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Author: Ferkin, Michael H.

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Odor-related behavior and cognition in meadow voles, *Microtus pennsylvanicus* (Arvicolidae, Rodentia)

Michael H. FERKIN

*The University of Memphis, Department of Biological Sciences, Ellington Hall, Memphis, TN 38152, USA;
e-mail: mhferkin@memphis.edu*

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Abstract. Mammals have the ability to identify particular conspecifics and in doing so use this information to discriminate between them, and respond in a manner that increases their survival and fitness. This narrative focuses on the behavioral challenges that voles face when they have to make decisions about mate choice, same-sex competition, odor communication, and sperm allocation. The narrative points out the different decisions that voles may make when they encounter the social information contained in the scent marks and over-marks of different conspecifics. The narrative demonstrates that the choices made by voles, and their resulting behaviors, may depend on several factors including the vole's own condition, age, and sex and those of nearby same- and opposite-sex conspecifics. The results of these studies are ecologically relevant as they reflect situations and challenges faced by free-living voles. The range of situations that voles find themselves and the decisions voles make when they encounter a potential mate or competitor become the backdrop of the narrative. Concentrating on the responses of a single model species was intentional. This approach may allow specific comparisons with other terrestrial mammals, facing similar behavioral and ecological challenges.

Key words: conspecific identification, scent marks, mating, competition

Introduction

The manner in which any animal, including a human, behaves depends on the information it receives from its environment (Dukas & Ratcliffe 2009, Ferkin 2011). The capacity to use this information to make decisions how an individual will behave when it encounters a same-sex or opposite-sex conspecific depends on that individual's sensory processes, perception, experience, and recall (Bekoff et al. 2002, Shettleworth 2010). For many terrestrial mammals, scent marks convey information about the donor to nearby conspecifics and heterospecifics (Johnston 1983, 2003, Hurst & Beynon 2004, Ferkin et al. 2010). These scent marks are typically deposited on prominent objects or along paths that are shared with

conspecifics (Brown & Macdonald 1985). Therefore, individuals will enter areas that contain single scent marks and overlapping scent marks, over-marks, which are comprised of scent marks from two or more conspecifics. These scent marks may be a signal that provides particular information about the donors to individuals that encounter these marks, which may affect how they respond to these donors. Typically, individuals spend more time investigating the scent marks of opposite-sex conspecifics than they do same-sex conspecifics (Ferkin & Seamon 1987). Consequently, scent marks can be used to attract mates (Johnston 1983). Individuals can use this information to accurately assess the condition of potential mates and competitors. These scent marks are viewed as

honest signals of the donor's quality or condition (Roberts 2007) because many of the substances used as scent marks are digestive exudates (Albone 1984). The response of individuals to scent marks as well as where individuals deposit their own scent marks may affect their subsequent interactions with conspecifics. Presumably, individuals may spend more time investigating the scent marks of more attractive than less attractive opposite-sex conspecifics. Similarly, individuals in better condition may scent mark and over-mark more often than would individuals in worse condition.

Consider a small mammal, such as a rodent, in its home range or territory. It is surrounded by scent marks, some are its own scent marks but most of the scent marks that it encounters are from conspecifics (Brown & Macdonald 1985, Gosling & Roberts 2001, McClintock 2002, Johnston 2003). Some of these scent marks are encountered singly; other scent marks may be overlapping, creating over-marks of two or more conspecifics. Let's imagine that this rodent is a male meadow vole, *Microtus pennsylvanicus*. Meadow voles are a seasonally breeding, non-monogamous microtine rodent that lives in northeastern USA (Madison 1980a, b); that uses olfaction, its primary sensory modality, to navigate through its world (Albone 1984), and chemical signals to communicate with conspecifics (Ferkin & Seamon 1987, Ferkin 2007, 2010, Vlautin et al. 2010) mates with multiple partners (Boonstra et al. 1993), although they have few direct interactions with opposite-sex conspecifics (Dewsbury 1990). How does our male vole respond when it encounters the scent marks from conspecifics? Also, does our vole respond in the same way to the scent marks from two different donors that he encounters separately and to overlapping scent marks, over-marks of the same two donors? Does the vole use a rule of thumb to govern its response? That is, do voles use an easily learned and easily applied procedure for making some determination. If so, was it a learned part of the vole's procedural memory? Does the vole always respond preferentially toward all opposite-sex conspecifics, and not so toward all same-sex conspecifics? Or, does the vole adjust its response by behaving preferentially to a particular conspecific? For example, do voles respond preferentially towards a familiar individual or an unfamiliar individual? If so, this would indicate that voles have a social memory for conspecifics, and use some form of decision making in social or sexual situations other than simply applying a rule of thumb. Our vole's response could also be affected

by its experience with a particular conspecific. The vole may recall the type of interaction it had with that conspecific, the location of the interaction, and when it occurred. This capacity would indicate that the vole has an understanding of the what, when and where of an event, akin to episodic-like memory. The vole may use this information to plan its route so that it may or may not encounter a particular conspecific. If it encounters a conspecific, it may use social information and its recollections to make decisions as to how it may respond in that situation. If so, this would suggest that our vole has the ability to remember the past, choose in the present, plan for the future, and make decisions based on this information. The extent to which voles have such capacities acts as a backdrop for explaining the actions of a male meadow vole as he wanders through his home range in an attempt to find a mate.

