Published in final edited form as:

Ethology. 2013 January 1; 119(1): . doi:10.1111/eth.12033.

Food deprivation and restriction during late gestation affects the sexual behavior of postpartum female meadow voles, *Microtus pennsylvanicus*

Ramona M. Sabau and Michael H. Ferkin¹

The University of Memphis, Department of Biological Sciences, Ellington Hall, Memphis, TN 38152 USA

Abstract

In many species of small mammals, including meadow voles, *Microtus pennsylvanicus*, females come into postpartum estrus (PPE) within 12–24 h of giving birth, allowing them to mate and become pregnant while raising the current litter. PPE females show increases in attractivity, proceptivity, and receptivity, the three components of sexual behavior, relative to females not in PPE. Several studies have shown that food deprivation and restriction reduce attractivity, proceptivity, and receptivity of females not in PPE. We tested the hypothesis that food deprivation and restriction during late gestation causes deficits and decreases the attractivity, proceptivity, and receptivity of females when they enter PPE. Our data support the hypothesis. On day 1 of lactation, females that were food deprived and food restricted produced scent marks that were significantly less attractive as those produced by control PPE females. Food deprivation but not food restriction caused females to no longer display significant preferences for the scent marks of males over those of females (proceptivity). Food deprivation and food restriction were sufficient to induce females to become significantly less sexually receptive than control females. Eleven of 12 control PPE females mated, 4 of 12 food-restricted females mated, and 3 of 12 food-deprived females mated. Dams facing food deprivation or restriction during late gestation may have to balance the benefits of mating during PPE with the increased costs associated with getting pregnant while they are lactating.

Keywords

Food deprivation; food restriction; sexual behavior; voles; postpartum estrus

Introduction

Sexual behavior in female mammals can be separated and characterized into three observable components: attractivity, proceptivity, and receptivity (Beach 1976). Attractivity refers to the relative stimulus values of cues and signals of different senders of the same sex, when assessed by receivers of the opposite sex (Beach 1976). Proceptivity refers to the sexually-appetitive responses of receivers to cues and signals of opposite-sex conspecifics (Beach 1976). Attractivity and proceptivity establish communication between potential mates, and allow them to coordinate behaviors that facilitate or inhibit direct interactions (Beach, 1976; Johnston 1979; Stopka & Macdonald 1998). For most terrestrial mammals, including rodents, these interactions are mediated by olfactory signals, such as scent marks, from the sender and the responses of receivers to these scent marks (Brown 1985; Johnston

¹Corresponding author: mhferkin@memphis.edu.

2003; Ferkin et al. 2004). Receptivity refers to a female's willingness to mate (Beach, 1976). Mating includes lordosis by the female and mounts, intromissions, thrusts, and ejaculations by males (Gray & Dewsbury 1975; delBarco-Trillo & Ferkin 2004, 2006).

The three components of sexual behavior can be affected by altering the amount of food available to a female (Bronson 1989; Wade et al. 1996; Pierce et al. 2005). For example, food-restricted or food-deprived female rats (*Rattus norvegicus*), musk shrews (*Suncus murinus*), house mice (*Mus musculus*), Syrian hamsters (*Mesocricetus auratus*), and meadow voles (*Microtus pennsylvanicus*) were less attractive to male conspecifics and often failed to show interest in responding to potential mates, and, if given an opportunity to mate, they usually did not mate (Bronson & Marsteller 1985; Wade & Schneider 1992; Gill & Rissman 1997; Jones & Wade 2002; Temple et al. 2000; Pierce et al. 2005). Typically, 48–72 h of food restriction and 24–48 h of food deprivation were sufficient to induce deficits in the sexual behavior of these female small mammals (Gill & Rissman 1997; Jones & Wade 2002; Temple et al. 2002; Pierce et al. 2005). However, it should be noted that these studies were carried out on female subjects that were not pregnant or lactating. We do not know if females that undergo food restriction or food deprivation during late gestation display similar deficits and decreases in their sexual behaviors when they later enter postpartum estrus. Females that are food restricted or food deprived late in pregnancy may be less likely than females that have continuous access to food to attract males, show interest in seeking out males, and mating with them.

For numerous species of terrestrial mammals, postpartum estrus, PPE, is a period of heightened attractivity, proceptivity, and receptivity that occurs shortly after the dam delivers her litter (Dewsbury et al. 1979; Gilbert 1984; Witt et al. 1990). Previous studies have shown that PPE females, which were not food restricted or food deprived during gestation, produced odors and scent marks that were more attractive to males than were those produced by females not in PPE (Ferkin & Johnston 1995; Zeigler et al. 1993; Lai et al. 1996; Lazaro-Perea et al. 1999; Vaughn et al. 2011). PPE females also spent more time and showed increases relative to females not in PPE in scent marking, over-marking, and self-grooming when they encountered the scent marks of males (Ferkin et al. 2004; Ferkin 2006). PPE females were more likely than females not in PPE to attract mates and to signal their interest in them (Witt et al. 1990; Rudd 1994; Ferkin 2006). PPE females also mated more readily and got pregnant more often than did females not in PPE (Gilbert 1984; Keller 1985; delBarco-Trillo & Ferkin 2007). Thus, PPE females are preferred as mates by male conspecifics (Ferkin et al. 2008). However, these females may no longer be preferred mates if they have undergone nutritional stress during gestation.

