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Meadow voles, *Microtus pennsylvanicus*, have the capacity to recall the “what”, “where”, and “when” of a single past event

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Abstract Some non-human animals may possess the ability to recall the “what”, “where”, and “when” of a single past event. 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 in two experiments. Briefly, male voles were allowed to explore an apparatus that contained two chambers. One chamber contained a day-20 pregnant female (24 h 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 postpartum estrus (PPE), a period of heightened sexual receptivity. 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 hours 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. The results of these and 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.

Keywords Recollection for what, when, and where · Voles · Reproductive state · Postpartum estrus

Introduction

Since Tulving’s (1972) paper describing the capacity of humans for episodic memory, much discussion, particularly within the last decade, has focused on whether non-human animals share the same capacity as do humans (Baddeley et al. 2001; Dere et al. 2006). Some authors argue that non-human animals may not share this ability with humans (Tulving 2001, 2002; Roberts 2002; Suddendorf and Busby 2003) in that episodic memory involves the *conscious* recollection of facts pertaining to specific and personal past experiences, essentially the recall of the “what, where and when” of personal events (Tulving 1983; Suddendorf and Busby 2003). They argue that to enable episodic memory, one must have a concept of subjective time, in that one must be able to comprehend events that happened in the past, present and potentially in the future. That is, one must

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be conscious of the fact that the recalled experiences have happened and are rooted in the past, rather than the recalled facts residing in the present (Roberts 2002). Secondly, some argue that a verbal language is a requirement for episodic memory (Nelson 1992; Suddendorf and Corballis 1997; Tulving 2002). Finally, others maintain that for episodic memory one must have a sense of self, and this self must be able to exist in subjective time (Suddendorf and Busby 2003).

In contrast, other authors believe that if the requirements for conscious recollection and a concept of self outside of the present are not included in the operational definition for episodic memory, then certain animals that have evolved the need for such capabilities may display aspects of it, such as food caching in scrub jays (Clayton and Dickinson 1998; Clayton et al. 2001, 2003, 2006; Griffiths and Clayton 2001). It has been reported that scrub jays remember the food type (what), the cache site (where), and the time during which the food items degraded (when). Briefly, jays were assigned to two different groups, a degraded group and a replenished group. The degraded group had pre-test training that included the birds learning that after a few days, the mealworms would degrade and become unpalatable. When tested four days after caching the meal worms and peanuts, the birds were more likely to locate the caches that contained meal worms rather than those that contained peanuts. However, when tested five days after caching, the scrub jays were more likely to locate caches containing peanuts. Additional experiments showed that scrub jays adjust their recaching behavior after pilfering of their food cache food by conspecifics. Clayton and colleagues suggested that scrub jays can mentally travel backwards and probably forwards in time, and that the birds recollect who watched them during their caching events and change their recaching behavior accordingly (Emery and Clayton 2001; Dally et al. 2006).

The literature is replete with studies claiming that a variety of animals can recollect the what, where, and when of a past event. For example, gorillas can remember after a single trial, the order of the food that was presented to them and who presented the food (Schwartz et al. 2005). In addition, studies on pigeons (Zentall et al. 2001), chimpanzees (Menzel 1999), mice (Dere et al. 2005), rats (Morris and Day 2003; Eacott and Norman 2004; Ergorul and Eichenbaum 2004; Babb and Crystal 2005; Eacott et al. 2005), and dolphins (Mercado et al. 1998) suggest the capacity for recollecting the what, when and where of a previous event. Yet, researchers have questioned the validity of these claims.

Several authors have criticized the methods and the interpretations of the findings of studies on the capacity of animals to recollect the what, where and when of past events. One argument against claims that animals display

such a capacity for recall is that the studies often fail to meet the content, structure, and flexibility criteria presented by Clayton and colleagues (2003, 2006). For example, it is not clear whether animals can form an integrated representation of what, when, and where, and use this information to solve novel problems (Schwartz et al. 2005; Dere et al. 2006). Some assert that these capabilities may only be attributed to humans (Tulving 2001; Roberts 2002; Suddendorf and Busby 2003). Authors also have questioned the degree to which animals may or may not display a capacity for what, when, and where for a past event and whether the methods are sufficient for measuring such a capacity. They raise the question of whether animals can demonstrate the capacity for the ‘when’ of a past event (Schwartz and Evans 2001; Zentall et al. 2001; Roberts 2002; Hampton and Schwartz 2004; Schwartz et al. 2005). In addition, some researchers argue that animals should be tested with ecologically relevant stimuli to gain a better understanding of the evolution of the recollection of what, when, and where of previous events (Clayton et al. 2001, 2003, 2006). However, others argue that an ethological approach weakens direct comparisons with humans and may restrict the number of species that can be studied (Dere et al. 2006). Finally, some researchers argue that since training is required for some animals to perform the task, especially those that are related to food and reward, animals may develop expectations or learn about what has to be recalled during the test trial, and not use retrospective memory retrieval to identify the what, where and when of a previous event (Zentall et al. 2001; Morris and Day 2003; Hampton et al. 2005; Schwartz et al. 2005).

Despite the controversy swirling around the ability of animals to recollect specific aspects of past events, 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). Thus, for many species of mammals, and particularly the majority of whom 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. They should be able to identify females that are in a heightened reproductive state, their location, and the amount of time that the females are in this heightened state. Such a capacity would benefit, for example, male meadow voles, *Microtus pennsylvanicus*; a microtine rodent. Adult male and female meadow voles live separately during the breeding season. At this time of year, female voles tend to occupy territories that are fixed spatially, but are dispersed widely across the home range of several males (Madison 1980). Female voles are induced ovulators and do not undergo estrous cycles (Milligan 1982; Meek and 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 postpartum estrus (PPE) (Keller 1985). PPE females are more likely to mate with a male than females that are not pregnant or lactating, or females that are pregnant, lactating or both (Ferkin et al. 2004; delBarco-Trillo and Ferkin 2007). Since female sexual receptivity varies and they enter PPE asynchronously, and since males increase their fitness by mating with as many females as possible (Boonstra et al. 1993), we hypothesize 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).

