Female Meadow Voles (*Microtus pennsylvanicus*) Demonstrate Same-Sex Partner Preferences

Karen J. Parker and Theresa M. Lee
University of Michigan

Female meadow voles (*Microtus pennsylvanicus*) are territorial during warm months but demonstrate social tolerance under low temperatures. In spring, females nest together and some pairs participate in communal nursing and rearing of young. Because communal nursing involves significant cooperation, selective pair-bonds may develop between 2 nestmates. Using a choice apparatus, the authors determined that (a) captive females demonstrated partner preferences for a nestmate; (b) partner preferences were enduring and persisted after dyadic separation; and (c) following the loss of a nestmate, females did not develop preferences for a new nestmate, even after extended cohabitation. Data support the hypothesis that captive meadow voles develop selective and enduring same-sex social bonds that may, under free-living conditions, facilitate communal nesting and cooperative rearing of young.

Although female meadow voles are territorial during the summer primary breeding season (Madison, 1980; Webster & Brooks, 1981), they demonstrate remarkable social tolerance toward conspecifics during the colder months of the year (Madison, FitzGerald, & McShea, 1984; McShea & Madison, 1984). Like many rodents (for a review, see Hayes, 2000), meadow voles often form stable mixed-sex nesting constellations in autumn that frequently consist of an adult female, her most recent litter, and 1 or more adult males (Madison et al., 1984). Communal nesting presumably allows rodents to capitalize on the thermoregulatory benefits afforded by group living (Howard, 1950), and strong social bonds may promote group cohesion during the colder months of the year. This prediction is supported by laboratory data that indicate that cohabitation facilitates the formation of selective and enduring opposite-sex pair-bonds between adult meadow voles (Parker, Phillips, & Lee, 2001).

Social movement occurs between communal groups in winter (Madison et al., 1984; Webster & Brooks, 1981) and may be male biased (McShea, 1990), with female group members remaining together throughout winter and into spring. In spring, communal groups do not dissolve with the onset of breeding, but they are closed to the immigration of new members (McShea, 1990; McShea & Madison, 1984). During this time, females are frequently observed nesting together, and at least some female pairs partici-

pate in communal nursing and rearing of young (McShea, 1990; McShea & Madison, 1984). Because communal nursing involves a significant amount of cooperation between the females involved, McShea and Madison (1984) hypothesized that female pair-bonds develop during winter communal nesting and may occur between relatives, most likely in the form of sister–sister, but possibly mother–daughter, partnerships (as demonstrated in house mice; Konig, 1994).

The selective nature of these female partnerships is supported by field data that indicate when a nesting partner disappears, no new partnership is formed (McShea & Madison, 1984). These social preferences are likely facilitated by familiarity, which typically results from individuals being reared together (Ferkin & Rutka, 1990; Paz y Mino & Tang-Martinez, 1999) or through cohabitation or repeated social interactions in adulthood (DeVries, Johnson, & Carter, 1997; Parker et al. 2001; Williams, Catania, & Carter, 1992). The role of familiarity in determining social preferences has been well established in many vertebrates (for a review, see Holmes, 1988), including meadow voles. In both field and laboratory experiments, female meadow voles prefer the odors of familiar to unfamiliar animals and engage in more affiliative and less agonistic behaviors during 5-min encounters with familiar animals compared with unfamiliar conspecifics (Ferkin, 1988a, 1989; Ferkin & Rutka, 1990). Similarly, field-trapped females that overwinter together readily share a nest site with one another, whereas nonnestmates behave agonistically toward one another and actively exclude unfamiliar females from the nest site (McShea, 1990).

Although the existence of selective pair-bonds has been demonstrated between opposite-sex meadow voles (Parker et al., 2001), we do not know whether female meadow voles form selective pair-bonds with other females, as hypothesized by McShea and Madison (1984). In the laboratory, pair-bonds have been operationally defined by quantifying the amount of time a test animal spends in lateral contact with both a familiar and unfamiliar animal in a choice apparatus (Williams et al., 1992). A subject exhibits a partner preference when it spends twice as much time in lateral contact with a familiar animal relative to an unfamiliar

conspecific (Insel, Preston, & Winslow, 1995). In this series of experiments, we examine (a) whether female meadow voles demonstrate selective partner preferences for a familiar nestmate compared with an unfamiliar female; (b) whether these selective social bonds endure a 3-week separation period; and (c) after the loss of a nestmate, whether females form new social bonds with a previously unknown female following extended cohabitation with the new nestmate. Data from these experiments allow us to determine whether female meadow voles develop selective and enduring same-sex social bonds that may, under free-living conditions, facilitate both communal nesting and cooperative rearing of young.

