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Age affects over-marking of opposite-sex scent marks in meadow voles, *Microtus pennsylvanicus*

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Abstract

Models of age-related effects on behavior predict that among short-lived species younger adults are more attractive and attracted to opposite-sex conspecifics than are older adults, whereas the converse is predicted for long-lived species. Although most studies of age-related effects on behavior support these predictions, they are not supported by many studies of scent marking, a behavior used in mate attraction. Over-marking, a form of scent marking, is a tactic used by many terrestrial mammals to convey information about themselves to opposite-sex conspecifics. The present study tested the hypothesis that the age of meadow voles, *Microtus pennsylvanicus*; a microtine rodent, affects their over- and scent marking behaviors when they encounter the marks of opposite-sex conspecifics. Sex differences existed in the over-marking behavior of adult voles among the three different age groups that were tested. Male voles that were 5-7 mo-old and 10-12 mo-old over-marked a higher proportion of the marks of females than did 2-3 mo-old male voles. Female voles that were 2-3 mo-old, 5-7 mo-old, and 10-12 mo-old over-marked a similar number of marks deposited by male voles. Overall, the data were not consistent with models predicting the behavior of short-lived animals such as rodents when they encounter the opposite sex. The differences in over-marking displayed by older and younger adult male voles may be associated with life history tradeoffs, the likelihood that they will encounter sexually receptive females, and being selected as mates.

Introduction

Age of the participants is a key feature in determining the responses of individuals to opposite-sex conspecifics (Trivers 1972; Manning 1985; Kokko 1998; Beck & Powell 2000). Several models have been suggested to predict the behavior of older and younger adults when they encounter opposite-sex conspecifics (Manning 1985, 1989; Promislow 1991; Forslund & Part 1995; Hansen & Price 1995; Kokko & Lindstrom 1996; Beck & Powell 2000). Collectively, these models of the age-related effects on behavior and reproduction provide two general predictions. One prediction is that in short-lived species such as song birds and rodents, younger adults are more attracted and attractive than older adults to opposite-sex conspecifics (Boonstra 1994; Forslund & Part 1995; Hansen & Price 1995). The other prediction is that in long-lived species such as primates and carnivores, older adults are more attracted and attractive than younger adults to opposite-sex conspecifics (Promislow 1991; Rose 1991; Brooks & Kemp 2001). However, when the age-related effects on mate selection have been tested, studies on odor communication have provided mixed results, particularly among short-lived mammals. Some studies, mainly on rats, indicate that shortly after puberty young adult males produce signals that are more attractive to female conspecifics than those from older adult males, who have not reached senescence (Doty et al. 1984; Mencio-Wszalek et al. 1992; Vega-Matusczyk et al. 1994). However, studies that have examined the effects of age in voles, a relatively short-lived rodent (Tamarin 1985), suggested that the scents of older adult males are more attractive

than those of younger adult males to female conspecifics (Ferkin 1999; Ferkin & Leonard in press).

Scent marking is a form of olfactory communication that many terrestrial mammals use to communicate their presence in an area as well as features of their identity, such as their age, to opposite-sex conspecifics (Thiessen & Rice 1976; Johnston 1983; Brown & Macdonald 1985; Roberts 2007). Nevertheless, the effects of age on the scent marking behavior of many terrestrial mammals remain unknown. Scent marking increased as adult golden lion tamarins, koalas, Jack Russell Terriers, and mice grow older (Kleiman & Mack 1980; Smith 1980; Cudd-Wirant et al. 2003; Arakawa et al. 2007). Other studies demonstrated that scent marking was higher at or near puberty and then declined as individuals aged in gray mouse lemurs, honey badgers, and Mongolian gerbils (Arkin et al. 2003; Begg et al. 2003; Aujard & Nemoz-Bertholet 2004; Cayetanot et al. 2005). One study reported that the frequency of scent marking was not affected by age after North American beavers reached puberty (Herr et al. 2006). Interestingly, many of the studies that examined the effects of age on scent marking focused on the behavior of individuals in areas that did not contain the marks of opposite-sex conspecifics.