Methods

Animals

The female and male meadow voles used in these experiments were second, third and fourth generation offspring of field-caught animals captured in New York, Ohio and Kentucky, USA. These voles were born and raised under long photoperiod (14 L:10 D, lights on at 0700 h, CST and off at 2100 h, CST). This photoperiod simulated a day length typical of the breeding season. Adult voles born and reared under long photoperiod are considered to be reproductively active (Meek and Lee 1993). All voles used in this experiment were weaned at 18 days of age, housed with littermates until 35 days of age, and then housed singly in clear plastic cages (27 L × 16.5 W × 12.5 H cm). Voles were housed in cages that contained wood chip substrate, cotton-nesting material, ad libitum food (Laboratory Rodent Diet #5008, PMI, Inc., St. Louis, MO, USA) and water. Cages were cleaned and cotton-nesting material replaced every week.

Reproductive condition of the female donors

All female voles were between 125 and 135 days of age when used in the tests. Female meadow voles do not undergo estrus cycles (Milligan 1982; Keller 1985). To represent different levels of female receptivity, we used females that were pregnant for 20 days (d-20 pregnant), in postpartum estrus (PPE), females that were not pregnant or lactating (reference, REF females) and day two lactating females. Gestation lasts 21 days in voles, thus d-20 pregnant female voles deliver their litters within 24 h. We used 36 different pregnant females in this study.

Immediately after parturition, these females enter postpartum estrous (PPE), a period of heightened sexual

receptivity, which lasts 8–12 h (Keller 1985; Ferkin et al. 2004; delBarco-Trillo and Ferkin 2007). The PPE females used in the present study had delivered pups 4–6 h prior to testing and were in postpartum estrus. The litter size of these PPE females was 4.3 ± 0.5 pups/litter (mean \pm SEM). In this study, 12 different PPE females were used in each of experimental conditions 3 and 5 (see [Experimental Procedure](#)).

In this study, we used 12 different REF females in experimental conditions 1, 2, 4, and 5 (see below). REF females were not currently pregnant or lactating (Ferkin and Johnston 1995). The REF females had previously delivered a litter about 3–4 weeks before being used in the experiment (see below). The REF females had lived singly for approximately 21 days before being used as scent donors.

In experimental conditions 4 and 5 (see below), we used 24 females that were in their second day of lactation ($n = 12$ different females for each condition). Lactation is 14–16 day in duration, and pups are weaned when they are 16–18 day old (Keller 1985). The d-2 lactating females were no longer in PPE and thus were no longer in a heightened state of sexual receptivity (Ferkin and Johnston 1995). The PPE females and d-2 lactating females had not lived with their mate for 17 and 18 days, respectively, prior to be used as donors (see below).

It is important to note that PPE female voles are in a heightened state of reproductive receptivity and readily mate with males (Keller 1985; Ferkin and Johnston 1995; delBarco-Trillo and Ferkin 2007). In contrast, REF females, d-20 females, and d-2 lactating females are not in a heightened state of sexual receptivity, and may not as readily mate with males as do PPE females. REF females, d-20 females, and d-2 lactating females are considered to be in a moderate state of sexual receptivity (Ferkin and Johnston 1995; delBarco-Trillo and Ferkin 2004, 2006). In addition, PPE females produce odors that are more attractive to males relative to those produced by females that are d-20 pregnant, d-2 lactating, or REF females; the later three groups of females produce odors that are similar in their attractiveness to males (Ferkin and Johnston 1995; Ferkin et al. 2004).

Male subjects

Subjects were 72 sexually experienced, male meadow voles between 90 and 150 days of age. Forty-eight males had mated with one of the current PPE or d-2 lactating females. Twenty-four males had not mated with the current PPE female or the day 2 lactating female. Overall, males were placed into three treatment groups according to their mating status: (1) the male mate of the particular female in the exposure phase (mates), (2) a male that mated with another female other than the particular female used in the exposure

phase, but within the pregnancy timeframe of the particular female used in exposure phase (non-mates) and (3) a male that was sexually experienced having previously sired a litter, but had not lived with a female for 35 days (no sex). The males in treatment group 1, mates and 2, non-mates, had not lived with their mate for 17 days prior to testing (see [Experimental procedure](#) below). The males in treatment group 3, no sex, lived singly for 35 days prior to the experiment.

Mating procedure

We established 85 breeding pairs of which 72 pairs copulated within 8 h of pairing. We included in this study the 60 males and females that produced litters, and disregarded the pairs that did not copulate within the 8-h period and those that copulated but did not produce pups. We verified that the males and females copulated by watching the recorded videotapes of each pairing. In doing so, we were able to identify whether and when copulations occurred to estimate onset of pregnancy and use females when they had been pregnant for 20 days. Thus, we were able to identify and subsequently use d-20 pregnant females. Gestation for voles is 21 days in our laboratory (M.H. Ferkin, unpublished data).

Apparatus

All behavioral observations were performed on voles placed in a T-shaped apparatus (Fig. 1). We used two opaque Plexiglas cages with wired tops for observation purposes. The large boxes served to house the female donors. There was a transparent divider with small holes between the females' living area and the area that males explored. This divider allowed males to investigate the female's living area without coming into direct contact with that female.

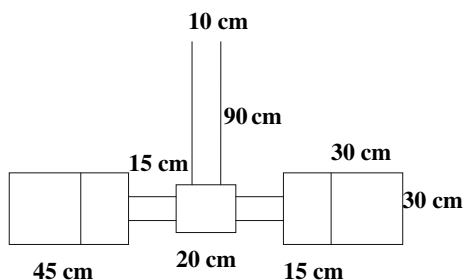


Fig. 1 The apparatus used to test for the capacity to display what, when, and where in voles. In the exposure phase, female voles were housed in chambers in the two arms of the apparatus. In the test phase, females were not present and the two arms of the apparatus were empty. During the exposure and test phases, male subjects were placed in the stem of the apparatus and allowed to explore the apparatus. Subjects could not enter the chambers that housed the females

Experimental procedure

We conducted an experiment, with five experimental conditions, in which male subjects were exposed to unique female donors. Each experimental condition contained two phases, an exposure phase and a test phase. In both phases of the five experimental conditions, a male meadow vole from one of the above treatment groups was placed into the starting box located at the base of the T (Fig. 1) for 30 s before the gate was lifted and the male was allowed to explore the entire apparatus. Each male underwent a single exposure and single test (see below).