Meadow voles were studied because they use scent marks and over-marks to facilitate and coordinate male-female encounters and interactions (Ferkin & Seamon 1987, Ferkin et al. 1999, Woodward et al. 1999, 2000). Male and female do not nest together and have infrequent encounters with one another (Madison 1980a, b, Dewsbury 1990). However, males and females mate with multiple partners (Boonstra et al. 1993, Berteaux et al. 1999). Males have large, overlapping home ranges that encompass the territories of one or more females (Madison 1980a). Voles may enter areas that contain the scent marks and over-marks of opposite-sex conspecifics that may reside there or that may be passing through.

When he enters such areas he may begin to self-groom. By self-grooming voles rub scent producing tissues on their body that release odiferous substances into the air (Thiessen 1977). These substances have two apparent functions within the realm of olfactory communication (Ferkin & Leonard 2010). First, self-grooming increases the release of scents that make the groomer more easily to detect (Ferkin et al. 1996). This allows nearby individuals to focus on the odors of the groomer. Several experiments have shown that when voles self-groom during an encounter with the scent marks of sexually receptive opposite-sex conspecifics, the groomer becomes more attractive to the opposite sex (Ferkin et al. 1996, 2001). Second, since groomers bring their own scents into contact with their own olfactory sensory apparatus, groomers may become more stimulated to find that nearby opposite-sex conspecific (Vaughn et al. 2010). In order to find that potential mate, the vole must locate that individual's scent marks, distinguish them from

the scent marks of other voles, and follow them to its scent donor. This process is the focus of the remainder of the paper.

Scent marks and over-marks

Let's go back to our male vole. He has entered a nearby runway and just encountered the scent marks from conspecifics. The manner in which the male encounters these scent marks, and that he expects to see them as he moves along these well-traversed paths, will become part of his perceptual memory. Such memories are dependent on nonmnemonic factors such as his attention, motivation, sensory responsivity, and motor capabilities, as well as the receptive fields of his olfactory cells (Williams 2002). Our vole may have learned a rule of thumb, which will allow him to respond a predictable way. That is, respond to the freshest scent marks since they may indicate that the donor may be nearby. This response may become more predictable and non-varying over time. Our vole, however, may encounter scent marks and over-marks of multiple conspecifics with whom he may or may not be familiar. To select the appropriate response to such scent marks, our vole will likely use some form of social recognition memory (Franklin & Ferkin 2006, 2008). This social memory will allow the vole to discriminate between the scent marks that he encounters and, in doing so, assign them to their donors. This social memory allows our male vole to categorize the scent marks as being from males or females (a category), as known (an individual), or as sexually receptive (a feature) (Franklin & Ferkin 2006). Forming this association may become more complex, however, if voles encounter the overlapping scent marks from two different conspecifics (Johnston et al. 1994, Ferkin et al. 1999). Overlapping scent marks from two different donors may provide additional information to the individual that it may not receive if it encountered the scent marks from the two donors separately (Hurst & Beynon 2004, Ferkin et al. 2010, 2011a, b, Vlautin et al. 2010).

The manner in which an individual responds to these scent marks may depend on whether the scent marks are encountered as single, separate marks or as the top- or bottom-mark of an over-mark. For example, when voles (*Microtus* spp.) and golden hamsters (*Mesocricetus auratus*) encounter the single and separate scent marks from two conspecifics of similar quality they show no preference between the scent marks from these two donors (Johnston 1983, Ferkin & Seamon 1987). However, when voles and hamsters are first exposed to the over-marks of the same

conspecifics, they later respond preferentially towards the mark of the conspecific that provided the top-scent mark than that of the conspecific that provided the bottom-scent mark (Johnston et al. 1994, 1995, 1997a, b, Ferkin et al. 1999, Woodward et al. 1999, 2000, Johnston 2003). Currently, we do not know how individuals respond to an area that contains both the over-marks and the single and separate scent marks from the same two conspecifics. That is, are they responding to the single scent marks, the over-marks, or both types of marks? This question is important in that in a given area an individual will likely encounter a combination of scent marks and over-marks of two same-sex conspecifics (Brown & Macdonald 1985, Ferkin & Pierce 2007).

Whether animals such as meadow voles differ in their responses to over-mark and to single scent marks from the same scent donors was addressed. The hypothesis that voles differ in the amount of time they will investigate the scent marks from two potential mates if they encounter them first as single scent marks or first as the top- and bottom-scent marks from an over-mark was tested (Ferkin et al. 2011a). A prediction of this hypothesis is that voles will spend more time investigating the mark of the top-scent donor over that of the bottom-scent donor when they encounter an area that contains more over-marks than single scent marks from two same-sex scent donors. This prediction is based on the premise that voles may be able to assess differences in features of the quality or condition of the donors (diet, age, reproductive state, social status) (Ferkin 2007, Roberts 2007) that differed in the proportion of over-marks to single scent marks they deposit. Presumably, higher "quality" voles will deposit a greater proportion of over-marks than scent marks than would lower "quality" voles. Alternatively, voles will spend more time investigating the mark of the top-scent donor over that of the bottom-scent donor independent of the proportion of over-marks and single scent marks from two same-sex scent donors they encounter. This prediction is based on the premise that voles may be able to compare features of two conspecifics that may not be possible if individuals encountered the scent marks of these conspecifics separately (Johnston et al. 1995, Woodward et al. 1999, 2000, Ferkin et al. 2010). Single scent marks may provide less comparative information about possible associations between the donors (Vlautin et al. 2010).

