

## Allocation of reproductive effort in *Mus domesticus*: responses of offspring sex ratio and quality to social density and food availability

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**Summary.** Female mammals in good condition can maximize their inclusive fitness by investing more in male offspring than in female offspring during periods of poor environmental quality. To test this hypothesis, we measured the effects of undernutrition and crowding before and during gestation on the sex ratio and weight of offspring at parturition and at weaning in *Mus domesticus*. Sex ratio was not significantly affected by density. Dams altered the sex ratio of their offspring in response to food availability, but only if variance in competitive success within the experimental subpopulation was evident. Thus *ad lib* fed females produced litters with an unbiased sex ratio, competitively successful females under moderate food availability produced a male-biased sex ratio, and severely food deprived females produced litters with a female-biased sex ratio. In groups that experienced competition for food, successful dams favoured male offspring during lactation. These results are consistent with the predictions of Trivers and Willard (1973). Analysis of within-cell variance and covariance suggests that the interaction of social structure and food availability provides specific cues for the dams' tactical reproductive choices.

### Introduction

The capacity to facultatively adjust the sex ratio of offspring may be favored by natural selection in polygynous species (Trivers and Willard 1973). This hypothesis depends on three assumptions.

First, a female in good condition is more likely to produce healthy offspring than one in poor condition. Second, healthy offspring have the advantage of greater size and strength at maturity. Third, in species where males compete for access to females, the sons of healthy females are more reproductively successful than the sons of unhealthy females. A daughter's reproductive success, on the other hand, should be relatively unaffected by her physical condition. Healthy females can therefore increase the number of their grandoffspring by biasing investment toward sons.

The social organization of *Mus domesticus* meets the assumptions of Trivers and Willard's sex allocation hypothesis. House mice are territorial and polygynous, and dominant males have a lasting advantage in mating (Bronson 1979; DeFries and McClearn 1970; Reimer and Petras 1967). Larger males win territory and dominance battles (Vessey 1967) and large male offspring size tends to be correlated with good maternal condition (Clutton-Brock and Albon 1982).

Crowding (Crowcroft and Rowe 1957) and caloric deprivation (Labov et al. 1986; Rivers and Crawford 1974) have been shown to produce biased sex ratios in mice. The purpose of this research was to investigate further the ecological cues for biased sex allocation in house mice (*Mus domesticus*). We manipulated food availability and social density in a factorial experiment to test the responses of female mice reproducing under combinations of these stressors when they were experienced only before and during gestation. We predicted, based on Trivers and Willard's (1973) hypothesis, that the following variables should increase under conditions of low social density or unrestricted food availability and decrease under conditions of high social density or restricted food availability: (1) indices of dams' physical condition

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at conception, parturition, and weaning, (2) litter size at parturition and weaning, (3) proportion of males in litter at parturition and weaning, (4) measures of caloric investment in male pups at parturition and weaning. Measures of (5) caloric investment in female pups at parturition and weaning were predicted to be equal in all treatment groups.

The first two of these variables measure the effects of experimental treatments on the dams' physical condition and reproductive effort, while the last three indicate sex-biased reproductive allocation.

## Methods

Two levels of density and three levels of food availability were combined in a factorial design. Mice were grouped at either low social density (5 females per bin, 207.1 cm sq per female) or high social density (20 females per bin, 51.8 cm sq per female). Food availabilities were: 1) *ad libitum* (5 gm/mouse/day), 2) moderate food (80% of *ad lib*) and 3) low food (65% of *ad lib*).

Food and density levels were previously established on the basis of their effect on the weight of nonpregnant mice in two pilot studies. The *ad lib* food and low density levels produced weight gains, the high density level maintained original weights, and the low food level produced a slow weight loss. Each of the 6 experimental cells (3 food  $\times$  2 density levels) included 20 females. Water was provided *ad lib* throughout the experiment.