Experimental condition 1 Male voles were exposed to an arena containing a d-20 pregnant female and a female that was not pregnant or lactating (REF female). 0.5 h later, male voles were allowed to investigate an empty arena.

During the exposure phase, male voles were placed into an apparatus that housed a REF female in one box and a d-20 pregnant female in the other box (Fig. 1). During the exposure phase, we recorded continuously for 10 min, the total amount of time male voles spent in the arms of the apparatus that housed each female donor (Fig. 1). We also noted the position of the home-boxes (left- or right-side of the apparatus) that housed each particular female donor. The position of a particular female's home-box in the left- or right-side of the apparatus was alternated for each male subject during the exposure phase. After the 10-min exposure, the male was returned to its own cage. Then, we disconnected the two-female home-boxes from the apparatus, and cleaned and disinfected the apparatus.

The second phase or the test phase took place 0.5 h after the exposure phase. During the test phase, the male voles were re-introduced into the apparatus that now contained boxes that housed no female donors; the boxes contained only clean wood chip bedding. We recorded continuously for 10 min, the total amount of time that male voles spent investigating the arm of the apparatus that previously housed the REF female that they were exposed to and the arm that previously housed the d-20 pregnant female.

Experimental condition 2 Male voles were exposed to an arena containing a d-20 pregnant female and a female that was not pregnant or lactating (REF female). Twenty-four hours later, male voles were allowed to investigate an empty arena.

Experimental condition 2 was the same as experimental condition 1. The test phase differed, however, with this notable exception. The test phase took place 24 h after the exposure phase. At this time, the d-20 pregnant female had delivered pups and had entered into postpartum estrus. During the test phase, the male voles were re-introduced into the apparatus that now contained boxes that housed no

female donors; the boxes contained only clean wood chip bedding (Fig. 1). We identified the initial choice of the males and recorded continuously for 10 min, the total amount of time that male voles spent investigating the arm of the apparatus that previously housed the REF female that they were exposed to and the arm that previously housed the d-20 pregnant female that they were exposed to, which was now currently in PPE.

Experimental condition 3 Male voles were exposed to an arena containing a d-20 pregnant female and a PPE female. 0.5 h later, male voles were allowed to investigate an empty arena.

Experimental condition 3 was similar in design to experimental condition 1, with these notable exceptions. During the exposure phase, a male meadow vole from one of the three treatment groups (mate, non-mate, or no sex) was allowed to explore the apparatus that contained a d-20 pregnant female in one box and a PPE female in the other box (Fig. 1). During the test phase, which occurred 0.5 h after the exposure phase, the male voles were re-introduced into the apparatus that now contained boxes that housed no female donors; the boxes contained only clean wood chop bedding. We identified the initial choice of the males and recorded continuously for 10 min, the total amount of time that they spent investigating the arm of the apparatus that previously housed the d-20 pregnant female that they were exposed to and the arm that previously housed the PPE female.

Experimental condition 4 Male voles were exposed to an arena containing a d-2 lactating female and a female that was not pregnant or lactating (REF female). 0.5 h later, male voles were allowed to investigate an empty arena.

Experimental condition 4 was similar in design to experimental condition 1, with these notable exceptions. During the exposure phase, a male meadow vole from one of the three treatment groups (mate, non-mate, or no sex) was allowed to explore the apparatus that contained a d-2 lactating female in one box and a REF female in the other box (Fig. 1). During the test phase, which occurred 0.5 h after the exposure phase, the male voles were re-introduced into the apparatus that now contained boxes that housed no female donors; the boxes contained only clean wood chop bedding. We identified the initial choice of the males and recorded continuously for 10 min, the total amount of time that they spent investigating the arm of the apparatus that previously housed the REF female that they were exposed to and the arm that previously housed the d-2 lactating female.

Experimental condition 5 Male voles were exposed to an arena containing a PPE female and a female that was not

pregnant or lactating (REF female). Twenty-four hours later, male voles were allowed to investigate an empty arena.

Experimental condition 5 was the same as experimental condition 2 in that the test phase of experimental condition 5 occurred 24 h after the exposure phase. During the exposure phase, a male meadow vole from one of the three treatment groups (mate, non-mate, or no sex) was allowed to explore the apparatus that contained a PPE female in one box and a REF female in the other box (Fig. 1). During the test phase, which occurred 24 h after the exposure phase, the male voles were re-introduced into the apparatus that now contained boxes that housed no female donors; the boxes contained only clean wood chop bedding. We identified the initial choice of the males and recorded continuously for 10 min, the total amount of time that male voles spent investigating the arm of the apparatus that previously housed the REF female that they were exposed to and the arm that previously housed the PPE female that they were exposed to, which was now currently in d-2 of lactation and no longer in PPE.

