

# Adult female prairie voles and meadow voles do not suppress reproduction in their daughters

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## Abstract

Reproductive suppression of young females by conspecific females has been reported from laboratory studies on several species of rodents, including the prairie vole, *Microtus ochrogaster*, but not meadow voles, *M. pennsylvanicus*. We exposed female prairie voles and meadow voles to two treatments: a mother and one 23–26-day-old daughter paired with a strange male and a 23–26-day-old daughter paired with a different strange male. We found no differences in the proportion of daughters breeding or the time to sexual maturation for daughters raised in the two treatments for either species. Thus, we have no indication that mothers had any adverse effect on reproductive efforts of their daughters. These results differ from previous studies that concluded young female prairie voles were reproductively suppressed by female relatives. The difference between our and previous studies on reproductive suppression is that we examined breeding in young females rather than proximate measures of growth and reproductive development. We question the evolutionary significance of reproductive suppression among related female microtine rodents, especially in that it has not been documented from field populations. © 2001 Elsevier Science B.V. All rights reserved.

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## 1. Introduction

A widely accepted paradigm in rodent behavioral ecology is that young females exhibit delayed growth and sexual maturation when reared in the presence of conspecific females (Wasser and Barash, 1983). This delayed sexual maturation, or reproductive suppression, may result from direct

contact with mothers or siblings or chemical signals from urine of related or grouped females (Batzli et al., 1977; Drickamer, 1977; Getz et al., 1983; Gubernick and Nordby, 1992; Heise and Rozenfeld, 1999) and reviewed in Carter and Roberts (1997) and Solomon and Getz (1997). The basic pattern of suppression is for the dominant female, usually the oldest and often mother of younger subordinate females, to breed while the younger females do not. The presence of the mother, female sibling, or urine from other fe-

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males is apparently sufficient to delay growth and suppress reproductive development. An explanation for this pattern is that competition for breeding exists among females and that older females suppress reproduction in younger females to reduce competition for limited resources. This reasoning seems well substantiated for carnivores (Macdonald and Moehlman, 1982; Creel and Waser, 1997; Moehlman and Hofer, 1997) and primates (Abbott, 1984; Digby, 1995; French, 1997), but less so for rodents such as voles and mice.

Reproductive suppression has been reported in numerous species of rodents (reviewed in Solomon and French, 1997), and has been studied extensively in house mice, *Mus domesticus*, (Drickamer, 1977; Massey and Vandenberg, 1980), prairie voles, *Microtus ochrogaster*, (Getz et al., 1983; Carter et al., 1986; Carter and Roberts, 1997), pine voles, *M. pinetorum* (Schadler, 1990; Solomon and Getz, 1997; Brant et al., 1998), California mice, *Peromyscus californicus* (Gubernick and Nordby, 1992), and others (Batzli et al., 1977; Solomon and French, 1997). In prairie voles and pine voles, the presence of the mother or siblings or even their urine supposedly exerts a suppressive effect on their daughters' or sisters' growth and reproduction (Batzli et al., 1977; Getz et al., 1983; Carter et al., 1986; Schadler, 1990). The mechanisms that suppress reproduction may be behavioral (Brant et al., 1998) or chemical, such as urine from the female (Getz et al., 1983; Schadler, 1990). Young female prairie voles delay growth in the presence of sibling and nonsibling females (Batzli et al., 1977). Social interactions among females (Batzli et al., 1977) or just urinary pheromones from female siblings were sufficient to inhibit body growth, uterine growth, and sexual development (Getz et al., 1983). Urinary cues alone however, did not suppress reproduction in pine voles, but the presence of the mother did (Brant et al., 1998).

Considerable literature has been published demonstrating that young females are reproductively suppressed by related females with few data to the contrary. Consequently, this paradigm has become widely accepted, despite the fact that reproductive suppression by related females has not

been demonstrated in the field (McShea and Madison, 1984; Lambin, 1994; Wolff, 1994; Wolff and Schaubert, 1996 and others). Delayed sexual maturation has been recorded in the field, especially at high densities, however it has not been determined whether this is caused by adult females, adult males, density, or some environmental factor (Wolff, 1992, 1997; Wolff et al., in review). As part of a long-term project studying the social behavior of monogamous and promiscuous rodents, we needed to confirm the widely held view that young female prairie voles were reproductively suppressed by female relatives, primarily their mothers. The objective of this study was to test the hypothesis that mothers would suppress reproduction in their daughters if they remained together in the same cage with a strange male; daughters that were isolated from their mothers and paired with a strange male would not be reproductively suppressed. Our study differed from previous studies in that we gave mothers and daughters the opportunity to breed rather than just measuring proximate cues of sexual maturation such as body growth, development of reproductive organs, and hormones (reviewed in Carter and Roberts, 1997; Solomon and Getz, 1997). In that reproductive suppression may in part be a function of mating system, we conducted a parallel study with the meadow vole, *M. pennsylvanicus*, which is promiscuous (Boonstra et al., 1993) to compare with the results of prairie voles, which are monogamous (Carter and Getz, 1993).

