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Female meadow voles, *Microtus pennsylvanicus*, respond differently to the scent marks of multiple male conspecifics

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Abstract

Many non-human animals are capable of discriminating a group or entity containing more objects from one containing less of the same objects. The capacity for making judgments of numerosness may also allow individuals to discriminate between potential mates. Female meadow voles (*Microtus pennsylvanicus*) may use judgments of relative numerosness to distinguish between potential suitors by selecting males that signal their interest by depositing more scent marks relative to other males. We used a familiarization-discrimination paradigm in the absence of training to test the hypothesis that female voles will discriminate between the different numerosities of scent marks of two male conspecifics that are similar in features of their phenotype and quality. During the exposure phase, we presented female voles with different ratios of feces scent marks from two males. During the test phase, we presented females with a single, fresh fecal scent mark from each of the two male donors, whose marks they had previously encountered during the exposure phase. In both phases, females spent more time investigating the scent mark(s) of the male that deposited more scent marks than that of the male that deposited fewer scent marks provided the difference in the ratio of scent marks provided by the male donors in the exposure phase was greater than or equal to 2. Our results are consistent with studies on a variety of taxa suggesting that numerosity discriminations are evolutionarily ancient and spontaneously available to non-human animals and humans.

Keywords

Numerosity; scent marks; meadow voles; rodent; discriminations

Introduction

Several studies have shown that a variety of non-human animals in different taxa can discriminate between a group and entity containing more objects from one containing fewer of the same objects (Beran 2001; Boysen 1997; Kilian et al. 2003; Machado and Keen 2002;

Pahl et al. 2013; Perdue et al. 2012; Rugani et al. 2011; Uller et al. 2003). This ability to make judgments of relative numerosity may allow animals to assess how much food is available and which patch contains the most food (Barnard et al. 2013; Beran et al. 2008; Hauser et al. 2003; Uller and Lewis 2009), track predators, assist in parenting, prevent brood parasitism, and discriminate between groups of intruders (Benson-Aram et al. 2011; McComb et al. 1994; Pahl et al. 2013; Wilson et al. 2000).

The capacity for making judgments of numerosity may also allow individuals to discriminate between potential mates. Carazo et al. (2009) found that male mealworm beetles (*Tenebrio molitor*) discriminated between the odors of females if the ratio between the female scent donors exceeded 1:2. By keeping track of the number of females and their odors, males can maximize their mating opportunities. Likewise, mammals may keep track of the odors and scent marks produced by conspecifics to find mates (Brown and Macdonald 1985; Hurst and Beynon 2004; Johnston 1983, 2003). For example, female meadow voles (*Microtus pennsylvanicus*) may need to keep track of the multiple male suitors who will deposit scent marks in or near their territory (Ferkin 2011; Ferkin et al. 2005). Vaughn and Ferkin (2011) discovered that male meadow voles spent more time investigating the scent mark of a female vole that had more scent marks of male conspecifics adjacent to it relative to the scent mark of a female vole that had fewer scent marks of male conspecifics adjacent to it if the ratio between the two numerosities was greater than 5:1. In another study, male voles were exposed to an area containing the overlapping scent marks of two female conspecifics (over-marks), in which the number of times each female donor provided the top-scent mark versus providing the bottom-scent mark varied (Ferkin et al. 2005). After being exposed to the over-marks, male voles were exposed to single, non-overlapping scent marks of the two scent donors. Male voles could discriminate between moderately large differences in the relative number of over-marks by the two scent donors, distinguishing between ratios in which one donor provided 6 top-scent marks and the other donor provided 1 top-scent mark (Ferkin et al. 2005). Thus, male voles may be more attracted to the female donor that deposited more over-marks. This donor is usually the female that is the current resident in that territory. Male voles may use differences in the amount of scent marks they find in an area to determine which female may be the resident female. Resident female voles have a higher fitness compared to that of female voles that are transients (Wolff 1993). Female meadow voles were able to discriminate between smaller differences in the relative number of over-marks by the two male scent donors, distinguishing between ratios in which one donor provided 4 top-scent marks and the other donor provided 3 top-scent marks (Ferkin et al. 2005). Thus, female voles are better at discriminating between numerosities that differ by smaller amounts compared to male voles. Males that scent mark at higher rates compared to males that mark at lower rates may be of higher quality (Roberts 2007). Accordingly, the ability to discriminate between the number of scent marks that various males deposit in her territory may allow females to select males of higher quality as potential mates (Ferkin 2011). Presumably, males that deposit more scent marks may be more interested in mating with that female or represent higher-quality phenotype (Ferkin 2011; Hurst and Beynon 2004; Roberts 2007).

