

## UNCORRECTED PROOF

# The duration of sociosexual behaviors in male meadow voles *Microtus pennsylvanicus* varies before, during, and after copulation

Ashlee A. VAUGHN<sup>1\*</sup>, Daniel A. FERKIN<sup>1</sup>, Javier delBARCO-TRILLO<sup>2</sup>, Michael H. FERKIN<sup>1</sup>

<sup>1</sup> Department of Biology, The University of Memphis, Memphis, TN 38152 USA

<sup>2</sup> Department of Evolutionary Anthropology, Duke University, Box 90383, Durham, NC, 27708, USA

**Abstract** The behaviors that surround copulation are characterized as sociosexual behaviors. These behaviors displayed by males that are directed at females may include allogrooming, wrestling, and chasing, approach, and time spent together. The data supported the hypothesis that the duration of sociosexual behaviors differs during the pre-copulatory, peri-copulatory, and post-copulatory phases of the mating bout in meadow voles. Voles spent more time approaching conspecifics during the pre- and peri-copulatory phases than during the post-copulatory phase. Voles spent more time allogrooming, wrestling, and chasing during the pre-copulatory phase than during the peri- and post-copulatory phases. Voles spent similar amounts of time together during the pre-, peri-, and post-copulatory phases. The data suggest that sociosexual behaviors displayed by males may be involved in setting the pace and temporal components of the mating bout. During the pre-copulatory phase particular behaviors by male voles may attract females, during the peri-copulatory phase some of these behaviors may stimulate or motivate the female to mate, and during the post-copulatory phase certain behaviors may prepare the male to mate again [*Current Zoology* 57 (1): – , 2011].

**Key words** Copulatory behavior, Meadow voles, Odors, Sociosexual behavior

Sociosexual behaviors are used by individuals to attract, show interest in, and mate with opposite-sex conspecifics (Beach, 1976). For example, males may approach females to indicate their willingness to mate with them (Clarke, 1956; Beyer et al., 1981; Thornton et al., 1991; Bercovitch et al., 2006; Alligood et al., 2009). Females may approach and withdraw from male conspecifics, and if the male does not follow her, she may again approach the male (Gavish et al., 1983; Bercovitch et al., 2006; Alligood et al., 2009). These behaviors may be the first steps in the courtship behavior (Grant and Mackintosh, 1963; Eisenberg, 1967; Dewsbury, 1972). Once attracted to a particular male, female rodents may remain in close proximity to him (Eisenberg, 1967; Carter et al., 1987). The sociosexual behaviors are likely to be involved in the pacing and temporal components of the mating

---

Received Apr. 25, 2010; accepted June 17, 2010

\* Corresponding author. E-mail: aavaughn@memphis.edu

© 2011 *Current Zoology*

bout (Stopka and Macdonald, 1998, 1999). For example, the duration of a male's sociosexual behaviors are likely to differ, depending on where in the copulation bout the male is at that time. During the pre-copulatory phase males may spend much of their time trying to attract females by approaching them (Gray and Dewsbury, 1975; Ferkin and Seamon, 1987; Witt et al., 1988, 1990; Bercovitch et al., 2006). Approaches may also reduce aggression, heighten the sexual motivation between opposite-sex conspecifics (Carter et al., 1987), and increase the amount of time that males and females spend together, which may be necessary for them to initiate mating (Grant and Mackintosh, 1963; Beach, 1976). During the peri-copulatory phase, sociosexual behaviors may insure that females remain sexually receptive and that males are able to complete the copulatory act and ejaculate (Mosig and Dewsbury, 1976; Alligood et al., 2009). Thus, allogrooming, chasing, and time together may increase in duration (Eisenberg, 1967; Dewsbury, 1972; Stopka and Gracíasová, 2001; Soini, 2005). During the post-copulatory phase, males may be preparing for the next pre-copulatory phase, presumably with another female (Vaughn et al., 2010; Ferkin and Leonard, 2010). There may be a decrease in approaches and the amount of time that the male and female remain together.