Ferkin et al. (2011a) found that male voles spent more time investigating the mark of the top-scent donor over that of the bottom-scent donor when they encounter an

area that contained more over-marks than single marks of two same-sex scent donors. By comparison, female voles spent more time investigating the mark of the top-scent donor over that of the bottom-scent donor when they encounter an area that did not contain more over-marks than single scent marks from two same-sex scent donors. Interestingly, the proportions of over-marks that male and female meadow voles needed to encounter to display a preference for the top-scent donor over the bottom-scent donor of an over-mark, 60 % for male subjects and 40 % for female subjects, were similar to the proportion of over-marks that males and females deposit when they encounter the scent marks from opposite-sex conspecifics. Previous work has shown that in the same size T-maze female voles over-marked more than 60 % of the scent marks from a female conspecific and that male voles over-marked more than 40 % of the marks of another male (Ferkin et al. 2004a, b). It is intriguing to consider that the proportion of over-marks that a same-sex conspecific deposits in an area is similar to the proportion of scent marks that need to be over-marked for an individual encountering these marks to respond preferentially to the top-scent donor over the bottom-scent donor (Ferkin 1999). This would suggest that over-marking is a not a random activity among voles as suggested by Wolff et al. (2002). Instead, the data support the hypothesis that over-marking allows the top-scent donor to signal a relationship or association with the bottom-scent donor (Johnston 2003, Ferkin et al. 2004a, b, Ferkin & Pierce 2007). Rather, the present findings support and extend the view that over-marking is a specialized type of odor communication that is directed at conspecifics (Rich & Hurst 1998, Johnston 2003, Ferkin et al. 2004a, b, Ferkin & Pierce 2007). The sex differences that existed in the response of female and male meadow voles to areas that contained different combinations of scent marks and over-marks of two scent donors may be attributed to differences in their natural history. Female meadow voles occupy territories that are visited by male conspecifics (Madison 1980a, b). Although females mate with multiple males (Boonstra et al. 1993), they should exert some degree of mate choice when they encounter the scent marks of males that visit their territories. Female voles may choose a male based on whether he is the top-scent donor of an over-mark (Johnston et al. 1997a, b, Ferkin et al. 1999). The top-scent male of an over-mark may be more likely than the bottom-scent male to be nearby (Wolff et al. 2002, Ferkin et al. 2005, 2008). It is also possible that position in the over-mark reflects differences

in quality between the top- and bottom-scent males (Rozenfeld et al. 1987, Rich & Hurst 1998, Johnston 2003, Ferkin 2007, 2010).

In contrast to females, male meadow voles occupy large home ranges and wander through the territories of one or more females. Thus, males are likely to encounter areas that contain the scent marks and over-marks of females that are residents in these territories or those of females that are looking for territories to occupy. Males will likely mate with both resident and transient females (Boonstra et al. 1993); however, they will have a greater chance of reproductive success by mating with females that are territory owners (Wolff 1993). Upon encountering the over-marks and scent marks of two sexually receptive females, males apparently respond preferentially to the top-scent female if she has over-marked at least 60 % of the scent marks of the bottom-scent female. At this point in time, it is not known if males view the top-scent females as territory owners, but since male fitness depends on the number of females that he mates with (Boonstra et al. 1993, Berteaux et al. 1999, delBarco-Trillo & Ferkin 2004) and if they are territory owners (Wolff 1993), male voles may respond preferentially to the top-scent female if she is more likely than the bottom-scent donor to be the resident (Ferkin & Pierce 2007).

Let's return to our male vole. Our male vole has encountered the scent marks and over-marks of two females. Typically, he would respond preferentially to the mark of the top-scent female but not to that of the bottom-scent female (Ferkin et al. 1999). He does so, because he may be unfamiliar with both the top- and bottom-scent females. However, our male vole would likely encounter the scent marks from females that possess territories in his home range (Madison 1980a, b). He may be familiar with the scent marks from these females relative to the scent marks from females that are new to his home range or have simply passed through it. It is likely that our male vole may respond differently to the scent marks from particular females if he is familiar with their scent marks. Several studies have examined the effects of familiarity on the preferences of rodents, including voles, to opposite-sex partner (Ferguson et al. 1986, Shapiro et al. 1986, Ferkin 1988, Řičánková et al. 2007). These studies suggest that for most rodents familiarity between opposite-sex conspecifics reduces agonistic behavior and increases affiliative behaviors towards one another (Blaustein et al. 1987, Cheetham et al. 2008). In this way, our male could increase his reproductive success by increasing his chances of interacting with novel females as opposed to familiar females.