In the Ferkin et al. (2005) study, we showed that meadow voles were capable of numerosity discrimination. However, in the present study, we quantify a female vole's numerosity discrimination. Accordingly, we tested two hypotheses. The first hypothesis was that female voles could make numerosity discriminations between scent marks of donors A and B; donors A and B were similar in phenotype and quality to one another. We considered the more investigated mark as being preferred by females (Ferkin and Johnston 1995; Ferkin et al. 2005; Vaughn and Ferkin 2011). During the exposure and test phases we also tested the second hypothesis that the amount of time female voles spent investigating the scent marks of donors A and B followed Weber's Law as it relates to the just noticeable difference in a stimulus in proportion to the magnitude of the original stimulus (e.g., Beran and Beran 2004; Carazo et al. 2009; Lewis et al. 2005; Rugani et al. 2011). Specifically, as the numerical magnitude increases, a larger difference between the sets is needed to obtain the same level of discrimination.

We also determined if these ratio effects were due to the differences in the proportion of the number of scent marks that they encountered. First, we exposed female meadow voles simultaneously to two sets of scent marks that differed in the number of scent marks within each set, measuring the amount of time they spent investigating each set. We predicted that females would spend more time investigating the larger set of scent marks over the smaller set of scent marks. Next, we presented the females voles with a single scent mark from each of the two male donors. We predicted that female voles would spend more time investigating the scent mark of the male that previously deposited more scent marks during the exposure phase than that of the male that previously deposited fewer scent marks.

We tested these predictions by using a familiarization-discrimination paradigm (Ferkin et al. 2005; Hauser et al. 2003; Vaughn and Ferkin 2011) in the absence of training to determine the capacity of female meadow voles for discriminating between two numerosities of scent marks from two potential mates. Our experimental paradigm consisted of two phases, an exposure phase and a test phase. We chose this format because, during the exposure phase, a female meadow vole may spend more time investigating a set with more scent marks simply because it takes her longer to process the additional information. Including a test phase in which the female encounters only one scent mark from each male allows us to determine if the amount of time she investigates a particular scent mark indicates a preference for that male.

General Methods

Animals

Voles were fourth to sixth generation offspring of field-caught animals captured in Ohio and Kentucky, USA. All voles used in this experiment were weaned at 21 days of age, housed with littermates until 35 days of age, and then housed singly in clear plastic cages (27 x 16.5 x 12.5 cm) thereafter. These cages contained wood chip bedding and cotton nesting material. Voles had continuous access to food (Harlan Teklad Rodent Diet, #8640, Madison, WI, USA) and water. These cages were cleaned once a week and the cotton nesting material was replaced every two weeks.

Female and male meadow voles were used in the following experiments. In each experiment, we used animals born and raised under a long photoperiod (14L: 10D; lights on at 0800 h, CST). This photoperiod simulates a day length typical of the breeding season. Female and male voles born and raised under a long photoperiod reach sexual maturity at 40 and 50 days of age, respectively, and as adults display similar responses to the odors and scent marks of conspecifics as do free-living voles during the spring and summer (Ferkin 2011; Ferkin and Johnston 1995). Female meadow voles do not undergo estrous cycles (Keller 1985) and are induced ovulators (Milligan 1982).

All the voles used in this study were between 65–95 days of age, sexually mature, but sexually inexperienced. Subjects were 132 female voles and scent donors were 64 male voles; subjects and scent donors weighed approximately 48.1 ± 3.9 g. To eliminate litter effects, we used no more than two individuals from the same litter as either subjects or scent donors. During the tests, subjects and scent donors were unfamiliar and unrelated to one another.