Virgin female mice (CD-1 albino, 120–140 days of age) were marked on the tail with felt pen for identification. After 2 weeks 4 female mice were removed and replaced by 4 males in the high density bins; one female was removed and replaced by a male in each low density bin. Mice were weighed every 2 days; if a mouse fell below 80% of its original weight, it was replaced by another to keep the densities constant (only two females needed to be replaced during the experiment). Females were monitored daily for the presence of a vaginal plug, which indicated day 1 of gestation. A pregnant female remained in its treatment group until Day 18 of gestation (about 2 days

before parturition) at which time it was removed and housed separately with *ad lib* food to prevent destruction of the litter by the mother or other adults. Of the 85 litters born and enumerated, 6 were lost entirely, resulting in different sample sizes for the parturition and weaning data. No dams died during lactation, and individual pup mortality was slight.

We determined the weight of the pups, litter size, the number of male and female pups, total male pup production (TMPP, the total weight of male pups in a given litter) and total female pup production (TFPP, the total weight of female pups in a given litter) at birth and at weaning (23 days of age). TMPP and TFPP were overall measures of investment in male pups and female pups. The sex ratio (proportion of males in a litter) was arcsine transformed for analysis.

We also measured the following indicators of the females' physical condition: dam's initial weight (weight at onset of experiment), dam's weight gain to the end of pregnancy (weight just before parturition minus initial weight), dam's residual weight gain (weight gain to end of pregnancy minus total weight of pups), dam's weight on Day 23 after parturition, and conception weight (for reproducing females, weight at the estimated time of conception; for non-reproducing females, weight at the time of peak number of conceptions in the group).

## Results I: Analysis of variance

The following fraction of each treatment group became pregnant: 95% of *ad lib* food/low density, 100% of *ad lib* food/high density, 95% of moderate food/low density, 93% of moderate food/high density, 40% of low food/low density, and 56% of low food/high density. Data were analyzed in a two-way analysis of variance for unequal cell frequencies with food and density as the main factors. All possible *a priori* paired comparisons of the food groups were also analyzed.

All indices of reproducing dams' condition except initial weight varied significantly for the food factor during the actual experimental treatments (Table 1). However, among reproducing females,

**Table 1.** Marginal means ( $\pm$ SE) of dam's weight (gm) at various reproductive stages, for the food and density factors. Underlining indicates pairs of means that do not differ at the  $\alpha=0.05$  level of significance

	Food factor				Density factor		
	Ad libitum	Moderate	Low	<i>P</i>	Low	High	<i>P</i>
<i>n</i>	35	33	17		45	40	
Dam's initial weight	25.50 $\pm$ 0.35	26.24 $\pm$ 0.32	25.32 $\pm$ 0.34	NS	25.32 $\pm$ 0.31	26.05 $\pm$ 0.25	NS
Dam's weight gain to end of pregnancy	26.13 $\pm$ 0.77	<u>19.60 <math>\pm</math> 1.00</u>	<u>19.39 <math>\pm</math> 1.45</u>	<0.01	23.35 $\pm$ 0.95	20.06 $\pm$ 0.88	<0.01
Dam's residual weight gain <sup>a</sup>	9.53 $\pm$ 0.51	<u>6.68 <math>\pm</math> 0.59</u>	<u>5.23 <math>\pm</math> 1.19</u>	<0.01	8.18 $\pm$ 0.57	5.96 $\pm$ 0.57	NS
<i>n</i>	36	36	35		60	47	
Conception weight <sup>b</sup>	<u>27.47 <math>\pm</math> 0.33</u>	27.23 $\pm$ 0.36	26.27 $\pm$ 0.42	<0.02	26.08 $\pm$ 0.31	26.89 $\pm$ 0.31	NS
<i>n</i>	32	32	14		40	39	
Dam's weight day 23	35.60 $\pm$ 0.58	34.82 $\pm$ 0.59	36.38 $\pm$ 0.69	NS	36.57 $\pm$ 0.57	34.70 $\pm$ 0.40	<0.05

<sup>a</sup> Weight gain to end of pregnancy – weight of pups; <sup>b</sup> Weight at conception; for nonreproducing females, weight at peak time of conceptions

**Table 2.** Marginal means ( $\pm$ SE): Parturition data. Weight given in grams. Underlining indicates pairs of means that do not differ at the  $\alpha=0.05$  level of significance