Statistical analyses

We used Sign tests to determine if the initial choice (initial visit) of male voles investigating the two arms of the arena were statistically different. We used one-way ANOVAs to compare the amount of time that males in the three treatment groups (mate, non-mate and no sex) spent investigating areas containing the female donors and areas that had previously contained them. To use the ANOVA, we had to create variables to test for the two phases of each experimental condition. For the exposure phase of experimental condition 1, the variable was calculated by dividing the time spent by the male investigating the d-20 pregnant female by the time spent by the male investigating the REF female. For the exposure phase of experimental condition 2, the variable was calculated by dividing the time spent by the male with the pregnant female by the time spent by the male with the REF female. For the test phase of experimental conditions 1 and 2, the variable was calculated by dividing the time spent by males investigating the arm of the apparatus that previously housed the d-20 pregnant female that they were exposed to, which was now currently in PPE in experimental condition 2, by the time spent by males investigating the arm of the apparatus that previously housed the REF female. For the test phase of experimental conditions 3 and 5, the variable was calculated by dividing the time spent by males investigating the arm of the apparatus that previously housed the PPE female that they were exposed to, which was now currently in day 2 of lactation in experimental condition 5, by the time spent by males investigating the arm of the apparatus that previously housed the d-20 pregnant female (experimental condition

3) or REF female (experimental condition 5). Prior to performing the ANOVA, these variables, as they were proportions, underwent an arc-sine and a square-root transformation. Last, we used paired *t*-tests to determine whether males spent different amounts of time investigating the areas that contained the paired female donors as well as the empty cages that had previously housed those paired females. Statistical significance was accepted at $\alpha < 0.05$ for all analyses.

Results

Experimental condition 1

Exposure phase: Pregnant female (d-20) versus reference female

Treatment condition of the male (mate, non-mate, or no sex) did not affect the amount of time that they investigated the area that housed the d-20 pregnant female and the area that housed the REF female ($F = 1.15$, $df = 2, 35$, $P = 0.328$). Males were initially exposed to d-20 pregnant females and REF females that were housed separately in opposite arms of the apparatus (Fig. 1). Males in the no sex group spent similar amounts of time during the exposure phase ($t = 1.30$, $df = 11$, $P = 0.220$) investigating the arm of the apparatus that housed the d-20 pregnant female and the arm of the apparatus that housed the reference female as did males that mated with that d-20 pregnant female ($t = 0.74$, $df = 11$, $P = 0.474$) and males that were mated with another pregnant female ($t = 0.89$, $df = 11$, $P = 0.392$; Fig. 2a). Male voles did not display a statistically significant initial choice (sign test $P = 0.1.22$). Six of 12 male voles first visited the cage containing the d-20 pregnant female, whereas the remaining six males first visited the cage containing the REF female.

Test phase: Pregnant female (d-20) versus reference female

The amount of time that males spent investigating the cage that contained the REF female and the cage that contained the d-20 pregnant female was not affected by whether the males were mates, non-mates, or no sex males ($F = 0.972$, $df = 2, 35$, $P = 0.388$). Male voles were initially exposed to d-20 pregnant females and REF females. 0.5 h later, males were exposed to an apparatus that would have housed that d-20 pregnant female and that REF female. Males in the no sex group spent similar amounts of time investigating the side of the apparatus that originally housed the day 20 female pregnant and the side of the apparatus that originally housed the REF female ($t = 1.12$, $df = 11$; $P = 0.286$; Fig. 2b). Likewise, male mates ($t = 1.56$, $df = 11$, $P = 0.147$,

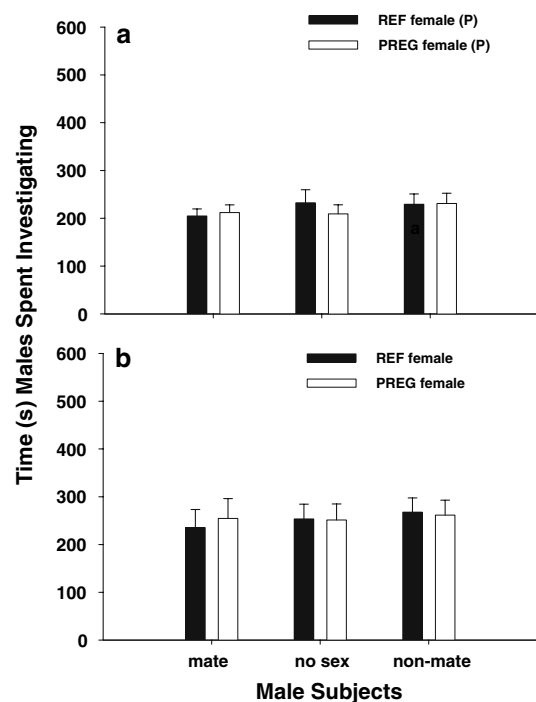


Fig. 2 The amount of time (s) \pm SEM that male voles (mates, no sex, and non-mates) spent investigating the sides of the apparatus **a** during the exposure phase that currently housed a REF female and a day 20 pregnant female (*P* indicates that the donor females were present). **b** The amount of time (s) \pm SEM during the test phase that male voles (mates, no sex, and non-mates) spent investigating the empty sides of the apparatus that would house a REF female vole and a day-20 pregnant female vole. The groups were not statistically different at $P > 0.1$

ns) and non-mates ($t = 1.39$, $df = 11$, $P = 0.19$; Fig. 2b) spent similar amounts of time investigating the arm of the apparatus that previously housed the d-20 pregnant female and the arm of the apparatus that housed the REF female. Male voles did not display a statistically significant initial choice (sign test $P = 0.774$). Seven of 12 male voles first visited the cage that would have contained the REF female, whereas the remaining five males first visited the cage that would have contained the d-20 pregnant female.

Experimental condition 2

Exposure phase: Pregnant female (d-20) versus reference female

Treatment condition of the male (mate, non-mate, or no sex) did not affect the amount of time that they investigated the area that housed the d-20 pregnant female and the area that housed the REF female ($F = 1.99$, $df = 2, 35$, $P = 0.151$). Males were initially exposed to a d-20 pregnant female and a REF female that were housed separately in opposite arms of the apparatus. Males in the no sex group spent similar amounts of time during the exposure phase

($t = 1.73$, $df = 11$, $P = 0.11$) investigating the arm of the apparatus that housed the d-20 pregnant female and the arm of the apparatus that housed the reference female as did males that mated with that d-20 pregnant female ($t = 0.81$, $df = 11$, $P = 0.45$) and males that were mated with another pregnant female ($t = 1.29$, $df = 11$, $P = 0.22$; Fig. 3a). Male voles did not display a statistically significant initial choice (sign test $P = 0.774$). Five of 12 male voles first visited the cage containing the d-20 pregnant female, whereas the remaining seven males first visited the cage containing the REF female.

