

Sex ratio manipulation and decreased growth of male offspring of undernourished golden hamsters (*Mesocricetus auratus*)

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Summary. The theory that female mammals in poor condition may increase individual fitness by skewing the sex ratio of their offspring toward daughters and by investing more resources in daughters than in sons was tested in hamsters. Newly mated experimental females were food-restricted during pregnancy and lactation (RR) or during lactation only (AR). Controls received food ad libitum. Maternal body weights were assessed daily from mating to 25 days postpartum. Litter survival (% litters with at least one pup surviving on any day), litter size, offspring sex ratios (= % males), and pup weights were monitored daily from birth (Day 1) to Day 25. All control and AR dams gave birth 16 days after mating. Gestation was extended by 1–3 days for 35.4% of RR dams. RR dams weighed significantly less at parturition than controls and AR females. During lactation, AR females showed the greatest weight loss and control females the least. AR weight loss exceeded that of RR females, possibly because the former maintained larger litters. Survival was highest for controls, intermediate for AR, and lowest for RR litters. Mean sex ratio at birth was significantly less for RR (40.7%) than for control (49.6%) and AR (48.8%) litters. RR sex ratio did not change significantly postnatally. Sex ratios of control and AR litters never differed statistically from 50%. Control male pups were significantly heavier than their sisters throughout the experiment. No significant gender differences were observed for AR pup weights after Day 2 postpartum. RR female offspring weighed more than their brothers throughout the experiment, and this difference was statistically significant immediately prior to the time that pups began to feed independently (Days 14–17). RR female pup weights were

similar to, and sometimes significantly greater than, weights of control daughters during the period of postnatal maternal investment. Control males were always heavier than males from the other treatments. Patterns of weight gain by AR and RR males varied with age. We conclude that underfed female hamsters are able to adjust the sex ratio of offspring prenatally and parental investment postnatally to favor daughters.

Introduction

The possibility that the sex ratio of offspring is a selected trait has intrigued biologists since the subject was addressed by Darwin (1859). Fisher (1930) concluded that, over its lifetime, a sexually reproducing organism should provide equal amounts of parental investment to male and female progeny. Sex ratio may be skewed if one sex is more costly to rear than the other. Favoring sons or daughters may also depend on parental condition and age during periods of investment, social factors such as the parent's dominance status within a population, the number of offspring in a litter, and the sex ratio of the population in which the parent lives (Silk et al. 1981; Barash 1982; Burley 1982; Simpson and Simpson 1982; Charnov 1982; Clutton-Brock and Albon 1982; Silk 1983; Meikle et al. 1984; McGinley 1984).

Trivers and Willard (1973) hypothesized that for species in which parents invest heavily in their young (e.g., mammals), a female may maximize reproductive success by facultative manipulation of offspring sex ratio based on her physical condition during periods of parental investment. Given that 1) males exhibit greater variance in reproductive success than females (e.g., polygynous or promiscuous mating systems where social dominance

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or possession of a territory is a prerequisite for mating), 2) male reproductive success depends at least partially on parental investment received prior to weaning, and 3) the amount of investment available to any offspring is proportional to the parent's physical condition, Trivers and Willard proposed that physiologically stressed (e.g., food-restricted) females may maximize individual fitness by skewing offspring sex ratio toward daughters. Daughters weaned in less-than-optimum condition would more likely breed as adults than would sons.

Facultative alteration of sex ratio may occur either before birth via differential mortality of fetuses of one sex or afterward by neglect or infanticide. While manipulation during pregnancy would minimize maternal investment of time and energy, selective elimination of young after birth may enable females to adjust the composition of their litters in response to changing conditions (Labov et al. 1985). Several studies have reported either prenatal (Rivers and Crawford 1974; Simpson and Simpson 1982; Hedricks and McClintock 1982; Burley 1982; Meikle et al. 1984) or postnatal (McClure 1981) alteration of offspring sex ratio by female parents. Investigation of this phenomenon during the entire period of maternal investment has not been undertaken.

In this study, both prenatal and postnatal manipulation of sex ratio and maternal investment were examined in food-restricted golden hamsters. Hamsters were considered ideal subjects for these experiments because mating in this species is probably promiscuous (Swanson 1983) and females produce excess offspring which they cull by infanticide (Day and Galef 1977). We hypothesized that food-restricted dams would deliver litters with sex ratios skewed toward daughters, and would selectively eliminate male offspring either via infanticide or neglect.