Nutritional stresses such as food deprivation and food restriction are an ecological challenge faced by small herbivores (Krackow 1989; Voltura & Wunder 1998; Zhao & Coa 2009), and might also be an important challenge for meadow voles. Meadow voles live in ephemeral and transitional grasslands, where food sources are patchy and vary in quality across the territories of female conspecifics (Getz 1985; Bergeron & Jodoin 1987; Bergeron et al. 1990). As females enter late gestation they become relatively sedentary (Madison 1980a, b, 1985) and may be limited to the forage that is available in their territory (Batzli 1985). Consequently, females during late gestation may become food restricted or food deprived. Food deprivation for 12–18 h can bring about changes in energy availability in voles (Mustonen et al. 2012), which may affect their behavior during postpartum estrus. The availability of food may determine whether a female vole that is food restricted or fasting late in pregnancy will have sufficient energy or be willing to mate and become pregnant again during postpartum estrus. Most free-living female meadow voles will mate during postpartum estrus (Dewsbury et al. 1979; Keller 1985). Not mating during postpartum estrus may lower the mating and reproductive success of free-living voles (Boonstra et al. 1993;

Berteaux et al. 1999), and have profound effects on their population density (Tamarin et al. 1984; Batzli 1985; Desy & Batzli 1989).

Thus, in the present study, we tested the hypothesis that food restriction and food deprivation during late gestation was sufficient to induce postpartum estrus female meadow voles to manifest deficits and decreases in the three components of sexual behavior: attractivity, proceptivity, and receptivity. Specifically, we predicted that such female voles would 1) produce scent marks that were no longer attractive to male conspecifics (attractivity), 2) no longer show a preference for the scent marks of male conspecifics to those of female conspecifics (proceptivity), and 3) no longer mate (receptivity) immediately after parturition, when they entered postpartum estrus.

Methods

Animals

The meadow voles used in the study were 4th–6th generation captive animals born and raised in a room that was maintained between 23–25° C and under long photoperiod (14:10 h light: dark, lights on at 0700 h, C ST). This photoperiod simulates the day length during the breeding season in free-living meadow voles (Zucker et al. 1980). All the female meadow voles used in the study were between 120–150 days of age, similar in body weight to one another (within 3–5 g), and sexually experienced, having previously delivered a litter, when they were 70–80 days of age. Female meadow voles are induced ovulators and do not undergo estrous cycles (Keller 1985). Male meadow voles were between 120–150 days of age, similar in body weight to one another (within 3–5 g), and sexually experienced, having previously sired a litter when they were 70–80 days of age. Males and females had continuous access to food (Harlan Teklad Rodent Diet, #8640, Madison, WI) prior to their inclusion in the study. We paired 40 males with 40 females for 24 h in breeding cages (37×21×15 cm; l, w, h). After 24 h, the males were removed from the breeding cages and returned singly to their home cages in the main colony. We adhered to the ‘Guidelines for the use of animals in research’ as published in Animal Behaviour (1991, 41, 183–186) and the laws of the country where the research was conducted.

Treatment Groups

We measured the amount of food eaten daily by pregnant females in the control groups during the 21 days of gestation. We did so, by providing females daily with 50 g of food placed in the hopper on the lids of their cages. Twenty-four h later, we removed the female from the cage and collected any food that remained in the hoppers and on the floor of the cage. This food was weighed to the nearest g (Ohaus GT4000 Automatic Balance, Florham Park, NJ). The difference between the amount of food placed in the hopper and the amount of food remaining 24 h later was considered to be that female’s food intake.

We were able to determine by tactile palpation which females were pregnant 10–14 days after pairing. Of the 40 pairs of voles that were allowed to mate, 36 pairs mated and later produced litters. Thus, we were able to assign pregnant females to three equal-sized groups. Females in group 1 (control) had continuous access to food during gestation. Females in group 2 had continuous access to food before day 18 of gestation, but were provided with 70% of the previous daily intake of control animals between day 18 and 20 of gestation, the last three days of gestation (FR). The mean duration of food restriction for female voles was 72.5 ± 2.1 h. Females in group 3 had continuous access to food until day 20 of pregnancy, when they were food deprived for 24 h before expected parturition (FD). The mean duration of food deprivation for female voles was 24.4 ± 1.8 h.