Sociosexual behaviors are likely to be involved in coordinating male-female interactions (Beach, 1976; Soini, 2005). A behavior that has been identified as facilitating encounters between opposite-sex conspecifics is self-grooming (Ferkin and Leonard, 2010), and has been studied recently in meadow voles *Microtus pennsylvanicus*. In that study, male voles were found to differ in the amount of time that they spent self-grooming different areas of their body before, during, and after coitus (Vaughn et al., 2010). The results of this study suggest that other sociosexual behaviors displayed by males and directed at females, such as allogrooming, wrestling, and chasing, approaches and time together may also differ in their duration across the pre-, peri-, and post-copulatory phases of a mating bout. If so, such findings would suggest that sociosexual behaviors displayed by males may be involved in setting the pace and temporal components of the mating bout. We tested the hypothesis that the duration of sociosexual behaviors differs during the pre-copulatory, peri-copulatory, and post-copulatory phases of the mating bout. We predicted that the behaviors that facilitate interactions with females, such as naso-nasal approaches would occur with the greatest duration during the pre-copulatory phase. During the peri-copulatory phase, behaviors that sustain contact and facilitate coitus, such as naso-anogenital approaches, allogrooming, wrestling, and chasing, and time spent together, should have increase in duration. During the post-copulatory phase, there should be a reduction in the duration of sociosexual behaviors, which along with no coitus may indicate the end of the copulatory bout. Being able to facilitate and coordinate male-female interactions would be especially important to meadow voles and other species in which the male and female do not nest together, have infrequent encounters, but mate with multiple partners and copulatory and reproductive success among males is highly skewed (Boonstra et al., 1993; Andersson, 1994; Clutton-Brock, 1998; Berteaux et al., 1999; Birkhead, 2000; LaDage and Ferkin, 2008).

## 1 Materials and Methods

### 1.1 Animals

We used meadow voles that were descendants of those captured in Pennsylvania, Kentucky, and Ohio, USA. Every 18–24 months, the voles in the colony were mated with captured free-living voles. In this study, meadow voles were born and raised under long photoperiod (14:10 h, L:D, lights on at 07:00 h CST). All voles were

weaned at 19 days of age, housed with littermates until 34 days of age, and thereafter housed singly in clear plastic cages ( $27 \times 16.5 \times 12.5$  cm). Cages contained bedding, cotton nesting material, water, and food (Harlan Teklad Rodent Diet, #8640, Madison, WI, USA). Meadow voles were housed in the animal facility at the University of Memphis. Female meadow voles are induced ovulators and do not undergo regular estrus cycles (Milligan, 1982). Adult female voles born and reared in long photoperiod are sexually receptive (Keller, 1985). Long-photoperiod meadow voles respond preferentially to the scent marks of opposite-sex conspecifics and readily mate with opposite-sex conspecifics (Meek and Lee, 1993; Ferkin and Johnston, 1995; Vaughn et al., 2008). However, to insure that mating occurred we injected female voles with 0.05 mg estradiol benzoate three days before pairing with a male (Dewsbury and Baumgardner, 1981; delBarco-Trillo and Ferkin, 2004; Vaughn et al., 2008, 2010). Voles used in this study were 120–150 days of age and sexually experienced, having previously sired or delivered a litter at least 30 days before being used in this experiment. None of the females, however, were pregnant or lactating when used in the experiment.

## 1.2 Testing Procedure

We established groups of male-female pairs. We used 51 male and 51 female voles to create these pairs. All testing was conducted during the first 2 hours of the light cycle (lights on at 07:00). We followed the procedures for pairing the males and females described in delBarco-Trillo and Ferkin (2004, 2006a). Briefly, an estradiol-primed female was introduced into a clean cage ( $37 \times 21 \times 15$  cm) lined with clean bedding. The focal male was introduced in the cage 5 min later. We video-taped the pairing with a Sony Handycam connected to a JVC 4 Head VCR Combo Video Cassette Recorder. No observer was present in the room during the recording of the male and female pair. During these pairings, the male voles were allowed to reach sexual satiety, which occurs when, after mating, there is a period of 30 min without any further copulation (Gray and Dewsbury, 1975; delBarco-Trillo and Ferkin, 2004). We used the free software Stopwatch+ (<http://www.cbn-atl.org/research/stopwatch.shtml>) to score the tapes.