General Method

Study Animals and Housing Conditions

Study animals, derived from wild-caught meadow voles (*Microtus pennsylvanicus*) trapped in northwestern Pennsylvania and southwestern New York, were born to continuously cohabiting breeding pairs housed in long-day lengths (14:10-hr light–dark cycle) in a colony at the University of Michigan. Wild-caught voles were periodically added to the captive colony, and study voles were 15–20 generations removed from the original colony founders. In the laboratory, meadow voles show dramatic seasonal changes in development (Lee, Smale, Zucker, & Dark, 1987), reproductive behavior (Meek & Lee, 1993a, 1993b), parental behavior (Parker & Lee, 2001; Reeves, 1994), and intraspecific social interactions and aggression (Ferkin, 1988a, 1988b; Ferkin & Gorman, 1992; Ferkin & Seaman, 1987), consistent with field studies, that can be driven entirely by changes in photoperiod. Consequently, weanling pups were removed from the dam and sire at 18 days of age, and both control and experimental voles were housed in same-sex sibling pairs under short-day lengths (10:14-hr light–dark cycle), a photoperiod characteristic of late autumn through early spring field conditions. It should be noted that long-day length females were not used as subjects in this study because they are highly territorial and the forced cohabitation required for these experiments induces significant agonism in same-sex, pair-housed, long-day length voles (personal observation). In all experiments, both control and experimental study voles lived in pairs until at least 51 days of age (see below for housing details specific to each experiment). A total of 149 females served as subjects in these experiments. Voles were housed in polypropylene cages (26.67 × 21.59 × 13.97 cm) on pine-shaving bedding with food (Purina 5015 Mouse Chow) and water available ad libitum. Animal rooms were maintained at 21 ± 2 °C with low ambient noise conditions.

Partner Preference Testing

Behavioral testing was conducted in a Plexiglas three-arm affiliation device (39.4 × 24.1 × 27.9 cm; Parker et al., 2001). The device consisted of three equal-sized compartments connected to each other by a runway on one side of the device. For experimental study voles, in one of the compartments, a designated vole from the test pair was loosely tethered with a 10.15-cm nylon tie and wire fishing clip secured to the back wall of the compartment. (Nylon ties were secured while test animals were lightly anesthetized with halothane.) This familiar stimulus vole was able to move freely in its end of the compartment. A second unfamiliar, unrelated stimulus vole of the same age and photoperiod as the first stimulus vole was tethered in an identical fashion in a second arm of the device. The third arm of the device remained empty. For control study voles, both tethered stimulus voles were unfamiliar, unrelated, and of the same age and photoperiod as the control vole (i.e., in the first experiment described below, control voles were not assessed for partner preferences with a familiar vole, although they were cohabiting with a nestmate). In both experimental and control conditions, tethered stimulus voles were allowed to explore the new

environment for 10 min before the test vole was introduced into the device. For all experimental conditions, only 1 study vole from each cohabiting (Experiment 1) or previously cohabiting (Experiment 2) pair was tested for partner preferences. Cohabiting voles were separated for no more than 20 min (from when the stimulus vole was tethered to when the test vole was introduced into the device). During the 180-min preference test, the test vole could move freely throughout the entire testing device. Each test was carried out during the lighted phase of the light–dark cycle and was videotaped with a Panasonic camera and wide-angle lens on a time-lapse VCR. Behavioral tests were later scored by a trained observer who was blind to experimental conditions. In several cases, videotaped tests could not be scored and were not included in statistical analyses.

