

MULTI-MALE MATING BY PAIRED AND UNPAIRED FEMALE PRAIRIE VOLES (*MICROTUS OCHROGASTER*)

by

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Summary

Promiscuous mating is common in female rodents; however what role the female plays in this choice of mates is not clear. Also, whether MMM occurs in the reportedly socially monogamous prairie vole, *Microtus ochrogaster*, and what role mate-guarding plays in deterring MMM is not known. We conducted two experiments to determine if female prairie voles that were not mate-guarded would copulate with multiple males during a given oestrous period. In experiment 1 using females that were unpaired, we allowed females to choose among three males that were tethered and unable to interact with one another, thus eliminating male-male competition and mate guarding. MMM occurred in 55% of 47 trials. Females mated most often with males with whom they spent the most time, thus social preference was a good predictor of sexual preference. The tendency to mate with multiple males increased over time, thus the length of time a male mate guards can affect paternity. In experiment 2 with females that had been paired with a male and were in post-partum oestrus, 5 of 12 (42%) females mated with more than one male and 3 of 12 (25%) females deserted their paired mate and paired with a new novel male. Thus multi-male mating was similar for paired and

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unpaired females. Our results suggest that female prairie voles that are not mate-guarded will mate with multiple partners.

Introduction

Multi-male mating is common among mammals and occurs extensively in rodents (*e.g.* Boonstra *et al.*, 1993; Agrell *et al.*, 1998; Berteaux *et al.*, 1999). Several hypotheses have been proposed to explain why females multiply mate (reviewed by Yasui, 1998; Jennions & Petrie, 2000) including both direct benefits (*e.g.* acquisition of nutrients, parental care and fertility insurance) and indirect effects (*e.g.* genetic diversity or genetic quality). These hypotheses assume that females choose to mate with multiple males. It is not known to what extent multi-male mating (MMM) results from forced copulations by males or if females play an active role in selecting multiple mating partners. Behavioural monogamy is relatively rare in mammals, occurring in less than 5% of species (Kleiman, 1977). However, in those species, the tendency for females to multiply mate may be the selective force for mate guarding, pairbonding and behavioural monogamy (Komers & Brotherton, 1997; Van Schaik & Kappeler, 1997). If this is the case, paired females may be just as likely to mate with multiple males as unpaired females. The role of the male in mate guarding and a female's tendency to solicit matings with multiple males is not known.

In this study we examine the role of the female in MMM in the prairie vole, *Microtus ochrogaster*. We chose the prairie vole because of its tendency to exhibit considerable variation in its mating system. Some evidence exists that under certain conditions, prairie voles form monogamous pairbonds (*e.g.* Thomas & Birney, 1979; Getz *et al.*, 1981, 1987, 1993; Young *et al.*, 1998), whereas in different situations or portions of their range, they may be more promiscuous (Fitch, 1957; Roberts *et al.*, 1998; Wolff & Dunlap, 2002). Numerous experiments have been conducted using prairie voles as a model for a behaviourally monogamous mammal (*e.g.* Williams *et al.*, 1992; Carter & Getz, 1993; Young *et al.*, 1998), however MMM has been observed in the laboratory (Dewsbury & Baumgardner, 1981; Wolff & Dunlap, 2002). MMM has not been studied in the field, but Carter & Getz (1993) report one multiply sired litter out of three examined. Whether a female mates with one or more partners may also depend on the length of time that she has to make this choice, *i.e.* is not mate-guarded. Also, what role the

female plays in multiple versus single-male mating and how this choice of mating partners might differ for paired versus unpaired females is not known. Previous studies have shown that female prairie voles show a social preference for their pairbonded partner (Williams *et al.*, 1992), however whether this translates to mate fidelity is not known. Even in species not known for forming pairbonds, females may show a social preference for a mating partner (*e.g.* meadow voles, *M. pennsylvanicus*, Parker *et al.*, 2001), however MMM still occurs (Boonstra *et al.*, 1993, Berteaux *et al.*, 1999).

Our overall objective was to determine the role of the female in choosing single or multiple mating partners in the prairie vole. Specifically we asked the following questions: (1) During a given estrous period, will female prairie voles mate with more than one male, (2) what is the time sequence with which a female shows a preference for a given male *versus* choosing to mate with multiple males, and (3) does the tendency for single- *versus* multi-male mating differ for females who are not paired versus those that are paired. In the field, 45% of females are unpaired and 55% are paired (Carter & Getz, 1993) so we tested females from both social situations that commonly occur in natural environments.

