Maternal nutrition and reproduction of daughters in wild house mice (*Mus musculus*)

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Food deprivation after weaning often has greater effects on the reproductive success of females than of males. However, if animals are deprived prenatally (that is, through food deprivation of the mother during gestation), the reproductive success of males may be more adversely affected than that of females because of a disruption in the organizational effects of testosterone in neonatal male mice. The hypotheses that daughters of female mice deprived of food during gestation would have lower reproductive success than control daughters, but that the impact of maternal food deprivation would be lower for daughters than it would be for sons, was tested. There was no difference in the proportion of daughters of food-deprived

and control mothers that produced one or two litters. However, the mean number of pups weaned in the second litters by daughters of control females (5.9 ± 0.57 SEM) was greater than the number of pups weaned by daughters of food-deprived females (4.5 ± 0.65 SEM). There were no differences in the mean birth or weaning body weights of offspring. Therefore, maternal food deprivation in mice may have a small but significant effect on the reproductive success of daughters. However, studies of sons born to females that were subjected to the same food deprivation protocol indicate that maternal food deprivation may have a much greater effect on the reproduction of sons than on that of daughters.

Introduction

Female mammals usually have a lower variance than do males in reproductive success (Alexander *et al.*, 1979; Clutton-Brock, 1988; Clutton-Brock and Parker, 1992), in part, because female mammals, unlike males, typically do not compete for access to mates and, therefore, usually have higher survivorship than males (for example, see Clutton-Brock, 1988; Meikle and Vessey, 1988; Paul and Kuester, 1990; Paul *et al.*, 1992). In addition, the probability of female mammals being chosen as mates does not vary as much as that of males (Clutton-Brock *et al.*, 1988; Meikle *et al.*, 1995). This sex-related asymmetry in reproductive success may result, in part, from an asymmetry in the way maternal condition (for example, nutritional state) influences the development and subsequent reproductive success of daughters and sons (Trivers and Willard, 1973; Clutton-Brock, 1988).

Food deprivation of both sexes shortly after weaning appears to have more serious effects on the reproductive success of females than of males (McClure, 1966; Bronson, 1985, 1989; Hamilton and Bronson, 1985). For example, food deprivation that is sufficient to reduce significantly the frequency of litters produced by female mice does not reduce the production or storage of spermatozoa in male mice, although body size of male mice can be affected significantly (Bronson, 1985; Hamilton and Bronson, 1985).

However, some evidence indicates that if offspring are deprived of nutrients or calories *in utero* because the mother is food-restricted, the reproductive success of sons may be more seriously affected than that of daughters (Labov *et al.*, 1986; Meikle *et al.*, 1995; Meikle and Westberg, 2001).

For example, in the house mouse (*Mus musculus*), sons born to females that are deprived of food during gestation have a lower body weight at weaning and as adults than sons born to well-nourished females (Wright *et al.*, 1988; Meikle and Thornton, 1995). The sons of food-deprived females are also more likely to be lower ranking than the sons of mothers fed *ad libitum*, and are more likely to have smaller preputial glands and seminal vesicles (Meikle and Westberg, 2001). In addition, oestrous females prefer the odours of sons born to females that are well nourished during gestation to those born to food-deprived females (Meikle *et al.*, 1995). The sons of females that are fed *ad libitum* are more frequently dominant in agonistic encounters than are sons of food-deprived females (Meikle and Westberg, 2001) and oestrous females prefer the odours of dominant males (Drickamer, 1992). Hence, evidence indicates that if a female mammal is deprived of food during gestation, her sons may be disproportionately represented among males that do not survive to maturity (for example, see Meikle and Vessey, 1988; Wasser and Norton, 1993; Meikle and Westberg, 2001) or among those that survive but have relatively low reproductive success (Clutton-Brock, 1988).

There are only limited data about the potential effects of

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the nutritional state of mothers during gestation on daughters. However, some evidence indicates that maternal nutrition does not have as large an impact on the reproductive success of daughters as it does on that of sons. For example, Wright *et al.* (1988) reported no differences in the birth body weights of daughters born to mothers that were either fed *ad libitum*, or moderately or seriously deprived of food during gestation. In fact, daughters born to the most seriously food-deprived mothers actually weighed more at weaning than those born to mothers that were either moderately deprived of food or fed *ad libitum*. Similarly, Meikle and Thornton (1995) reported no differences in the birth or weaning body weights of daughters born to females that were slightly deprived of food during gestation compared with those born to mothers fed *ad libitum*. Drickamer and Meikle (1988) found that depriving mothers of food during gestation had no effect on the timing of the first oestrus, or the body weights at weaning or sexual maturity of their daughters.