Using a computer-aided scoring program (designed by Steve Parus, Chemistry Department, University of Michigan), the observer recorded counts and durations of amicable and agonistic behavior between the test vole and each stimulus vole. The amount of time the test vole spent alone in the third arm of the device was also calculated. Behavior was amicable when the test vole engaged in side-by-side contact with a stimulus vole (after Williams et al., 1992). Behavior was aggressive when the test vole engaged in charging, attacking, biting, or boxing with a stimulus vole (after Ferkin 1988a). However, because aggression between the test and stimulus voles was exceedingly rare, as is common for short photoperiod-housed voles (Ferkin & Seaman, 1987), agonistic interactions did not occur often enough to warrant statistical analysis.

Statistical Analyses

Preferences were determined by quantifying the number of minutes test subjects spent in side-by-side contact with each stimulus vole (e.g., the familiar and unfamiliar vole; DeVries et al., 1997; Insel et al., 1995; Parker et al., 2001; Williams et al., 1992). We determined that a selective partner preference existed when a subject spent twice as much time in lateral contact with a familiar vole relative to an unfamiliar conspecific (after Insel et al., 1995). Subjects' contact times with the familiar and unfamiliar vole were compared using paired t tests within each condition (i.e., experimental and control conditions at each test time). Differences were considered significant when $p < .05$. Repeated measures analysis of variance was used to determine whether test voles spent more time in contact with reunited nestmates (Experiment 2) and new nestmates (Experiment 3) or less time alone (Experiment 3) across the three test times. Partner preferences were calculated using a preference ratio ([time spent with the nestmate/total time spent with both stimulus voles] × 100) for each time point. We generated a C-matrix and used difference contrasts to determine which test times significantly differed. In post hoc tests, the alpha error was adjusted to protect against multiple comparisons (i.e., differences were considered significant when $p < .0167$). Systat (Version 9.0) was used for all analyses.

Experiment 1

The goal of Experiment 1 was to determine whether adult females, housed together since birth, demonstrate selective partner preferences for a familiar nestmate compared with an unfamiliar female. This experiment was designed to quantitatively evaluate whether continuously cohabiting female meadow voles possess the capacity to form selective social bonds with a nestmate as was hypothesized by McShea and Madison (1984) but has never before been tested. Sibling pairs were selected as study voles because, under free-living conditions, winter immigration appears to be male biased (McShea, 1990) and it is therefore likely that the females that overwinter together are relatives (sister–sister pairs) that remain together from the previous breeding season.

Experiment 1 Method

Both experimental and control voles resided in nestmate pairs from weaning until the beginning of the experimental procedure. At roughly 11 weeks of age, partner preference testing (as described above) occurred. The experimental condition included eight cohabiting nestmate pairs, but only 1 vole from each pair was assessed for partner preferences. Thus, in the experimental condition, test voles ($n = 8$) were placed in a preference apparatus and allowed to choose between spending time with a familiar nestmate ($n = 8$), with an unfamiliar female ($n = 8$), or alone. The control condition included nine cohabiting nestmate pairs, but only 1 vole from the pair was assessed for partner preferences. Unlike the experimental condition, the nontest nestmate did not serve as a familiar stimulus vole. Thus, control test voles ($n = 9$) chose between spending time with either of 2 unfamiliar females ($n = 18$) or alone.

Experiment 1 Results: Partner Preferences in Cohabiting Nestmates

Experimental test voles exhibited strong partner preferences for their nestmate compared with an unfamiliar female, $t(7) = 4.783$, $p < .002$. Moreover, experimental test voles spent 70% of the preference test in lateral contact with their nestmate, whereas they spent only 6% of the test with the unfamiliar female (see Figure 1). Control test voles did not demonstrate a significant preference for either unfamiliar stimulus vole and spent the majority of time (74%) alone.

Experiment 2

The goal of Experiment 2 was to assess the enduring nature of same-sex social bonds by separating continuously cohabiting female nestmates for 3 weeks, a separation period that constitutes 12%–25% of a free-living, short-day length meadow vole's life span, and reuniting them in the preference apparatus (Madison et al., 1984). Previous studies in prairie voles, a closely related and highly social species (which live year-round in family groups), indicate that sibling recognition persists following 15, but not 20, days of separation (Paz y Mino & Tang-Martinez, 1999). Consequently, we used this time frame to determine whether selective social bonds persist following an extended separation in female meadow vole dyads. We also tested whether 1 or 10 days of cohabitation after reunion would reactivate partner preferences in the event that these preferences were not demonstrated at reunion or, if they were evident, whether renewed cohabitation would strengthen the preference.