Ferkin et al. (2010) tested the hypothesis that the amount of time individuals investigate the scent marks from opposite-sex conspecifics is affected by their olfactory experience with those conspecifics. Male and female meadow voles spent more time investigating the scent marks from the opposite-sex conspecific with which they had four days of olfactory experience than those of a novel, opposite-sex conspecific. In addition, it was discovered that voles exposed to a mixed-sex over-mark in which they had no prior olfactory experience with the top or bottom-scent donor, later spent more time investigating the scent mark of the opposite-sex conspecific that provided the top or bottom-scent mark in the over-mark than that of a novel, opposite-sex conspecific. Male and female voles spent similar amounts of time investigating the scent mark of a novel, opposite-sex donor and the scent mark of the bottom-scent, opposite-sex conspecifics. Lastly, female voles exposed to a mixed-sex over-mark that contained the scent mark of an opposite-sex conspecific with which they had four days of olfactory experience, later spent more time investigating the mark of a novel male than that of the male that provided the bottom or top-scent mark in the over-mark (Ferkin et al. 2010). In contrast, males spent more time investigating the mark of the female that provided the top-scent mark in the over-mark, but spent similar amounts of time investigating the mark of the novel female and the mark of the female that provided the bottom-scent mark in the over-mark. These results suggest that the manner in which voles responds to over-marks was affected by their familiarity with the top- or bottom-scent donor (Ferkin et al. 2010).

Episodic-like memory in male voles

Now imagine that our male has located the scent marks from a female. He needs to identify the reproductive state of the female. He is more likely to mate with a female that is in postpartum estrus (PPE), a period of about 12-24 hours after parturition, in which females are highly attractive and responsive to male conspecifics (Ferkin & Johnston 1995, Ferkin et al. 2004b, 2008b). However, finding a PPE female may be a daunting task because postpartum estrus is relatively short, lasting 12-24 hours after parturition (Keller 1985), and that male and female meadow voles do not share a nest and likely to have few repeated encounters with one another (Dewsbury 1990). How does our male vole locate a PPE female, determine how long she will be in PPE, or recall the location of a pregnant female that will soon enter PPE?

During the breeding season, female voles tend to occupy territories that are fixed spatially, but are dispersed widely across the home range of several males (Madison 1980a, b). Female voles are induced ovulators and do not undergo estrous cycles (Milligan 1982, Meek & Lee 1993). Thus, the reproductive condition and sexual receptivity varies among female voles during the breeding season. That is, female voles may be pregnant, lactating, both pregnant and lactating, neither pregnant nor lactating, or in a period of heightened sexual receptivity during PPE (Keller 1985). Postpartum estrus females are more likely to mate with a male and become pregnant relative to females that are not pregnant or lactating, or females that are pregnant, lactating or both (Keller 1985, delBarco-Trillo & Ferkin 2007). Since female sexual receptivity varies and they enter PPE asynchronously (Keller 1985), and since males increase their fitness by mating with as many females as possible (Boonstra et al. 1993), it was hypothesized that after a single visit to a female, male voles will later recollect her previous reproductive state (what); her location (where), and how long she will be in that reproductive state (when).

Despite the controversy swirling around the ability of animals to recollect specific aspects of past events (Clayton & Dickinson 1998, Roberts 2002, Suddendorf & Busby 2003, Crystal 2009), it is not difficult to imagine that some animals may use information from such past events to secure a mate. An important feature that often characterizes most non-human mammals is that females do not mate with males when they are not in a heightened state of sexually receptivity (Bronson 1989). For many species of mammals, including meadow voles (Madison 1980a, b), the majority in which opposite-sex conspecifics live separately during the breeding season, males should be able to discriminate among females in different states of sexual receptivity. Thus, in those species, male may be able to identify females that are in a heightened reproductive state, their location, and the length of time that the females are in this heightened state. Episodic memory involves encoding and retrieving the contents of a personal past episode. This type of memory includes what happened, where it took place and when it occurred (Tulving 1972). Recalling the “what”, “when”, and “where” of a past event is a feature of episodic-like memory (Clayton & Dickinson 1998). Researchers have argued that ecological pressures, such as recalling food patches, tool use and mates may have allowed non-human animals to have the capacity for the “what, when,

and where” of a past event (Roberts et al. 2008, 2009, Crystal 2010, Salwiczek et al. 2010, Basile & Hampton 2011). We tested the hypothesis that male meadow voles possess the capacity to recall the what, where, and when of a single past event associated with mate selection (Ferkin et al. 2008b). Briefly, male voles were allowed to explore an apparatus that contained two chambers. One chamber contained a day-20 pregnant female (24 hour prepartum). The other chamber contained a sexually mature female that was neither pregnant nor lactating (REF female). Twenty-four hours after the exposure, the males were placed in the same apparatus, which was empty and clean. At this time, the pregnant female would have entered PPE. Males initially chose and spent significantly more time investigating the chamber that originally housed the pregnant female (now a PPE female) than the chamber that originally housed the REF female. Male voles also explored an apparatus containing a chamber with a PPE female and one chamber containing a REF female. Twenty-four h later, males were placed into an empty and clean apparatus. The males did not display an initial choice and they spent similar amounts of time investigating the chamber that originally housed the PPE female (now a lactating female) and the chamber that originally housed the REF female. We recently extended these findings by allowing male voles to enter an apparatus containing a female that was in PPE and a female that was day-20 pregnant. The males spent more time near the chamber containing the PPE female compared to the chamber containing the day-20 pregnant female. The males were placed in the empty apparatus 24 hours later and spent more time investigating the chamber that would have housed the d-20 pregnant female, who would now be in PPE, than they investigated the chamber that formerly housed the PPE female, who would now be d-2 lactation (Fig. 1). These results and those from additional experiments suggest that male voles may have the capacity to recall the “what”, “where”, and “when” of a single past event, which may allow males to remember the location of females who would currently be in heightened states of sexual receptivity (Ferkin et al. 2008b).