Taken together, this evidence indicates that the potential reproductive success of sons of food-deprived females is significantly lower than that of sons born to females fed *ad libitum* during gestation. However, there does not appear to be such a large difference in the reproductive success of daughters born to food-deprived and control (fed *ad libitum*) mothers. It is possible that sons are more seriously affected because maternal food deprivation disrupts the organizational effects of testosterone that occur in neonatal male mice (Breedlove and Arnold, 1980; Lung and Cunha, 1980) and, therefore, has significant adverse effects on their development and reproductive success (Meikle and Westberg, 2001). No such organizational effects are anticipated for female mice (Breedlove and Arnold, 1980; Breedlove, 1992); however, the direct impact of maternal food deprivation during gestation on the reproductive success of daughters has not been examined.

The aim of the present study was to test the hypothesis that in wild house mice, the reproductive success of females born to mothers deprived of food during gestation would be lower than the reproductive success of daughters born to females fed *ad libitum*. This study is a continuation of earlier studies in which the effects of maternal food deprivation on the development and reproductive potential of sons and daughters were examined (Meikle and Drickamer, 1986; Drickamer and Meikle, 1988; Meikle *et al.*, 1995; Meikle and Thornton, 1995; Meikle and Westberg, 2001). In the present study, a food deprivation protocol was used that in previous studies has been shown to have large effects on male reproductive success, specifically, adult body weight, attractiveness to oestrous females, ability to win agonistic encounters and mass of accessory sex glands (Meikle and Thornton, 1995; Meikle *et al.*, 1995; Meikle and Westberg, 2001). The results of these studies indicate that the reproductive success of sons of food-deprived mothers may be significantly lower than that of sons of control mothers. Hence, the second aim of the present study was to test the

hypothesis that any difference in the reproductive success of daughters of food-deprived and control mothers is smaller than the potential difference in the reproductive success of sons of the two types of mother.

Food deprivation of mothers during gestation may reduce the ability of adult daughters to invest in offspring; therefore, it was hypothesized that a smaller proportion of the daughters of food-deprived mothers would produce first or second litters than daughters of control mothers. In addition, it was predicted that there would be fewer pups in litters of daughters of food-deprived mothers at birth and especially at weaning compared with litters born to daughters of control mothers.

Materials and Methods

House mice (*Mus musculus*) were obtained from an outbred colony that was established with approximately 80 wild mice captured from five sites in Frederick County, MD. All animals were housed individually after weaning (21–22 days) in opaque polypropylene cages (15 cm × 28 cm × 15 cm; Ancare Corp., Bellmore, NY). The colony rooms were maintained at 22°C and at 30–70% relative humidity with a 14 h light:10 h dark photoperiod. Water was available *ad libitum* as was Purina 5015 Mouse Chow® except as described below. For experimental animals, primiparous females were assigned randomly to either food-deprived ($n = 60$) or control ($n = 48$) groups. More females were assigned to the deprived treatment group because female mice deprived of food during gestation have lower fertility (Meikle and Thornton, 1995; Meikle and Westberg, 2001).

Female mice in the control and food-deprived groups were paired randomly with adult males (no sibling pairs). At 10 days after pairing, males were removed and females were deprived of food for 24 h and then for 24 h on every third day for a subsequent 10 days (food deprivation for a total of 4 days). Food was available *ad libitum* on the other days and also after birth for all animals. Two cotton nestlets were provided for each female as nesting material. The wild animals used were captured either by hand or in a plastic bag for close inspection. The presence of copulatory plugs was not examined to avoid stressing the females by frequent capture and restraint. The gestation period of wild female house mice is 19–21 days (Rugh, 1968); therefore, it was possible to estimate the day of conception in relation to the timing of food deprivation from the day of birth.

In some food deprivation studies, female mice were fed an invariable and inadequate diet (that is, below the level of consumption that animals choose if fed *ad libitum*) each day (for example, see Rivers and Crawford, 1974; McClure, 1981; Labov *et al.*, 1986). However, fluctuations in food availability and dominance rank-related access to food may occur daily for species like mice (Jakobson, 1981; Ward, 1981; Bronson, 1985). Hence, in the present study, female mice were deprived of food during gestation on an intermittent (that is, at 3 day intervals) basis. More frequent removal of food during gestation results in very low birth

rates (Drickamer and Meikle, 1988). Females that are deprived of food for 24 h every third day during the second half of gestation give birth to litters that are smaller than those of control females (Meikle and Thornton, 1995). In addition, although female mice deprived of food for 24 h every third day regain much of their lost body weight during the 2 day period of *ad libitum* feeding, these mice weigh significantly less at parturition than control females (Meikle and Thornton, 1995).