Experiment 2 Method

Both experimental ($n = 12$ pairs) and control ($n = 14$ pairs) voles resided in same-sex sibling pairs from 19–50 days of age, after which time both experimental and control voles were separated from their familiar nestmates and housed individually for 3 weeks. (In the case of the experimental animals, the nontest, stimulus vole was also housed alone.) All study voles remained so housed until the beginning of the experimental procedure. At 11 weeks of age, the first partner preference test (described above) occurred. As in Experiment 1, experimental test voles ($n = 12$) were placed in the preference apparatus and allowed to choose between spending time with the separated stimulus nestmate ($n = 12$), with an unfamiliar female ($n = 12$), or alone. Control test females ($n = 14$) chose between spending time with either of 2 unfamiliar stimulus females ($n = 28$) or alone. Following testing, experimental test voles were reunited with their separated nestmate (but control test voles were not). Reunited nestmates cohabited for 24 hr and were again tested for partner preferences as before. Experimental test females were again tested for partner preferences
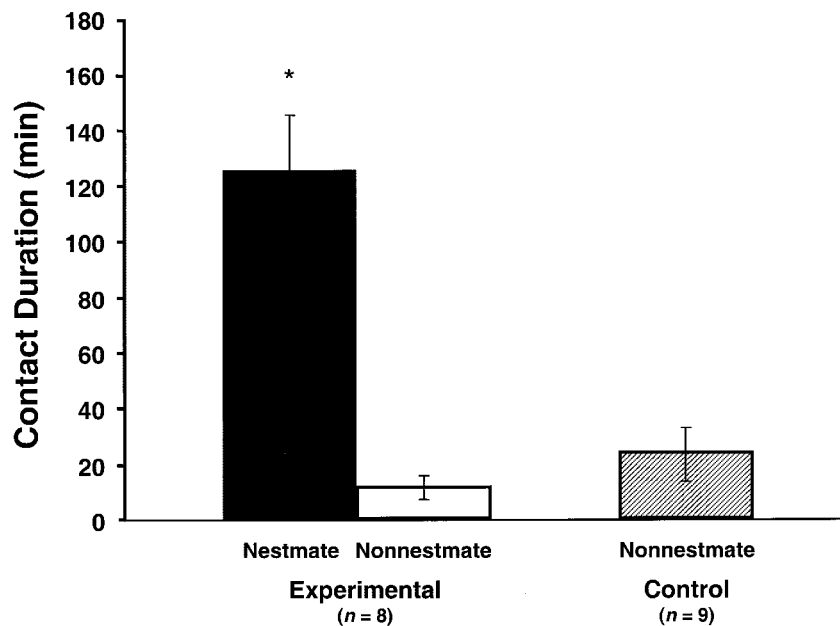

Figure 1. Mean ($\pm$ *SE*) duration of side-by-side contact with nestmate (solid bar) and nonnestmate (open bar) during 180-min partner preference tests. The hatched bar indicates the average amount of time control females spent with 1 of the nonnestmates. An asterisk indicates a minimum significant difference ($p < .05$) within the experimental group between time spent with the 2 stimulus voles.

after 10 days of cohabitation. Previous laboratory data indicate that preferences for 2 unfamiliar stimulus animals do not differ in unpaired animals across test times (Parker, 2000), and consequently, unpaired females were not evaluated during the second and third test times to reduce the number of voles used in these experiments and simplify data analysis.

Experiment 2 Results: Partner Preferences in Reunited Nestmates

After a 3-week separation period, experimental test voles exhibited strong partner preferences for their separated nestmate (compared with an unknown female) at reunion (Time 1), $t(11) = 3.278$, $p = .007$; after 24 hr of cohabitation (Time 2), $t(8) = 4.345$, $p = .002$; and after 10 days of cohabitation (Time 3), $t(9) = 4.442$, $p = .002$ (see Figure 2). Partner preference ratios did not significantly increase over time (Time 1 $= 81\%$; Time 2 $= 86\%$; Time 3 $= 92\%$), $F(2, 14) = 1.449$, $p = .268$. As expected, control test voles did not demonstrate partner preferences and spent the majority of time (40%) alone (see Figure 2).