Previous studies have showed that 48–72 h of food restriction and 24–48 h of food deprivation were sufficient to induce deficits in sexual behavior of female musk shrews (*Suncus murinus*) and meadow voles that were not pregnant or lactating (Gill & Rissman 1997; Jones & Wade, 2002; Temple et al. 2002; Pierce et al. 2005). We chose to use similar durations of food restriction and deprivation during gestation to determine whether female voles in poor nutritional condition display the heightened sexual behaviors characteristic of postpartum estrus. We selected a 30% food restriction of what control PPE females consumed. We did so, because this may be typical of what a female vole may encounter in the field (Batzli 1985), and because our results from a pilot study showed that all dams survived and none cannibalized young when they underwent such a food restriction during the last 3 days of gestation.

In addition, we used 24 females from our colony that had continuous access to food, and were not currently pregnant or lactating; these females were in behavioral estrus and designated as reference (REF) females (Ferkin & Johnston 1995). We compared the sexual behavior of REF females to that of females in groups 1–3. Several studies have shown that male meadow voles spend more time investigating the scent marks of PPE females than those of REF females (Ferkin & Johnston 1995; Vaughn et al. 2011) and that PPE females are more interested in males and mating with them relative to female meadow voles not in PPE (Ferkin et al. 2004; delBarco-Trillo & Ferkin 2007).

Attractivity

Scent Donors and Subjects—Forty-eight females were selected to be scent donors. Donors were placed on the dietary regimens detailed above so that there were 12 females in each group: 12 REF females, 12 control PPE females, 12 FR females, and 12 FD females. Subjects were 48 male voles that had continuous access to food. Males were randomly chosen from a pool of sexually experienced male voles that were unrelated to and unfamiliar with the female scent donors used in the attractivity tests. We did not use more than two individuals from the same litter in any experimental group to eliminate the potential for litter effect. We used a Latin Squares design to allow PPE females to serve as scent donors in the attractivity tests and then as subjects in the proceptivity tests and receptivity tests (Pierce et al. 2005). That is, some PPE females were subjects in the proceptivity tests first, some were first subjects in receptivity tests, and others were first used as donors in attractivity tests. We used female subjects, male studs, and male and female scent donors that were unfamiliar and unrelated to the voles with which they were tested.

Testing procedure—Each male underwent a single 5-minute attractivity test that followed the procedures detailed by Pierce and colleagues (Pierce & Ferkin 2005; Pierce et al. 2005, 2007). Briefly, we recorded the amount of time in seconds that males spent investigating the anogenital area scent marks of the following pairs of female scent donors: 1) a FR PPE female versus a PPE female that was not food restricted (PPE); 2) a FD PPE female versus a PPE female that was not food deprived; 3) a FR PPE female versus a REF female; 4) a FD PPE female versus a REF female; 5) a FR PPE female versus a FD PPE female.

Each male subject was exposed to the scent marks of a unique pair of opposite-sex donor. These two scent marks were placed on a clean, glass microscope slide (2.5×7.6 cm). Each slide was divided in three equal sections. Each section was 2.5 cm long. One end section contained a scent mark from one female donor, while the other end section contained a scent mark from the other female donor. The middle section contained no stimulus odor. The methods of attractivity test followed those detailed in Pierce et al. (2005). Briefly, the anogenital area of a scent donor was rubbed for approximately 5 seconds against the left- or

right side of a clean slide; the middle portion was clean and contained no scent marks. The position of the scent marks of the two different females that were used as scent donors were alternated for each test. After both scent marks had been placed on the slide, we suspended the slide on a clip and hook apparatus 1 cm above the substrate, against the wall opposite the subject's nest. During the 5-minute attractivity test, we recorded continuously the amount of time that male subject licked or sniffed (the subject's nose comes within approximately 1–2 cm) each scent mark and the clean section of the slide. The test began when the slide was placed into the cage of the male subject (Pierce et al. 2005). All male subjects investigated both scent marks, spending more time investigating the two scent marks than the section of the slide containing no scent marks.

Fresh scent marks from the anogenital area were obtained for each trial from each female scent donor. The anogenital area may contain components of scent from multiple sources such as urine, feces, sex organs, and sebaceous glands but are responded to similarly by conspecifics (Ferkin & Johnston 1995); the anogenital area scent marks are deposited by voles in their runways (Ferkin et al. 2004). The experimenter wore disposable latex gloves to minimize human scent transfer while handling all slides. All attractivity tests took place within 4–8 h of parturition. Thus, each of these now lactating females would have been in postpartum estrus. The investigator coding the behaviors was blind to the treatment conditions of the female voles in the attractivity tests, as well as the proceptivity and receptivity tests listed below.

Proceptivity

Scent Donors and Subjects—We used a scent preference test to determine whether nutritional stress induced before parturition induced differences in proceptive behavior of PPE females. Scent donors were 36 REF females and 36 sexually experienced males that had not been paired with any of the subject females and had not been used as subjects for the attractivity tests. The subjects were the 36 females from diet-treatment groups 1–3. Each subject was tested once with a unique pair of male and female scent donors.