Methods

Animals and husbandry. Multiparous, adult female golden hamsters (*Mesocricetus auratus*, LVG-LAK strain) from an outbred colony were born and maintained at Princeton University and were between 170–280 days old at the beginning of the study. Each female was housed individually in a plastic cage (30 × 36 × 16 cm) covered with a wire mesh top. Bedding of wood shavings in the cages was changed weekly until parturition and added to occasionally after the birth of litters to minimize disturbance to dams. Animals were maintained in a colony room at 23° C and 14L: 10D photoperiod (lights on at 2200 h). Tap water was available ad libitum. Wayne Rodent Blox (Formula 8604-00) was provided as described below.

Procedure. Each animal was assigned randomly to one of three treatments after being mated with a sexually experienced male. Control females ($n=24$) were fed ad libitum during both preg-

nancy and lactation. AR females ($n=65$) received food ad libitum during pregnancy, but were placed on a restricted diet until their pups were 25 days old. A third group of females (RR, $n=65$) was food-restricted from the day of mating until their offspring were 25 days old.

Females were weighed daily to the nearest gram from mating until parturition. Dams that maintained litters were weighed daily through the postpartum period. During pregnancy, each RR female received approximately 75% of the amount of chow consumed daily by controls of the same body weight. The postparturitional deprivation formula also accounted for the amount of food likely to be consumed by a female's offspring:

$$F = 0.75 [(W_f \times r_f) + (W_y \times r_y)]$$

where F = food ration, W_f = maternal body weight, W_y = total body weight of a female's pups, r_f = food/maternal body weight, r_y = food/total body weight of young on a given day (all weights in grams).

Pups were sexed and weighed to the nearest 0.1 g within 12 h of birth and daily thereafter until Day 25. Gender was determined by observing ano-genital distances (ano-genital distance in males is approximately twice that in females; Huck, unpublished observation). Litter survival (= % of dams with at least one surviving pup on any day), the number of pups/litter, and sex ratio (= % males) were also recorded daily.

Statistical analyses. Differences in sex ratios among groups and within groups over time, comparisons of maternal body weights, and number of pups per litter were assessed using one-way analyses of variance (ANOVA). The effects of treatment and gender on pup weights were analyzed using ANOVAS with pups nested within litters (Ray 1982). Newman-Keuls' Multiple-Range Test (corrected for unequal sample sizes) was employed to test for differences between any two treatments when an ANOVA indicated significant treatment effects (Bruning and Kintz 1977).

Results

Preparturitional and postparturitional maternal weights

Maternal body weights during pregnancy are presented in Fig. 1a. With one exception, there were no significant effects of treatment on maternal body weights for the first nine days of gestation (for Day 7, AR > RR, $P < 0.05$). From Day 10 until parturition, control and AR dams were significantly heavier than RR females ($P < 0.001$ for each day). Control and AR maternal weights did not differ significantly from each other at any time during pregnancy.

Gestation was prolonged for some RR dams. All control and AR females gave birth to litters on Day 16, but gestation was as long as 19 days for 23 RR subjects (17 days: 17 dams; 18 days: 4 dams; 19 days: 2 dams) (Fig. 1a).

Body weights of all females that maintained litters declined during lactation (Fig. 1b). Control dams were significantly heavier than RR dams from Days 1–25 postpartum. Control and AR females maintained similar body weights from birth

