this study were second- or third-generation laboratory-reared animals (parental stock was from western Tennessee). Animals were outbred with wild stock annually. All subjects were 65–180 days old, males were sexually experienced, and females were nulliparous. Previous studies with prairie voles show that nulliparous and parous females respond similarly to males in these types of experiments (Thomas, 2002; Wolff et al., 2002). Animals

were housed singly in standard 18 cm × 29 cm × 13 cm polycarbonate cages and provided with surplus food (PMI Rodent Chow 5008, St. Louis, MO) and water. Beta chip laboratory bedding and cotton nestlets were provided in each cage. Although animals were housed individually, cages were stored on shelves so individuals had visual and olfactory contact with each other. Animals were maintained on a 14 h L:10 h D cycle with lights on at 07:00 h. Temperature was maintained at $21 \pm 2^\circ\text{C}$. We conducted all trials between 08:00 and 12:00 h in a USDA-approved laboratory outside the main animal facility.

3. Experiment 1

This experiment was performed to determine if male prairie voles scent mark differentially in the presence of a novel male or a novel female.

3.1. Methods

Twenty-four hours prior to the experiment, nulliparous females were placed in large (28 cm × 42 cm × 15 cm) cages divided into two chambers (28 cm × 21 cm × 15 cm) by a screen partition. Unrelated sexually mature males were placed in the other half of the cages. These male–female pairs were left for 24 h to induce receptiveness in the females (Carter et al., 1987). At no time were these pairs allowed to directly interact; these males were not used in any other portion of this study.

To initiate the experiment, one male was placed in each of two compartments in a three-chamber apparatus (Fig. 1). The two smaller chambers were 25 cm × 25 cm × 40 cm and the larger chamber was 25 cm × 50 cm × 40 cm. All males were sexually experienced and of similar weight (± 2 g). The walls between the chambers were made of Plexiglas with a 10 cm × 10 cm wire-mesh gate for exchange of visual and olfactory cues, but not direct contact. The floor of the apparatus was covered with white photocopy paper as a substrate for scent marking. One male was placed in each of the subject's chambers and left for 30 min during which time he scent marked the substrate; we assumed that during this period the two males would familiarize themselves with each other. All

scent marks were from anogenital glands; none were urinary or fecal marks. After 30 min, the paper was removed and replaced with a clean sheet. A female was then placed in the stimulus chamber for 30 min. During this time, males had visual and olfactory contact with the female through the Plexiglas walls and wire-mesh gate. After a second 30 min time period, the animals were temporarily removed so we could count scent marks.

The area covered by scent marks was estimated by overlaying the scent-marked paper with an acetate grid sheet divided into 0.5 cm² squares. Scent marks were visualized under a longwave UV light (Desjardins et al., 1973). Scent marks were traced onto the transparency and each block containing a mark was counted. This procedure gave a relative estimate of the proportion of area that was marked. We counted the total scent marks in each subject's chamber. We then focused on the scent marks in two smaller areas: one in front of the gate separating the two males and one in front of the female's gate (Fig. 1). Each of these two regions was 48 cm² in area. This procedure allowed us to determine if scent marking was directed toward male opponents, toward the female, or equally on all areas of the paper within the chamber. Eighteen trials

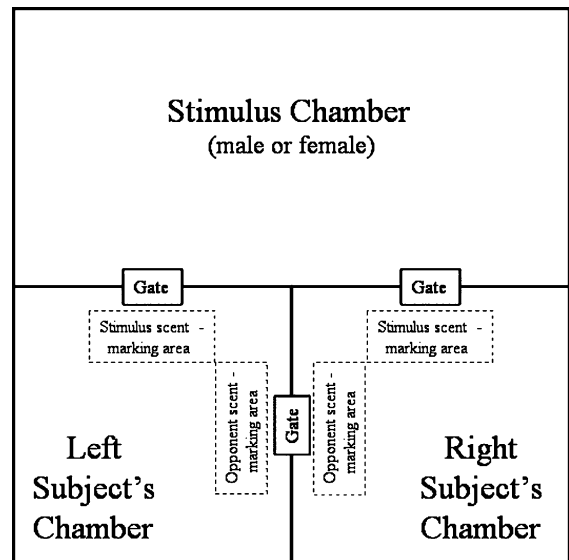


Fig. 1. Diagram of the scent marking and mate choice apparatus in which one male was placed in each front compartment and a stimulus animal (male or female) was placed in the rear compartment.