The female offspring of control and food-deprived females were caged individually at 21 days of age. On some occasions, data were collected for more than one daughter from each litter. In those cases, the average scores for the sisters from each litter were calculated and used as single data points for statistical analysis. At all times during the experiments described below, the daughters of control and food-deprived mothers were fed *ad libitum*. These animals are referred to as 'control daughters' and 'deprived daughters' to highlight the fact that only their mothers were deprived of food during gestation.

When the daughters of control and food-deprived mothers were 90 days old, 30 daughters were selected randomly from each group (all mice were within 1 week of age of each other) for comparison of the reproductive success of individually caged control and deprived daughters. Each control and deprived daughter was weighed and paired with a male chosen randomly. At day 10 after pairing, the male was removed and at day 19 after pairing cages were checked each day for the presence of offspring. On the day each litter was born, the female was weighed, the litter sexed, and all male and female pups were weighed, as they were at 21 days (weaning). The mean body weight for male and female offspring at birth and at weaning was then calculated.

Daughters of food-deprived and control females were paired with a second male about 2 months after the first pairing. Female mice that produced a litter with the first male were able to produce a second litter with the second male. In addition, female mice that did not produce a litter with the first male were able to produce a first litter with the second male, which may have been more attractive to them than the first male (for example, see Drickamer *et al.*, 2000). Data on litters from the second pairing were collected as for those from the first pairing.

Statistical analysis

Levene's test (SPSS Inc., 1996) was used to determine whether variances were homogeneous. As it was not possible to correct for unequal variances in the secondary (at birth) sex ratio data by any transformations, the sex ratio results were analysed using non-parametric statistics (Siegel, 1956). For all tests for which we had predictions, one-tailed probabilities are reported. Two-tailed probabilities were used for all other tests and all means are $\pm$ SEM. The number of litters for which the mean birth body weights or mean weaning body weights are available, are lower than the

number of litters born because some pups were partially consumed at birth and in a few litters some or all pups died before weaning. Power analyses (Howell, 1982) for all comparisons of the number of pups born and weaned by daughters of food-deprived and control mothers were also performed.

Results

Food-deprived mothers produced litters 20–24 days after pairing with a male. Hence, conceptions occurred approximately 6–10 days before the food deprivation treatment began. Control mothers produced litters 20–26 days after pairing. The greater the time it took for food-deprived mothers to give birth to a litter (that is, the closer that food deprivation occurred with respect to conception) the smaller the size of the litter ($R^2 = 0.93$, $F_{1,3} = 38.25$, $P < 0.025$), indicating that food deprivation caused resorption of some embryos.

Among the adult daughters of food-deprived and control mothers, there was no difference in the proportion of females that gave birth after being paired with one male (control: 19 of 30 = 0.63; deprived: 16 of 30 = 0.53; $\chi^2 = 0.62$, $df = 1$, $P > 0.1$). The proportion of daughters of food-deprived and control mothers that did not produce a litter after pairing with the first male did not differ when daughters were paired with a second male (total producing at least one litter: 24 of 30 = 0.80% of daughters of control mothers and 22 of 30 = 0.73% of daughters of food-deprived mothers; $\chi^2 = 0.12$, $df = 1$, $P > 0.1$). In addition, all 19 daughters of control mothers and 16 daughters of food-deprived mothers that had a litter after the first pairing also had a litter after the second pairing.

The mean number of pups born in the first litters did not differ between control and deprived daughters ($t = 0.88$; $df = 44$; $P > 0.1$) (Fig. 1). However, the mean number of pups born in the second litters was higher for controls than for daughters of food-deprived mothers ($t = 1.75$, $df = 33$, $P = 0.05$; Fig. 1). For first and second litters combined, there was no difference in the mean number of pups born to daughters of control and food-deprived females ($t = 0.49$; $df = 44$; $P > 0.1$; Fig. 1). As the difference between the mean numbers of total pups born in both litters was relatively small (0.6 ± 0.83 pups per litter), the power of the analysis was low (δ approximately 0.10).