General methods

Animals

All animals used in this experiment were second and third generation offspring from the vole colony at the University of Memphis. Original prairie voles for the colony were wild caught in southwestern Shelby County, Tennessee and outbred annually. Prairie voles are normally social, however to avoid pregnancies and to standardize social experience, animals were housed singly for 14-21 d prior to the study. Animals were housed individually in polycarbonate cages (29 × 18 × 13 cm) and maintained on a 14 : 10 L : D cycle. Although housed individually, cages were placed on racks so animals would have visual and olfactory but not tactile contact with same-sex conspecifics. Males and females were housed in separate rooms. Food and water were provided *ad libitum* and temperature was maintained at 21 ± 2°C. Animals used in this experiment were 60-120 d old.

Apparatus

We conducted the experiment using a four-chambered apparatus following the design and methods of Berteaux *et al.* (1999). This apparatus consisted of a wooden box divided into four chambers. Each of the three adjacent front chambers was 25 × 25 cm and the rear chamber was 25 × 75 cm, extending the length of all three front chambers. A 10 × 10 cm doorway provided access from the larger back chamber to each of the three front chambers; the front

chambers had no direct connection to each other. The front wall of the apparatus was made of Plexiglas to allow observation and videotaping of the three front chambers. Food, water, and bedding were provided in each chamber. The photoperiod was maintained as in the lab colony.

Experiment 1

This experiment was conducted to determine if parous females that were not currently paired with a male would mate with multiple males when given the opportunity. Females used in this experiment had given birth to one litter, but had not been paired with a male for the previous 30 d and had been separated from their litters for at least 2 wk. These females represent the 81% of females in the field that lose their mates and do not form new pairbonds, but continue to reproduce with wandering males (Pizzuto & Getz, 1998).

Methods

Test trials

To initiate a trial, three unrelated, sexually experienced males >90 d old of similar age (± 15 d) and weight (± 2 g) were chosen for each experiment. One male was tethered in each of the smaller chambers to a steel bar using a flexible steel wire with a swivel clip attached to a plastic cable-tie collar. Males had free movement within their chambers but could not enter the rear (female's) chamber or each other's chambers. The openings to the rear chamber initially were blocked with sliding doors made of hardware cloth. We added an unrelated, parous female that was unfamiliar with any of the males to the rear chamber for a 24-hour acclimation period. Females had visual, olfactory and some tactile contact with males through the hardware cloth doors. We assumed that females would use this time to assess the three males and to become hormonally primed for mating (Hasler & Conway, 1973).

Following the 24-hour acclimation period, we removed the doors giving the female access to each of the males. We videotaped the events for the next 24 h using a time-lapse VCR and a video camera with night vision. After 24 h, we returned the voles to their home cages and observed the females for pregnancy and parturition. Each videotape was watched in its entirety and the numbers of copulations (defined by the number of mounts with thrusting; Gray & Dewsbury, 1973; Dewsbury & Hartung, 1982) and mating partners were recorded as well as the amount of time each female spent in each male's chamber (usually, but not always in physical contact). We were not able to detect ejaculations, so we used copulations as our measure of mating. We define social preference as the male with which a female spent the most time; sexual preference as the male(s) with which a female mated.

Behavioural analyses

We tested for a position effect (bias in male chambers) using ANOVA with the time spent in each chamber as a dependent variable and chamber number as the independent variable (blocked by trial). We then ranked the males based on the number of copulations with females. When two males had the same number of copulations, they were each given an intermediate rank. Using this ranking as a measure of sexual preference, we tested for an association between sexual preference and social preference. For this analysis, we used time spent with each male (female totally in the chamber of a given male, and usually but not always in physical contact) and the copulation order (who the female copulated with first, second and/or third) as the response variables and sexual preference as the predictor variable. We also blocked by trial. Because of non-normal data, we performed a multivariate analysis of variance (MANOVA) on the ranks (Conover, 1999). Finally, we compared latency to mating for females who mated with one male to females who mated with multiple males using ANOVA.

In addition to the above analyses, we tested how the length of observation affected the results. Many previous studies observed matings for only 1 to 2 hours (Shapiro *et al.*, 1986; Shapiro & Dewsbury, 1986; Horne & Ylönen, 1996), but this period was insufficient to predict mating preferences in meadow voles (Berteaux *et al.*, 1999) or prairie voles (Solomon, 1993). Therefore, we re-analyzed our data using only those observations from the first two hours of tape. We then tested for correlations between the 2-h data and the 24-h data set using the mating order, time spent, and number of copulations using Spearman's rank correlation.