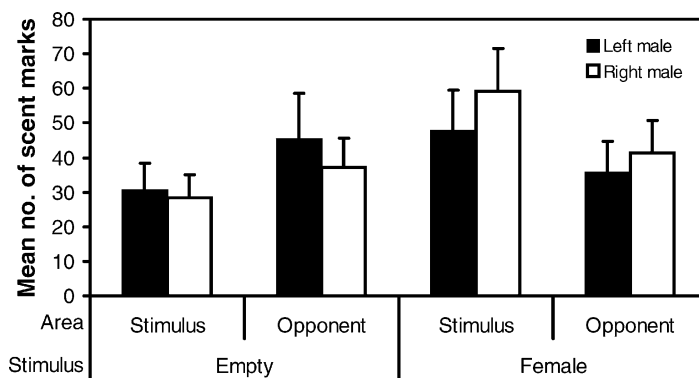


Fig. 2. Patterns of scent marking (mean \pm S.E. number of squares marked) when a female is the stimulus animal. Stimulus refers to the occupant of the stimulus chamber, and area refers to the area marked (see Fig. 1).

were conducted. The observer counting scent marks was blind to the treatment being scored.

3.2. Statistical analysis

We tested for a difference in the total area marked (throughout the entire arena) with and without the stimulus female present using a split-plot ANOVA. The sub-plot factor was subject (as designated by the male's position, right or left, in the apparatus). We then analyzed the data for the specific areas marked using a nested split-plot ANOVA. This analysis was identical to the previous analysis, except that we nested the area marked (in front of the stimulus chamber or in front of the opponent) within the subject. We used a square-root transformation on all data to meet assumptions of normality. Alpha level was 0.05 for all tests. All values are given as mean \pm S.E. unless otherwise noted. We did not control for an order effect in this study, but preliminary trials and previous work (e.g. Wolff et al., 2002) showed that order was not a factor in the frequency or placement of scent marks.

3.3. Results

The total area scent marked during the second 30 min when the female was present (215.0 ± 26.9 ($\bar{X} \pm$ S.E.) squares marked) was not significantly greater than during the first 30 min (174.0 ± 28.7 squares marked) when the female was not present ($F_{1,34} = 1.54$, $P = 0.224$). There was no difference in numbers of scent marks deposited by males

in the left and right chambers ($F_{1,34} = 1.09$, $P = 0.303$). There was no difference in the area an individual marked in front of the male or female gates ($F_{2,102} = 0.27$, $P = 0.764$), however, the interaction between the presence of a stimulus animal and the area marked bordered on significance ($F_{3,102} = 2.30$, $P = 0.082$; Fig. 2). This interaction was due to an increase in the number of marks placed in front of the stimulus chamber when a female was present, but without a concurrent decrease in the area marked in front of the opponent or throughout the chamber. Thus, males place more marks in front of an occupied chamber than an empty chamber (see also experiment 3 below).

4. Experiment 2

This experiment was performed to determine how the scent-marking pattern of male prairie voles affects agonistic interaction and female mate choice.

4.1. Methods

Immediately following experiment 1, the gate between the two males was opened for 10 min to allow males access to each other. Each vole was uniquely identified. Encounters were videotaped and pertinent agonistic behaviors (attacks, chase, and avoidance) and one non-agonistic behavior (mutual touching: two animals sitting side-by-side or otherwise in contact with one another in a non-aggressive fashion) were

recorded (Wolff, 1993). After a 10 min interaction period, each male was tethered with a flexible steel wire with a swivel clip attached from a plastic collar (nylon wire ties) to a steel bar mounted across the top of the compartment so animals could not leave their chambers. Tethering did not inhibit the animals from any normal activities such as moving, eating, or mating. The substrate was covered with shavings and food and water were provided ad libitum to each male. The gates leading to the female's chamber were then removed allowing the female access to both males for 22 h. All aspects of the study were videotaped with a time-lapse recorder. All copulatory behaviors (a mount and thrust with intromission was considered a copulation (Shapiro and Dewsbury, 1986); we could not detect ejaculation) were recorded from the videotapes. The arena was cleaned after each trial. Eighteen trials were conducted.