Testing Procedure—All proceptivity tests were conducted within 4–8 h of parturition. We followed the methods for proceptivity testing developed by Pierce and collaborators (Pierce et al. 2005) and are similar to the attractivity test we described above, with one notable exception. In the proceptivity test, females were exposed to a glass slide that contains the scent mark of a REF female and the scent mark of an unfamiliar male conspecific. During the 5-minute long proceptivity tests, we recorded the amount of time subject females in each group investigated the end of the slide containing the scent mark of the male scent donor and the end containing the scent mark of the female scent donor. The pups of the lactating female subjects were not removed from the cage during the proceptivity test. Female voles were considered to display proceptive behavior if they spent significantly more time investigating the odors of a male conspecific than those of a female conspecific (Pierce & Ferkin 2005; Pierce et al. 2005, 2007).

Receptivity

Subjects—Subjects were 36 female voles from diet-treatment groups 1–3 and 36 male voles; the male voles for this test were not used in the attractivity and the proceptivity tests. We used the same methods in testing receptivity as described by Pierce et al. (2005). Briefly, each stud male was paired with a single female from one of the dietary groups in a clear, plastic cage (37×21×15 cm; l, w, h), containing hardwood shavings, nesting material and water. Pups were kept with the dam in the cage until weaning on day 18; no pups were attacked or injured.

Testing Procedure—All receptivity tests were occurred within 4–8 h of parturition. Introduced pairs were allowed to interact for 4 h; meadow voles typically mate within this 4-h period (delBarco-Trillo & Ferkin 2004, 2007; Vaughn et al. 2008, 2011). We recorded each 4-h paring (Sony Handycam DCR-SR68). During playback, we scored the number of ejaculations by each male and his latency to first ejaculation, which was the amount of time (seconds) that elapsed between the male's introduction into the female's cage and his first ejaculation. We observed lordosis but did not measure it. Female meadow voles display lordosis only after males mount them; they do not display lordosis prior to mounting as do rats (delBarco-Trillo & Ferkin 2006). Thus, measures of mounting and lordosis are highly correlated (Dewsbury 1972, 1975). We used mating success as an indicator of female sexual receptivity. Specifically, we recorded whether or not female meadow voles mated during their interaction with stud males (Berteaux et al. 1999; Vaughn et al. 2011). We also measured ejaculation by males; the final component of the copulatory behavior (Dewsbury 1972, 1975) as an indicator of male responsiveness to females. The ejaculation is characterized by a short series of rapid thrusts and intromissions followed by a noticeable relaxation of the male meadow vole's pelvic region area and extension of his leg (Gray & Dewsbury 1975; delBarco-Trillo & Ferkin 2004, 2006a, b, 2007).

Statistical Analyses

We used matched-paired t-tests to determine whether significant differences existed in the amount of time each subject spent investigating the scent marks of the two donors for that attractivity and proceptivity tests (SPSS Version 16; Pierce et al. 2005). Each subject was tested once and with a unique pair of scent donors. We used Chi-Square tests to compare the number of females that mated in the PPE control group with the numbers of females that mated in the food-restricted group and those that mated in the food-deprivation group (receptivity test). We used the number of females that mated in the control PPE group as the expected value for the Chi-Square tests. We used two separate one-way ANOVA's to determine if males paired with control PPE females, food-restricted females, or food-deprived females differed in their number of ejaculations and latency to first ejaculation. In all statistical analyses, significant differences were accepted at $\alpha = 0.05$.

Results

Effects of food restriction and food deprivation on attractivity

Food restriction and food deprivation during late gestation were sufficient to induce day 1 lactating (PPE) females to produce scent marks that were no longer as attractive to males as those produced by control PPE females. Male voles spent more time investigating the scent marks of control PPE females than those of FD females ($t_{11} = 12.01$, $p < 0.001$; Fig. 1) as well as the scent marks of FR females ($t_{11} = 3.76$, $p = 0.001$; Fig. 1). Male voles spent similar amounts of time investigating the scent marks of REF females compared to the scent marks of FD females ($t_{11} = 0.485$, $p = 0.31$) and the scent marks of FR females ($t_{11} = 1.099$, $p = 0.014$; Fig. 1). Males also spent similar amounts of time investigating the scent mark of a FR female and that of a FD female ($t_{11} = 0.892$, $p = 0.19$).

Effects of food restriction and food deprivation on proceptivity

We found that food restriction of 30% of the intake of control PPE females resulted in no effect on our measure of proceptivity. FR PPE females spent more time investigating scent of males than those of females ($t_{11} = 2.610$, $p = 0.01$; Fig. 2). Similarly, control PPE females spent more time investigating the odors of opposite sex conspecifics ($t_{11} = 4.68$, $p < 0.001$; Fig. 2). In contrast, FD PPE females spent similar amounts of time investigating the scent of opposite-sex and same- sex conspecifics ($t_{11} = 0.138$, $p = 0.44$; Fig. 2), suggesting an inhibition of proceptive behavior.