It is likely that age affects the scent marking behavior of individuals when they enter areas containing the marks of opposite-sex conspecifics. Many studies have shown that many terrestrial mammals deposit scent marks near or on top of the scent marks of opposite-sex conspecifics (Brown & Macdonald 1985; Hurst 1990; Johnston et al. 1994; Ferkin & Pierce 2007), a phenomenon known as over-marking (Macdonald 1980; Johnston 2003). Studies showed that male and female prairie voles (*Microtus ochrogaster*) and meadow voles (*M. pennsylvanicus*) adjust the number and location of scent marks that they deposit in areas previously marked by particular conspecifics. Male and female meadow and prairie voles target the scent marks of opposite-sex conspecifics and over-mark their scent marks (Ferkin et al. 2004a). Male meadow voles also over-marked more of the scent marks of females that were in postpartum estrus, a high state of sexual receptivity, than they did relative to females in moderate and lower states of sexual receptivity (Ferkin et al. 2004b). Similarly, females in postpartum estrus over-marked more of the scent marks of males than did females in moderate and lower states of sexual receptivity (Ferkin et al. 2004b). By differentially over-marking the scent marks of particular opposite-sex conspecifics, voles, and potentially other terrestrial mammals that scent mark, may be able to communicate particular information to a variety of opposite-sex conspecifics. Studies have suggested that over-marking the scent marks of an opposite-sex conspecific allows the top-scent donor to indicate its interest in the bottom-scent donor, possibly as a potential mate (Hurst 1990; Woodward et al. 2000; Ferkin & Pierce 2007).

The goal of the present experiment is to determine if the age of a meadow vole influences scent marking and over-marking behaviors. We test this hypothesis by examining the scent marking and over-marking behaviors among three different age classes of meadow voles (2-3 mo-old, 5-7 mo-old, and 10-12 mo-old) in response to the scent marks of 5-7 mo-old opposite-sex conspecifics. In doing so, we will also assess whether the behavior of meadow voles match those predicted by models for the effects of age on behavior of short-lived animals, such as rodents (Spruijt et al. 1989; Promislow 1991; Rose 1991; Boonstra 1994). Specifically, these models predict that voles that have recently passed puberty (2-3 mo-old) should be more likely than older voles (5-7 mo-old and 10-12 mo-old) to deposit more scent marks and over-marks in areas containing the scent marks of opposite-sex conspecifics.

Materials & Methods

Animals

Meadow voles were housed in the animal facility at the University of Memphis. The colony consisted of meadow voles captured in Pennsylvania, Kentucky, and Ohio, USA. Every 18-24 months, the voles in the colony were mated with captured free-living voles. Meadow voles used in the present study were born and raised under long photoperiod (14:10 h, L: D, lights on at 0700h CST). Long-photoperiod male and female voles reach sexual maturity by between one and two months of age (Keller 1985). Female meadow voles are induced ovulators and do not undergo regular estrus cycles (Milligan 1982). Adult female voles born and reared in long photoperiod are sexually receptive (Keller 1985). In the present study, all female voles were sexually receptive and of similar reproductive condition. Long-photoperiod female and male voles spend more time investigating and prefer the scent marks of long-photoperiod opposite-sex conspecifics than those of short-photoperiod opposite-sex conspecifics (Ferkin & Johnston 1995).

All voles used in this study were weaned between 19-21 days of age, housed with littermates until 33-36 days of age, and thereafter housed singly in clear plastic cages (18 × 12.5 × 10 cm). Cages contained cotton nesting material, water and food (Laboratory Rodent Diet # 5008, PMI, St. Louis, MO, USA). Voles used in this study did not have sexual experience.

Age Classes

The 2-3 mo-old, 5-7 mo-old, and 10-12 mo-old voles encompass the adult cohorts found in free-living vole populations (Negus & Berger 1988; Sheridan & Tamarin 1988). The 2-3 mo-old voles represent those individuals that are sexually mature, having recently passes through puberty (Nadeau 1985); we consider these voles as being young adults (Ferkin 1999). The 10-12 mo-old voles represent those individuals that are sexually mature, have not yet reached senescence (Slade 1995), and in field populations are fewest in number (Sheridan & Tamarin 1988; Negus & Berger 1988; Ferkin, Pugh & Tamarin unpubl. data). We consider these voles as being old adults (Ferkin 1999). The 5-7 mo-old voles represent those individuals that are sexually mature, and in field populations are greatest in number (Sheridan & Tamarin 1988; Negus & Berger 1988; Ferkin, Pugh & Tamarin unpubl. data). We consider these voles as being middle-aged adults. Voles of similar age cohorts were used in previous studies of age-related effects on olfactory behavior in voles (Ferkin 1999; Ferkin & Leonard in press).