Experiment 3

In captive prairie voles, same-sex partner preferences develop between previously unfamiliar voles within 24 hr of cohabitation (DeVries et al., 1997; Williams et al., 1992), after test females have been separated from a previous nestmate for 2 weeks. However, in free-living meadow voles, new partnerships are not formed when a nestmate disappears in the field (McShea & Madison, 1984). Thus, the goal of Experiment 3 was to determine whether female meadow voles would form new social bonds following cohabitation with a previously unknown female, after the permanent removal of a nestmate.

Experiment 3 Method

As in Experiment 2, study voles resided in same-sex pairs from 19–50 days of age and were subsequently separated into individual housing for 3 weeks. At 11 weeks of age, the first partner preference test (described above) occurred. Test voles ($n = 10$), separated from their original nestmate for 3 weeks, chose between spending time with either of 2 unfamiliar stimulus females ($n = 20$) or alone. Following testing, test females were housed with the stimulus female with which they spent the most time in side-by-side contact during the preference test. Females cohabited in these newly formed dyads for 24 hr, and test voles were tested for partner preferences as before. Test voles were again tested for partner preferences after 10 days of cohabitation. For each test subject, the stimulus voles were the same for all three preference tests. To limit the number of voles used in these experiments, we used 10 test voles in this experiment that also served as control test voles in Experiment 2. These voles were only tested once as control test voles and were then paired with a previously unfamiliar animal and tested after 1 day and 10 days of cohabitation as described above.

Experiment 3 Results: Partner Preferences in Newly Paired Nestmates

As expected, after 0 days of cohabitation, test females did not exhibit partner preferences for either unfamiliar female, $t(9) = 0.402$, $p = .697$. In contrast to previous reports in prairie voles (DeVries et al., 1997), meadow vole females did not form partner preferences for a new nestmate after 1 day of cohabitation
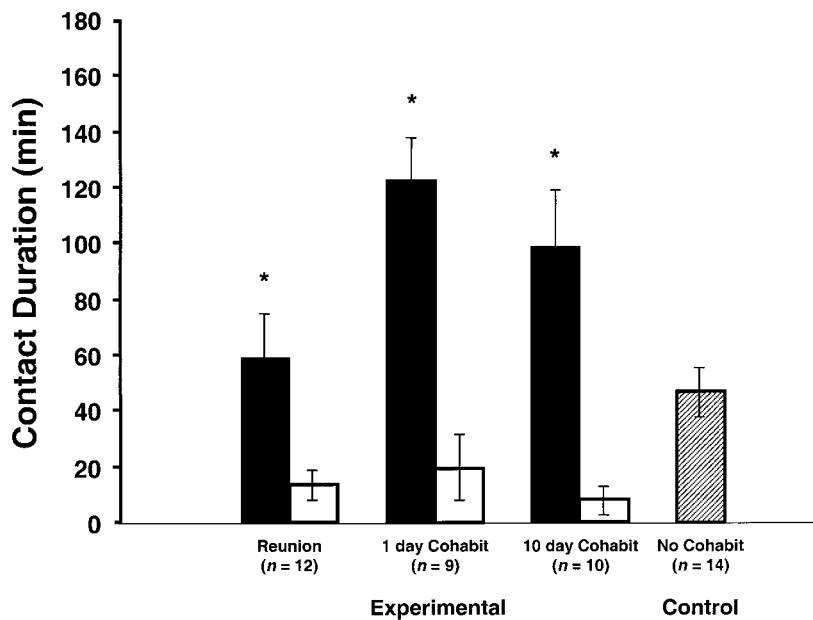