	Food factor				Density factor		
	Ad libitum	Moderate food	Low food	<i>P</i>	Low	High	<i>P</i>
<i>n</i>	35	33	17		45	40	
Litter size	10.83 $\pm$ 0.40	<u>8.90 <math>\pm</math> 0.46</u>	<u>9.07 <math>\pm</math> 0.28</u>	<0.01	10.24 $\pm$ 0.38	9.25 $\pm$ 0.35	NS
Number of males	<u>5.24 <math>\pm</math> 0.33</u>	<u>5.16 <math>\pm</math> 0.36</u>	3.35 $\pm$ 0.41	<0.01	5.33 $\pm$ 0.35	4.35 $\pm$ 0.25	NS
Number of females	<u>5.60 <math>\pm</math> 0.34</u>	3.77 $\pm$ 0.26	<u>5.66 <math>\pm</math> 0.43</u>	<0.01	4.88 $\pm$ 0.31	4.90 $\pm$ 0.29	NS
Proportion of males	0.47 $\pm$ 0.16	0.57 $\pm$ 0.02	0.37 $\pm$ 0.14	<0.01	0.51 $\pm$ 0.03	0.47 $\pm$ 0.02	NS
Mean male pup weight	<u>1.57 <math>\pm</math> 0.02</u>	<u>1.47 <math>\pm</math> 0.05</u>	<u>1.67 <math>\pm</math> 0.06</u>	<0.05	1.51 $\pm$ 0.04	1.59 $\pm$ 0.03	NS
Mean female pup weight	1.51 $\pm$ 0.02	1.43 $\pm$ 0.05	1.51 $\pm$ 0.04	NS	1.43 $\pm$ 0.04	1.52 $\pm$ 0.04	NS
Total male production	<u>8.24 <math>\pm</math> 0.52</u>	<u>7.64 <math>\pm</math> 0.55</u>	5.57 $\pm$ 0.72	<0.02	8.05 $\pm$ 0.56	6.84 $\pm$ 0.38	NS
Total female production	<u>8.36 <math>\pm</math> 0.47</u>	5.28 $\pm$ 0.40	<u>8.46 <math>\pm</math> 0.65</u>	<0.001	7.12 $\pm$ 0.49	7.26 $\pm$ 0.41	NS

**Table 3.** Marginal means ( $\pm$ SE): Weaning data. Weights given in grams. Underlining indicates pairs of means that do not differ at the  $\alpha=0.05$  level of significance

	Food factor				Density factor		
	Ad libitum	Moderate	Low	<i>P</i>	Low	High	<i>P</i>
<i>n</i>	32	32	15		40	39	
Litter size	10.66 $\pm$ 0.31	<u>9.10 <math>\pm</math> 0.44</u>	<u>8.58 <math>\pm</math> 0.32</u>	<0.001	10.17 $\pm$ 0.32	9.05 $\pm$ 0.34	<0.05
Number of males	<u>5.25 <math>\pm</math> 0.34</u>	<u>5.41 <math>\pm</math> 0.36</u>	3.35 $\pm$ 0.46	<0.01	5.50 $\pm$ 0.35	4.36 $\pm$ 0.26	<0.05
Number of females	<u>5.41 <math>\pm</math> 0.32</u>	3.66 $\pm$ 0.26	<u>5.23 <math>\pm</math> 0.32</u>	<0.001	4.68 $\pm$ 0.31	4.67 $\pm$ 0.24	NS
Proportion of males	0.49 $\pm$ 0.03	0.60 $\pm$ 0.02	0.38 $\pm$ 0.05	<0.001	0.54 $\pm$ 0.03	0.48 $\pm$ 0.2	NS
Mean male pup weight	<u>11.26 <math>\pm</math> 0.28</u>	<u>11.70 <math>\pm</math> 0.46</u>	13.45 $\pm$ 0.68	<0.02	11.52 $\pm$ 0.39	12.11 $\pm$ 0.36	NS
Mean female pup weight	<u>10.77 <math>\pm</math> 0.28</u>	<u>11.16 <math>\pm</math> 0.36</u>	12.94 $\pm$ 0.54	<0.005	11.17 $\pm$ 0.35	11.52 $\pm$ 0.30	NS
Total male production	<u>57.79 <math>\pm</math> 3.45</u>	<u>60.18 <math>\pm</math> 3.56</u>	43.98 $\pm$ 6.52	<0.05	61.33 $\pm$ 3.74	50.90 $\pm$ 2.71	<0.05
Total female production	57.79 $\pm$ 3.21	39.33 $\pm$ 2.50	68.28 $\pm$ 4.95	<0.001	51.97 $\pm$ 3.73	52.25 $\pm$ 2.59	NS