Test phase: PPE female versus reference female

The amount of time that males spent investigating the cage that contained the REF female and the cage that contained the d-20 pregnant female was not affected by whether the males were mates, non-mates, or no sex males ($F = 1.34$, $df = 2, 35$, $P = 0.27$). Male voles were initially exposed to a d-20 pregnant female and a REF female. Twenty-four hour later, males were exposed to an apparatus that would have housed that pregnant female, which had delivered her pups and entered postpartum oestrus (PPE) and a REF female.

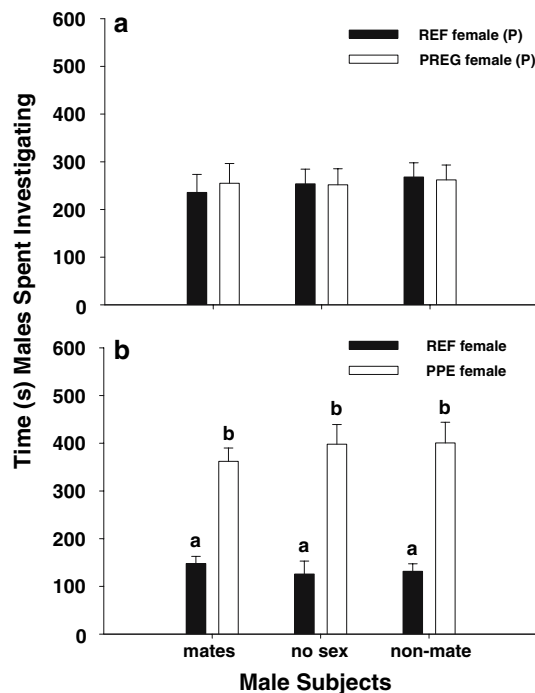


Fig. 3 The amount of time (s) \pm SEM that male voles (mates, no sex, and non-mates) spent investigating the sides of the apparatus **a** during the exposure phase that currently housed a REF female and a day 20 pregnant female (P indicates that the donor females were present). **b** The amount of time (s) \pm SEM during the test phase that male voles (mates, no sex, and non-mates) spent investigating the empty sides of the apparatus that would house a REF female vole and a PPE female vole. Histograms capped with different letters are statistically different at $P < 0.001$

Males in the no sex group spent significantly more time investigating the side of the apparatus that originally housed the day 20 female pregnant compared to the side of the apparatus that originally housed the REF female ($t = 5.42$, $df = 11$; $P = 0.001$; Fig. 2b). Likewise, male mates ($t = 3.81$, $df = 11$, $P = 0.003$) and non-mates ($t = 4.79$, $df = 11$, $P = 0.006$; Fig. 3b) spent more time investigating the arm of the apparatus that previously housed the d-20 pregnant female than they did investigating the arm of the apparatus that housed the REF female. Male voles displayed a statistically significant initial choice (sign test $P = 0.038$). Ten of 12 male voles first visited the cage that would have contained the PPE female, whereas the remaining two males first visited the cage that would have contained the REF female.

Experimental condition 3

Exposure phase: d-20 pregnant female versus PPE female

The amount of time that males spent investigating the cage containing the d-20 pregnant female and the cage containing the PPE female was not affected by whether the males were mates, non-mates, or no sex males ($F = 2.41$, $df = 2, 35$, $P = 0.10$). Males were exposed to a d-20 pregnant female and a PPE female housed in opposite arms of the apparatus. Males in the no sex group ($t = 3.14$, $df = 11$, $P = 0.01$), mates ($t = 2.59$, $df = 11$, $P = 0.025$) and non-mates ($t = 4.03$, $df = 11$, $P = 0.002$) spent more time investigating the areas that housed the PPE female than they did investigating areas that housed d-20 pregnant female donors (Fig. 4a). Male voles displayed a statistically significant initial choice (sign test $P = 0.038$). Ten of 12 male voles first visited the cage containing the PPE female, whereas the remaining two males first visited the cage containing the d-20 pregnant female.

Test phase: d-20 pregnant female versus PPE female

The amount of time that males spent investigating the two empty cages was not affected by whether the males were mates, non-mates, or no sex males ($F = 0.416$, $df = 2, 35$, $P = 0.66$). 0.5 h after the exposure phase, male voles were exposed to an empty apparatus that would have housed a d-20 pregnant female and a PPE female. Males in the no sex group ($t = 3.72$, $df = 11$; $P = 0.003$), male mates ($t = 3.11$, $df = 11$, $P = 0.009$) and non-mates ($t = 4.13$, $df = 11$, $P = 0.0017$) spent more time investigating the arm of the apparatus that previously housed the PPE female than they did investigating the arm of the apparatus that housed the d-20 pregnant female (Fig. 4b). Male voles displayed a statistically significant initial choice (sign test $P = 0.038$). Ten of 12 male voles first visited the cage that would have

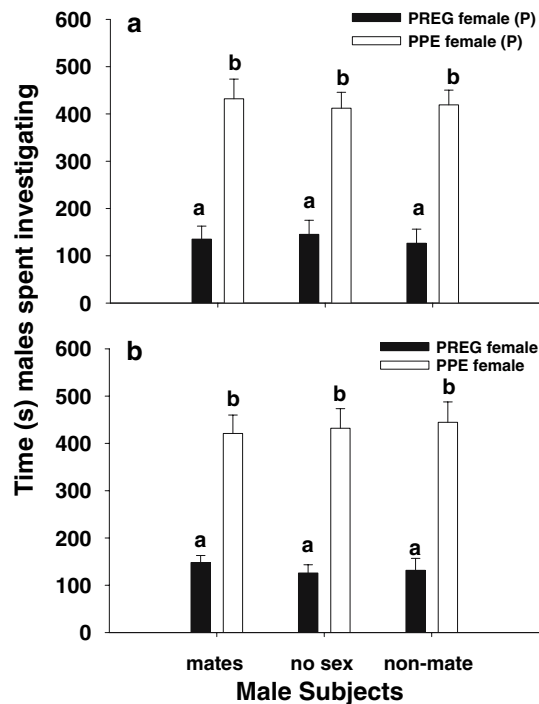


Fig. 4 The amount of time (s) \pm SEM that male voles (mates, no sex, and non-mates) spent investigating the sides of the apparatus **a** during the exposure phase that currently housed a day 20 pregnant female and a PPE female vole (*P* indicates that the donor females were present). **b** The amount of time (s) \pm SEM during the test phase that male voles (mates, no sex, and non-mates) spent investigating the empty sides of the apparatus that would house a day 20 pregnant female vole and a PPE female vole. Histograms capped with different letters are statistically different at $P < 0.001$