Effects of food restriction and food deprivation on receptivity

We found that 18 females, 11 of 12 females from the control PPE group, 4 of 12 females from the food-restricted group, and 3 of 12 females from the food-deprived group mated when paired with an unfamiliar, male conspecific. The proportion of food-deprived and the food-restricted females that mated was significantly less than that of the control PPE females that mated ($\chi^2 = 4.45$, $df = 1$, $p = 0.035$ and $\chi^2 = 5.81$, $df = 1$, $p = 0.016$, respectively; Fig. 3). Of the females that mated, those in the control PPE group, those in the food-restricted group, and those in the food-deprived group did not differ in our measures of copulatory behavior. The number of ejaculations received by control females (mean $\pm$ SEM, 6.1 ± 1.1), food-deprived females (5.7 ± 1.3), and food-restricted females (5.8 ± 1.4) were similar ($F_{2, 12} = 0.68$, $p = 0.52$). There were also no significant differences in the latency to first ejaculation ($F_{2, 12} = 1.42$, $p = 0.27$) for males paired with control females (mean $\pm$ SEM, 2890.4 ± 235.1 seconds), food-deprived females (3050.3 ± 319.3 seconds), or food-restricted females (3353.7 ± 372.6 seconds).

Discussion

Female meadow voles that underwent either food restriction or food deprivation during late gestation showed deficits and reductions in their sexual behavior (attractivity, proceptivity, and receptivity during postpartum estrus). Food deprivation on day 20 of gestation, the day before parturition, and 30 % food restriction starting on day 18 of gestation were sufficient to induce female meadow voles on day 1 of lactation, when the females would enter PPE, to produce anogenital area scent marks that were not as attractive to males as those produced by control PPE females. We also found females that were food deprived or food-restricted produced scent marks that were as attractive as those produced by REF females; females that are not pregnant, lactating or in PPE. Previous work has shown that REF females produce odors that are less attractive than those produced by PPE females to males (Ferkin & Johnston 1995; Vaughn & Ferkin 2011). Our data suggest that PPE females in poorer nutritional states may not be attractive to potential mates. Male meadow voles may use such information to distinguish between potential mates (Pierce et al. 2005; Hobbs & Ferkin 2012). Male meadow voles respond preferentially to the scent marks of control PPE females because these females have shorter latencies to mate, allow males to have fewer ejaculations, reducing their sperm investment, and are more likely to get pregnant relative to females that are not in PPE, such as REF females (Gilbert 1984; Keller 1985; delBarco-Trillo & Ferkin 2007) and those females that were food deprived or food restricted (Pierce et al. 2005). In contrast, the odors and scent marks produced by female meadow voles that were food deprived or food restricted indicate to males their poor nutritional state and their likelihood of not mating (Pierce & Ferkin 2005; Hobbs & Ferkin 2012).

Interestingly, food restriction and food deprivation during late gestation had different effects on the proceptivity of PPE females. PPE females that were food restricted during late gestation and control PPE females maintained their preferences for the scent marks of male conspecifics over those of female conspecifics. In contrast, females that were food deprived during late gestation no longer expressed a preference for the scent marks of male conspecifics; food-deprived PPE females spent similar amounts of time investigating the scent marks of male and female voles. Similarly, Pierce et al. (2005) found REF female voles that were food deprived for six h spent similar amounts of time investigating the scent marks of male and female conspecifics. Taken together, our findings suggest that food-restricted females may still be motivated or interested in locating potential mates, whereas food-deprived females may not be as motivated or interested in locating potential mates because they may not have the energy to meet the costs associated with becoming pregnant while they are currently lactating (Hobbs et al. 2012). The decline in proceptive behaviors among food-deprived females may reflect the fact these females have to rely entirely on

limited energetic reserves for their maintenance and that of their pups. Small mammals such as voles can survive only 2–3 days without food (Bronson 1989). Typically, voles eat small meals throughout the day (Batzli 1985). A 30% food restriction may not cause dams to rely entirely on stored energy to meet the high costs of entering postpartum estrus and lactation. Thus, 30% food-restricted females may be more inclined to seek out mates during postpartum estrus than would food-deprived females, who may have used their remaining energy stores to support their current litter. As such, female meadow voles may be less likely to approach or seek out potential mates when they encounter their scent marks nearby.

Food deprivation and food restriction during late gestation affected a female vole's sexual receptivity postpartum. Eleven of 12 control PPE females (92%) copulated. Several studies have shown that nearly all female voles that enter PPE mate (Keller 1985; Witt et al. 1990; delBarco-Trillo & Ferkin 2006b, 2007). We discovered that only 3 of 12 food-deprived dams (25%) and 4 of 12 of the food-restricted dams (33%) copulated during the receptivity test. Female meadow voles that are not receptive will not allow males to mount (Dewsbury 1972, 1975; Gray & Dewsbury 1975; delBarco-Trillo & Ferkin 2006a, b). Male meadow voles also did not attempt mount females if they were not interested in those females (Pierce et al. 2005) and if the females cause the males to ejaculate outside of their vagina (delBarco-Trillo & Ferkin 2007). Male and female voles both exert control over mating. We know of no comparable studies that have examined the effects of food deprivation on sexual behavior of postpartum estrus females. However, female mammals that were not lactating or in postpartum estrus also respond to food deprivation by reducing their copulatory behavior or willingness to mate (Wade et al. 1996; Gill & Rissman 1997). For example, Pierce et al. (2005) found that six h and 24 h of food deprivation were sufficient to inhibit sexual receptivity in 8 of 9 females and 10 of 10 females that were not pregnant or lactating (REF females in our study), respectively.