those in the low food treatment groups did better than expected, with weight gains not significantly smaller than those in the moderate food treatment groups. This may be attributable to the fact that delayed pregnancies in the low food groups allowed the females to achieve a minimum weight gain before conceiving. The dams' weight did not differ significantly among the food groups at the end of the lactation period after three weeks of *ad lib* food and individual housing.

Density affected weight gain to the end of pregnancy and weight at weaning, but not the other two measures of dams' condition (Table 1). There were no significant food  $\times$  density interactions.

The condition of all females was analyzed by including the weight of non-reproducing females at the time when most conceptions occurred (Table 1). The marginal means for the food factor but not the density factor differed significantly in the expected direction. This result suggests that the fe-

males in the poorest condition did not reproduce in the low food treatment groups.

At parturition, litter size varied significantly for the food factor but not the density factor (Table 2). At weaning, litter size was significant for the density factor as well (Table 3). The loss of one very small litter is responsible for the apparently anomalous increase in mean litter size in the moderate food treatment during lactation. No significant food  $\times$  density interactions were observed.

These results partially support our predictions that litter size should be reduced by the experimental stress factors. Food availability influenced litter size during pregnancy, but mean litter size did not differ between moderate and low food treatments. Density apparently did not influence litter size until the lactation period.

Litter size was further partitioned into the number of male and female pups to determine whether one sex was overrepresented. The differ-

ence between groups for the number of male pups born was significant for the food factor, with *ad lib* and moderate food groups having the most male pups and low food groups having the least (Table 2). At weaning, the mean number of males differed among both food and density treatment groups. There were no significant food  $\times$  density interactions.

Differences among the groups in number of female pups born were significant for the food factor, but not for the density factor, at both parturition and weaning. Dams in the low and *ad lib* groups had the most female pups while dams from the moderate food groups had the fewest (Table 2).

The difference among groups for the proportion of males was significant for food, but not for density (Tables 2 and 3). There were no food  $\times$  density interactions. The low food groups had the lowest sex ratio as predicted, but moderate food groups had the highest, a result that only partially agrees with our predictions.

Total male pup production was significant at birth and weaning for the food factor (Table 2), and at weaning for density (Table 3). Total female pup production was significant for the food factor but not for density at parturition (Table 2) and at weaning (Table 3).

The correlated variables litter size, number of males, and total male pup production varied significantly in response to the density factor. However, these differences do not strongly support our initial predictions about the effect of density, because they occurred after 3 weeks of solitary housing and were isolated among a general pattern of non-significant responses.

Male pup weight differed significantly among the food treatments at birth (Table 2), and male pups were heaviest in the low food treatment. At weaning, low food group pups of both sexes were significantly heavier than either of the other two groups (Table 3). Density did not affect pup weight, and there were no significant food  $\times$  density interactions. These results do not support our prediction of male-biased caloric investment by the dams in favorable conditions.

### Discussion I: Analysis of variance

The analysis of treatment means provided ambiguous results with respect to our original predictions from Trivers and Willard's hypothesis. First, although the average condition of all females responded to the experimental conditions, those females that actually reproduced in the low food groups did not differ significantly in condition

from those in moderate food groups. Second, though social density appeared to influence average female condition, it had relatively little effect on measures of reproductive effort and sex allocation (Tables 2 and 3). Third, though food availability appeared to influence sex allocation, it did so in an unexpected direction: Dams in the moderate food groups produced male-biased litters. Fourth, both male and female offspring from the low food group received increased investment during lactation under conditions of individual housing and *ad lib* food. These results suggested that additional analyses were required to evaluate the interactions of food availability, density, and within-treatment variability on reproductive effort and sex allocation.