Results

Behavioural analysis

Data were analyzed for 47 trials in which mating occurred. Females mated with more than one male in 26 of 47 (55%) trials (16 females mated with two males and 10 mated with all three). On average, females mated with 1.77 ± 0.11 ($\bar{x} \pm SE$) males. We analyzed data for 28 of 47 trials for which we had complete data on the time spent with each male. We detected no position effect in that no significant difference occurred in the time each female spent in each of the three front chambers, regardless of the male present in each chamber ($F_{2,54} = 0.74$, $p = 0.482$). Females showed a social preference for the male with whom she copulated the most (Fig. 1; Wilk's Lambda = 0.425, $p < 0.001$). This difference was due to the total time spent with each male ($F_{4,52} = 11.49$, $p < 0.001$), but not the order of copulations ($F_{4,52} = 2.08$, $p = 0.097$). Females who mated with only one male mated later (average hour in which mating occurred = 11.36 ± 2.17) than females who mated with more than one male (average hour in which mating occurred = 5.92 ± 1.47 ; $F_{1,23} = 4.93$, $p = 0.037$).

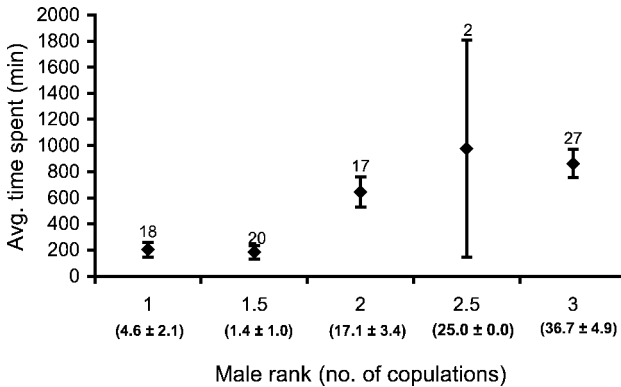


Fig. 1. Mean (\pm SE) time spent in males' chambers as a function of sexual preference. Male number refers to the ranked order of number of copulations (higher numbers represent more copulations). Numbers above each category refer to sample sizes; numbers below each category are the average number of copulations (\pm SE) for males in each category. Note that most males with a ranking of 1.5 had 0 copulations (*i.e.* the female only mated with one male in that trial).

The duration of observation affected the percent of females mating and the number of females mating with multiple males. All measures were correlated for the 2-h analysis and the full 24-h analysis (Spearman's $\rho = 0.456$ for mating order, 0.667 for time spent, and 0.547 for number of copulations; all $p < 0.001$). The percentages of females that mated with one, two, or three males, while changing over 24 h, remained in the same relative order (*i.e.* most females mated with one male and the fewest females mated with three males; Fig. 2). Longer observation times resulted in an increase in the number of females mating (18% after 2 h to 75% by 24 h) and in the number of females mating with more than one male (7% mated with 2 males, 0% with three males after 2 h versus 18% mated with two males and 25% mated with three males by 24 h).

Experiment 2

This experiment was conducted to determine if a paired female will desert her current mate and mate with a different male and/or mate with multiple males. In the field, this situation could arise when new males become available as mates either through loss of their females, immigration of new males into the population, or by males employing a wandering strategy

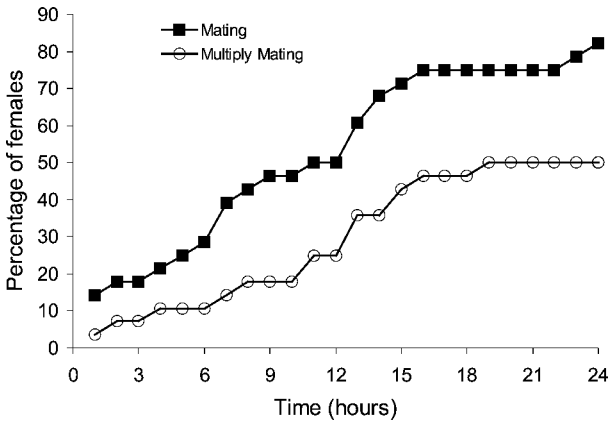


Fig. 2. Percent of trials (total $N = 28$) in which mating occurred (matings) and in which multiple male mating occurred (multiple matings).

(Getz *et al.*, 1993). The resident female then has the opportunity to mate with males other than her original mate.

Methods

In a second series of trials, single unrelated males and females from the colony were housed in breeding cages together until the female was obviously pregnant. The photoperiod and conditions were as described above. Approximately 1-2 d before the birth of a litter, we tethered the male of the pair in the center chamber of the 4-chamber apparatus. Two unrelated (novel) males of similar age (± 15 d) and weight (± 2 g) were tethered in the remaining two chambers. The pregnant female was then placed into the chamber of her paired male. All doors were left open so the female had access to each of the males. Prairie voles show post-partum oestrus (Carter *et al.*, 1986), and therefore we expected these females to copulate following parturition. We then videotaped the trial, allowing the female to give birth, and continued to tape until 2 d after parturition. Each videotape was analyzed from the time of parturition, and the numbers of copulations and mating partners were recorded. Tapes were also observed for any copulations prior to parturition, but none occurred.