Collection of stimulus odors for the exposure and test phases

Fresh fecal scent marks were obtained for each exposure and test phase from each scent donor. The experimenter wore disposable latex gloves to minimize human scent transfer while handling all slides. Feces contain sexually distinct odor cues for meadow voles (Ferkin and Johnston 1995) and are deposited by free-living male voles during their daily travels.

Exposure phase

The exposure phase took place in the female subject's home cage; each female was exposed to a unique combination of male scent donors. We followed the methods for determining odor preferences that were employed by Vaughn and Ferkin (2011). Briefly, we presented female voles with a plastic slide (2.70 cm x 10.83 cm; w x l) that contained feces scent marks from the following combinations (ratios) of scent marks from two different male conspecifics: 1) 5 scent marks from the first male (donor A) versus (vs.) 4 scent marks from a second male (donor B); 2) 5 vs. 3; 3) 5 vs. 2; 4) 5 vs. 1; 5) 4 vs. 3; 6) 4 vs. 2; 7) 4 vs. 1; 8) 3 vs. 2; 9) 3 vs. 1; 10) 2 vs. 1; and 11) 3 vs. 3.

We divided the plastic slide into three equal sections (each section was 3.61 cm in length); one end section of the slide contained the fresh feces scent marks from donor A and the other end section contained the fresh feces mark(s) from donor B. Except for the control condition (3 vs. 3), donor A always contributed more scent marks than did donor B. The middle section of the slide contained no scent marks. To deposit the scent marks on the slide, we gently rubbed a fecal bolus of one of the male donors against one of the end sections of the slide for 3–5 seconds; we rubbed the feces of the other male donor across the other end section of the same slide and so on until all the scent marks were placed on the slide. One minute separated the deposition of the scent marks on the slide. The scent mark from each male was approximately 0.5 cm x 0.2 cm (l x w) and placed within 5 mm of the center of their respective end section of the slide in a roughly circular pattern; the marks did

not touch or overlap. For each trial, we alternated the placement of the male scent donors' scent marks on the left or right side of the slide.

Five minutes after the last scent marks were placed on the slide it was suspended in the home cage of the female subject. A single observer blind to the number of scent marks placed on the slides recorded continuously for 5 minutes the amount of time that female voles investigated (the subject licked the slide or its nose came within 2 cm of the slide) the three sections of the slide. The trial began when the slide was placed into the cage of the subject. Each exposure slide was used once and then cleaned with 70% ethanol and dried prior to use in subsequent trials. In all the exposure trials, females spent little time (1.1 ± 0.2 seconds, mean $\pm$ SEM) investigating the clean, middle section of the slide. Thus, we did not include that measure in the data analysis.

Test Phase

One minute after the exposure phase, each female subject underwent a single 5-minute test trial; this test trial duration has been used previously in voles (Ferkin and Johnston 1995). Briefly, females were presented with a clear, glass slide that contained a single, fresh fecal scent mark (1.2 cm x 0.5 cm; 1 x w) from each of the two male donors whose marks they encountered during the exposure phase. As in the exposure phase, each slide prepared during the test phase was divided into three equal sections. The middle section contained no stimulus odor. One end section contained the scent mark of donor A and the other end section contained the scent mark of donor B; the placement of the scent mark on the right or left side of the slide was alternated for each trial.

The slide was suspended in the female's cage 5 minutes after the last scent mark was placed on it. During each 5-minute test phase, the observer recorded continuously the amount of time each subject investigated the two scented sections of the slide and the middle section of the slide. Each slide was used in only one trial and discarded. In the test trials, female voles spent little time (0.6 ± 0.3 seconds, mean $\pm$ SEM) investigating the clean, middle section of the slide. Thus, we did not include that measure in the data analysis.

