Food availability and secondary sex ratio variation in wild and laboratory house mice (*Mus musculus*)

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Summary. Female house mice deprived of food intermittently for 1 week before mating gave birth to fewer male young, but litters of females deprived of food for 2 weeks did not differ from control litters. Since mean weights of females did not differ between the two treatments, our results suggest that females were initially stressed by food deprivation, but recovered in the second week.

Introduction

Recent data and theory suggest that secondary sex ratios (sex ratio at birth) of mammals can vary in relation to maternal nutritional status (Trivers & Willard, 1973; Rivers & Crawford, 1974; Clutton-Brock, Albon & Guinness, 1981; Verme, 1983; Labov, Huck, Vaswani & Lisk, 1986). Trivers & Willard (1973) proposed that, since the reproduction of males varies more than that of females in polygynous and promiscuous species, the development and subsequent reproduction of sons is probably more closely associated with maternal 'condition' (e.g. size, dominance rank, nutritional state) than is the reproduction of daughters. The model therefore predicts that, all else equal, females in poor condition give birth to more daughters than sons, while females in good condition gave birth to more sons than daughters.

There have been a few reports of offspring sex ratio variation in rodents in relation to maternal nutritional status. Female albino house mice (*Mus musculus*) fed a low-fat diet (<1% lipid) gave birth to fewer male than female young (Rivers & Crawford, 1974). Labov et al. (1986) also reported that females of the LVG/LAK strain of golden hamster (*Mesocricetus auratus*) gave birth to fewer male offspring and that males grew more slowly than females when their mothers were consistently underfed (kept at about 75% of full body weight). In addition, when female wood rats (*Neotoma floridanus*) were underfed during lactation (about 70–90% of maintenance requirement for non-reproductive females) their sons did not gain weight as rapidly as and had higher mortality than did their daughters, apparently due, in part, to maternal rejection of male offspring (McClure, 1981).

In the above studies females were fed an inadequate diet on a daily basis. However, large fluctuations in food availability and dominance rank-related access to food may occur daily for species like mice (Jakobson, 1981; Ward, 1981; Bronson, 1985). We therefore tested the Trivers–Willard model by alternately depriving female house mice of food and feeding them *ad libitum* every other day just before mating. In addition, we compared the responses of wild and albino laboratory mice to this treatment, since the latter are not subject to natural selection by food scarcity and resource competition as are their wild conspecifics.

Materials and Methods

We used nulliparous females from a random-bred ICR/Alb-derived strain (N = 97) and F₁ progeny of wild mice (*M. musculus*) trapped at a poultry farm in West Simsbury, Connecticut.

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(N = 74). Each adult female (>60 days old) was housed alone in an opaque polypropylene cage (15 x 28 x 15 cm) for 10 days before the experiments. The colony rooms were maintained at 21–25°C and 30–70% relative humidity with lights on from 06:00 to 18:00 h. Wayne Lab Blox and water were provided ad libitum to all mice.

Females were deprived of food for 2 weeks or 1 week before mating. The 2-week deprivation group was begun first; all food was removed every other day, but was available ad libitum on alternate days (i.e. no food on 7 of 14 days). The 1-week deprivation group (no food on 4 of 7 days) was begun so that both groups of females (and controls) could be mated on the same day. After the last day of deprivation, all females were given food for 1 full day and then 1 randomly-selected adult male was added to each female's cage and was removed after 10 days. To avoid additional stress on females, particularly wild ones, the occurrence of vaginal plugs was not recorded. Food was available ad libitum from mating until the end of the experiment. Cages were checked each morning and new litters were sexed and weighed.

These experiments were conducted twice for wild (36 and 38 females mated) and laboratory mice (52 and 45 females mated) and only one litter from each female was used. Different nulliparous females were used for data on body weights during the 1- and 2-week treatments, again to avoid stressing the mated females. Laboratory females were easily weighed but wild females often jumped out of their cages when the lids were removed. Their cages were therefore opened on the bottom of a large drum so that females could run into a weighing tube (5 x 25 cm) that was closed at one end and lying against the side of the drum. On each day 10 females for each treatment were weighed (30 wild and 30 laboratory mice).