Male voles were able to recollect the reproductive states of the females they encountered in the exposure phase and in the test phase spent more time in areas that would have been expected to contain PPE females and displayed initial choices for such areas. This finding indicates that male meadow voles likely recollect the point in time when they previously encountered a female in a particular reproductive state (Ferkin et al.

2008b). Such a capacity in voles seems to be consistent with their space use and social biology. Recall, during the breeding season, male meadow voles occupy large overlapping home ranges, which encompass the territories of one or more females (Madison 1980a, b). The females may be widely dispersed over a male’s home range. To coordinate breeding and reduce sperm competition, our male vole may keep track of the reproductive condition of nearby female conspecifics, and visit them when they are in PPE (Ferkin et al.

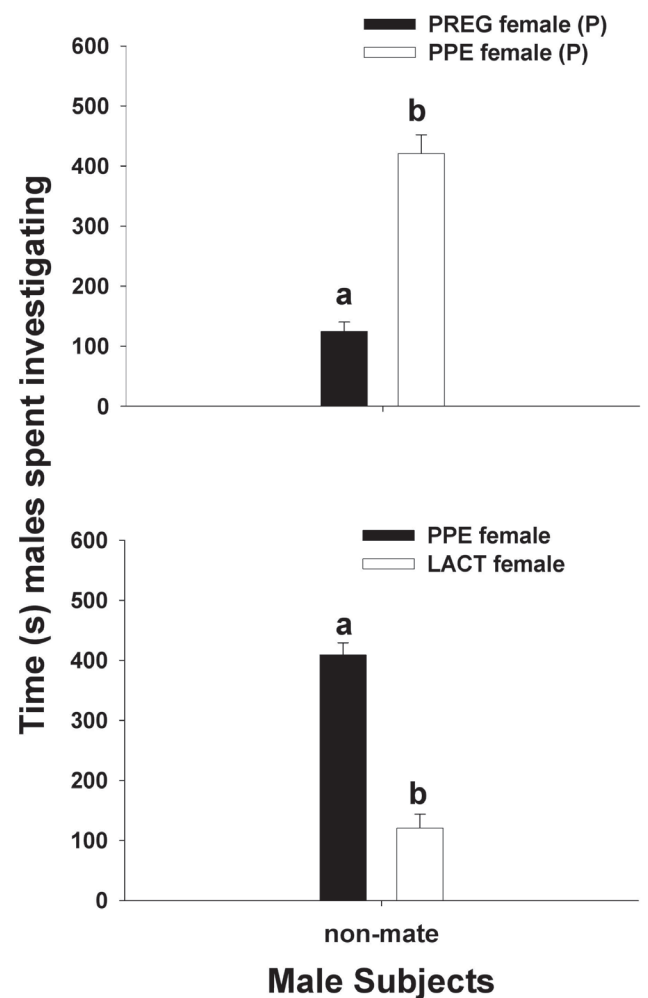


Fig. 1. The amount of time (s) \pm SEM that male voles, *Microtus pennsylvanicus*, spent investigating the sides of the apparatus (a) during the exposure phase that currently housed a postpartum estrus (PPE) female and a day 20 pregnant (PREG) female (P – indicates that the donor females were present). (b) The amount of time (s) \pm SEM during the test phase that male voles spent investigating the empty sides of the apparatus that would house a lactating day 2 (LACT) female vole and a PPE female vole. Histograms capped with different letters are statistically different at $p < 0.05$ (paired t-test).

2008b). A preference by males for a PPE female is consistent with the fact that such males should get a bigger payoff in reproductive success when they locate and mate with a PPE female than they would by locating and attempting to mate with a female that was not in PPE. PPE females are in heightened sexual receptivity, require a shorter copulatory bout, and are more likely to become pregnant than are females in other reproductive states (Keller 1985, delBarco-Trillo & Ferkin 2007).

We do not know whether voles achieve this through mental time travel, similar to the ability of bonobos and orangutans to anticipate the need for particular tools (Mulcahy & Call 2006) or through a feed forward system where the subject knows later on where something is and its state, rather than having to mentally revisit past events (e.g. Suddendorf & Busby 2003). There are many future oriented mechanisms that make species act in ways that are in tune with where important things like food, mates, or shelter are likely to be found (Suddendorf & Corballis 1997). The results do not clearly show that male voles mentally reconstruct a past situation *per se* (Ferkin et al. 2008b). What the results do show is that the voles spend more time where they could reasonably expect a receptive female to be now. This finding suggests that voles have the capacity of prospecting (Ferkin et al. 2008b). However, it does not tell us the mechanism underlying prospecting. Alternatively, our male meadow vole may anticipate the identity (what), location (where) and when females enter and leave postpartum estrus (when), which is achieved through the use of episodic memory and mental access to a past event and subsequent extrapolation into the future (Franklin & Ferkin 2006, 2008, Ferkin et al. 2008b). Nonetheless, having the capacity to identify a potential mate, locate it and visit it when it is sexually receptive may benefit other animals in which the reproductive condition of females varies and opposite-sex conspecifics live separately during the breeding season (Ferkin et al. 2008b), or when males are attempting to monopolize mates (Trivers 1972).