### Within-treatment variation

Since mice were housed in groups, the experimental factors (food availability and crowding) may have influenced social interactions, creating within-treatment variance among the mice. Such within-treatment variance could have several results. First, mice might vary within treatments with respect to competitive success and physical condition, both of which function as cues for sex allocation bias in the model of Trivers and Willard (1973). If this is the case, we must look beyond treatment or marginal means for evidence relevant to their hypothesis. Second, as a result of within-treatment variance in competitive success and physical condition, individual mice may differ in their reproductive effort (e.g., litter size, offspring survival, offspring weight gain), and some dams might not reproduce at all. Thus, we expect that females should contribute differentially and non-randomly to the treatment mean. Third, functional relationships between reproductive variables (for example, the relationship between litter size and pup weight) might vary among treatments.

Between-treatment variation in reproductive functional relationships and within-treatment variance in competitive success, physical condition, and reproductive effort could influence our experimental results dramatically. Understanding these relationships may help us to explain the observed patterns in treatment means in terms of facultative reproductive tactics of female mice.

### Results II: A revised model and further analysis

Female mice in our experiment appeared to vary their reproductive effort within as well as between treatments. First, as noted above, the proportion of reproducing females varied dramatically with

**Table 4.** Parturition data: Variation among food treatment groups (pooled for density) in (1) litter size and (2) the relationship between number of males and litter size

Food treatment group	Litter size range	s <sup>2</sup> litter size	CV ( $\pm$ SE) litter size	Estimated slope (b): regression of number of males of litter size	Test of H <sub>0</sub> : $\beta=0.5$
Ad lib	One litter of 3, otherwise 8–15	5.419	21.50 $\pm$ 2.69	0.484	NS
Moderate	3–15	6.875	29.46 $\pm$ 3.78	0.650	<0.05
Low	7–11	1.309 <sup>a</sup>	12.61 $\pm$ 2.18	0.365	NS

<sup>a</sup> Estimated variance in litter size for low food group differs significantly from moderate ( $F_{32,16}=5.25$ ,  $P<0.005$ ) and from high ( $F_{34,16}=4.13$ ,  $P<0.005$ )

food availability. Second, the moderate and low food treatments (pooled over density) had significantly reduced mean litter size compared with the ad lib group (Table 2), while the variance and coefficient of variation in litter size for the low food group was significantly lower than for the other groups (Table 4).

These patterns in litter size suggest that the mice were closely adjusting their reproductive effort in response to the constraints imposed by food availability and within-treatment social structure. We propose the following model to explain how the facultative adjustment of reproductive effort might have influenced our cell and marginal means for sex ratio. We do not consider explicitly the effects of density, as density at the levels assigned in this experiment did not significantly affect most variables and did not, in most cases, interact with food availability.

#### Revised model

Dams in the *ad lib* food treatments experienced relatively little competition for food and a favourable, homogeneous environment. With few cues predicting variance in reproductive success of their offspring, Trivers and Willard's hypothesis predicts that they should invest equally in male and female pups.

Dams in the moderate food treatments experienced considerable competition for food, and an individual's physical condition would tend to be correlated with competitive success. Within this group, then, if the most successful competitors produced the largest litters, Trivers and Willard's hypothesis predicts the largest litters should be biased in favour of males. Less successful females, in poor condition, might bias their small litters toward female offspring within this treatment, but the influence of large litters would outweigh that of small litters and produce an overall male-biased sex proportion for the group.

In the low food treatments, there was severe competition, with only the most successful females reproducing. These females, though they were in relatively good condition, experienced a competitive and heterogeneous environment with poor resources. Trivers and Willard's hypothesis predicts that they should bias parental investment toward female offspring, regardless of litter size.

This revised model is *a posteriori* and thus not testable with our experimental cell means. However, we present below other results, largely independent of the cell means, that support the processes assumed by our model.