Results

Although female laboratory mice gave birth to about twice as many young as did wild females (Table 1) and weighed about twice that of wild females (Fig. 1), the responses of the two types were quite similar. Wild and laboratory females deprived of food for 1 week before mating gave birth to a lower proportion of sons (0.40 and 0.46, respectively) than did control females (0.61 and 0.56, assuming each birth independent; \( \chi^2 = 8.49 \) and 6.60, d.f. = 1, \( P < 0.01 \) and \( P < 0.02 \), N = 193 and 689 young born respectively). As a result, the wild and laboratory females deprived of food for 1 week produced about half as many male-biased litters as did control females (25% and 30% vs 62% and 59%; Fisher exact probability, \( P < 0.01 \) and \( P < 0.02 \) respectively).

<table>
<thead>
<tr>
<th>Mouse type</th>
<th>Group</th>
<th>Fertility* (%)</th>
<th>Mean litter size*</th>
<th>No. of young born**</th>
<th>Mean birth wt* (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wild</td>
<td>Control</td>
<td>21/28 (0.75)</td>
<td>5-1</td>
<td>66/42</td>
<td>1.2 1.1</td>
</tr>
<tr>
<td></td>
<td>1-week</td>
<td>16/27 (0.59)</td>
<td>5-3</td>
<td>34/51</td>
<td>1.3 1.2</td>
</tr>
<tr>
<td></td>
<td>2-week</td>
<td>15/19 (0.79)</td>
<td>5-8</td>
<td>51/36</td>
<td>1.3 1.2</td>
</tr>
<tr>
<td>Laboratory</td>
<td>Control</td>
<td>32/37 (0.86)</td>
<td>11.6</td>
<td>209/163</td>
<td>2.0 1.9</td>
</tr>
<tr>
<td></td>
<td>1-week</td>
<td>27/40 (0.68)</td>
<td>11.7</td>
<td>147/170</td>
<td>2.0 1.9</td>
</tr>
<tr>
<td></td>
<td>2-week</td>
<td>16/20 (0.80)</td>
<td>11.6</td>
<td>96/90</td>
<td>1.9 1.9</td>
</tr>
</tbody>
</table>

* No differences amongst treatments (\( P > 0.05 \)).
** \( P < 0.05 \) (see text).
There were no differences in the proportions of males born to wild and laboratory females deprived of food for 2 weeks (0.59 and 0.52, N = 87 and 186 young respectively) and control females. In fact, wild females deprived of food for 2 weeks gave birth to a greater proportion of sons ($\chi^2 = 5.96$, d.f. = 1, $P < 0.05$) and more male-biased litters (Fisher exact probability, $P < 0.05$) than did wild females deprived for 1 week, although this was not the case for laboratory mice ($P > 0.1$ for $\chi^2$ and Fisher exact probability tests). The same pattern of secondary sex ratio skew occurred in all experiments.

There were no differences in mortality rates of male and female young and so the sex ratios of litters at weaning did not differ significantly from those at birth. During the first experiment, 7 wild females close to each other on the cage rack died (apparently from a contagious respiratory disease) and were not included in this analysis. No females died during the second experiment.

There were no significant differences in mean litter sizes for the different treatments ($F_{2,49} = 1.70$ and $F_{2,72} = 0.02$, respectively; $P > 0.1$; Table 1) and so there was no relationship between sex ratio and litter size as suggested by McGinley (1984). There also were no differences in fertility amongst treatments for wild or laboratory mice ($\chi^2 = 2.55$ and 4.05 respectively, d.f. = 2, $P > 0.1$ for both), although fertility tended to be lower for both types deprived of food for 1 week (Table 1). Females did not differ in the time it took them (from introduction of the male) to bear litters ($F_{2,49} = 1.82$ and $F_{2,72} = 0.44$ for wild and laboratory mice respectively, $P > 0.1$ for both), which suggests that females that produced litters were fertilized during their first oestrous cycle after males were introduced. In addition, there was no difference in the timing of birth of male-biased and female-biased litters for the different treatments (Yates $\chi^2$s all <2.43, d.f. = 1, $P > 0.1$ for all).