Bottom scent donors and subjects

The bottom-scent donors were 5-7 mo-old voles who were the opposite sex of the top-scent donor. Thus, we established six types of over-marking dyads with a 5-7 mo-old opposite-sex conspecific as the bottom-scent donor and as the top-scent donor 1) a 2-3 mo-old male vole (n = 30), 2) a 2-3 mo-old female vole (n = 30), 3) a 10-12 mo-old male (n = 30), 4) a 10-12 mo-old female vole (n = 30), 5) a 5-7 mo-old male vole (n = 30), and 6) a 5-7 mo-old female vole (n = 30). The top- and bottom-scent donors were unfamiliar and unrelated to one another and matched for weight (within 5 grams); the average weight of the voles used in this study was 46.3 ± 4.9 grams. No scent donor was used more than once.

Arena

Subject voles were allowed to scent mark in a T-shaped arena. This arena was constructed of green acrylic sides, which was placed on top of a paper substrate. Each arm and the stem of the arena was 25 cm (length) × 13 cm (width) × 16 cm (height). The color, shape and size of the arena simulate an intersection of two natural vole runways (Ferkin et al. 2001, 2004a, b, Ferkin 2007). White photocopy paper served as the substrate on the floor of the arena. The

experimenter wore disposable floor-exam gloves when handling the paper to prevent the introduction of human scents.

Over-marks and testing procedure

The anogenital area scents from each donor were collected for each trial. Voles typically rub and drag their anogenital area across the substrate when scent marking (Ferkin et al. 2001, 2004a, b; Ferkin 2007). Thus, to collect scent marks from the bottom-scent donors, we gently dragged the donor's anogenital area against on a sheet of white copy paper, which was placed into an empty T-shaped arena that contained no bedding. We have used identical procedures in previous over-marking studies on voles (Ferkin et al. 2001, 2004a, b; Ferkin 2007). Briefly, the bottom-scent donors provided a fixed number (16 marks) of scent marks that were placed in one arm of the arena (Ferkin 2007). The paper contained 16 anogenital area scent marks (two equidistant rows of 8 marks) from a male or a female vole (the bottom-scent donor); each anogenital area scent mark was approximately 0.4-0.5 cm in length and 0.1-0.2 cm in width. This method of scent deposition allowed the investigator to control for the size and the number of marks deposited by the bottom-scent donor and to prevent a bias in the scent marking behavior of the bottom-scent donor (Ferkin et al. 2004a, b; Ferkin 2007). Under UV light, each of these 16 marks was visualized and circled by a pen with blue ink to distinguish them from marks that would be deposited by the subject (top-scent donor, see below). Sixteen marks were selected as it was approximately the mean number of marks deposited by meadow voles while exploring an empty arena for 10 min (Ferkin 2007). Previous tests indicated that the presence or color of the ink used in tracing has no effect on the marking behavior of voles (Ferkin et al. 2001, 2004a, b; Ferkin 2007). The resulting configuration of the T-arena was such that it contained an arm that contained the scent marks of the bottom-scent donor (the scented arm) and an arm that was not marked by that donor (the clean arm).

Fifteen min after marks of the bottom-scent donor were placed in the arena the top-scent donor was placed into the stem of the arena. The top-scent donor was allowed to explore and scent mark within the T-maze for 10 min and was then returned to its home cage. The paper substrate was allowed to dry for 5 min. Under UV illumination (Blak-Ray Longwave UV lamp, UVP Model B100 AP) in an otherwise dark room, we recorded the number and location of scent marks that the top-scent donor deposited in the T-maze (Ferkin et al. 2004a, b; Ferkin 2007). Scent marks deposited included feces, urine, and anogenital area secretions. Under UV light, feces appears as brown streaks or boli, urine appears as blue spots, and anogenital area secretions appear as silver-white slivers. Although these three types of marks may have different signal values, we are not aware of them, and for this study, as in previous studies, we assumed their signal values to be similar (Ferkin et al. 2004a, b; Ferkin 2007). Thus, one urine mark, two anogenital area marks, and two fecal boli were considered to represent five marks. The three types of scent marks convey sexually discriminable information to conspecifics (Ferkin & Johnston 1995). We used red ink to trace the outline of the scent marks deposited by the top-scent donor. This allowed the observer to distinguish between the marks of the top-scent donor from those of the bottom-scent donor, whose scent marks were previously traced in blue ink.