During the pre-copulatory, peri-copulatory, and post-copulatory phases we recorded selected sociosexual behaviors in male voles. We selected the following behaviors because they are frequently observed in rodents (Clarke, 1956; Grant and Mackintosh, 1963; Myers and Krebs, 1971; Dewsbury, 1972; Ferkin and Seamon, 1987), and may support mating. Specifically, we recorded the amount of time males spent: (a) directly interacting with the female outside of coitus; this included the time males spent allogrooming females, the time males spent boxing/wrestling, and the time males spent chasing the female; these behaviors were recorded if the males initiated them; (b) the amount of time the male approached within 2 cm of the female but did not engage in coitus and did not spend time in allogrooming, wrestling with, and chasing the female; these approaches were subdivided according to the olfactory investigation by the male of the female's face (naso-nasal approaches), the female's anogenital area (naso-anogenital area approaches), and other body regions of the female not including her head and anogenital region (naso-other approaches); and (c) the time males and females spent together sitting or lying side-by-side, and not involved in coitus or the other behaviors listed above. These sociosexual behaviors are displayed by captive and free-living voles (Clarke, 1956; Myers and Krebs, 1971; Tamarin, 1985; Ferkin and Seamon, 1987).

We measured the amount of time that male voles spent performing these behaviors before (the pre-copulatory phase), during (the peri-copulatory phase), and after copulation (the post-copulatory phase) in 51 trials. The pre-copulatory phase included the 10 min before the start of the first copulatory bout, unless mating occurred before that time. The peri-copulatory phase included the time from the first ejaculation until 10 minutes after the first ejaculation or until the male started the second ejaculatory series. Thus, the peri-copulatory phase consisted of the full inter-copulatory interval between the first and the second ejaculatory series or the first 10 min of that inter-copulatory interval if it lasted more than 10 min. The post-copulatory phase lasted for 10 min and was recorded starting when the male and female were no longer engaged in coitus.

### 1.3 Statistics

We created a continuous variable for each sociosexual behavior we tested. This variable was the quotient of the total amount of time that the male spent involved in that behavior divided by the total time in that phase. Kolmogorov-Smirnov tests indicated that the data were not normally distributed. Statistical analyses were performed using SPSS 16 for Windows. We then used the Friedman test to determine whether differences existed in the sociosexual behaviors of male voles during the pre-copulatory, peri-copulatory, or post-copulatory phases. We performed Wilcoxon sign ranks tests to determine if differences existed between males in the amount of time they spent involved in the sociosexual behaviors in the multiple paired comparisons. Statistically significant differences were accepted at  $P < 0.05$ . All values reported in the figures are shown as mean  $\pm$  SEM.

## 2 Results

### 2.1 Sociosexual behaviors across the pre-copulatory, peri-copulatory, and post-copulatory phases

Male meadow voles differed in the duration of their sociosexual behaviors directed toward females during the pre-copulatory, peri-copulatory, and post-copulatory phases. Males spent different amounts of time involved in allogrooming, wrestling, and chasing females during the pre-copulatory, peri-copulatory, and post-copulatory phases ( $\chi^2 = 23.19$ ,  $P < 0.0005$ ; Fig. 1). During the pre-copulatory phase, males spent more time involved in allogrooming, wrestling, and chasing females than they did during the peri-copulatory phase and the post-copulatory phase ( $P < 0.0005$  for both comparisons). In addition, males differed in the amount of time that they spent approaching the females during the pre-copulatory, peri-copulatory, and post-copulatory phases ( $\chi^2 = 13.22$ ,  $P = 0.001$ ). Males spent more time approaching females during the pre-copulatory phase and peri-copulatory phase than they did during the post-copulatory phase ( $P < 0.0005$  for both comparisons). Male voles, however, spent similar amounts of time in side-by-side contact with female voles during the pre-copulatory, peri-copulatory, and post-copulatory phases ( $\chi^2 = 5.65$ ,  $P = 0.059$ ).

### 2.2 Sociosexual behaviors within the pre-copulatory, peri-copulatory, and post-copulatory phases

During the pre-copulatory, peri-copulatory, and post-copulatory phases, male voles differed in the combined total time they spent engaged in allogrooming, wrestling, and chasing females, in approaching females, and in side-by-side contact with female voles ( $\chi^2 = 72.15$ ,  $P < 0.0005$ ; Fig.1). Male voles, however, spent more time during the pre-copulatory phase involved in allogrooming, wrestling, and chasing females than they spent

approaching females and engaged in side-by-side contact with females ( $P \leq 0.001$  for all comparisons). During the pre-copulatory phase males spent more time approaching females than they spent in side-by-side contact with females ( $Z = -4.23, P < 0.0005$ ).