Although food restriction and food deprivation during late gestation affected the proportion of dams that mated during PPE, such treatment did not affect our measures of copulatory behavior of the pairs that did mate. The latency to mate was similar for all females that mated in our study. In addition, dams received between 4–6 ejaculations from their paired males, independent of whether she was a control, food deprived, or food restricted during late gestation. The number of ejaculations per copulatory bout reported in this study also matched those reported in meadow voles that were exposed to different risks of sperm competition (Gray & Dewsbury 1975; delBarco-Trillo & Ferkin 2004; Vaughn et al. 2008, 2011). This suggests that the number of ejaculations by male meadow voles during a copulatory bout may be independent of the condition of the female and the context.

In the wild, meadow voles are opportunistic breeders (Tamarin 1977), and PPE female meadow voles are preferred mates (Keller 1985; Ferkin & Johnston 1995; Vaughn & Ferkin 2011). However, dams that were exposed to 30% food restriction or food deprivation during late gestation do not display behaviors that signal their heightened levels of attractivity, proceptivity, and receptivity to male conspecifics. These dams are likely not to mate after parturition. By not mating during PPE, dams may be able to direct their limited energy into their current litter without having to shift their energy into a concurrent pregnancy (Trivers 1972). Thus, nutritionally-stressed dams will have lower lifetime reproductive success (Boonstra et al. 1993; Berteaux et al. 1999). As a result, population density may decline (Tamarin 1977; Tamarin et al. 1984; Batzli 1985; Desy & Batzli 1989).

Acknowledgments

We thank Nicholas Hobbs, Christian Vlautin, and Daniel Ferkin for reading earlier drafts of this manuscript. We also thank Susan Foster and two anonymous reviewers, who provided constructive comments and suggestions. This

research was supported by NIH grants HD 049525 and an ARRA supplement, and NSF grant IOB 0444553 to MHF.

Literature Cited

- Batzli, GO. Nutrition. In: Tamarin, RH., editor. Biology of the new world *Microtus*. American Society of Mammalogists; Provo, UT: 1985. p. 779-811.
- Beach FA. Sexual attractivity, proceptivity, and receptivity in female mammals. *Horm Behav.* 1976; 7:105–138. [PubMed: 819345]
- Bergeron JM, Jodoin L. Defining “high-duality” food resources of herbivores: the case for meadow voles (*Microtus pennsylvanicus*). *Oecologia.* 1987; 71:510–517.
- Bergeron JM, Brunet R, Jodoin L. Is space management of female meadow voles (*Microtus pennsylvanicus*) related to nutritive quality of plants? *Oecologia.* 1990; 82:531–536.
- Berteaux D, Bety J, Rengifo E, Bergeron JM. Multiple paternity in meadow voles (*Microtus pennsylvanicus*): investigating the role of the female. *Behav Ecol Sociobiol.* 1999; 45:283–291.
- Boonstra R, Xia X, Pavone L. Mating system of the meadow vole, *Microtus pennsylvanicus*. *Behav Ecol.* 1993; 4:83–89.
- Bronson FH, Marsteller FA. Effect of short-term food deprivation on reproduction in female mice. *Biol Reprod.* 1985; 33:660–667. [PubMed: 4052528]
- Bronson, FH. Mammalian reproductive biology. University of Chicago Press; Chicago: 1989.
- Brown, RE. The rodents II: suborder myomorpha. In: Brown, RE.; Macdonald, DW., editors. Social odours in mammals. Clarendon University Press; Oxford: 1985. p. 345-457.
- delBarco-Trillo J, Ferkin MH. Male mammals respond to a risk of sperm competition conveyed by odours of conspecific males. *Nature.* 2004; 431:446–449. [PubMed: 15386011]
- delBarco-Trillo J, Ferkin MH. Female meadow voles cause external ejaculations in male meadow voles. *Behaviour.* 2006a; 143:1425–1437.
- delBarco-Trillo J, Ferkin MH. Similarities between female meadow voles mating during postpartum estrus and raising two concurrent litters and females raising only one litter. *Reprod Fert Develop.* 2006b; 18:751–756.
- delBarco-Trillo J, Ferkin MH. Female meadow voles, *Microtus pennsylvanicus*, experience a reduction in copulatory behavior during postpartum estrus. *Ethology.* 2007; 113:466–473.
- Desy EA, Batzli GO. Effects of food availability and predation on prairie vole demography: a field experiment. *Ecology.* 1989; 70:411–421.
- Dewsbury DA. Patterns of copulatory behavior in male mammals. *Quarterly Review of Biology.* 1972; 47:1–33. [PubMed: 4553708]
- Dewsbury DA. Diversity and adaptation in rodent copulatory behavior. *Science.* 1975; 190:947–954. [PubMed: 1188377]
- Dewsbury DA, Evans RL, Webster DG. Pregnancy initiation in postpartum estrus in three species of muroid rodents. *Horm Behav.* 1979; 13:1–8. [PubMed: 391690]
- Ferkin MH, Johnston RE. Effects of pregnancy, lactation and postpartum oestrus on odour signals and the attraction to odours in female meadow voles, *Microtus pennsylvanicus*. *Anim Behav.* 1995; 49:1211–1217.
- Ferkin MH, Lee DN, Leonard ST. The reproductive state of female voles affects their scent marking behavior and the responses of male conspecifics to such marks. *Ethology.* 2004; 10:257–272.
- Ferkin MH, Combs A, delBarco-Trillo J, Pierce AA, Franklin S. Meadow voles, *Microtus pennsylvanicus*, have the capacity to recall the “what”, “where”, and “when” of a single past event. *Anim Cogn.* 2008; 11:147–159. [PubMed: 17653778]
- Ferkin MH. The amount of time that a meadow vole, *Microtus pennsylvanicus*, self-grooms is affected by its reproductive state and that of the odor donor. *Behav Processes.* 2006; 73:266–271. [PubMed: 16876967]
- Getz, LL. Habitats. In: Tamarin, RH., editor. Biology of New World *Microtus*. American Society of Mammalogists; 1985. p. 286-309. Special Publication
- Gilbert AN. Postpartum and lactational estrus: a comparative analysis in Rodentia. *J Comp Psychol.* 1984; 98:232–245. [PubMed: 6478785]