Females gave birth in 12 of the 16 trials and in all 12 trials mated after giving birth. We tested for differences in the number of copulations females had with their paired partner versus unfamiliar novel males. For all 12 trials, the copulations with the two novel males in each trial were summed (for the two trials in which the female mated with both novel males) and a one-tailed paired t -test was used to determine the effect of pairing on number of copulations. This test was one-tailed to test the hypothesis that if females are truly monogamous, they should not mate with a novel male once they are paired.

Results

Mating occurred in the 12 of 16 trials in which paired females gave birth. Five of the 12 (42%) females mated with multiple males, however no female mated with all three males. Nine females mated with their original partner; of these, three also mated with one of the novel males. Of the three females who did not mate with their original partner, two mated with both novel males. Paired males had significantly more copulations (9.8 ± 2.2) than novel males (3.1 ± 1.5 ; paired t -test: $t_{11} = 2.15$, $p = 0.027$, one-tailed). When only those females who mated with their original partner and a novel male are considered, the sample size ($N = 3$) is too small for a statistical comparison. For these three trials, females mated with their original partner $9.67 (\pm 2.33)$ times and with the novel male $6.33 (\pm 4.84)$ times, however the high average for novel males was due to one novel male receiving 14 matings (in the same trial the original partner received nine matings). The numbers of males mated by paired (1.42 ± 0.15) and unpaired (1.77 ± 0.11) females were not statistically different (Fisher's exact test, $p = 0.243$). After giving birth, three of the 12 (25%) females deserted their paired partner and moved their new pups into chambers of novel males. Interestingly, none of these males committed infanticide.

Discussion

Our results indicate the following. (1) Given the opportunity, some female prairie voles will mate with more than one male. (2) Social preference, as measured by time spent with a male, was related to sexual preference as measured by number of copulations, but not order of copulations. Therefore, time spent with a male was a good predictor of which male the female would mate with the most (see also Witt *et al.*, 1990). (3) The percent of females mating and the percent mating with multiple partners increased over time. (4) Paired females were as likely to be promiscuous as were unpaired females, at least under the conditions of this experiment when their mates were unable to mate guard and additional males were in close proximity.

Field (Getz *et al.*, 1981, 1993; Carter & Getz, 1993) and laboratory (Thomas & Birney, 1979; Williams *et al.*, 1992; Solomon, 1993) studies have indicated that prairie voles from Illinois are socially monogamous.

However, under the conditions of our study, female prairie voles from Tennessee were not sexually monogamous, rather MMM occurred in 55% of trials with unpaired females. This frequency of MMM is substantial, but less than that for meadow voles in which 79% of females mated with multiple males (Berteaux *et al.*, 1999). Field (Madison, 1980; Boonstra *et al.*, 1993) and laboratory (Shapiro & Dewsbury, 1986; Berteaux *et al.*, 1999) studies have shown that meadow voles are not socially monogamous, but do show partner preferences under some conditions (Parker *et al.*, 2001). Under the conditions of our study, and using the same experimental design that Berteaux *et al.* (1999) used with meadow voles, both species showed considerable tendency for MMM. This result suggests that either prairie voles from Tennessee are behaviourally much different than those from Illinois, prairie vole mating behaviour is highly variable, monogamy is only maintained by mate guarding, or prairie voles in general are not as monogamous as indicated from previous studies. We are currently conducting field and laboratory studies to discern among these alternatives.

A female's sexual preference (who she mates with most) was the same male with which she spent the most time, but not the male with whom she first mated. Females that mated earlier had a greater tendency to multiply mate than females that mated later, perhaps because they were less discriminating; monogamous females may have taken longer to discern among alternative mates. We attempted to control for as much phenotypic variance in males as possible (sexual experience, and age differed by less than 15 d and mass by 2 g), so if females were discriminating on age or weight they were doing so within narrow limits. More likely, females are choosing mates based on some other criteria, which might be an indicator of 'good genes' (Trivers, 1972; Kodric-Brown & Brown, 1984), compatible genes (reviewed in Penn & Potts, 1999), or potential male parental investment (Emlen & Oring, 1977). However, in that 55% of females mated with multiple males, females apparently were not seeking an exclusive mating partner.