*Parturition: Evidence for variance in competitive ability.* The revised model assumes that food availability influences the level of competition and hence the within-treatment variance in dam's condition. If competition for food was more intense in the moderate and low food treatment groups than in the *ad lib* food groups, the variance in dam's weight should increase over time in the groups with reduced food availability, but not in the *ad lib* group. This was the case for weight of all females at the peak time of conception and for weight of reproducing females just after parturition (Table 5).

**Table 5.** Comparison of variance in dams' initial weight with (1) variance in all dams' weight at time of peak conception and (2) variance in reproducing dams' weight immediately after parturition, for each level of food availability

Group	F ratio	P	F ratio	P
	s <sup>2</sup> conception wt/s <sup>2</sup> initial wt		s <sup>2</sup> parturition wt/s <sup>2</sup> initial wt	
Ad lib food	0.942	NS	1.660	NS
Moderate food	1.434	NS	2.649	<0.005
Low food	3.153	<0.005	4.843	<0.001

If a female's initial weight gave her an advantage in competition for food, we would expect initial weight to be correlated with litter size where such competition took place. This was the case in the pooled moderate food treatment groups ( $r = 0.349$ ,  $P < 0.05$ ) but not in the *ad lib* groups. In the low food groups, variance in litter size was minimal and did not significantly correlate with dam's initial weight.

*Parturition: Evidence relevant to sex allocation.* The revised model makes several predictions about the ways in which sex allocation might appear as within-treatment covariance.

First, if litter size is an indication of the success of the dam under competition for food, then females with larger litters in competitive situations should have more male offspring. To test this hypothesis, we regressed the number of male pups on litter size within each treatment. The expected slope was 0.5 if there was no bias in sex allocation across litter size. The regression coefficients did not differ significantly with respect to density, so the density data were pooled within food levels. For the *ad lib* and low food treatments, we were unable to reject the null hypothesis that  $\beta = 0.5$  (Table 4). However, in the pooled moderate food groups, the slope was significantly greater than 0.5. These results are consistent with the above revised model and may explain why the moderate food treatment produced a higher overall sex proportion than the *ad lib* treatment.

If condition of the female alone was the most important cue for biased sex allocation, there should be a positive correlation between measures

of the dam's condition and the sex ratio of her litter. However, there was no significant correlation between measures of biased sex allocation and either (1) dam's weight gain to end of pregnancy (a measure which includes total pup production and her own weight gain) or (2) dam's weight just after parturition (a measure of condition independent of litter size).

*Weaning: Evidence for the residual effects of competition.* The negative correlations between mean pup weight and litter size increased or remained high throughout the lactation period in all treatment groups except *ad lib* food/low density (Table 6), despite the fact that all dams were housed separately with *ad lib* food during lactation. The pattern on day 23 was almost identical for male and female pup weights.

These results suggest that, after competition for limited food, even those dams capable of rearing large litters provide fewer calories per pup than those rearing smaller litters, irrespective of the pups' sex. However, dams that had experienced little competition for food (the *ad lib*/low density group) provided the same investment per pup regardless of litter size.

To test the assertion that large size at weaning of both male and female pups (Table 3) in the low food groups is not attributable to small litter size, weaning weights from the pooled low food groups were compared to those from comparably-sized litters, 8–11 pups, from the *ad lib* food/low density group. Mean weaning weight was significantly greater in the pooled low food groups for male pups ( $P < 0.02$ ) and female pups ( $P < 0.01$ ) com-

**Table 6.** Within-cell correlations between mean pup weight and litter size, at birth and at weaning for ad libitum, moderate, and low food groups with low and high densities. The low food/high density treatment group had almost no variance in litter size and was not included in the analysis

Group	Correlations between mean pup weight and litter size at birth		Correlations between mean pup weight and litter size at weaning	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Ad lib food				
Low density	-0.313	NS	-0.363	NS
High density	-0.510	<0.05	-0.773	<0.001
Moderate food				
Low density	+0.373	NS	-0.486	<0.05
High density	-0.566	<0.02	-0.747	<0.001
Low food				
Low density	-0.863	<0.001	-0.851	0.005
Pooled	-0.138	NS	-0.603	<0.001
Heterogeneity	$F_{10,73} = 3.636$	<0.001	$F_{10,67} = 2.463$	<0.02