During the peri-copulatory phase, male voles spent different amounts of time involved in sociosexual behaviors ( $\chi^2 = 97.52, P < 0.0005$ ). Males spent more time in the combined behaviors of allogrooming, wrestling, and chasing females than males spent in side-by-side contact with females ( $Z = -2.43, P = 0.015$ ). Males also spent more time in side-by-side contact with females than they spent approaching females ( $Z = -1.97, P = 0.048$ ).

Lastly, during the post-copulatory phase, males spent different amounts of time involved in sociosexual behaviors ( $\chi^2 = 72.97, P < 0.0005$ ). When the total times were combined, male voles spent similar amounts of time of allogrooming, wrestling, and chasing female voles, approaching females, and in side-by-side contact with females ( $P < 0.0005$  for all comparisons).

### **2.3 Differences in naso-nasal, naso-anogenital and naso-other approaches across the pre-, peri-, and post-copulatory phases**

During the pre-copulatory phase, peri-copulatory phase, and post-copulatory phase, male voles differed in the amount of time they spent in naso-nasal approaches, naso-anogenital area approaches, and naso-other approaches ( $\chi^2 = 12.62, P = 0.002$ ; Fig. 2). Males spent more time during the pre-copulatory phase and peri-copulatory phase involved in naso-nasal approaches than they did during the post-copulatory phase ( $P < 0.01$  for both comparisons). Males, however, spent similar amounts of time involved in naso-nasal approaches during the pre-copulatory and peri-copulatory phases ( $Z = -0.449, P = 0.654$ ).

Males spent different amounts of time when they approached the anogenital area of females across the pre-copulatory, peri-copulatory, and post-copulatory phases ( $\chi^2 = 19.96, P < 0.0005$ ). During the pre-copulatory phase, males spent more time involved in naso-anogenital approaches than they did during the peri-copulatory and post-copulatory phases ( $P < 0.0005$  for both comparisons). During the peri-copulatory phase, males spent more time involved in naso-anogenital approaches than they did during the post-copulatory phase ( $Z = -3.57, P < 0.0005$ ).

Males spent different amounts of time approaching other body regions on females (naso-other) across the pre-copulatory, peri-copulatory, and post-copulatory phases ( $\chi^2 = 6.19, P = 0.045$ ). Male voles spent more time involved in approaching other body regions on females during the peri-copulatory phase than they did during the pre-copulatory phase ( $Z = -2.04, P = 0.041$ ).

### **2.4 Differences in naso-nasal, naso-anogenital and naso-other approaches within the pre-, peri-, and post-copulatory phases**

During the pre-copulatory phase, males differed in the amount of time they spent in naso-nasal approaches, naso-anogenital approaches, and naso-other approaches ( $\chi^2 = 35.92, P < 0.0005$ ; Fig. 2). Males spent more time in naso-nasal approaches and naso-anogenital area approaches than they did in naso-other approaches ( $P < 0.0005$  for both comparisons). Likewise, during the peri-copulatory phase, males differed in the amount of time they spent in naso-nasal approaches, naso-anogenital approaches, and naso-other approaches ( $\chi^2 = 19.41, P < 0.0005$ ; Fig. 2). Males spent more time in naso-nasal approaches than in naso-anogenital approaches and naso-other approaches ( $P < 0.05$  for both comparisons). During the post-copulatory phase, males also differed in the amount

of time they spent in naso-nasal approaches, naso-anogenital approaches, and naso-other approaches ( $\chi^2 = 26.26$ ,  $P < 0.0005$ ; Fig. 2). Males spent more time in naso-nasal approaches than in naso-anogenital approaches and naso-other approaches ( $P < 0.005$  for both comparisons).