4.2. Results

Agonistic behavior was minimal throughout the experiment. The most commonly observed behavior was mutual touching, which accounted for 106 (77%) of 137 interactions. Only 31 (23%) of the interactions included agonistic behavior and 27 of these occurred in 2 trials. Males frequently entered each other's chambers and sat side-by-side without any overt aggression. Both males often sniffed the female through the mesh gate without exhibiting agonistic behavior toward each other. Agonistic behaviors were insufficient to predict a hierarchical relationship between individuals and were not used to predict female mate choice nor were they compared to male scent-marking patterns.

We conducted 18 trials, of which 11 females (61%) mated, as measured by copulation, with 1 male, 4 females (22%) mated with both males, and 3 females did not mate. The 15 females that did mate copulated an average of 15.2 ± 3.73 ($\bar{X} \pm S.E.$) times. Seven of the 15 females became pregnant but we were not able to determine paternity. We found no significant relationship between female mating preference and the male who marked the most total area (9 of the 15; Fisher's exact test, $P = 0.689$) or the most area in front of the female (Fisher's exact test, $P > 0.999$). In fact, males with which the 11 females mated exclusively scent marked less than those with which fe-

males did not mate (70.3 ± 24.3 and 106.5 ± 25.2 total marks; and 22.6 ± 9.7 and 53.0 ± 11.3 in front of the female).

5. Experiment 3

The first experiment showed that males deposited scent marks in all areas of their chambers including those in front of a male opponent. The numbers of marks deposited was slightly, though not significantly, greater when a stimulus female was placed in an adjacent chamber (see above). In experiment 1, we could not determine if the increased numbers of marks in front of the female chamber were because the animal was a female, or if they would mark similarly to any stimulus animals, such as another male. Thus, in experiment 3, we repeated the same experimental design using a male as the stimulus animal to determine if males mark differently in the presence of a stimulus male than a female. This experiment allowed us to differentiate between the sexual attraction hypothesis (males should mark more toward females than males), male–male competition hypothesis (males should mark more towards a male competitor than a female), and individual identity hypothesis (males should mark relatively equally in all areas) for male scent marking.

5.1. Methods

Animals used in this experiment had not been used in the previous experiments. We placed two males in the apparatus as in experiment 1 for 30 min. After the initial 30 min, the substrate was removed and replaced with a clean sheet of paper. An adult male was placed in the stimulus chamber and scent marking was again recorded for 30 min. After the two 30 min trials, the numbers of scent marks in the same regions as above (in front of the two gates) were counted. Twelve trials were conducted.

5.2. Results

Males did not deposit more scent marks in the presence of a stimulus male than vacant area ($F_{1,22} = 0.55$, $P = 0.468$; Fig. 3), nor did they mark more in front of one gate than the other ($F_{2,66} = 1.28$,

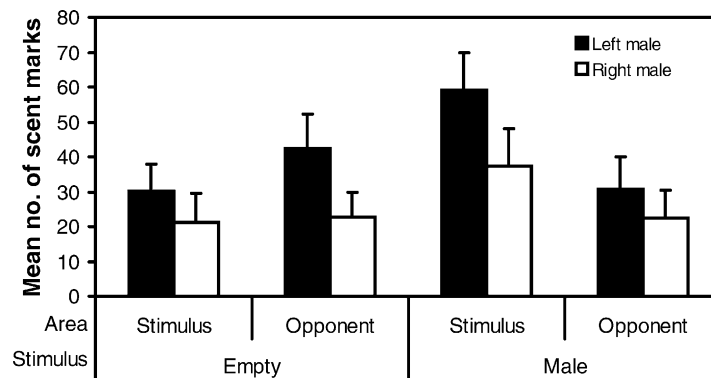


Fig. 3. Patterns of scent marking (mean \pm S.E. number of squares marked) when a male is the stimulus animal. Stimulus refers to the occupant of the stimulus chamber, and area refers to the area marked (see Fig. 1).

$P = 0.286$). However, as with the female experiment above, statistical interaction between area marked and the presence or absence of the stimulus male bordered on significance ($F_{3,66} = 2.66$, $P = 0.055$). This difference was due to a slight increase in marking in front of the stimulus chamber during the second 30 min trial, and not a decrease in marking in other areas of the chamber.