- Gill CJ, Rissman EF. Female sexual behavior is inhibited by short and long-term food restriction. *Physiol Behav.* 1997; 61:387–394. [PubMed: 9089757]
- Gray GD, Dewsbury DA. A quantitative description of the copulation behavior of meadow voles (*Microtus pennsylvanicus*). *Anim Behav.* 1975; 23:261–267.
- Hobbs NJ, Ferkin MH. The response of male meadow voles, *Microtus pennsylvanicus*, to same- and mixed-sex over-marks depends on the reproductive state of the top- and bottom-female scent donors. *Behaviour.* 2012 In Press.
- Hobbs NJ, Ferkin MH. Effects of food availability on proceptivity: a test of the reproduction at all costs and metabolic fuels hypotheses. *Behav Proc.* 2012 In Press.
- Johnston RE. Olfactory preferences, scent marking and “proceptivity” in female hamsters. *Horm Behav.* 1979; 13:21–39. [PubMed: 521019]
- Johnston RE. Chemical communication in rodent: from pheromones to individual recognition. *J Mammal.* 2003; 84:1141–1162.
- Jones JE, Wade GN. Acute fasting decreases sexual receptivity and neural estrogen receptor-alpha in female rats. *Physiol Behav.* 2002; 77:19–25. [PubMed: 12213498]
- Keller, BL. Reproductive patterns. In: Tamarin, RH., editor. *Biology of New World Microtus*. 8. American Society of Mammalogists; 1985. p. 725-778. Special Publication
- Krackow S. Effect of food restriction on reproduction and lactation in house mice mated post partum. *J Reprod Fert.* 1989; 86:341–347.
- Lai SC, Vasilieva NY, Johnston RE. Odors providing sexual information in Djungarian hamsters: Evidence for an across-odor code. *Horm Behav.* 1996; 30:26–36. [PubMed: 8724176]
- Lazaro-Perea C, Snowden CT, Arruda MF. Scent-marking behavior in wild groups of common marmosets (*Callithrix jacchus*). *Behav Ecol Sociobiol.* 1999; 46:313–324.
- Madison DM. An integrated view of the social biology of *Microtus pensylvanicus*. *The Biologist.* 1980a; 62:20–33.
- Madison DM. Space use and social structure of meadow voles, *Microtus pennsylvanicus*. *Behav Ecol Sociobiol.* 1980b; 7:65–71.
- Madison, DM. Activity rhythms and spacing. In: Tamarin, RH., editor. *Biology of new world Microtus*. American Society of Mammalogist; Shippensburg, Pennsylvania: 1985. p. 373-419.
- McShea WJ, Madison DM. Measurements of reproductive traits in a field population of meadow voles. *J Mammal.* 1989; 70:132–141.
- Mustonen AM, Kakela R, Halonen T, Karja V, Vartiainen E, Nieminen P. Fatty acid mobilization in voles-model species for rapid fasting response and fatty liver. *Comp Biochem Physiol A Mol Integr Physiol.* 2012; 163:152–160. [PubMed: 22643335]
- Pierce AA, Ferkin MH. Re-feeding and the restoration of odor attractivity, odor preference and sexual receptivity in food-deprived female meadow voles. *Physiol Behav.* 2005; 84:553–561. [PubMed: 15811390]
- Pierce AA, Ferkin MH, Williams TK. Food deprivation induced changes in sexual behavior of meadow voles, *Microtus pennsylvanicus*. *Anim Behav.* 2005; 70:339–348.
- Pierce AA, Ferkin MH. Food deprivation and the role of estradiol in mediating sexual behaviors in meadow voles. *Physiol Behav.* 2007; 90:353–361. [PubMed: 17112551]
- Rudd CD. Sexual behavior of male and female tammar wallabies (*Macropus eugenii*) at post-partum oestrus. *J Zool.* 1994; 232:151–162.
- Stopka P, Macdonald DW. Signal interchange during mating in the wood mouse *Apodemus sylvaticus*: The concept of active and passive signaling. *Behaviour.* 1998; 135:231–249.
- Tamarin RH. Reproduction in the island beach vole, *Microtus breweri*, and the mainland meadow vole, *Microtus pennsylvanicus*, in southeastern Massachusetts. *J Mammal.* 1977; 58:536–548. [PubMed: 336824]
- Tamarin RH, Reich LM, Moyer CM. Meadow vole cycles within fences. *Can J Zool.* 1984; 62:1796–1802.
- Temple JL, Schneider JE, Scott DK, Korutz A, Rissman EF. Mating behavior is controlled by acute changes in metabolic fuels. *Am J Physiol Reg Integr Comp Physiol.* 2002; 282:R782–R790.