### 3 Discussion

Male meadow voles displayed differences in the duration of the sociosexual behaviors they directed toward females during the pre-copulatory phase, peri-copulatory phase, and post-copulatory phase of the mating bout. It was not surprising to find that males spent more time approaching females during the pre-copulatory phase and the peri-copulatory phase than during the post-copulatory phase. Approaching a female vole would allow a male vole to signal his interest in her. By doing so, males may learn more about the willingness of these females to mate (Clarke, 1956; Eisenberg, 1967; Beyer et al., 1981; Ferkin and Seamon, 1987; Thornton et al., 1991). Also during the pre-copulatory phase, male voles spent much time allogrooming, wrestling, and chasing the female. Male woodrats that chased females more often had more copulations than did males that did not chase females as often (Alligood et al., 2009). During the pre-copulatory phase, male voles also spent time approaching and investigating the nasal and anogenital areas of the females. It is interesting, however, that male and female meadow voles spent little time in side-by-side contact with one another during the pre-copulatory phase. In contrast, in prairie voles, a monogamous species, males and females spend much time in side-by-side contact prior to copulation (Carter et al., 1987; Insel et al., 1997). We suggest that by spending little time in side-by-side contact, male and female meadow voles may proceed more quickly to the peri-copulatory phase and the post-copulatory phase, which may shorten the duration of the copulatory bout. Our findings support and augment the view that the prevalence of allogrooming, wrestling, chasing, and approaches during the pre-copulatory phase are behaviors involved in courtship or facilitating coitus (Clarke, 1956; Dewsbury, 1972; Stopka and Graciasová, 2001). It is possible that the long duration of sociosexual behaviors during the pre-copulatory phase may allow males and females to continually update their assessment of their potential partner's condition and quality to determine if mating should occur (Stopka and Macdonald, 1998, 1999; Soini, 2005; Bercovitch et al., 2006; Ferkin and Leonard, 2010).

During the peri-copulatory phase males continued to approach and investigate the nasal and anogenital areas of females. There was also an increase in the amount of time male voles were involved in nasal-other investigation of female voles. Taken together, the odors of male and female voles during the peri-copulatory phase may be stimulatory to the participant, allowing them to continue to mate (Ferkin and Leonard, 2010). Male meadow voles also spent time during the peri-copulatory phase allogrooming, wrestling, and chasing the female. Since female voles may run away from males during copulation (delBarco-Trillo and Ferkin, 2006b), these interactions may insure that males can continue to mate until they finish their copulatory behavior, which is composed of several ejaculations (Dewsbury, 1972; Gavish et al., 1983; Soini, 2005; delBarco-Trillo and Ferkin, 2006b). Our data support and extend the hypothesis that sociosexual behaviors during the peri-copulatory phase may prolong coitus to insure that the male ejaculates and/or serve to stimulate the female to continue to be sexually receptive towards that male (Gray and Dewsbury, 1975; Witt et al., 1988, 1990).

During the post-copulatory phase there was no difference in time male voles spent in approaching females, allogrooming, wrestling, and chasing females, or in side-by-side contact with females. At this point, the current mating bout has been completed and male meadow voles may be more interested in finding new potential mates rather than attempting to mate again with a current mate (Andersson, 1994; Birkhead, 2000). Similarly, the current female may no longer be interested in interacting or mating again with that male vole (Ivy et al., 2005; LaDage and Ferkin, 2006; LaDage et al., 2008). Studies on non-monogamous rodents, including meadow voles indicate that females prefer to associate and mate with novel males rather than previous mates (Ferguson et al., 1986; Shapiro et al., 1986). Our data are consistent with and augment the hypothesis that during the post-copulatory phase, sociosexual behaviors may prepare males to mate with another female (Hart et al., 1987; Sachs et al., 1988; Mooring et al., 1996; Ferkin and Leonard, 2010).

Overall, our findings in male voles extend the view that sociosexual behaviors by male mammals are involved in coordinating interactions with female conspecifics (Beach, 1976; Soini, 2005) and establishing the pacing and temporal components of the mating bout (Stopka and Macdonald, 1998, 1999). Thus, the amount of time that a male spends involved in signaling his interest in that female by approaching her, spending time in contact with her, and grooming her may differ between males in monogamous and non-monogamous species. In monogamous species of mammals males may display sociosexual behaviors that are relatively longer in duration and with greater frequency to lengthen the copulatory bout to both reinforce the pair bond or as a form of mate guarding among new pairs (Kleiman, 1977; Dewsbury, 1981), but not among established pairs (Witt et al., 1988, 1990). It is possible, however, that in non-monogamous species of mammals, including meadow voles (Madison, 1980; Boonstra et al., 1993), males display sociosexual behaviors across the mating bout that are shorter in duration and have fewer occurrences. This may allow such males to shorten the copulatory bout with a particular female, and increase the amount of time that he has to locate and mate with multiple females (Andersson, 1994; Clutton-Brock, 1998; Birkhead, 2000).