There were also no differences in the mean numbers of pups weaned in the first litters ($t = 0.62$; $df = 41$; $P > 0.1$). The number of pups weaned by control females in the second litters was greater than the number of pups weaned by daughters of food-deprived females ($t = 1.72$; $df = 27$; $P = 0.05$, Fig. 2). In addition, for first and second litters combined, the mean number of pups weaned for control and food-deprived daughters did not differ ($t = 0.45$; $df = 35$; $P > 0.1$; Fig. 2). Again, because the differences in the mean numbers of total pups weaned from both litters was so small (0.6 ± 0.93 pups per litter), the power of the analysis was relatively low (δ approximately 0.10).

Fig. 1. Mean number ($\pm$ SEM) of pups born to daughters of control (■) and food-deprived (□) females in first and second litters, and in both litters combined for the wild house mouse *Mus musculus*. Number of litters shown in parentheses. *Significantly different from control group of second litter ($P < 0.05$).

Fig. 2. Mean number ($\pm$ SEM) of pups weaned by daughters of control (■) and food-deprived (□) females in first and second litters, and in both litters combined for the wild house mouse *Mus musculus*. Number of litters shown in parentheses. *Significantly different from control group of second litter ($P < 0.05$).

The mean body weights at first mating of the daughters of control and food-deprived females did not differ ($t = 0.08$; $df = 58$; $P > 0.1$) or at first parturition ($t = 0.06$; $df = 44$; $P > 0.1$; Table 1). The body weights of females at mating and at parturition for their second litters did not differ ($t = 1.2$; $df = 33$; $P > 0.1$ and $t = 0.4$; $df = 33$; $P > 0.1$, respectively; Table 1). There were also no differences between the daughters of control and deprived females in

the mean body weights of their male or female offspring at birth ($t = 0.9$ and 0.4 , respectively; $P > 0.1$) or at weaning ($t = 0.7$ and 0.6 , respectively; $P > 0.1$) for first litters (Table 1), or at birth (both $t < 0.26$; $P > 0.1$) or at weaning (both $t < 0.4$; $P > 0.1$) for second births (Table 1).

For daughters of control and deprived females, the mean body weights of males and females at birth and at weaning were regressed on litter size to determine whether there was any evidence of trade-off between litter size and the mean body weights of the pups (for example see, Krackow, 1997). The number of pups born to control females was not associated with the mean birth ($R^2 < 0.03$; $F < 0.2$; $P > 0.5$, respectively) or weaning body weights ($R^2 < 0.04$; $F < 0.25$; $P > 0.5$, respectively) of male or female pups. However, the more pups born to food-deprived mothers, the lower the mean birth body weights ($R^2 = 0.27$; $F_{1,31} = 11.3$; $P < 0.005$) and mean weaning body weights of sons ($R^2 = 0.29$; $F_{1,27} = 10.8$; $P < 0.005$). In addition, the more pups born to the daughters of food-deprived females, the lower the weaning body weights ($R^2 = 0.20$; $F_{1,27} = 10.8$; $P < 0.015$), but not the birth body weights ($R^2 = 0.06$; $F_{1,31} = 2.0$; $P > 0.1$), of their daughters.

Daughters of control females gave birth to a greater proportion of sons (0.58) in their first litters than did the daughters of food-deprived females (0.44; Mann–Whitney U test = 141; $P < 0.05$), although the proportions at weaning did not differ ($U = 112$; $P > 0.05$). In second litters, there was a trend towards control daughters giving birth to more sons ($U = 53$; $P = 0.075$), although at weaning this trend was weaker ($U = 48.5$; $P > 0.1$).

Discussion

The results of the present study indicate that daughters of food-deprived mothers have slightly lower reproductive success than do daughters of control mothers. If these results are representative of reproduction of wild mice in nature, daughters of mothers fed *ad libitum* wean on average about one more pup from their first two litters compared with daughters of food-deprived mothers. In addition, the difference in the number of pups weaned may increase in third and subsequent litters. However, estimates of survivorship among females in populations of wild mice (Singleton, 1989; Singleton and Redhead, 1990; Triggs, 1991) indicate that the average female in the wild probably does not produce more than (or even as many as) two litters.