We combined the data from experiments 1 and 3 to increase the sample size when there is no stimulus animal present (36 total trials). In the absence of a stimulus animal, even with this larger sample size, males did not mark more in front of their opponent than the (empty) stimulus chamber ($F_{2,87} = 1.47$, $P = 0.235$). We also used the combined data in a separate analysis to test for differences in the marking behavior of males when the stimulus animal was male versus female. Combined, males marked more in front of a novel stimulus than their opponent ($F_{2,84} = 5.74$, $P = 0.005$), but the frequency of marking did not differ between a male and female stimulus ($F_{1,28} = 0.69$, $P = 0.412$).

6. Discussion

Our results are consistent with those of other studies on scent marking in voles that show males deposit scent on any bare substrate (e.g. Johnston et al., 1997a,b; Kohli and Ferkin, 1999; Ferkin, 1999a,b; Thomas and Wolff, 2002). Males placed significantly more scent marks in front of a stimulus animal (male

or female), but females did not choose mates based on the frequency of scent marks. In a similar study with prairie voles, females exposed to substrates marked by two males did not use the frequency or placement of scent marks (over marks) in choosing mates when the males were presented simultaneously (Thomas, 2002). In the current experiment and that of Thomas, females were presented with both potential mates at the same time and were likely using cues other than the frequency of scent marking for assessing male quality, which are probably more informative. Our results, and those of other studies, suggest that the frequency of scent marking by itself is not effective in advertising male attractiveness.

Males deposited scent in all areas of their chambers in all trials, but increased their frequency of scent marking in the presence of stimulus males (as they did with females). However, when two males were allowed to interact after a 30 min scent-marking bout, they showed minimal agonistic behavior and often interacted amicably during olfactory, visual, and partially tactile contact with a female through a mesh gate. Scent marking in front of the gate opening did not deter neighboring males from entering each other's chambers. Due to the low levels of aggression we were not able to detect a hierarchy between males or show a relationship among agonistic behavior, dominance, scent marking, and mate choice by females. This low level of aggression has been observed in other laboratory studies, but is probably not indicative of the level of agonistic behavior exhibited in natural environments (Getz et al., 1993).

In this study, and those of Thomas and Wolff (2002) and Thomas (2002), male voles scent marked relatively evenly on all substrate in their chambers. In this study, but not the other two, the frequency of marking increased in the presence of another individual (male or female), but the overall results from these scent-marking studies is that male voles mark everywhere, independent of a stimulus animal. Our results are most consistent with the individual identity hypothesis in that males marked on all substrate similarly in the presence of a male or female stimulus and that the presence of either sex did not influence a male hierarchical relationship or mate choice by females. The increased scent marking in the presence of a novel individual, though not originally predicted, is not inconsistent with individual identity hypothesis in that the scent in front of the stimulus animal provides a mechanism for self-advertisement directly to another individual. This increase in marking, while not documented in similar studies, does not seem to function in mate attraction or defense and may simply be a method of advertising individual identity to a novel animal. If the latter is true, this does not contradict the individual identity hypothesis. Also, because we have not been able to demonstrate that over marking or counter marking occurs in prairie voles (Thomas and Wolff, 2002; Thomas, 2002; Wolff et al., 2002) the frequency and placement of scent marks are not likely used directly as male competitive strategies. However, in that scent marking is so common in mammals, especially in a social context (Gosling and Roberts, 2001) it must have important evolutionary consequences. Therefore, we agree with others (e.g. Ferkin et al., 1997; Humphries et al., 1999; Hurst et al., 2001) that quality of scent is more important than quantity in animal communication. The frequency of scent marking by male prairie voles may function primarily to advertise an individual's presence in an area, but scent quality may provide more information about an individual's competitiveness, genetic quality, or sexual attractiveness.

Our study has limitations in that animals were not able to move freely in their environment nor did they have established territories as adults usually do in the wild. However, wild voles typically wander over unfamiliar areas and encounter strange males and females as they did in this study (Getz et al., 1993). We do not know how voles scent mark in the wild, but

scent-marking behavior is rather stereotyped in the laboratory and occurs in a predictable pattern even under different experimental protocols. The results from this study also are similar to those from several other studies that address different but related questions using similar techniques. Therefore, we are confident that our results represent natural behavior and adequately test the three designated hypotheses for the frequency of scent marking in male prairie voles. However, from this study and others in our laboratory, we conclude that the frequency of scent marking is not a reliable indicator of the ultimate function of scent deposition. Future studies should focus on scent quality more so than quantity or placement (see Hurst et al., 2001).

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