**Acknowledgements** We thank the editor and three anonymous reviewers for their helpful comments and suggestions. This research was supported by NSF grant IOB-0444553 and NIH grant HD-049525 to M.H. Ferkin.

## References

- Alligood CA, Wheaton CJ, Daneault AJ, Carlson RC, Savage A, 2009. Behavioral predictors of copulation in captive key largo woodrats *Neotoma floridana smalli*. Behav Process 81: 337–342.
- Andersson M, 1994. Sexual Selection. Princeton, N.J: Princeton University Press.
- Beach FA, 1976. Sexual attractivity, proceptivity, and receptivity in female mammals. Horm. Behav. 7: 105–138.
- Bercovitch FB, Bashaw MJ, del Castillo SM, 2006. Sociosexual behavior, male mating tactics, and the reproductive cycle of giraffe *Giraffa camelopardalis*. Horm. Behav. 50: 314–321.
- Berteaux D, Bêty J, Rengifo E, Bergeron J, 1999. Multiple paternity in meadow voles *Microtus pennsylvanicus*: investigating the role of the female. Behav. Ecol. Sociobiol. 45: 283–291.
- Beyer C, Contreras JL, Morali G, Larsson K, 1981. Effects of castration and sex steroid treatment on the motor copulatory pattern in the rat. Physiol Behav 27: 727–730.

- Birkhead TR, 2000. Promiscuity: An evolutionary history of sperm competition. Cambridge, MA: Harvard University Press.
- Boonstra R, Xia X, Pavone L, 1993. Mating system of the meadow vole *Microtus pennsylvanicus*. Behav. Ecol. 4: 83–89.
- Carter SC, Witt DM, Schneider J, Harris ZL, Volkening D, 1987. Male stimuli are necessary for female sexual behavior and uterine growth in prairie voles *Microtus ochrogaster*. Horm Behav 21: 74–82.
- Clarke JR, 1956. The aggressive behaviour of the vole. Behaviour 9: 1–23.
- Clutton-Brock TH, 1998. Reproductive skew, concessions and limited control. Trends Ecol. Evol. 13: 288–292.
- delBarco-Trillo J, Ferkin MH, 2004. Male mammals respond to a risk of sperm competition conveyed by odours of conspecific males. Nature 431: 446–449.
- delBarco-Trillo J, Ferkin MH, 2006a. Male meadow voles respond differently to risk and intensity of sperm competition. Behav Ecol 17: 581–585.
- delBarco-Trillo J, Ferkin MH, 2006b. Female meadow voles *Microtus pennsylvanicus* cause their mates to ejaculate outside their reproductive tract. Behaviour 143: 1425–1437.
- Dewsbury DA, 1972. Patterns of copulatory behavior in male mammals. Q. Rev. Biol. 47: 1–33.
- Dewsbury DA, 1981. An exercise in the prediction of monogamy in the field from laboratory data on 42 species of muroid rodents. The Biologist. 63: 138–162.
- Dewsbury DA, Baumgardner DJ, 1981. Studies of sperm competition in two species of muroid rodents. Behav. Ecol. Sociobiol. 9: 121–133.
- Eisenberg JF, 1967. A comparative study in rodent ethology with emphasis on evolution of social behavior. Proc. US Nat. Mus. 122: 1–55.
- Ferguson B, Fuentes SM, Sawrey DK, Dewsbury DA, 1986. Male preferences for mated versus unmated females in two species of voles (*Microtus ochrogaster* and *M. montanus*). J. Comp. Psychol. 100: 243–247.
- Ferkin MH, Johnston RE, 1995. Meadow voles *Microtus pennsylvanicus* use multiple sources of scent for sex recognition. Anim. Behav. 49: 37–44.
- Ferkin MH, Leonard ST, 2010. Self-grooming as a form of olfactory communication in related behaviors. In: Kalueff AV, LaPorte JL, Bergner CL ed. Neurobiology of Grooming Behavior. Cambridge, UK: Cambridge University Press, in press.
- Ferkin MH, Seamon JO, 1987. Odor preference and social behavior in meadow voles *Microtus pennsylvanicus*: Seasonal differences. Can. J. Zool. 65: 2931–2937.
- Gavish L, Carter CS, Getz LL, 1983. Male-female interactions in prairie voles. Anim. Behav. 31: 511–517.
- Grant EC, Mackintosh JH, 1963. A comparison of the social postures of some common laboratory rodents. Behaviour 21: 246–259.
- Gray GD, Dewsbury DA, 1975. A quantitative description of the copulatory behaviour of meadow voles *Microtus pennsylvanicus*. Anim Behav 23: 261–267.
- Hart BL, Korinek E, Brennan P, 1987. Postcopulatory genital grooming in male rats: Prevention of sexually transmitted infections. Physiol. Behav. 41: 321–325.
- Insel TR, Young L, Wang Z, 1997. Central oxytocin and reproductive behaviours. Rev. Reprod. 2: 28–37.
- Ivy TM, Weddle CB, Sakaluk SK, 2005. Females use self-referent cues to avoid mating with previous mates. Proc. Biol. Sci. 272: 2475–2478.