Studies on long-lived species, such as humans, indicate that maternal food deprivation may increase rates of disease (for example, cardiovascular disease) among adult post-reproductive offspring (for an example see, Barker, 1999). However, because house mice have relatively short lifespans (Singleton, 1989; Singleton and Redhead, 1990; Triggs, 1991), it seems unlikely that such disease-related differences in survivorship among control and deprived daughters would have a strong impact on their lifetime reproductive success. In addition, on the basis of other measurements, there is no strong evidence to indicate that

Table 1. Mean body weights ($\pm$ SEM) of control and deprived daughters at mating and birth, and of pups for each litter at birth and weaning for first and second litters in the wild house mouse, *Mus musculus*

	Control mice	<i>n</i>	Deprived mice	<i>n</i>
First Litter*				
Daughters				
Maternal weight (g) at mating	16.9 (0.5)	30	16.8 (0.5)	30
Maternal weight (g) at birth	19.8 (0.5)	24	19.8 (0.5)	22
Pups				
Weight (g) of male pups at birth	1.3 (0.04)	21	1.3 (0.4)	20
Weight (g) of male pups at weaning	9.5 (0.3)	19	9.2 (0.4)	18
Weight (g) of female pups at birth	1.2 (0.05)	20	1.3 (0.05)	21
Weight (g) of female pups at weaning	8.8 (0.3)	18	8.6 (0.3)	18
Second Litter*				
Daughters				
Maternal weight (g) at mating	19.5 (0.7)	19	18.5 (0.3)	16
Maternal weight (g) at birth	22.0 (0.6)	19	21.8 (0.5)	16
Pups				
Weight (g) of male pups at birth	1.4 (0.04)	15	1.4 (0.06)	12
Weight (g) of male pups at weaning	9.8 (0.2)	14	10.1 (0.4)	11
Weight (g) of female pups at birth	1.3 (0.04)	15	1.7 (0.37)	12
Weight (g) of female pups at weaning	9.4 (0.2)	14	9.1 (0.3)	11

*No significant differences were found between deprived and control house mice.
Values in parentheses are $\pm$ SEM of body weights.

daughters of food-deprived and control mothers differ in their survivorship. For example, no body weight differences at parturition or at mating were found in the present study between the daughters of control and food-deprived females. Wright *et al.* (1988) reported that daughters of food-deprived mothers actually weighed more at weaning than daughters of control mothers.

The offspring of daughters of control and food-deprived females did not differ in their mean birth or weaning body weights, although the mean body weights of sons and daughters of food-deprived mothers decreased with increasing litter size. However, there is no clear indication that the offspring of daughters of control and food-deprived females would be at a disadvantage in terms of survival or reproductive success (DeFries and McLearn, 1970; Fuchs, 1981; Krackow, 1993; König, 1994). Finally, the timing of first oestrus in daughters of mothers deprived of food during gestation is not delayed (Drickamer and Meikle, 1988). Although the results reported here indicate that the lifetime reproductive success of control and deprived daughters does not differ by much, some evidence indicates that the same level of maternal food deprivation has large effects on the lifetime reproductive success of sons. For example, the brothers of the daughters of food-deprived mothers used in these experiments had smaller preputial glands and seminal vesicles than those of the brothers of daughters of control females (Meikle and Westberg, 2001). Sons of food-deprived mothers were about 50% less frequently dominant to sons of control mothers than vice-versa (Meikle and Westberg, 2001). In addition, Meikle *et al.* (1995) found that males born to mothers subjected to the

same food deprivation protocol as that used in the present study were half again less attractive to oestrous females than were males born to control mothers. Hence, sons of control mothers are more likely to have greater survivorship and be able to establish and maintain a territory more readily than sons of food-deprived mothers. Sons born to control mothers are also likely to be chosen more frequently as mates than are sons of food-deprived mothers. The extent to which these factors that may influence reproduction differ in sons of control and food-deprived mothers indicates that the lifetime reproductive success of control sons may be several times higher than that of sons of food-deprived females (Meikle *et al.*, 1995; Meikle and Westberg, 2001).

It is not surprising that maternal food deprivation during gestation has less effect on the reproductive success of daughters than that of sons. Poor maternal nutrition may disrupt testosterone-mediated organizational effects in males (Breedlove and Arnold, 1980; Lung and Cunha, 1980; Breedlove, 1992), resulting in adult mice devoid of the physical or behavioural characteristics that predispose them to be dominant during intrasexual agonistic encounters or attractive to potential mates. Female mice do not undergo such organizational effects and, therefore, may be relatively immune from the serious effects of mild food deprivation of their mothers during gestation. However, only a direct measure of reproduction of sons and daughters of control and food-deprived females in natural or semi-natural conditions will allow a rigorous comparison of the relative impact of maternal nutrition on the lifetime reproductive success of sons and daughters.

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