Statistics

In both the exposure and test phases, we used separate paired *t*-tests to determine if females spent different amounts of time investigating the scent marks of donor A and donor B. By doing so, we could test the first hypothesis that female voles make numerosity discriminations between the scent marks of donors A and B. We considered the more investigated mark as being preferred by females (Ferkin and Johnston 1995; Ferkin et al. 2005; Vaughn and Ferkin 2011). We also tested the second hypothesis that the amount of time female voles spent investigating the scent marks of donors A and B followed Weber's Law during both the exposure and test phases. To do so, we created a continuous variable, the amount of time spent investigating the scent marks from donor A divided by the sum of the amount of time female voles spent investigating the marks of donors A and B. The quotient was arcsine square root transformed. We found that the data were not normally distributed (Shapiro-Wilk test, $P > 0.05$). Thus, we used a Kruskal-Wallis analysis of variance followed by Student-Newman-Keuls for post-hoc pairwise comparisons. We

calculated the correlation between this ratio for both the exposure and test phases and the ratio of scent marks provided by donor A to that of donor B during the exposure phase using Spearman's rho. Significant differences were accepted at $\alpha = 0.05$ for all statistical analyses.

Results

Exposure phase

During the exposure phase, female meadow voles spent more time investigating the scent mark(s) of donor A compared to those of donor B when the ratio of scent marks of donor A to donor B was 5:3, 5:1, 4:2, 4:1, or 3:1 (Table 1, Figure 1A). However, females spent similar amounts of time investigating the marks of donor A and donor B when the ratio of their scent marks was 5:4, 5:2, 4:3, 3:2, 3:1, or 3:3 (Table 1, Figure 1A).

During the exposure phase, the ratio of time spent investigating the scent marks of donor A to the total time spent investigating scent marks was significantly correlated with the ratio of the number of scent marks provided by donor A to those provided by donor B ($\rho = 0.318$, $P = 0.0002$). As the ratio of the number of scent marks provided by donor A to that of donor B increases, the ratio of time spent investigating donor A's scent marks to the total time spent investigating scent marks also increases.

A Kruskal-Wallis Analysis of Variance revealed that group significantly affected the proportion of time spent investigating the marks of donor A to that of time spent investigating the scent marks from donors A and B ($H_{10} = 28.77$, $P = 0.001$). Post-hoc pairwise comparisons using the Student-Newman-Keuls method revealed the following differences: female voles exposed to the ratios of 5:4, 5:3, 5:1, 4:3, 4:2, 4:1, 3:2, 3:1, and 2:1 showed a significantly stronger preference for donor A compared to females exposed to ratios of 3:3 or 5:2 (Figure 2A). Females exposed to a ratio of 5:2 showed a stronger preference for donor A relative to females exposed to the ratio of 3:3 (Figure 2A).

Test phase

During the test phase, females spent more time investigating the single scent mark of donor A compared to donor B when the ratio of scent marks during the exposure phase was 5:3, 5:2, 5:1, 4:2, 4:1, 3:2, and 3:1 (Table 1, Figure 1B). However, female voles spent similar amounts of time investigating the single scent marks of donor A and donor B when the ratio of their scent marks during the exposure phase was 5:4, 4:3, 2:1, or 3:3 (Table 1, Figure 1B).

During the test phase, the ratio of time spent investigating the scent marks of donor A to the total time spent investigating scent marks was significantly correlated with the ratio of the number of scent marks provided by donor A to those provided by donor B ($\rho = 0.302$, $P = 0.0004$). As the ratio of the number of scent marks provided by donor A to that of donor B during the exposure phase increases, the ratio of time spent investigating donor A's scent marks to the total time spent investigating scent marks during the test phase also increases.

Our findings suggest that the amount of time that female voles investigated the scent marks of donors A and B may be following Weber's Law. That is, as the numerical magnitude increases, a larger difference between the sets is needed to obtain the same level of

discrimination. A Kruskal-Wallis Analysis of Variance revealed that group significantly affected the proportion of time spent investigating the mark of donor A to that of time spent investigating the scent marks from donors A and B ($H_{10} = 25.27$, $P = 0.005$). Post-hoc pairwise comparisons using the Student-Newman-Keuls method revealed the following differences: female voles exposed to the ratios of 5:4, 5:2, 5:3, 5:1, 4:2, 4:1, 3:2, 3:1, and 2:1 showed a significantly stronger preference for donor A compared to females exposed to ratios of 3:3 or 4:3 (Figure 2B). Females exposed to a ratio of 3:3 showed a stronger preference for donor A relative to females exposed to the ratio of 4:3 (Figure 2B).