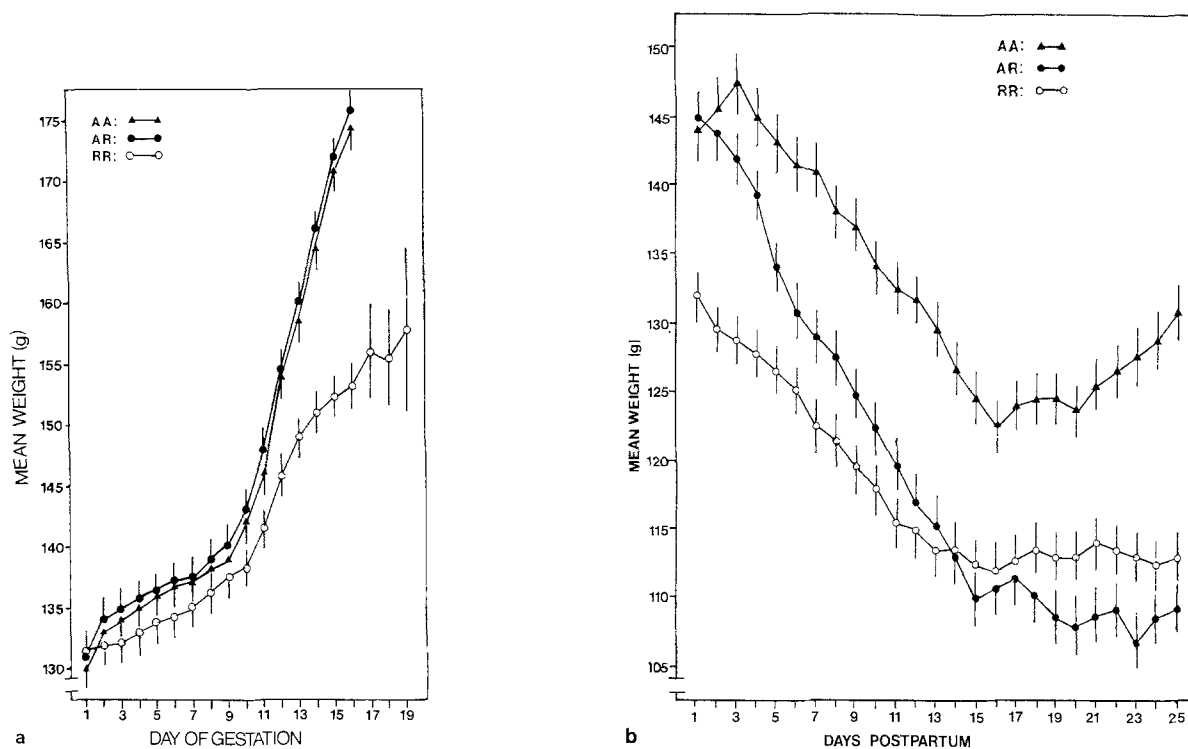


Fig. 1. a Body weights (mean \pm SE) of dams during pregnancy. AA=Controls: Food provided ad libitum during both pregnancy and for 25 days postpartum; AR=Food provided ad libitum during pregnancy and then postpartum restriction; RR=Food restriction during both pregnancy and postpartum period. Gestation was extended by 1–3 days in 35.4% of RR dams. Refer to text for statistical analyses of differences among treatments. **b** Postpartum body weights (mean \pm SE) of dams. AA=Controls: Food provided ad libitum during pregnancy and 25 days postpartum; AR=Food provided ad libitum during pregnancy and then postpartum restriction; RR=Food restriction during pregnancy and postpartum period. Refer to text for statistical analyses of differences among treatments

through Day 4. By Day 6, body weights of AR females declined and remained statistically similar to those of RR dams.

Control pups began to feed on solid food on approximately Days 12–13 while AR and RR pups were observed to consume chow beginning on Days 9–11. By Day 17, offspring were feeding independently of their dams. As a result, body weights of control females increased after Day 17 and, by Day 25, returned to levels that did not differ from those prior to pregnancy ($F_{1,22}=0.81$, NS). In contrast, AR and RR maternal weights did not rebound. By the conclusion of the experiment, body weights of these dams had returned to only 83% ($F_{1,46}=18.8$, $P<0.001$) and 86% ($F_{1,31}=25.1$, $P<0.001$), respectively, of that recorded immediately after mating.

Offspring sex ratios

Control and AR dams delivered litters whose sex ratios did not differ significantly from each other or from 50% (Table 1). Sex ratio at birth for RR offspring was significantly less than that for the other two groups and from 50% ($F_{2,151}=6.1$,

Table 1. Number of litters and mean values \pm SE of litter sizes, sex ratios, and pup weights on day of parturition. Controls: food provided ad libitum during both pregnancy and for 25 days postpartum; AR: Food provided ad libitum during pregnancy and then postpartum restriction; RR: Food restriction during both pregnancy and postpartum period

	Treatment		
	Control	AR	RR
Number of litters	24	65	65
Number of males/litter	6.29 \pm 0.39	5.62 \pm 0.22	3.42 \pm 0.22
Number of females/litter	6.42 \pm 0.42	5.89 \pm 0.24	5.03 \pm 0.29
Sex ratio (% males)	49.6 \pm 2.8	48.8 \pm 1.6	40.7 \pm 2.1
Weight of male pups (g)	2.53 \pm 0.03	2.50 \pm 0.02	2.34 \pm 0.03
Weight of female pups (g)	2.41 \pm 0.03	2.43 \pm 0.02	2.28 \pm 0.02