The scent marks from PPE females and those from male conspecifics

In some species, such as meadow voles, in which females and males copulate with multiple partners (Boonstra et al. 1993, Berteaux et al. 1999), it is likely that the female may have already mated with one or more of the males that deposited their scent marks near her scent mark. Males may use this social information, particularly from the presence of scent marks of other

males, to assist them in selecting females as mates (Dugatkin 1992, Valone 2007). Such information could induce males to avoid a female that has attracted a number of male suitors. Such a female may have mated with these suitors, which may increase the likelihood of sperm competition for the next male (Parker et al. 1996, Birkhead 2000), and cause the male to increase the amount of sperm he allocates in his ejaculate (delBarco-Trillo & Ferkin 2004, 2006a, Vaughn et al. 2008). Conversely, social information may induce males to become more attracted to a female that has many suitors. This behavior is known as mate copying (Dugatkin 1992), and for the most part has been studied from the perspective of females selecting males as mates that they have observed with other females (Galef et al. 2008).

Males may also choose a female based on the information about her current reproductive state that is conveyed in her scent marks. This information is important because there are female mammals, such as voles that do not undergo regular estrous cycles (Milligan 1982) and the reproductive condition and sexual receptivity of females varies (Keller 1985). Males are more attracted to the scents produced by conspecific PPE females than they are to the scents produced by conspecific females that are not in PPE (Zeigler et al. 1993, Ferkin & Johnston 1995, Lazaro-Perea et al. 1999, Ferkin et al. 2008b). A consequence of the preference for PPE females is that many males may visit a PPE female and leave their scent marks near her nest.

Let's say that our male vole finally encounters a female in PPE. He still has to make a decision about choosing her as a mate. This PPE female may have already attracted a number of males to her (Ferkin & Johnston 1995, Ferkin 2006). Thus, the nest site of a PPE female will likely have the scent marks from males nearby and adjacent to her scent marks. How does our male respond, given that mating with a female whose nest contains the scent marks from other males, increases his sperm investment or reduces the likelihood of his siring the litter (delBarco-Trillo & Ferkin 2004, 2006a, Vaughn et al. 2008)? In a recent study, Vaughn & Ferkin (2011) tested the hypothesis that the presence of scent marks from males adjacent to those of a female may indicate to the investigating male how many males have visited this female, which may affect how attractive she is to other males. We tested the hypothesis by exposing male meadow voles to the scent mark of a PPE female and a female that was not in PPE, a reference female (REF female), a female that was in a moderate state of sexual receptivity, and then

placing the scent marks of 0, 1 or 5 males adjacent to the scent marks of these two female scent donors.

Vaughn & Ferkin (2011) found that males spent more time investigating the scent mark of a female adjacent to the scent marks of more males than the scent mark of a female adjacent to the scent marks of fewer males. This suggests that the presence of the scent marks of rival males may increase the interest of that male for that female or somehow increases the attractiveness of her scent mark to him. The fact that males spent more time with the REF females adjacent to the scent marks of five males compared to the time that males spent investigating the scent mark of a PPE females with the scent marks of zero or one male adjacent to it, offers the possibility that male voles may choose a female, independent of her reproductive state that has been visited by many males. Such a preference for a female, although she may not be in PPE, is similar to mate copying by female in other species when they select lower quality males that have been observed with a female over higher quality males that have been alone (Dugatkin 1992). Given that female meadow voles mate multiply (Bertheaux et al. 1999), it is likely that a female that has scent marks of males adjacent to her own scent mark may have already mated with one or more of these nearby males it may be costly to male meadow voles to choose her as a potential mate (delBarco-Trillo & Ferkin 2004, 2006a, Pound & Gage 2004, Vaughn et al. 2008).

Vaughn & Ferkin (2011) also found that male subjects exposed only to the scent marks of male conspecifics spent more time investigating the scent marks of five males compared to the scent mark of one male and the scent marks of five different males more than five scent marks of the same male. Males may be attracted to the larger numbers of scent marks because they represent a stronger stimulus than would a smaller number of scent marks, akin to some type of sensory bias (Ryan & Rand 1993), because the time to process such social information increases as the number of scent marks increases (Ferkin et al. 2011a, b), or because males have the capacity for relative numerosness and select more scent marks over fewer scent marks (Ferkin et al. 2005, 2008a).

Why should a male vole select a female vole as a mate if it increases the likelihood of sperm competition, an increased sperm allocation, and a decreased chance of siring the litter? It is possible that the costs of selecting a female that has possibly mated with many males may be offset by the benefit of mating with a female that has already been assessed by other males and found to be of sufficient quality. Alternatively,

a male may benefit from mating with this female if she will require little or no courtship (Vaughn et al. 2010, 2011) and may not be as stringent in assessing his condition or quality. The latter two conjectures support the notion that competition among males for potential mates is intense (Boonstra et al. 1993) and that females may encourage multiple mating (Bertheaux et al. 1999). Female voles may gain indirect and direct benefits from mating with multiple males (Hobbs & Ferkin in press). It is less clear, what males are gaining from mating with a “popular” female. For males, such a mating may represent a tradeoff between the costs and benefits associated with mating with a popular female.