- Trivers, RL. Parental investment and sexual selection. In: Campbell, BG., editor. Sexual selection and the descent of man 1871–1971. Aldine -Atherton; Chicago: 1972. p. 136-179.
- Vaughn AA, Ferkin MH. The presence and number of male competitor's scent marks and female reproductive rate after the response of male meadow voles to female conspecifics' odours. *Behavior*. 2011; 148:927–943.
- Vaughn AA, delBarco-Trillo J, Ferkin MH. Sperm investment in male meadow voles is affected by the condition of the nearby male conspecifics. *Behav Ecol*. 2008; 19:1159–1164. [PubMed: 19529815]
- Vaughn AA, delBarco-Trillo J, Ferkin MH. The duration and occurrence of sociosexual behaviors in male meadow voles, *Microtus pennsylvanicus*, varies before, during, and after copulation. *Curr Zool*. 2011; 57:43–49.
- Voltura MB, Winder BA. Effects of ambient temperature, diet quality, and food restriction on body composition dynamics of the prairie vole, *Microtus ochrogaster*. *Physiol Zool*. 71:321–328. [PubMed: 9634179]
- Wade GN, Schneider JE. Metabolic fuels and reproduction in female mammals. *Neurosci Biobehav Rev*. 1992; 16:235–272. [PubMed: 1630733]
- Wade GN, Schneider JE, Li HY. Control of fertility by metabolic cues. *Am J Physiol*. 1996; 270:E1–E19. [PubMed: 8772468]
- Witt DM, Carter CS, Chayer R, Adams K. Patterns of behavior during postpartum oestrus in prairie voles, *Microtus ochrogaster*. *Anim Behav*. 1990; 39:528–534.
- Zhao ZJ, Cao J. Plasticity in energy budget and behavior in Swiss mice and striped hamsters under stochastic food deprivation and refeeding. *Comp Biochem Physiol A Mol Integr Physiol*. 2009; 154:84–91. [PubMed: 19447188]
- Ziegler TE, Eppler G, Snowdon CT, Porter TA, Belcher AM, Kuderling I. Detection of the chemical signals of ovulation in the cotton-top tamarin, *Saguinus oedipus*. *Anim Behav*. 1993; 45:313–322.
- Zucker I, Johnston PG, Frost D. Comparative, physiological and biochronometric analyses of rodent seasonal reproductive cycles. *Progr Reprod Biol*. 1980; 5:103–133.

Figure 1.

Mean + SEM time (seconds) during the 5-minute long attractivity tests that male meadow voles spent investigating the anogenital scent marks of 1) control (C) females, PPE females that had continuous access to food and those that were food restricted for 3 days prior to parturition (FR), 2) control PPE females and females that were food deprived for 24 h prior to parturition (FD), 3) FD females and FR females, 4) females that were not pregnant and lactating and that had continuous access to food (REF) and FD females, and 5) REF females and FR females. * Asterisk indicates significant differences between pairs at $p < 0.001$.

Figure 2.

Mean + SEM time (seconds) during the 5-minute long proceptivity tests that control PPE females (C), food-restricted females (FR), and food-deprived females (FD) spent investigating the anogenital scent mark of a male conspecific and that of a female conspecific. * Asterisk indicates significant differences between pairs at $p < 0.001$.

Figure 3.

The proportion of control PPE females (C), food-restricted females (FR), and food-deprived females (FD) that mated postpartum. Bars capped with different letters indicate significant differences among treatments at $p < 0.05$.