We considered over-marks to be marks by the top-scent donor that overlapped or touched those deposited by the bottom-scent donor (Ferkin et al. 2004a, b; Ferkin 2007). We counted the total number of scent marks deposited by the top-scent donor. We also counted the number of marks of the bottom-scent donor that were over-marked by the top-scent donor. Next, we calculated the proportion of the bottom-scent donor's marks that were over-marked by those of the top-scent donor's marks. These variables match those collected in other studies of over-marking in voles (Ferkin et al. 2004a, b; Ferkin 2007).

Statistical Methods

The data were analyzed using a 3-way ANOVA with sex (male or female), arm (scented or unscented), and age (2-3 mo-old, 5-7 mo-old, and 10-12 mo-old) of the top-scent donors as main effects. To assess statistical differences across groups and within levels the data were analyzed by using *a posteriori* multiple pairwise comparisons (Holm-Sidák method). We used a 2-way ANOVA with sex (male or female) and age (2-3 mo-old, 5-7 mo-old, and 10-12 mo-old) of the top-scent donors as main effects followed by *a posteriori* multiple pairwise comparisons (Holm-Sidák method). Statistical significance was determined as $p < 0.05$.

Results

Number of scent marks deposited by the top-scent vole in the arena

The number of scent marks deposited in the arena by subject voles was not affected by their sex ($F_{1, 89} = 1.71$, $p = 0.194$) or age ($F_{2, 89} = 1.146$, $p = 0.322$) (Fig. 1), but was affected by whether those marks were placed in the previously scented or unscented arm of the arena ($F_{1, 89} = 23.497$, $p = 0.0001$). There was no interaction between sex and age ($F_{2, 89} = 0.923$, $p = 0.401$), sex and arm of the arena ($F_{1, 89} = 1.481$, $p = 0.226$) and age and arm of the arena ($F_{2, 89} = 1.059$, $p = 0.357$) and age, sex, and arm of the arena ($F_{2, 89} = 1.562$, $p = 0.215$). Subjects, independent of their sex and age class, however, deposited a greater number of scent marks in the arm of the arena that contained the scent marks of the bottom-scent donor than the arm of the arena that contained no scent marks ($t = 23.63$, $df = 89$, $p < 0.00$; Fig. 2).

Over-marking by the top-scent donor

The proportion of marks of the bottom-scent donor that were over-marked by the top-scent donor was affected by the sex ($F_{1, 89} = 8.47$, $p < 0.005$) and the age class of the top-scent voles ($F_{2, 89} = 14.24$, $p < 0.001$; Fig. 3). There was also a significant interaction between sex and age class of the top-scent donors ($F_{2, 89} = 328.53$, $p < 0.001$). Post hoc comparisons revealed that female voles over-marked a greater proportion of scent marks of the bottom-scent donor than did male voles (Holm-Sidák method, $p < 0.05$). The multiple paired comparisons also indicated that 5-7 mo-old and 10-12 mo-old male voles over-marked a higher proportion of the scent marks of female voles than did 2-3 mo-old male voles (Holm-Sidák method, $p < 0.05$; Fig. 3). Males that were 5-7 and 10-12 mo-old over-marked a similar proportion of the scent marks of female voles (Holm-Sidák method, $p > 0.05$; Fig. 3). Female voles that were 2-3 mo-old, 5-7 mo-old, and 10-12 mo-old over-marked a similar number of marks deposited by male voles (Holm-Sidák method, $p > 0.05$; Fig. 3).

Discussion

Over-marking the scent marks of opposite-sex conspecifics is a behavior that is observed in a number of terrestrial mammals (Macdonald 1980; Brown & Macdonald 1985; Hurst 1990; Johnston 2003; Ferkin & Pierce 2007). A potential function of this behavior is to facilitate communication between the sexes (Ferkin & Pierce 2007), which depending on the species may be a form of mate guarding or mate attraction (Woodward et al. 2000). In the present study, we discovered that age of the scent donors affected the over-marking behavior of male but not female voles. Specifically, 5-7 mo-old and 10-12 mo-old male voles over-marked a higher proportion of female marks than did 2-3 mo-old male voles. Higher rates of over-marking by older adult males relative to younger adult males may affect the likelihood of that younger and older adult males communicate with female conspecifics. Female meadow voles do not form pair bonds and may mate with multiple males (Boonstra et al. 1993). However, male voles may wander through the territories of many females before they encounter a sexually receptive female (Madison 1980; Dewsbury 1990). Females may return