## 2. Materials and methods

Prairie voles and meadow voles used in this study were second- or third-generation laboratory-reared outbred animals. Prairie voles were from Tennessee and meadow voles were from Michigan. Subjects were housed in standard 28 × 42 × 15 cm polycarbonate cages and provided with surplus food (PMI Rodent Chow 5008, St. Louis, MO) and water. Beta chip laboratory bedding and cotton nestlets were provided in each cage. Animals were maintained on a 14:10 light:dark photoperiod with lights on at 07:00 h.

We used standard laboratory breeding cages in this study to create the greatest amount of physical and olfactory contact and competition between mothers and daughters.

To initiate the experiment, parous 90–150-day-old females that had been isolated for at least 30 days were bred with an experienced stud male who remained with the female until parturition. Stud males were removed to avoid the confounding effects of inbreeding avoidance of daughters and post-partum mating by mothers. Litters were weaned at 23–26 days of age. A mother and one daughter remained in their home cage and a strange unrelated 60–90-day-old male was added to the cage (mother–daughter, MD treatment). One daughter from the same or another litter was placed in a separate breeding cage with a different strange male (daughter, D treatment). We then compared the pregnancy rates and time of conception of mothers and daughters in the MD treatment with daughters in the D treatment. Males were left in the cages until after one or both females gave birth and were obviously pregnant with their second litter or for a period of 60 days if the daughter had not bred by that time. In preliminary trials, if breeding were to occur, it occurred within 60 days, usually before 35 days so we set 60 days as the length of the trial. Thirteen trials were conducted with prairie voles and 14 trials with meadow voles. No animals died during the study.

### 3. Results

#### 3.1. Prairie voles

Ten of 13 (77%) mothers and nine of 13 (69%) daughters in both the MD and D treatment groups gave birth ( $X^2 = 1.34, P > 0.50$ ; Fig. 1). The mean number of days from pairing to parturition did not differ significantly between mothers (28.2, SD = 7.33) and daughters (33.7, SD = 8.67) in the MD treatment ( $F_{1,17} = 2.216, P = 0.154$ ) or between daughters (D treatment = 34.8, SD = 12.62) in MD and D treatments ( $F_{1,16} = 0.047, P = 0.830$ ). Six of the nine daughters in the MD treatment gave birth within 2 days of their mothers, often on the same day. We could not always determine litter sizes for mothers and daughters in the MD group because litters were often born synchronously, but mean litter sizes for mothers and daughters in the MD treatments was 3.5 compared to 3.4 for daughters in the D treatment ( $F_{1,9} = 0.540, P = 0.481$ ). Pups of different ages (based on size) were frequently nursing from either the mother or daughter. The mean length of time between birth of daughters and time they gave birth to their first litters was 53.9 (SD = 6.18) days. Assuming a 21-day gestation, most daughters conceived when they were about 33 days old, or 7–10 days after pairing. All offspring survived to weaning.

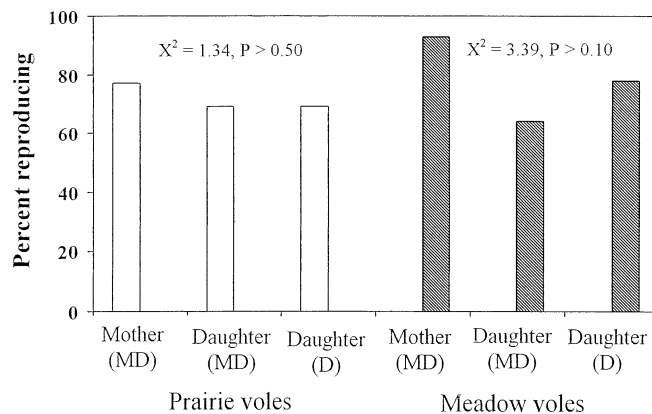


Fig. 1. The percent of mothers and daughters that gave birth in the mother–daughter (MD) and daughter (D) treatments.  $N = 13$  for prairie voles and 14 for meadow voles.

### 3.2. Meadow voles

Thirteen of 14 (93%) mothers and nine of 14 (64%) daughters in the MD treatment and 11 of 14 (78%) daughters in the D treatment gave birth ( $X^2 = 3.386$ ,  $P > 0.10$ ; Fig. 1). The mean number of days from pairing to parturition did not differ significantly between mothers (22.3,  $SD = 0.603$ ) and daughters (23.9,  $SD = 1.63$ ) in the MD treatment ( $F_{1,20} = 1.073$ ,  $P = 0.312$ ) or between daughters (D treatment = 26.2,  $SD = 2.16$ ) in the two treatments ( $F_{1,17} = 0.704$ ,  $P = 0.413$ ). Assuming a 21-day gestation period, daughters with their mothers usually bred within 1 day of pairing (seven of nine daughters gave birth 21–22 days of pairing) compared to daughters without their mothers who gave birth 3 days later. The other two females conceived 8 and 14 days after pairing. All pups survived to weaning.