$P<0.003$). Interestingly, the percentage of males in RR litters decreased as the length of gestation increased beyond Day 16 (Day 16: 41.3 \pm 2.4%; Day 17: 40.7 \pm 2.5%; Day 18: 28.5 \pm 10.4%; Day

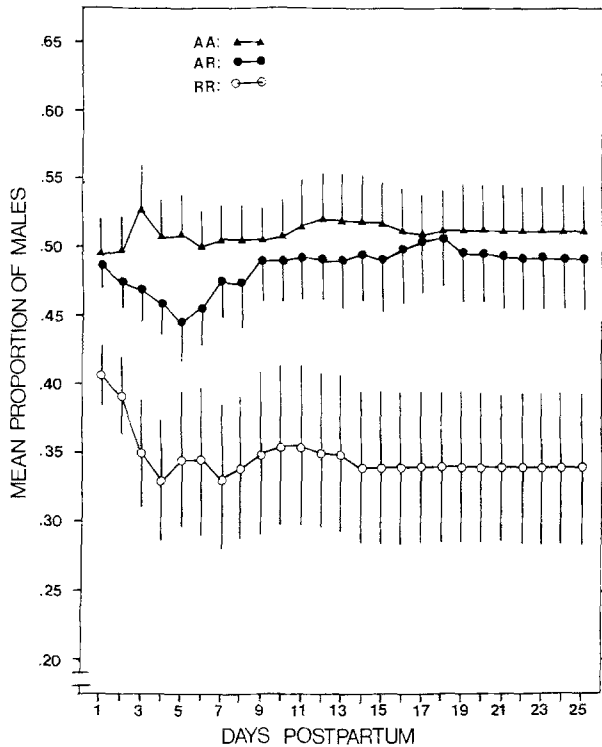


Fig. 2. Proportion of males (mean \pm SE) remaining in AA, AR, and RR litters from birth through Day 25 postpartum. AA = Controls: Food provided ad libitum during both pregnancy and 25 days postpartum; AR = Food provided ad libitum during pregnancy and then postpartum restriction; RR = Food restriction during both pregnancy and postpartum period

19: $22.1 \pm 11.1\%$; all values expressed as mean \pm SE). However, these differences are not statistically significant ($F_{3,61} = 1.92$, $P = 0.14$).

Postpartum sex ratio increased for control and AR litters (controls: from 49.6% to 51.1%; AR: from 48.8% to 50.6%) and decreased for RR offspring (from 40.7% to 34.0%), but none of these differences within groups is statistically significant (Fig. 2). However, the number of AR and RR litters containing only females increased significantly whereas the number of all-male litters did not (Ta-

ble 2). Control litters never contained offspring of only one gender (Table 2).

Litter size and survival

The mean numbers of male and female pups/litter at birth for each treatment are shown in Table 1. A two-way ANOVA indicated significant differences among treatments ($F_{2,302} = 30.8$, $P < 0.001$) and between sexes ($F_{1,302} = 10.9$, $P < 0.001$) as well as a significant interaction between treatment and gender ($F_{2,302} = 5.4$, $P < 0.005$). However, there were no significant differences in the number of either male or female pups born to control and AR dams. RR litter sizes were significantly less than that for the other two treatments (control and AR data pooled), and most of this difference was attributed to a reduction in the number of RR male offspring ($\bar{x} = 2.4$ fewer males vs. $\bar{x} = 1.0$ fewer females). Although there was a significant treatment effect for the number of daughters born (Table 1), Newman-Keuls' analysis indicated that only control and RR values differed significantly.

Postpartum litter survival was associated with the amount of food deprivation (Fig. 3). One hundred percent of control litters survived to Day 25. AR litter survival decreased to 78% by Day 25. RR litter survival was lowest, with only 49% of the original litters remaining after Day 8.

Pup mortality within surviving litters was also dependent on levels of food deprivation (Fig. 4). Control litter size declined by 3.5 offspring. Surviving RR litters decreased by an average of 5.1 pups. Mortality within AR litters was greatest (average reduction of 6.9 pups/litter), but the final average litter size (4.6 pups) was intermediate to that for the other two treatments. Virtually all pup mortality occurred during the period of maternal investment. Of 1602 pups born, 1056 were eliminated by Day 17. Only four pups died during the final eight days of the experiment.