**Table 7.** Estimated slope of regression of male pup weight at weaning on female pup weight at weaning, with tests of  $H_0: \beta = 1.0$ . Density pooled within food treatment levels. All slopes significantly different from 0

Group	Estimated slope	Test of $H_0: \beta = 1.0$
Ad lib food ( $n = 32$ )	0.909	NS
Moderate food ( $n = 32$ )	1.234	$t_s = 4.89, P < 0.001$
Low food ( $n = 13$ )	1.109	NS

pared with the *ad lib* food/low density litters of 8 to 11 pups. This greater investment per pup was achieved by lactating dams without weight loss (Table 1).

These observations suggest that dams that have competed successfully for scarce resources invest more in offspring of both sexes than those that have always experienced little competition, regardless of litter size.

*Weaning: Evidence for differential investment during lactation.* Trivers and Willard (1973) suggest that mothers in good condition should favour males throughout the period of parental investment. Dams biasing the sex ratio of their litters in favour of males could reinforce their tactical decision by investing more in their sons during lactation. However, there were no significant correlations within or across treatment groups between either male or female pup weight at 23 days of age and the sex ratio.

Independent of the sex ratio, there was evidence that dams favour males over females during lactation when they are successful enough to produce large pups after exposure to food-limited situations. Table 7 shows the results of the regression of male pup weight on female pup weight at 23 days. If dams invest equally in male and female offspring, the slope of this regression is expected to be 1.0. In the moderate food groups, the slope was significantly greater than 1, suggesting that dams in those groups investing most heavily in their offspring during lactation tend to favour males.

### General discussion

We observed several tactics for suppression or reduction of reproductive effort during the experiment. The first, pregnancy blocks and delays, have been documented in other mouse populations in response to food restriction (Bruce 1963; McClure 1959, 1966). The second, facultative variation of

litter size, has also been observed in both mice and hamsters as a response to food availability (Rivers and Crawford 1974; Labov et al. 1986; Bronson 1984).

Social stratification among females and corresponding variance in their access to resources and reproductive success have been described in wild-caught house mice (Hurst 1987). The different patterns of reproductive suppression in the treatment groups of this experiment suggest strongly that these female mice were also responding to a stratified social and nutritional environment. In moderate food groups, even the most unsuccessful mice produced offspring, and there was a continuous distribution of litter sizes from very small to large. Females in the low food groups, however, appeared to face a dichotomous choice in reproductive commitment – total suppression or a moderate, closely circumscribed effort. Any behavioral model seeking to elucidate strategies of reproductive effort allocation in interacting groups of mice would need to include dynamics that produce a continuum of reproductive effort under moderately restricted food availability and a bimodal distribution under severe conditions.

Female mice also seem to respond to temporal environmental heterogeneity. Even though all dams were housed separately and given *ad lib* food from the time of parturition, their investment in their offspring during lactation varied both within and between treatment groups.

These results suggest a model of reproductive effort allocation that takes into account the quality and variability of the environment and its effect on both the current and future reproductive effort of a female. Such a model might predict that dams in a uniform good environment (such as the *ad lib* food treatments) could maximize lifetime reproductive success by producing large litters weaned as early as possible, since the offspring would enter a relatively benign environment and the dam would benefit from beginning a new pregnancy immediately. On the other hand, a dam accustomed to poor and unpredictable conditions would maximize her lifetime reproductive success by weaning her offspring at a heavier weight, sacrificing some resources she might have put into a subsequent litter in order to ensure the success of her current reproductive effort (Williams 1966).

The results of König and Markl (1987) differ from ours, as they found a negative relationship between litter size and weaning weight even under uncrowded conditions with *ad lib* food. In addition, they report that female mice pregnant with a second litter weaned the first offspring at a lighter

weight than non-pregnant controls and concluded that an appropriate response to environmental unpredictability would be weaning as early as possible. However, their mice were of wild-caught stock, and thus may not have the same capacity to nourish large litters as our laboratory strain. Also, there was no opportunity for post-partum mating in our experiment, a stress that would change expectations for present and future reproductive success and thus might require different tactics of lactation investment.