to their territories and encounter the scent marks of males that have over-marked their scent mark. At a functional level of analysis, older males may increase the likelihood that they are detected by females by over-marking their scent marks more than did younger males. Higher levels of over-marking by older adult males compared to younger adult males may also be a reliable indicator of features of their quality or competitive ability, which may be used by females to assess potential mates (Rich & Hurst 1999; Ferkin & Pierce 2007). In previous studies, female voles responded preferentially to scent marks of older adult voles than to those of younger adult voles (Ferkin 1999; Ferkin & Leonard in press). Differences in over-marking the scent marks of females by older and younger adult male voles may also be explained by sex differences in the development of this behavior. Older voles may produce more urine, a component of scent marks (Ferkin et al. 1995), than do younger adult males (Drickamer 1995). Thus, older male voles may have more urine to contribute to producing over-marks than do younger male voles. Older adult male voles may be better than younger male voles at identifying the scent marks of sexually receptive female conspecifics, which allows older males to over-mark more of their over-marks (i.e., Doty et al. 1984; Mencio-Wszalek et al. 1992; Eliasson & Meyerson 1994). It is also possible that the accuracy with which an adult male deposits its scent marks on top of or near to those deposited by a female conspecific improves with age.

The age of female voles did not affect the proportion of scent marks of male voles that they over-marked. Two-3 mo-old, 5-7 mo-old, and 10-12 mo-old female meadow voles over-marked a similar number of marks deposited by male voles. Our results suggest that older adult female voles and younger adult female voles are as likely to indicate to males their presence in an area by over-marking their scent marks. Previous work, however, has shown that female meadow voles in a heightened state of sexual receptivity, such as during postpartum estrous, over-marked a larger percentage of male marks than did female voles in other states of sexual receptivity (Ferkin et al. 2004b). It appears that for female meadow voles, their ability or willingness to attract a mate may depend more on their state of sexual receptivity than on their age (Ferkin et al. 2004b, 2008; Ferkin & Pierce 2007; Ferkin & Leonard in press). This is not too unusual in that most sexually receptive females, independent of their age, may be selected as potential mates by male conspecifics (Trivers 1972).

Overall, the data from present study on meadow voles do not support the models which predict that short-lived animals display behaviors during interactions with opposite-sex conspecifics that favor younger adults over older adults (Spruijt et al. 1989; Boonstra 1994; Forslund & Part 1995; Hansen & Price 1995). The over-marking behavior of female meadow voles was also not consistent with these models. The models for short-lived animals did not explain the finding that 2-3 mo-old, 5-7 mo-old and 10-12 mo-old female voles did not differ in the amount of scent marks they depositing in an arena that was previously marked by an opposite-sex conspecific. The frequency of scent marking in adult North American beavers was also not affected by their age (Herr et al. 2006). However, many studies have shown that an individual's age affected its scent marking. Scent marking was highest after puberty and then decreased with age in gray mouse lemurs (Aujard & Némoy-Bertholet 2004; Cayetanot et al. 2006) and in honey badgers (Begg et al. 2003). Scent marking increased after puberty and continued to do so as the individuals aged among golden lion tamarins (Kleiman & Mack 1980), male mice (Arakawa et al. 2007), and a female Russell Terrier (Cudd-Wirant et al. 2006). At present, it is not clear if current models of aging can be used to predict the scent marking and over-marking behavior of many terrestrial mammals. Our data correspond to the models that predict that the tactics that older and younger adult male voles use to communicate with opposite-sex conspecifics may be best explained by life history tradeoffs, the likelihood that male and female conspecifics interact, and mate choice (Partridge & Endler 1987; Kokko 1998; Beck & Powell 2000).

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Figure 1.

The number (mean $\pm$ SEM) of scent marks deposited by meadow voles (subjects) in an arena that was previously scent marked by an opposite-sex conspecific. No statistical differences were found in the number of scent marks deposited by male and female voles ($p > 0.1$).

Figure 2.

The number (mean $\pm$ SEM) of scent marks deposited by meadow voles in the arm of the arena that was previously scent marked by an opposite-sex conspecific (scented arm) and the arm of the arena that was not previously scent marked (clean arm). Bars capped with different letters are statistically different at $p < 0.001$.

Figure 3.

The proportion (mean $\pm$ SEM) of scent marks deposited by male voles and female voles in an arena that was previously scent marked by an opposite-sex conspecific. Bars capped with different letters are statistically different at $p < 0.05$.