contained the PPE female, whereas the remaining two males first visited the cage that would have contained the d-20 pregnant female.

Experimental condition 4

Exposure phase: REF female versus d-2 lactating female

Treatment condition of the male (mate, non-mate, or no sex) did not affect the amount of time that they investigated the area that housed the d-2 lactating female and the area that housed the REF female ($F = 1.28$, $df = 2, 35$, $P = 0.29$). Males were initially exposed to a d-2 lactating female and a REF female that were housed separately in opposite arms of the apparatus (Fig. 5a). Males in the no sex group spent similar amounts of time during the exposure phase ($t = 1.30$, $df = 11$, $P = 0.22$) investigating the arm of the apparatus that housed the d-2 lactating female and the arm of the apparatus that housed the reference female as did males that mated with that d-2 lactating female ($t = 0.74$, $df = 11$, $P = 0.47$) and males that were mated with another lactating female ($t = 0.89$, $df = 11$, $P = 0.39$; Fig. 5a). Male voles did not display a statistically significant initial choice

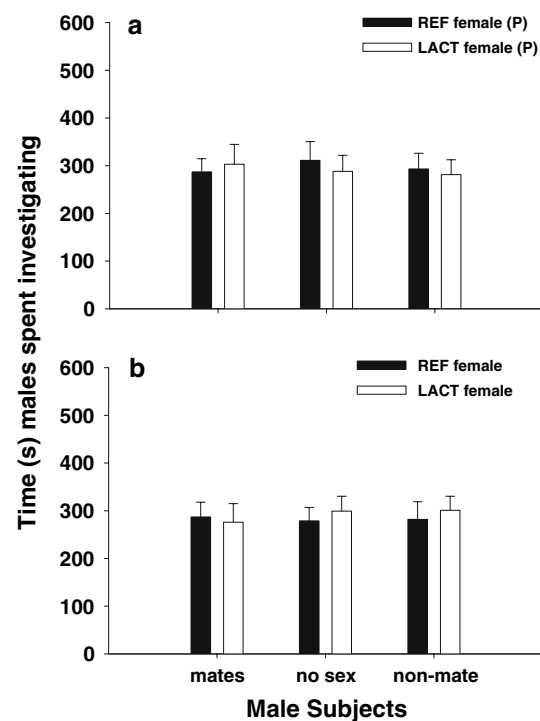


Fig. 5 The amount of time (s) \pm SEM that male voles (mates, no sex, and non-mates) spent investigating the sides of the apparatus **a** during the exposure phase that currently housed a REF female and a day 2 lactating female (*P* indicates that the donor females were present). **b** The amount of time (s) \pm SEM during the test phase that male voles (mates, no sex, and non-mates) spent investigating the empty sides of the apparatus that would house a REF female vole and a day 2 lactating female vole. The groups were not statistically different at $P > 0.1$

(sign test $P = 0.38$). Eight of 12 male voles first visited the cage containing the d-2 lactating female, whereas the remaining four males first visited the cage containing the REF female.

Test phase: REF female versus d-2 lactating female

The amount of time that males spent investigating the cage that contained the REF female and the cage that contained the d-2 lactating female was not affected by whether the males were mates, non-mates, or no sex males ($F = 0.79$, $df = 2, 35$, $P = 0.46$). Male voles were initially exposed to a d-2 lactating female and a REF female. 0.5 h later, males were exposed to an apparatus that would have housed that d-2 lactating female and that REF female. Males in the no sex group spent similar amounts of time investigating the side of the apparatus that originally housed the d-2 lactating female and the side of the apparatus that originally housed the REF female ($t = 1.33$, $df = 11$; $P = 0.21$; Fig. 5b). Likewise, male mates ($t = 1.82$, $df = 11$, $P = 0.096$) and non-mates ($t = 1.27$, $df = 11$, $P = 0.23$; Fig. 5b) spent similar amounts of time investigating the arm of the apparatus that

previously housed the d-2 lactating female and the arm of the apparatus that housed the REF female. Male voles did not display a statistically significant initial choice (sign test $P = 0.77$). Six of 12 male voles first visited the cage that would have contained the REF female, whereas the remaining six males first visited the cage that would have contained the d-2 lactating female.

Experimental condition 5

Exposure phase: REF female versus PPE female

Treatment condition of the male (mate, non-mate, or no sex) did not affect the amount of time that they investigated the area that housed the PPE female and the area that housed the REF female ($F = 1.66$, $df = 2, 35$, $P = 0.20$). Males were initially exposed to a PPE female and a REF female that were housed separately in opposite arms of the apparatus. Males in the no sex group spent more time during the exposure phase ($t = 3.81$, $df = 11$, $P = 0.0029$) investigating the arm of the apparatus that housed the PPE female than the arm of the apparatus that housed the REF female as did the males mated with that PPE female ($t = 2.94$, $df = 11$, $P = 0.013$) and the males that were mated with another female ($t = 4.07$, $df = 11$, $P = 0.0019$; Fig. 6a). Male voles displayed a statistically significant initial choice (sign test $P = 0.006$). Eleven of 12 male voles first visited the cage containing the PPE female, whereas the remaining male first visited the cage containing the REF female.