However, Vaughn & Ferkin (2011) also discovered that differences in the reproductive condition of the female scent donors could also affect the response of males to the scent marks of the female donors. Interestingly, males spent more time investigating the scent marks of PPE females to those of the REF females when the number of scent marks of males that were adjacent to the scent marks of the female donors was the same. Likewise, males preferred the scent marks of PPE females to those of REF females if there were no scent marks of males adjacent to either of the scent marks of the female donors. Taken together, these observations allowed Vaughn & Ferkin (2011) to suggest that a male vole’s preference for a female may be guided by two simple rules of thumb. First, select a female if she has more male suitors than another female, independent of the reproductive state of either female. Second, if however, the number of male suitors is the same for each female, select the female that is in a more heightened state of sexual receptivity.

Relative numerosness in voles

We have shown that meadow voles can discriminate between the donors of the top and bottom scents of an over-mark by spending more time investigating the mark of the top-scent donor than that of the bottom-scent donor when the two marks are offered separately (Johnston et al. 1997a, b, Ferkin 1999, Woodward et al. 2000). In free-living populations of voles, however, the identity of the top- and bottom-scent donors may vary, especially if the two scent donors are in close proximity to one another. Thus, at any given time in a particular area, an individual may have some of its marks on top of those deposited by another individual or below those deposited by that individual. It is not known whether voles can discriminate between these two different scent-marking individuals and identify

the individual whose scent marks was on top more often than the other individual. Is it possible that voles have a sense of number? If so, the simplest explanation is that voles can make a relative size judgement – such as distinguishing an area containing more of one individual's over-marks as compared to less of another individual's of over-marks. If voles can identify the more frequent top-scent donor from the less frequent top-scent donor and respond accordingly, it may be an indication that they have the capacity for relative numerosness (Davis & Perusse 1988, Beran 2001, Hauser et al. 2003). An important feature of this ability is that animals do not have to count the number of objects in the two groups (Beran et al. 2008).

We determined if voles displayed relative numerosness by exposing them simultaneously to a set of over-marks by one individual and a smaller or larger set of over-marks by another individual. We found that voles responded preferentially to the donor who was the top-scent donor on more of the over-marks as compared to the donor who was the bottom-scent on most of the over-marks. This finding suggested that voles displayed the capacity for distinguishing more from less. Specifically, after investigating such over-marks male and female voles showed a preference for the individual whose scent marks was on top most often (Ferkin et al. 2005, 2008a). Females were capable of spontaneously discriminating between areas in which donor A's marks were on top of donor B's marks four times relative to the three times donor B's marks were on top of donor A's marks. Males could make a similar discrimination if donor A's marks were on top of donor B's marks six times relative to the one time donor B's mark was on top of one of donor A's marks (Ferkin et al. 2005). Female voles behaved as if they were able to make finer discrimination of relative numerosness than did male voles.

The asymmetry in relative numerosness by male and female voles is intriguing in that the literature is replete with studies suggesting that sex differences exist in mathematical skills that favor males over females, particularly in primates and humans (Geary 1996). One argument is that males have better spatial and navigational abilities than females, which provides them with a greater need and capacity to solve problems in geometry and other mathematics-related activities (Geary 1996). The fact that male meadow voles have better spatial ability as compared to female meadow voles (Gaulin et al. 1990), but the former has poorer prenumerical ability than the latter is interesting (Ferkin et al. 2005). The findings suggest

that sex differences in distinguishing more over-marks from fewer over-marks are somehow separate from the spatial ability of meadow voles. Moreover, for voles it appears that spatial ability may be a poor predictor of relative numerosness, and vice versa. Female biases in relative numerosness may be the developmental link for more complex numerical processes, such as subitizing, estimation, and counting, and arithmetic reasoning in this species (Gallistel 1990, Boysen & Capaldi 1993, Hauser et al. 2003).

Sperm allocation

Our male vole has finally succeeded in finding a female and is mating with her. However, the scent marks of other males are near the nest of this female, suggesting that she may have already mated with one of more of these males (Boonstra et al. 1993, Salo & Dewsbury 1995, Berteaux et al. 1999). Thus, the incidence of sperm competition is likely to be high (Parker et al. 1996, Pizzari et al. 2003, 2008, Pound & Gage 2004). Male voles have developed physiological, morphological, behavioral strategies to confront the normal occurrence of sperm competition (Dewsbury 1982, Boonstra et al. 1993, delBarco-Trillo & Ferkin 2004). Briefly, male voles allocate different amounts of sperm during copulation after they assess the risk and intensity of sperm competition as indicated by the presence of scent marks of conspecific males found near a sexually receptive female. When a male meadow vole was paired with a female vole and both were exposed to the odor of a male conspecific, the copulating male will increase his sperm investment by over 116 % (delBarco-Trillo & Ferkin 2004). A male vole's sperm investment, however, does not rise as high if he is exposed to the scent marks of five males (delBarco-Trillo & Ferkin 2006a), suggesting that male voles are able to assess differences in the number of potential mates near a receptive female. Interestingly, the male did not alter his sexual behavior (delBarco-Trillo & Ferkin 2004, 2006a, b, c, 2007, Vaughn et al. 2008) as has been shown in other animals (Stockley & Preston 2004).