## 4. Discussion

Our results do not support previous studies on rodents that the presence of mothers suppresses reproduction in their daughters for either prairie voles or meadow voles. Mothers and daughters often conceived at the same time, gave birth synchronously, and raised pups communally. The presence of the mother had no measurable effect on fitness of their daughters and we had no evidence of infanticide. Even in cases in which mothers bred first and daughters a few days later, pregnancy by mothers did not affect subsequent breeding by daughters (see Payman and Swanson, 1980). Thus, our results differ from those of numerous previously cited studies showing suppression of daughters by related females (op cited). Our experimental design differed from those of Batzli et al. (1977) and Getz et al. (1983) who examined inhibition of growth and sexual development of young female voles. Our study was designed to determine if young females would breed or not. Young females in both MD and D treatments usually bred within 7–10 days of being paired with a strange male for prairie voles and 1–2 days for meadow voles.

The paradigm for reproductive suppression of young female rodents has been developed from studies in the laboratory, whereas field evidence suggests that daughters commonly breed in the presence of related females. Breeding of mothers and daughters in the same nest or at least the same territory has been shown for several species of mice and voles, such as montane voles, *Microtus montanus*, (Jannett, 1978), meadow voles, *M. pennsylvanicus*, (McShea and Madison, 1984), Townsend's voles, *M. townsendii*, (Lambin, 1994), white-footed mice, *Peromyscus leucopus*, (Wolff, 1994), gray-tailed voles, *M. canicaudus* (Wolff and Schaubert, 1996), and others (Wolff, 1985; Tamarin et al., 1990). Breeding by daughters at their mothers' nesting areas also occurs in prairie voles (McGuire and Getz, 1995) especially at high densities when strange males have access to the young females (Hofmann and Getz, 1988). In a field experiment with gray-tailed voles in which we created artificially high densities of >150 adult females/ha, we had no indication that mothers were suppressing growth or reproduction in their daughters (Wolff et al., in review). The greatest competition for resources should be at high densities when young females remain near their natal site (McGuire and Getz, 1991; Carter and Roberts, 1997); however communal and cooperative breeding in rodents seems to be most frequent at the highest densities (Jannett, 1978; Lambin, 1994; Wolff, 1994).

Reproductive suppression has been demonstrated in the laboratory with promiscuous or polygynous species (e.g. house mice, Drickamer, 1977; California voles, *M. californicus*, Batzli et al., 1977; and common voles, *Microtus agrestis*, Heise and Rozenfeld, 1999) as well as with monogamous species such as prairie voles (Getz et al., 1983; Carter et al., 1986; Carter and Roberts, 1997), pine voles, (Schadler, 1990; Brant et al., 1998), and California mice (Gubernick and Nordby, 1992). Therefore, reproductive suppression, at least in the laboratory, does not appear to be associated with a particular type of mating system. One of the hypotheses for monogamy in rodents, especially prairie voles, is that they live in relatively poor habitats compared to polygynous or promiscuous species (Carter and Getz, 1993). If

this were the case, competition among females would be greater than for species in more productive habitats. Thus reproductive suppression might be more likely to occur in monogamous species than promiscuous species. The results from this study do not support this supposition in that we failed to demonstrate reproductive suppression in either monogamous prairie voles or promiscuous meadow voles. To the best of our knowledge, reproductive suppression by related females has not been demonstrated in the field for any species for which it has been shown in the laboratory.

Arguments have been made for how reproductive suppression of relatives can be adaptive (Batzli et al., 1977; Massey and Vandenbergh, 1980; Brant et al., 1998), however these explanations have not been tested. Reproductive suppression of female kin should occur only if the dominant female's inclusive fitness were decreased by having her daughters breed, something that has not been demonstrated. In fact, the way a mother can maximize her inclusive fitness is for her daughters to breed as quickly and often as possible as long as it does not decrease the direct fitness of the mother. Reproductive suppression would not appear to be adaptive in species such as prairie voles or meadow voles or perhaps other short-lived, grassland voles that are rarely at their carrying capacity and do not defend food resources (Wolff, 1993; Wolff and Peterson, 1998). Thus, our results for prairie voles and meadow voles are consistent with predictions from inclusive fitness theory. Before further studies are conducted on mechanisms of reproductive suppression in the laboratory, we recommend that field studies be conducted to document its relevance in an animal's natural environment.

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