Females quickly regained the weight that they lost during food deprivation (Fig. 1). The mean

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**Fig. 1.** Mean body weights of Control, 1-week and 2-week food-deprived females during the 2-week period before mating.
percentage weight loss after each day of food deprivation differed by less than 1.2% between the 1- and 2-week treatments for wild (15.2 and 16.3% respectively; $t = 0.64$, 18 d.f., $P > 0.1$) and laboratory (12.9 and 13.3% respectively; $t = 0.23$, 18 d.f., $P > 0.1$) females. In addition, the birth weights of male young and female young in the three groups did not differ ($F_{2,49} = 0.98$ and $F_{2,72} = 1.14$ for wild and laboratory mice respectively, $P > 0.1$ for both; Table 1).

Discussion

These results are ambiguous with respect to the predictions of the Trivers & Willard (1973) model. A monotonic decrease in number of males born to females deprived of food for 2 weeks was expected. Since weight losses did not differ between 1- and 2-week-deprived animals, and since the weight loss was entirely regained after 24 h with food *ad libitum* (Fig. 1), the decreased number of males born to females deprived for 1 week probably did not result from an actual energy deficit (Bronson & Marsteller, 1985). The weight similarities and behavioural differences we observed between 1- and 2-week-deprived animals suggest that a physiological stress response to food deprivation every other day may account for their secondary sex ratios. Female hooded rats that were stressed by restraint before mating also gave birth to fewer sons than did non-stressed control females (Lane & Hyde, 1973).

The similarity in secondary sex ratios of control and 2-week food-deprived females suggests that females recovered from every other day food availability after about 1 week. In addition, although behavioural data were not systematically recorded, we observed a dramatic difference in the behaviour of wild mice deprived of food for 1 and 2 weeks. During the first week of deprivation females in the 2-week group were lethargic after 24 h without food, as were 1-week deprived females. However, after 1 week of deprivation, the 2-week animals were nearly as active as control females. In fact, during the first week of deprivation, many wild females remained still when the tops of their cages were removed and could be lifted by the tail with forceps and placed in the weighing tube. During the second week of deprivation, however, those same females usually leaped from their cages when the top was removed.

In circumstances of intermittent, extreme food deprivation during development or before mating, female rodents usually became reproductively dysfunctional (McClure, 1966; Hamilton & Bronson, 1985) and if severe deprivation occurs early during lactation females are likely to kill and eat young (Bronson & Marsteller, 1985). However, less severe circumstances of chronic undernourishment (Rivers & Crawford, 1974; Labov *et al.*, 1986) result in smaller litters and a decreased proportion of males. The 1-week deprivation schedule that we used appears to have been even less severe than the above treatments since 1-week deprived females gave birth to a lower proportion of males, but litter sizes did not differ from controls (Table 1).

The mechanism by which the 1-week sex ratios varied was not obvious from these results. Since litter sizes did not differ it appears that there were no sex-specific differences in mortality of embryos, if one assumes equal numbers of fertilized ova amongst all females. It is possible that X and Y chromosome-bearing spermatozoa were differentially available for and/or capable of fertilizing ova (Bennett & Boyse, 1973; Meikle, Tilford & Vessey, 1984).

In situations where limited food is available, dominant females probably are able to appropriate more food than are lower-ranking females. Dominant female house mice also produce a greater proportion of male-biased litters than do lower-ranking females (Drickamer, 1985; Fisher exact probability, $P < 0.05$). These dominance-related sex ratios may be the result of adrenal stress from losing agonistic encounters (Louch & Higginbotham, 1967; Meikle *et al.*, 1984). Whether variation in the secondary sex ratio in response to stress or an energy deficit is adaptive remains to be answered (Trivers & Willard, 1973; Clutton-Brock *et al.*, 1981).
Food and sex ratio in house mice

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References


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