Figure 2. Mean ($\pm$ *SE*) duration of side-by-side contact with nestmate (solid bars) and nonnestmate (open bars) during 180-min partner preference tests at reunion and after 1 day and 10 days of cohabitation following a 3-week dyadic separation. The hatched bar indicates the average amount of time control females spent with 1 of the nonnestmates. Asterisks indicate a minimum significant difference ($p < .05$) between time spent with the 2 stimulus voles by experimental females at each testing time point.

with that nestmate, $t(9) = 1.018$, $p = .335$, nor did they form preferences following 10 days of extended cohabitation, $t(9) = 1.049$, $p = .322$ (see Figure 3). Repeated measures analysis of partner preference ratios yielded similar results (Time 1 = 53%; Time 2 = 58%; Time 3 = 63%), $F(2, 16) = 0.319$, $p = .732$. However, cohabitation did induce greater sociality in test females, $F(2, 17) = 7.943$, $p = .003$, as they spent significantly less time in the empty tube after 24 hr ($p = .013$) and 10 days ($p = .010$) of cohabitation, an average of 18% of the total test time, compared with the time spent in the empty tube during the first preference test, which constituted 41% of the total test time.

General Discussion

This series of experiments examined whether female meadow voles demonstrate same-sex partner preferences and, if so, whether these preferences were selective, enduring, and exclusive. Data from these experiments determined that female meadow voles exhibit selective partner preferences for a female with which they have been housed (a nestmate) and spend little time in contact with an unfamiliar female (see Figure 1). These partner preferences were enduring, as following a 3-week dyadic separation test, females demonstrated strong preferences for previous nestmates upon reunion (see Figure 2). Following the permanent removal of a nestmate, females did not develop partner preferences for a new nestmate, even after extended cohabitation with the new nestmate (see Figure 3). Collectively, these data support the hypothesis that female meadow voles develop selective and enduring same-sex social bonds that may, under free-living conditions, facilitate both communal nesting and cooperative rearing of young.

Research on voles has focused on the role of social cues in the development of partner preferences. In female prairie voles, 24 hr of nonsexual cohabitation is sufficient to activate the onset of partner preferences in newly paired same-sex dyads (DeVries et al., 1997). In female meadow voles, our results indicate that association at the natal nest and extended post-weaning cohabitation trigger strong and enduring preferences for familiar nestmates. However, unlike prairie voles, adult female meadow voles do not form same-sex preferences for a new nestmate following 24 hr of nonsexual cohabitation, nor are preferences demonstrated following 10 days of continuous cohabitation with a new female.

It is unclear why prairie voles form new same-sex partner preferences in adulthood but meadow voles do not. One possible explanation is that these laboratory data may reflect species differences in free-living social organization. Prairie voles live year-round in social groups and may be predisposed to form social bonds more readily with other conspecifics. In contrast, social living is a seasonal, rather than constitutive, feature of meadow vole social systems. As a result, meadow voles may require long periods of dyadic cohabitation to facilitate the development of partner preferences in otherwise territorial and asocial females.

Besides this proximate explanation, extended periods of dyadic cohabitation required to establish partner preferences in meadow voles may also serve an adaptive purpose. In the spring, female meadow voles are frequently observed nesting together in pairs, and some paired females participate in communal nursing (McShea, 1990; McShea & Madison, 1984). Because the fitness costs associated with choosing a "bad" partner are high (i.e., increased risk of offspring mortality if the partner does not engage in adequate maternal attendance), females should be selective in their choice of nursing partners. Because a necessary component of reciprocal nursing partnerships is the ability to recognize the partner, it is therefore interesting to note that meadow voles were able to "remember" their familiar nestmates (indexed by ready affiliation at reunion) even after a 3-week dyadic separation (see Figure 2).