- Keller BL, 1985. Reproductive patterns. In: Tamarin R ed. *Biology of New World Microtus*. 8<sup>th</sup> edn. Lawrence, KS: American Society of Mammalogists, 725–778.
- Kleiman DG, 1977. Monogamy in mammals. *Q. Rev. Biol.* 52: 39–69.
- LaDage LD, Ferkin MH, 2006. Male leopard geckos *Eublepharis macularius* can discriminate between two familiar females. *Behaviour* 143: 1033–1049.
- LaDage LD, Gutzke WHN, Simmons RA II, Ferkin MH, 2008. Multiple mating increases fecundity, fertility and relative clutch mass in the female leopard gecko *Eublepharis macularius*. *Ethology* 114: 512–520.
- Madison DM, 1980. An integrated view of the social biology of *Microtus pennsylvanicus*. *The Biologist* 62: 20–33.
- Meek LR, Lee TM, 1993. Female meadow voles have a preferred mating pattern predicted by photoperiod, which influences fertility. *Physiol Behav* 54: 1201–1210.
- Milligan SR, 1982. Induced ovulation in mammals. In: Finn, CA ed. *Oxford Reviews of Reproductive Biology*. Vol. 4. London: Clarendon Press, 1–46.
- Mooring MS, McKenzie AA, Hart BL, 1996. Grooming in impala: role of oral grooming in removal of ticks and effects of ticks in increasing grooming rate. *Physiol. Behav.* 59: 965–971.
- Mosig DW, Dewsbury DA, 1976. Studies of the copulatory behavior of house mice *Mus musculus*. *Behav. Biol.* 16: 463–473.
- Myers JH, Krebs CJ, 1971. Genetic, behavioral, and reproductive attributes of dispersing field voles *Microtus pennsylvanicus* and *Microtus ochrogaster*. *Ecol Monogr* 41: 53–78.
- Sachs BD, Clark JT, Molloy AG, Bitran D, Holmes GM, 1988. Relation of autogrooming to sexual behavior in male rats. *Physiol Behav* 43: 637–643.
- Shapiro LE, Austin D, Ward SE, Dewsbury DA, 1986. Familiarity and female mate choice in two species of voles (*Microtus ochrogaster* and *M. montanus*). *Anim Behav* 34: 90–97.
- Soini P, 2005. Sociosexual behavior of a free-ranging *Cebuella pygmaea* (Callitrichidae, platyrrhini) troop during postpartum estrus of its reproductive female. *Amer J Primatol* 13: 223–230.
- Stopka P, Graciasová R, 2001. Conditional allogrooming in the herb-field mouse. *Behav. Ecol.* 5:5 84–589.
- Stopka P, Macdonald DW, 1998. Signal interchange during mating in the wood mouse *Apodemus sylvaticus*: The concept of active and passive signaling. *Behaviour* 135: 231–249.
- Stopka P, Macdonald DW, 1999. The market effect in the wood mouse *Apodemus sylvaticus*: Selling information on reproductive status. *Ethology* 105: 969–982.
- Tamarin RH, 1985. *Biology of New World Microtus*. Special Publication No.8. The Lawrence, KS: American Society of Mammalogists.
- Thornton JE, Irving S, Goy RW, 1991. Effects of prenatal antiandrogen treatment on masculinization and defeminization of guinea pigs. *Physiol. Behav.* 50: 471–475.
- Vaughn AA, delBarco-Trillo J, Ferkin MH, 2008. Sperm investment in male meadow voles is affected by the condition of the nearby male conspecifics. *Behav. Ecol.* 19: 1159–1164.
- Vaughn AA, delBarco-Trillo J, Ferkin MH, 2010. Self-grooming by male meadow voles differs across copulation but is not affected by the risk and intensity of sperm competition. *Behaviour* 147: 259–274.
- Witt DM, Carter CS, Carlstead K, Read LD, 1988. Sexual and social interactions preceding and during male-induced oestrus in prairie voles, *Microtus ochrogaster*. *Anim. Behav.* 36: 1465–1471.