Discussion

The results of our familiarity-discrimination paradigm suggest female voles were able to discriminate between different numerosities of scent marks provided by two male conspecifics that are similar in features of their phenotype and quality. During the exposure phase, female meadow voles were simultaneously exposed to two sets of scent marks that differed in number. We found that female voles spent more time investigating the larger set of scent marks over the smaller set of scent marks in five out of six groups where the difference between numbers in the ratio was greater than or equal to 2 (5:3, 5:1, 4:2, 4:1, and 3:1, with 5:2 being the exception). During the test phase, female voles were exposed simultaneously to a single scent mark from each of the two male donors. We discovered that female voles recalled the donor that provided more scent marks during the exposure phase. During the test phase, females spent more time investigating the single scent mark of the male that previously deposited more scent marks than that of the male that previously deposited fewer scent marks if the difference in the ratio of scent marks provided by the male donors in the exposure phase was greater than or equal to 2 (5:3, 5:2, 5:1, 4:2, 4:1, and 3:1). Interestingly, when exposed to a ratio of 3 scent marks from donor A and two scent marks from donor B (3:2), females spent a similar amount of time investigating the scent marks from both donors. However, during the test phase, females spent more time investigating the mark of donor A than the mark of donor B. Our results provide strong evidence that female meadow voles are capable of numerosity discrimination based on scent marks and that such a system works when an operational ratio of scent marks of male donors is 1.7:1. Overall, these findings support and augment those of Ferkin et al. (2005), who showed previously that voles were capable of discrimination of different numerosities.

Similar ratio effects were reported by Carazo et al. (2009), who found that male beetles discriminated between the odors of females in the ratios 1 vs. 4 and 1 vs. 3 females. However, male beetles could not discriminate between ratios of 1 vs. 2 or 2 vs. 4 females, suggesting that males were capable of chemically discriminating between two odor sources based on the number of females contributing to the odor, if the ratio exceeds 1:2. Vaughn and Ferkin (2011) discovered that male voles spent more time investigating the scent mark of a female vole that had 5 male scent marks adjacent to her scent mark relative to the scent mark of a female vole that had 1 or 0 scent marks adjacent to her scent mark. Male meadow voles also discriminated between the numbers of times an opposite-sex conspecific provided the top-scent mark versus providing the bottom-scent mark if the ratio of providing the top-scent mark to providing the bottom-scent mark was either 7:0 or 6:1 (Ferkin et al. 2005). In contrast, female voles could distinguish between the top- and bottom-scent donors if the

ratios were 7:0, 6:1, 5:2, and 4:3, indicating that females could make finer discriminations of relative numerosness compared to male voles (Ferkin et al. 2005). Similarly, cotton-topped tamarins (*Saguinus oedipus*) presented with auditory stimuli discriminated sequences of 4:8, 4:6, and 8:12 syllables but could not do so if the sequences were 4:5 and 8:10 syllables (Hauser et al. 2003). In these studies, the responses of individuals to the different numerosities were largely due to differences and magnitude changes in the proportion of stimulus intensity and not to differences in the absolute number of stimuli.

It is possible, however, that the numerosity discriminations made by female voles may be due to the total amount of scent marks from each male they encountered, rather than the number of separate scent marks. Quantity estimation can be accomplished using non-numerical continuous cues such as amount estimation, which can co-vary with numerosity (Argillo et al. 2011; Carazo et al. 2012; Shifferman 2011). However, previous work has shown that meadow voles do not select the donor that provided scent marks that covered more surface area than those of another donor. Voles spent similar amounts of time investigating the scent marks and scent marking in response to small and large scent marks of two opposite-sex conspecifics of similar body mass, age, and reproductive condition (Ferkin et al. 1999, 2004a, b; Wolff et al. 2002). Thus, we believe that it is likely that the discrimination by female voles in the present study depended on the difference in the number of scent marks provided by the male scent donors during the exposure phase.