In some rodents, communal nursing occurs between either unrelated or related females (for a review, see Hayes, 2000) and is thought to increase offspring growth, weaning, and survival rates
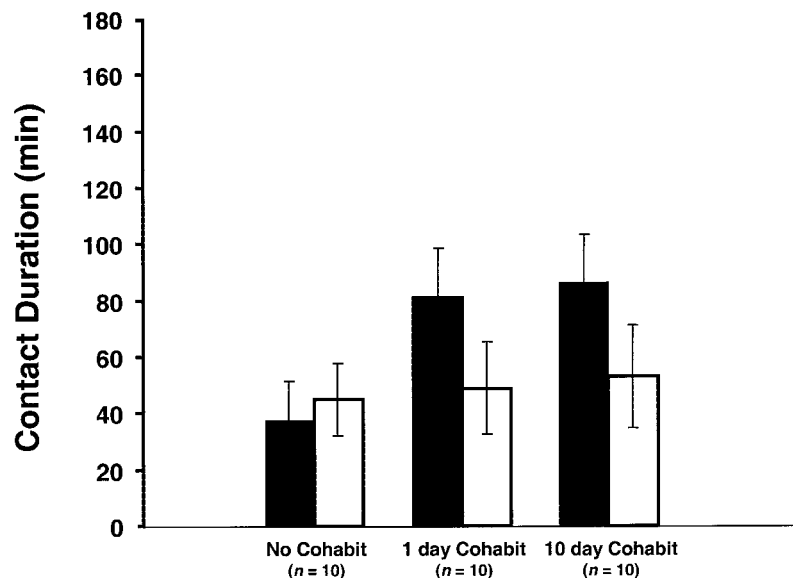

Figure 3. Mean ($\pm$ *SE*) duration of side-by-side contact with a new nestmate (solid bars) and nonnestmate (open bars) during 180-min partner preference tests after 0, 1, and 10 days of cohabitation.

compared with young that are not communally reared (Konig, 1994; Mennella, Blumberg, McClintock, & Moltz, 1990; Saylor & Salmon, 1971). Moreover, among relatives, successful corearing of offspring confers not only direct but also inclusive fitness benefits (Hamilton, 1964; Konig, 1994). Although the genetic relatedness of communally nursing meadow vole dyads in free-living populations is unknown, our data nevertheless suggest that long periods of cohabitation—perhaps initiated in the natal nest—foster the development of selective social bonds, which may, in turn, facilitate the familiarity required for successful corearing of young.

The prediction that selective bonds are required to facilitate communal nursing raises the question of whether animals that lose a preferred partner will form new partnerships. In spring field studies, females do not appear to form new partnerships after losing a nestmate (McShea & Madison, 1984). This is corroborated by our data that indicate that after separation from a long-term nestmate, captive meadow voles do not form social bonds with new females after 10 days of cohabitation (see Figure 3). Whether females eventually form new partnerships following longer periods of cohabitation is unknown and merits future investigation.

Although meadow vole females did not develop preferences for a new nestmate, it should be noted that they nevertheless displayed little aggression and spent the majority of test time in social contact with other females. In winter field studies, meadow voles form transient rather than stable social groups (Madison et al., 1984; Webster & Brooks, 1981), which may occur as a result of nestmate mortality (McShea, 1990). Under these socioecological conditions, manifestation of general sociability and infrequent agonism may promote affiliative tendencies between previously unfamiliar females, permitting voles to opportunistically conserve heat under low temperatures.

In summary, our data indicate that female meadow voles develop selective and enduring same-sex partner preferences when housed under laboratory short day lengths, a photoperiod that corresponds to late autumn through spring field conditions. The existence of social bonds in this species may promote dyadic cohesion during communal nesting to allow voles to capitalize on the thermoregulatory benefits afforded by group living. Selective partner preferences may also serve as a critical social substrate for successful communal nursing, as demonstrated in other social rodents, including house mice (Konig, 1994). If, like house mice, meadow voles preferentially nest and nurse with close relatives, the possibility that selective partner preferences are the product of kin selection should be considered.

Additional studies in captive meadow voles are needed to differentiate the roles that early association in the natal nest (i.e., filial imprinting as determined through cross-fostering experiments) and extended cohabitation in adulthood play in the formation of selective and enduring partner preferences. Comparative studies between long and short photoperiod-housed meadow voles would also be valuable in determining whether partner preferences and communal nursing in the laboratory occur selectively and only under circumstances that may confer a fitness benefit under free-living conditions (i.e., under short, but not long, photoperiods).

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> 750 First Street, NE
> Washington, DC 20002-4242

The first review of nominations will begin December 8, 2003. The deadline for accepting nominations is **December 15, 2003**.