The absence of a strong density effect in all groups may be attributable to the treatment's not being intense enough. Other investigators have observed adverse effects on mice at higher densities (Christian and LeMunyan 1968; Keeley 1962). However, there are several reasons why we need not assume a simple positive relationship between density and stress in mice. First, if density increases the variance in competitive success, there may be an upper limit to that variance; beyond a certain point, an individual gains nothing by gathering excess resources. Second, there may be a maximum group size beyond which mice do not interact (Petras 1967). This would cause a large group of mice to subdivide, so an individual might continue to perceive a normal social environment within its smaller group even at high densities.

With respect to food availability, we have presented some evidence for biased sex allocation, but only in response to a combination of factors – the female's own physical condition, the population's variance in competitive success, and environmental quality and variability. Measures of the dam's condition alone were unrelated to sex allocation in this experiment. Our revised model of the experiment takes these factors into account, and is consistent with our observation of male-biased sex allocation only among the most successful dams in the moderate food groups and female-biased sex allocation among the most successful females in the low food groups. Females in the *ad lib* food groups experienced little competition and therefore would expect little variance in reproductive success of their offspring, so their failure to bias sex allocation is consistent with Trivers and Willard's hypothesis as we applied it in the revised model. However, further experiments including behavioural observations are needed for a definitive investigation of the relationship among female social structure and competitive success, food availability, environmental predictability, and sex allocation.

Studies of mice in natural environments are consistent with this interpretation. Reimer and Pe-

tras (1968), Smith (1954), and Laurie (1946) found sex proportions of 50% in mouse populations in a variety of environments with consistently plentiful food supplies (food storage depots and granaries). Populations with moderate or variable food sources tend to be divided into territories of differing quality, giving some males a reproductive advantage (Wolff 1985). Brown (1953) censused such a population on a farm and found the sex proportion to be 60 percent males. Wild populations of mice inhabiting temporary and unstable environments such as corn ricks or well-protected seed warehouses show a female bias (Laurie 1946; Southern and Laurie 1946; Evans 1949) with the sex proportion in Evans' population estimated at 40%. It is unclear, however, whether this effect is due to more female offspring being born, or to males dispersing from the poor food resource (Newsome 1971; Rowe et al. 1964).

Trivers and Willard (1973) predict that large litters, because they produce smaller weanlings, should be female-biased. However, the prediction depends on the assumption that body size is the major determinant of offspring reproductive success. If large litters are an indication of the dam's competitive ability, and if offspring reproductive success is more dependent on inherited behavioural characteristics than on body size, then we would expect that large litters in moderately competitive situations should be male biased, which is what we observed.

König and Markl (1987) noted no evidence for biased sex allocation during lactation, even among dams stressed by a second pregnancy. We found some support for biased sex allocation during lactation; however, in general male pup weight at weaning was unrelated to measures of dam's condition.

The lack of a clear bias of caloric investment in favour of males could result from the tradeoff between two factors that determine a male's success in keeping a high-quality territory: the male's weight, and early possession of the territory (Vessey 1967; Urich 1938; Jones and Nowell 1974). Thus a dam may have a choice of tactics to improve the success of her male offspring – early weaning, giving them a head start in gaining a territory, or longer lactation, giving them an advantage in weight. The choice between these tactics may well depend on the dam's perception of the quality and variability of the environment.

Predictions from simple verbal models like that of Trivers and Willard are difficult to test appropriately, because they do not specify all components of fitness for the two sexes and because con-



flicting selection pressures may result in very different sex ratios from the ones specified by the simple model. Clutton-Brock and Iason (1986) discuss this problem in some detail and conclude that formal, comprehensive model-building and parameter estimation for individual species are needed before truly falsifiable predictions about sex allocation as an adaptation can be made. Future research in this area should be based on more complete models of the relationship between environmental factors, social interactions, and the sex-specific fitness of offspring.

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