Test phase: REF female versus d-2 lactating female

The amount of time that males spent investigating the cage that previously contained the REF female and the cage that previously contained the PPE female (now d-2 lactating female) was not affected by whether the males were mates, non-mates, or no sex males ($F = 1.09$, $df = 2, 35$, $P = 0.34$). Male voles were initially exposed to a REF female and a PPE female. 24 h later, males were exposed to an apparatus that would have housed a female that was no longer in PPE but now in d 2 of lactation and a REF female. Males in the no sex group spent similar amounts of time investigating the side of the apparatus that originally housed the PPE females and the side of the apparatus that originally housed the REF female ($t = 1.19$, $df = 11$; $P = 0.25$; Fig. 5b). Likewise, male mates ($t = 0.48$, $df = 11$, $P = 0.64$) and non-mates ($t = 0.73$, $df = 11$, $P = 0.48$; Fig. 6b) spent similar amounts of time investigating the arm of the apparatus that previously housed the PPE female than they did investigating the arm of the apparatus that housed the REF female. Male voles did not display a statistically significant initial choice (sign test $P = 0.77$). Six of 12 male voles first visited the cage that would have contained the REF female,

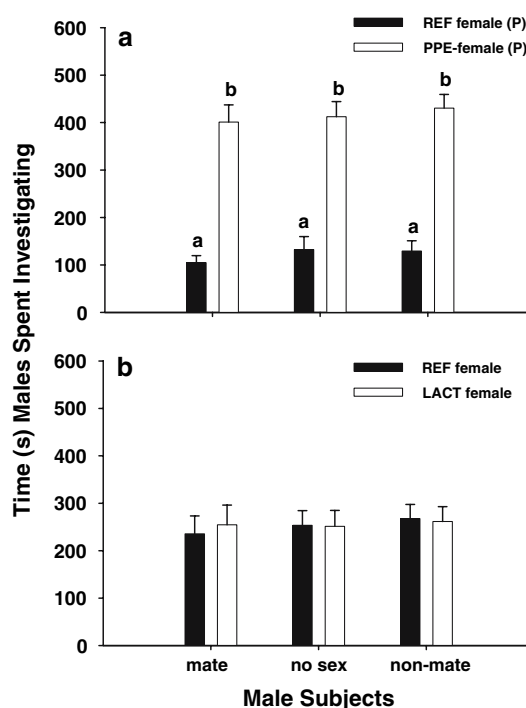


Fig. 6 The amount of time (s) \pm SEM that male voles (mates, no sex, and non-mates) spent investigating the sides of the apparatus **a** during the exposure phase that currently housed a REF female and a PPE female (P indicates that the donor females were present). **b** The amount of time (s) \pm SEM during the test phase that male voles (mates, no sex, and non-mates) spent investigating the empty sides of the apparatus that would house a REF female vole and a day 2 lactating female vole. Histograms capped with different letters are statistically different at $P < 0.001$

whereas the remaining six males first visited the cage that would have contained the d-2 lactating female.

General discussion

The present experiment examined the responses of male meadow voles that initially were exposed to female voles in different reproductive states, and later entered areas that previously housed these females. Our findings suggest that male meadow voles respond preferentially to PPE females or to areas that would be expected to contain PPE females relative to REF females, d-2 lactating females, and d-20 pregnant females or to areas that had, but would no longer, contain PPE females. Briefly, male meadow voles exposed to both d-20 pregnant females and females that were neither pregnant nor lactating (REF females), when tested one day later, when the pregnant females had delivered their pups and entered postpartum estrus (PPE), initially chose and spent more time investigating areas that previously housed the formerly pregnant females compared to areas that previously housed the REF females. That is, male voles spent more time investigating areas that would have been

expected to contain PPE females than those of REF females. In addition, male voles initially exposed to PPE females and REF females, one day later, when the previously PPE female was in day 2 of lactation, did not initially chose and spent similar amounts of time investigating areas that previously housed the formerly PPE females and those that previously housed the REF females. We also found that male voles exposed to a d-20 pregnant female and a REF female, 0.5 h later spent similar amounts of time in the location that would contain the d-20 pregnant female and in the location of the REF female. In addition, male voles exposed to a PPE female and a d-20 pregnant female, 0.5 h later initially chose and spent more time in the location that would contain that PPE female than in the location of the d-20 pregnant female. Lastly, we found that male voles exposed to a d-2 lactating female and a female that is neither pregnant nor lactating (REF female), 0.5 h later spent similar amounts of time in the location that would contain that d-2 lactating female and the location of the REF female. These results are consistent with previous work suggesting that male meadow voles prefer the scent marks of PPE females to those of d-20 pregnant females, d-2 lactating females or REF females (Ferkin and Johnston 1995). The data are also congruent with those suggesting that male meadow voles preferentially scent mark and visit areas inhabited by PPE females as compared to those inhabited by pregnant, lactating, or REF females (Ferkin et al. 2004). Such a preference may provide male meadow voles benefits such as reduced latency to copulation and shorter intervals between successive copulations by mating with PPE females (delBarco-Trillo and Ferkin 2007).

Our data, especially from experimental condition 5, indicate that male voles did not simply develop a conditioned place preference for a particular location. In experimental condition 5, during the exposure phase, voles were presented with a PPE female and a REF female. The male preferred the PPE female over the REF female. This result was not surprising in that previous work showed that males are more attracted to PPE females than they are to REF females (Ferkin and Johnston 1995; Ferkin et al. 2004; Ferkin 2006). If male voles formed a conditioned place preference, they would have spent more time during the test in the side of the apparatus that would have been paired with the rewarding stimulus, a PPE female (Tzschentke 1998). This result was not observed. During the test phase male voles explored an empty apparatus. The males spent similar amounts of time investigating the side of the apparatus that previously housed the PPE female during the exposure phase and the side of the apparatus that previously housed the REF female. At the time of the test phase, the formerly PPE female would no longer be in PPE, but would be in the second day of lactation. Males are similarly attracted to females that are in d-2 of lactation and REF females (Ferkin

and Johnston 1995). Our results cannot be explained as the voles developing a conditioned place preference.