A. A. VAUGHN: Sociosexual behavior in meadow voles

Witt DM, Carter CS, Chayer R, Adams K, 1990. Patterns of behaviour during postpartum oestrus in prairie voles *Microtus ochrogaster*. Anim. Behav. 39: 528–534.

## Figure Legends

**Fig. 1** The mean  $\pm$  SEM time (s) that male meadow voles spent during the pre-copulatory, peri-copulatory, and post-copulatory phases allogrooming, wrestling, and chasing, approaching, and in side-by-side contact with a female

Bars capped with asterisk(s) denote significant differences at: \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

**Fig. 2** The mean  $\pm$  SEM time (s) that male meadow voles spent during the pre-copulatory, peri-copulatory, and post-copulatory phases displaying naso-nasal approaches, naso-anogenital approaches, and naso-other approaches directed at a female

Bars capped with asterisk(s) denote significant differences at: \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

Figure 1

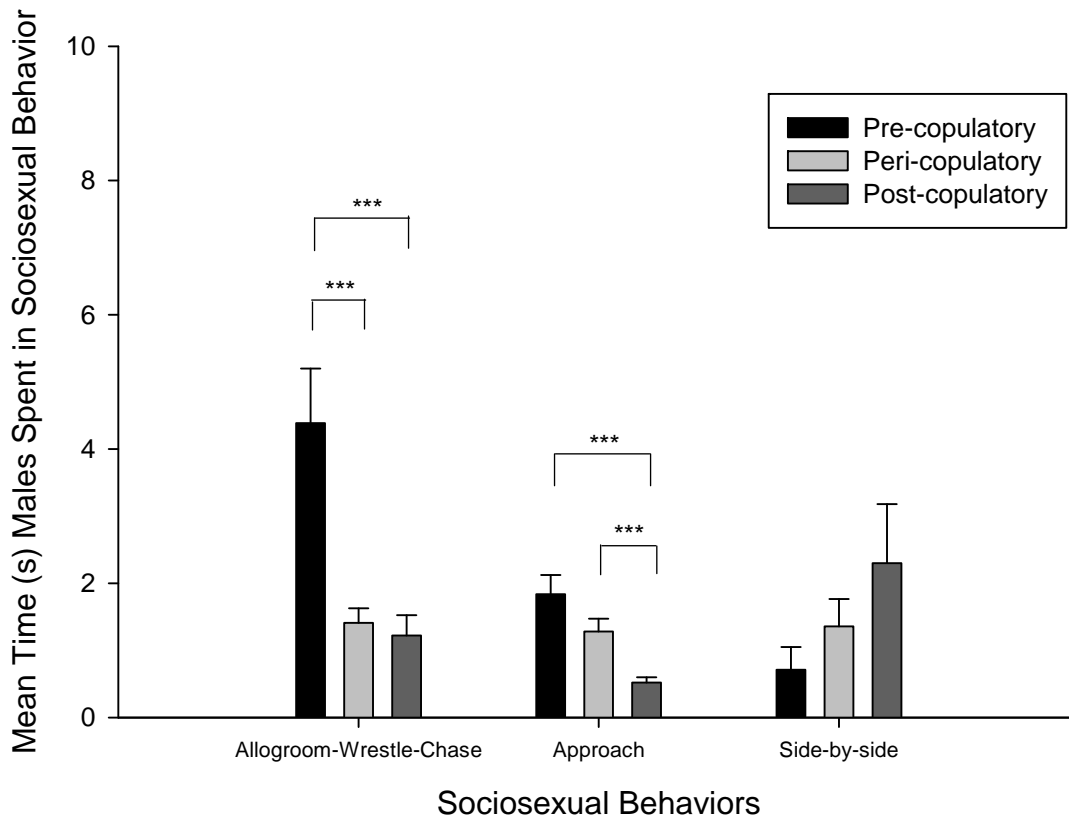


Figure 2