Our results also show that the preference of female meadow voles increases as the ratio between the number of scent marks of the male donors increases and that this numerosity discrimination is independent of absolute size. We suggest that the numerosity discrimination made by female voles in the present study were most likely due to differences and magnitude changes in the proportion of stimulus intensity and not differences in the amount of surface area covered by the scent marks provided by male scent donors. That is, the preferences of female voles for the scent marks of male donors seem to follow Weber's Law. Thus, the present study using scent marks joins other studies using chemical, visual, and auditory cues (Beran 2001; Hauser et al. 2003; Pahl 2013) that support the view that non-human animals have the capacity for numerical discrimination that is modulated by Weber's Law (Beran and Beran 2004; Carazo et al. 2009; Lewis et al. 2005; Rugani et al. 2011; Uller and Lewis 2009). Collectively, these studies on a variety of taxa demonstrate that numerosity discriminations are evolutionarily ancient and spontaneously available to non-human animals (Barnhard et al. 2013; Beran 2008; Hauser 2000; Hauser et al. 2003; Pahl et al. 2013; Rugani et al. 2011) and humans (Boysen and Capaldi 1993; Brannon et al. 2006; Lipton and Spelke 2003; Uller et al. 2013).

Also of interest is the extent to which female voles may use judgments of relative numerosness to facilitate decision processing surrounding mate choice. Most terrestrial mammals deposit scent marks along well-traversed paths and on prominent objects in an area, where they can be encountered by conspecifics (Brown and Macdonald 1985; Gosling and Roberts 2001; Thiessen and Rice 1976). Individuals may use the "public information" provided by scent marks to assist them in selecting potential mates (Ferkin 2011; Hurst and Beynon 2004; Johnston 1983, 2003; Roberts 2007). Many terrestrial mammals mate with multiple partners (Birkhead 2000). Thus, more than one male will deposit their scent marks

near the scent marks of a sexually receptive female to signal their presence in an area (Brown and Macdonald 1985; Ferkin 2011; Wolff et al. 2002). Female mammals may use judgments of relative numerosity to distinguish between the marks of multiple male scent donors (Ferkin et al. 2005; this study) and identify scent donors, allowing female voles to choose as mates males that are of higher relative quality. Presumably, males of higher quality or phenotype may deposit more scent marks than males of lower quality in the territories of female conspecifics (Hurst and Beynon 2004; Roberts 2007). Females may select the former males as potential mates, which may provide them with indirect fitness benefits such as mating with a vigorous courting male (Kokko et al. 2003).

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Figure 1.

The mean amount of time (+ SEM) in seconds that female meadow voles spent investigating (a) the differing number of scent marks of two male scent donors during the exposure phase and (b) the single scent marks of the same two male donors during the test phase. Asterisk (*) indicate a significant difference ($P < 0.05$) between the pairs.

Figure 2.

The mean proportion of time ($\pm$ SEM) spent investigating either (a) the scent marks of donor A to the total time investigating the scent marks of donors A and B during the exposure phase or (b) the single scent mark of donor A to the total time spent investigating the single scent marks of donors A and B during the test phase. Columns capped by different letters are statistically different from one another (Student-Newman-Keuls method, $P < 0.05$).

Table 1

Paired *t*-test values for the exposure and test phases of the 11 ratios tested.

Ratio	Exposure Phase	Test Phase
5:4	$t_{11} = 0.319, P = 0.755$	$t_{11} = 1.358, P = 0.202$
5:3	$t_{11} = 2.333, P = 0.040$	$t_{11} = 3.421, P = 0.006$
5:2	$t_{11} = 0.342, P = 0.739$	$t_{11} = 3.340, P = 0.007$
5:1	$t_{11} = 5.726, P < 0.001$	$t_{11} = 3.649, P = 0.004$
4:3	$t_{11} = 1.708, P = 0.116$	$t_{11} = 0.322, P = 0.754$
4:2	$t_{11} = 3.260, P = 0.008$	$t_{11} = 3.667, P = 0.004$
4:1	$t_{11} = 2.441, P = 0.033$	$t_{11} = 4.236, P = 0.001$
3:2	$t_{11} = 1.059, P = 0.312$	$t_{11} = 2.757, P = 0.019$
3:1	$t_{11} = 5.470, P < 0.001$	$t_{11} = 2.855, P = 0.016$
2:1	$t_{11} = 1.352, P = 0.204$	$t_{11} = -0.580, P = 0.574$
3:3	$t_{11} = -0.261, P = 0.799$	$t_{11} = -0.211, P = 0.837$