Given that male meadow voles adjust their sperm investment during mating when exposed to the scent marks of other males, it begs the question as to whether they adjust their sperm investment based on the information contained in the scent marks of competing males. For example, do males adjust their sperm investment if they encounter the scent marks of males that differ in some feature of their quality? Vaughn et al. (2008) discovered that males are able to adjust their sperm investment when they encounter

the scent marks of males that were not food deprived for 24 hour but do not increase their sperm investment during copulation when they are exposed to the scent mark of a male that was food deprived for 24 hour. Indeed, sperm investment was similar in the presence of the scent mark of a food-deprived male and in the absence of any scent marks from male conspecifics. These findings suggest that food-deprived males may represent a reduced risk of sperm competition relative to males that were not food deprived. The results of Vaughn et al. (2008) support and extend the hypothesis that sperm investment of a copulating male mammal will increase if he encounters the scent marks of a conspecific male that represents a stronger risk of sperm competition (delBarco-Trillo & Ferkin 2004, 2006a).

It appears that male voles can allocate different amounts of sperm when they encounter males that represent different relative risks of sperm competition (delBarco-Trillo & Ferkin 2004, 2006a, Vaughn et al. 2008). The ability to adjust sperm investment depending on both the relative risk of sperm competition and the intensity of sperm competition may be a strategy employed by males to use sperm prudently (Parker et al. 1996, Pizzari et al. 2003, 2008, Pound & Gage 2004). If there are multiple competitors, then the likelihood of siring the offspring of a particular female will decrease. The presence of other males causes a male to increase the amount of his ejaculate. An increase in ejaculate can increase the likelihood that a male inseminates a female, but it also limits the amount of sperm that he has remaining to inseminate additional females. This represents a possible tradeoff between the potential fitness he may gain from investing more sperm in the current female and the potential fitness he may lose if he makes this expenditure and locates additional females. The ability to adjust sperm investment may be an advantage to individuals in species characterized by a promiscuous mating system (Gomendio et al. 1998, Birkhead 2000), a social system where male mammals visit the territories of females that likely contain the scent marks of males that are able to represent different relative risks of sperm competition (delBarco-Trillo & Ferkin 2004, 2006a, b, c, Vaughn et al. 2008).

Concluding thoughts

A goal of this narrative was to *provide insight into the behavior of meadow voles*. I did so, by taking a look into the decisions facing meadow voles when they encounter the scent marks of potential mates and

same-sex competitors. We found that sex differences existed in the responses of voles to conspecifics. We found that within a sex, conspecifics varied in their responses. The results of these studies support the speculation that these responses may be a product of sexual selection. We also discovered that voles display a suite of behaviors that allow them to meet the challenges of finding mates. Specifically, voles can use information provided by scent marks to respond preferentially to the top-scent donors of an over-mark and seek out females in PPE more than they seek out female not in PPE (Ferkin et al. 1999, 2004a). Voles can also distinguish between individuals independent of whether their scent marks were encountered first as over-marks or as single marks (Ferkin et al. 2011a). It was also discovered that our male vole has the capacity to remember the past, choose in the present, and plan for the future. Males have an episodic-like memory for the what, when, and where of locations of females that differ in their reproductive state (Ferkin et al. 2008b). Voles are also able to discriminate between the top- and bottom-scent donors in an area after their position in over-marks may switch, indicating that they have the capacity for relative numerosness (Ferkin et al. 2005, 2008a).

The narrative also details studies that show that mate choice is more complex than previously thought (Ferkin & Seamon 1987, Wolff et al. 2002). We also found that voles adjust their behaviors when they encounter potential mates and that their responses depend on whether same-sex conspecifics are nearby. We also found that male voles spent more time investigating the scent mark of the PPE female to that from the REF female when the scent marks of both females were adjacent to either zero scent marks of males or were both adjacent to the scent marks of five males (Vaughn & Ferkin 2011). It may be beneficial for male voles to be attracted to the scent marks of a PPE female. Our data suggest that when only female reproductive state differs, males choose to spend more time investigating the scent marks of females in a heightened state of sexual receptivity (Vaughn & Ferkin 2011).

Overall, our data indicate that a combination of factors may influence a male's preference for the scent marks of potential mates. Males respond to features of a female's condition, such as her reproductive state as well as the number of males that may be nearby. In addition, male voles adjust their sperm allocation when they encounter the scent marks of male conspecifics near the nest of female that they are engaged in coitus (delBarco-Trillo & Ferkin 2004, 2006a, Vaughn et

al. 2008). The presence of other males causes a male to increase the amount of his ejaculate. An increase in ejaculate can increase the likelihood that a male inseminates a female, but it also limits the amount of sperm that he has remaining to inseminate additional females. This represents a possible tradeoff between the potential fitness he may gain from investing more sperm in the current female and the potential fitness he may lose if he makes this expenditure and locates additional females. Thus, it appears that voles, like other animals share the ability to identify particular conspecifics and in doing so use this information to discriminate between them, and respond in a manner that increases their own survival and/or fitness

(Dugatkin 1992, Franklin & Ferkin 2006, 2008, Galef et al. 2008).

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