Do male meadow voles possess the capacity to recollect the what, when, and where of a single past event? The capacity to recollect the what, when, and where of a past event has been suggested for pigeons (Zentall et al. 2001), chimpanzees (Menzel 1999), mice (Dere et al. 2005) and rats (Eacott and Norman 2004; Ergorul and Eichenbaum 2004; Eacott et al. 2005), but the conclusions of many of these studies have been viewed cautiously by researchers. The most glaring concern raised by researchers is that animals may show a recollection for the what, where and “which”, but they may not recollect the “when” (Suddendorf and Corballis 1997; Menzel 1999; Schwartz and Evans 2001; Roberts 2002; Eacott and Norman 2004; Schwartz et al. 2005). Much of the concern about whether animals can recollect the “when” may reflect the different operational definitions for the “when” component (Zentall et al. 2001; Eacott et al. 2005; Clayton et al. 2001; Dere et al. 2006). For example, Dere et al. (2006) state that the when component can be operationalized by presenting the animals two or more distinct events, and evaluating whether they are able to remember their order of occurrence. They argue that the scrub jays in Clayton and Dickinson (1998) study did not have to recollect the sequence of events. In our study, male voles were not forced to remember any order of events either. Thus under the Dere et al. (2006) operational definition of the “when”, we did not address the “when” component. However, we tested male voles 24 h after the exposure phase, and the male voles may have recollected “when” as how long it has been since they encountered a particular female vole, which is akin to how long ago a scrub jay cached a particular food item (Clayton and Dickinson 1998; Griffiths et al. 1999). Overall, our data suggest that male voles may have the capacity to recollect the what, where and when of single past event. If so, our experiment may be the first to suggest that male non-human animals may have the capacity to identify a potential mate, locate her, and later visit her when she can be expected to be most sexually receptive.

On the other hand, Roberts (2002) takes exception with this definition of “when” because the memory for time is different, and states that recollection of “when” implies a temporal structure for past time within which events can be located. He argues that recollection for how long ago could be dependent on elapsed time or temporal distance since an event (Roberts 2002). Thus, male voles may have learned that a weaker memory trace for a PPE female may indicate that that female is no longer in PPE, and that a stronger memory trace for a PPE female may indicate that the female is still in PPE. It is also possible that male voles may have learned a rule of thumb. That is, if a short period of time passes between the exposure phase and the

test phase, then maintain the preference shown in the exposure phase, but if the interval of time is long (say 24 h or one complete light:dark cycle), then prefer each similarly in the exposure phase. However, such rules may be highly specific, condition dependent, and associated with particular females (Roberts 2002). Finally, it is also possible that male voles recollect the specific point in time when they previously encountered a female in a particular reproductive state, which would indicate that they have both a sense of time and the ability to recollect the when of a past event.

In our study, male voles had a single one-time experience with two females that differed in their respective reproductive states. In addition, the stimuli were novel to these male voles. Male voles received no previous training with females used in our experiment. Thus, we were able to avoid a point of contention raised by researchers who argue that training of subjects to perform the tasks used to test for what, where and when may affect the behavior of animals by conditioning them or making them familiar with aspects of the test. For example, pigeons were trained to perform tasks that would indicate that they have the capacity for forming episodic-like memories (Zentall et al. 2001). In these cases, animals may be relying on the learning of a rule of thumb and the recall of a past event to perform the behavioral task (Zentall et al. 2001; Schwartz and Evans 2001; Roberts 2002; Morris and Day 2003; Suddendorf and Busby 2003; Schwartz et al. 2005). Some researchers argue that to show episodic-like memory individuals must have a one-time experience with novel stimuli that evokes a recollection of the what, when, and where of the past event (Morris and Day 2003; Dere et al. 2006). In our study, previous training can be ruled out as an explanation for the behavior of the male voles in our test. According to this definition (Morris and Day 2003; Dere et al. 2006), male meadow voles in our experiments may have displayed episodic-like memory.

The fact that 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, indicates that male meadow voles likely recollect the point in time when they previously encountered a female in a particular reproductive state. Such a capacity in voles seems to be consistent with their space use and social biology. During the breeding season, male meadow voles occupy large overlapping home ranges, which encompass the territories of one or more females (Madison 1980). The females may be widely dispersed over a male's home range. Male and female voles also have few repeated interactions with the same opposite-sex conspecifics

(Dewsbury 1990; Boonstra et al. 1993). In addition, females are induced ovulators and do not undergo estrous cycles, but their reproductive condition may vary, with some females being pregnant, others lactating, others not pregnant or lactating and still others undergoing postpartum estrus (PPE) (Milligan 1982; Keller 1985; Ferkin et al. 2004). However, meadow voles are promiscuous, mating with multiple partners, and in some cases having litters of mixed paternity (Boonstra et al. 1993; delBarco-Trillo and Ferkin 2004). To coordinate breeding and reduce sperm competition, male voles appear to keep track of the reproductive condition of nearby female conspecifics based on past exposure.

At present, 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 and 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 and Busby 2003; Busby and Suddendorf 2005). 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 and Corballis 1997). Our results do not clearly show that male voles mentally re-construct a past situation *per se*. What our data 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 prospection. However, it does not tell us the mechanism underlying prospection. Alternatively, male meadow voles 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 (Clayton et al. 2003; Franklin and Ferkin 2006).

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 (Clayton et al. 2001), or when males are attempting to monopolize mates (Huck et al. 2004). PPE females are more attractive and sexually receptive to males relative to females in other reproductive states (Ferkin and Johnston 1995; Ferkin et al. 2004). PPE females readily mate with males, usually within a few minutes of pairing, whereas females in other reproductive states may take several hours to mate when paired with a male (Keller 1985). Males may increase their mating opportunities if they have the capacity to recall the identity and location of a female, and to predict the time when the female enters into heightened sexual receptivity.

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