Berteaux *et al.* (1999) found that the length of observation in mate-choice trials affected the results and interpretations of female mating behaviour. Berteaux *et al.* reported that most copulations occurred early in the trials; however more females mated multiply as the length of the trial increased. A similar analysis of our data indicated a strong correlation between the first 2 h of each videotape and the full 24 h. However, the total number

of copulations and number of males with which a female copulated did change after the initial 2-h period in our data, complementing the results of Berteaux *et al.* For prairie voles, a 2-h observation time was sufficient to predict sexual and social preference, but not necessarily the number of males with whom a female ultimately mated. Longer observation times led to more multiple matings and an increased proportion of females mating (Fig. 2). Thus, the length of the observation period appears to be important in these kinds of studies in that it may affect the ultimate interpretation of mate choice and/or the frequency of MMM.

Paired females were as promiscuous as unpaired females mating with multiple males in 42% and 55% of trials, respectively. Although no paired females mated with all three males, the relative number of females choosing one, two or three males were the same for unpaired and paired females as revealed by the Fisher's exact test. Additionally, 25% (3 of 12) of paired females dissolved their current pair relationships and showed a social preference for a novel male. Because we chose the original male with which the female was paired, it is not surprising that some females left their current partner and chose a different male. In a related study in our laboratory, 38% of female prairie voles that had been paired with a less-preferred male deserted their current mate and paired with novel or preferred males and an additional 38% mated with multiple males (Thomas & Wolff, in review). When given the option to choose their own mates, females may exhibit lower rates of mate desertion and MMM. In field studies, dissolution of a pairbond occurs in about 10% of paired individuals (Getz *et al.*, 1993), but extra-pair copulations may be more frequent if males do not mate guard.

Our study was designed to determine female mating behaviour in the absence of mate guarding. We do not know if this is realistic compared to natural situations, but it is doubtful that males can guard females throughout their entire oestrous periods. Unpaired females should have access to multiple mating partners, but wanderers also visit territories of paired females (Hofmann & Getz, 1988; McGuire & Getz, 1998). Our results indicate that paired females will multiply mate or even switch partners. Our findings that 55% of unpaired females mated with more than one male and 42% of paired females copulated with males other than their paired male are of particular interest. Because females actively chose these additional mates, if genetic monogamy occurs in the field in this species, it is probably maintained by mate guarding as suggested by McGuire & Getz (1998). Furthermore, Fitch

(1957) described anecdotal evidence of male-male competition for access to a female in the field that could be interpreted as mate guarding. Our observation of promiscuity among females may be due to the proximity of the three males to the females, and, while this could be a laboratory artifact, prairie voles are known to live in complex breeding units at times during the year (Getz *et al.*, 1987). Also, at high densities, numerous males have access to a given female's nesting area (Hofmann & Getz, 1988), which provides opportunity for MMM. Our results suggest that the reproductively mature females in such aggregates could be mating promiscuously.

Our results differ from those of other socially monogamous rodents. Paternity analyses from field populations of California mice, *Peromyscus californicus* (Ribble, 1991) and old-field mice, *Peromyscus polionotus* (Foltz, 1981) confirm genetic monogamy. Both of these species characteristically exist at low densities and consequently pairs may be relatively isolated from neighboring or intruding males. Paternal care is also essential in California mice (Gubernick & Teferi, 2000), where it is not in prairie voles (Getz & McGuire, 1993). Although density, access to additional males, failure to mate guard, and needs for paternal care may partially explain differences in mating systems, other aspects of the social system, such as tendency for males to commit infanticide (Gubernick, 1994; Agrell *et al.*, 1998) may also affect a female's tendency to multiply mate.

It is not the purpose of this paper to discern among alternative hypotheses for why female voles mate with multiple partners, but in a related study, we were able to reject the hypothesis that MMM increases litter size or the probability of conception (Wolff & Dunlap, 2002). Other genetic benefits may occur (*e.g.* Jennions & Petrie, 2000), but one possible explanation for MMM among rodents is that females copulate with neighboring males to confuse paternity to deter infanticide of their offspring (Agrell *et al.*, 1998; Ebensperger, 1998). We did not observe infanticide in this study, but have in other studies in our laboratory (unpubl.) and have good evidence that it occurs in the field (Mahady & Wolff, 2002).

Unfortunately, we were not able to determine paternity with an appropriate level of confidence in this study, but our preliminary results suggest that multiple paternity is substantially lower than the frequency of MMM. We are currently perfecting the techniques for determining paternity in prairie voles such that we will be able determine the relationship between MMM and multiple paternity. Our next step will be to determine if and to what extent litters

of prairie voles from a variety of social and geographic natural settings are multiply sired.

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