Table 2. Numbers of litters from which male or female pups were absent. Controls: Food provided ad libitum during both pregnancy and for 25 days postpartum; AR: Food provided ad libitum during pregnancy and then postpartum restriction; RR: Food restriction during both pregnancy and postpartum period

	Control			AR			RR		
	Total litters	Males absent	Females absent	Total litters	Males absent	Females absent	Total litters	Males absent	Females absent
Day 1	24	0	0	65	0	0	65	2	1
Day 17	24	0	0	48	5	4	32	10	4
X^2_1		0.0	0.0		4.8 ^a	3.4 ^a		13.2 ^a	3.3 ^a
P		NS	NS		<0.03	<0.07 (NS)		<0.001	<0.07 (NS)

^a X^2 value corrected for continuity

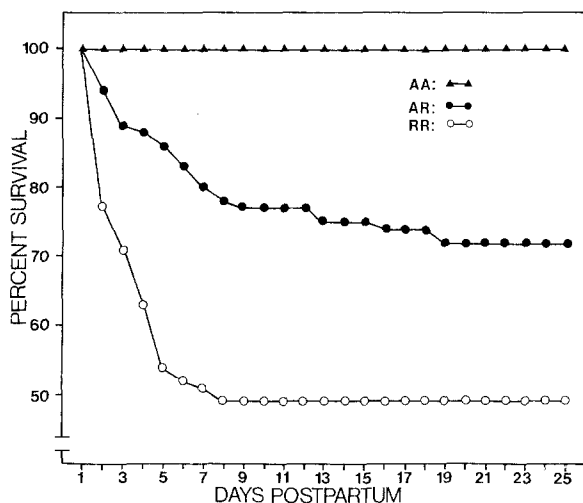


Fig. 3. Litter survival (= % of dams with at least one surviving pup) of AA, AR, and RR dams from birth to Day 25 postpartum. AA=Controls: Dams fed ad libitum during both pregnancy and 25 days postpartum; AR=Dams fed ad libitum during pregnancy and then postpartum restriction; RR=Dams food-restricted during both pregnancy and postpartum period

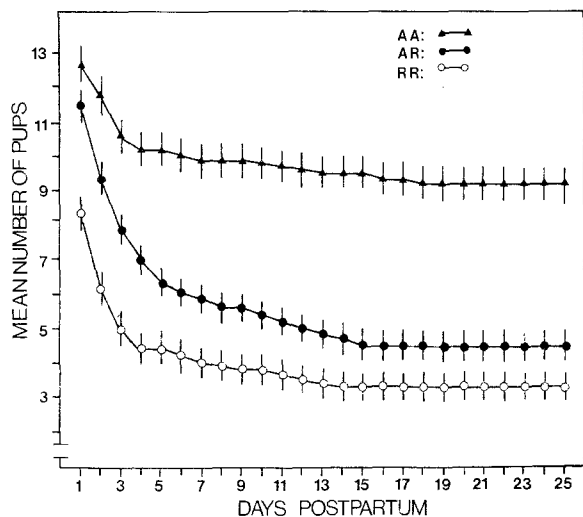


Fig. 4. Litter sizes (mean number of pups \pm SE) of surviving litters of AA, AR, and RR dams. AA=Controls: Dams fed ad libitum during both pregnancy and 25 days postpartum; AR=Dams fed ad libitum during pregnancy and then postpartum restriction; RR=Dams food-restricted during both pregnancy and postpartum period

Weights of pups

Parturition. A two-way analysis of variance indicated significant differences in mean pup weights per litter among treatments ($F_{2,299}=12.7$, $P<0.001$) and between sexes ($F_{1,299}=3.9$, $P=0.049$), but no significant interaction between these variables ($F_{2,299}=0.26$, $P=0.77$). Both RR male

and female pups weighed significantly less at birth than their control and AR counterparts (Table 1). Newborn control and AR males were significantly heavier than their sisters, but this difference was not observed among RR offspring.

Litter size and weights of individual pups are usually inversely proportional in rodents (e.g., Layne 1968). Control and AR litters exhibited this inverse relationship at birth (Control: $r=-0.420$, $DF=22$, $P=0.04$; AR: $r=-0.548$, $DF=63$, $P<0.001$), but litters delivered by RR dams did not ($r=-0.144$, $DF=63$, $P=0.25$).

Postnatal. Patterns of weight gain for male and female pups differed among treatments. Control male pups always weighed more than their sisters and, with the exception of Days 1 and 2, these differences were statistically significant (Fig. 5a). No significant differences were found between the weights of AR males and females at any time (Fig. 5b). In contrast, weights of RR female offspring always exceeded those of RR males (Fig. 5c), and these differences were statistically significant on Days 3, 4, 6, 7 and 8.

Separate comparisons of males (Fig. 6a) and of females (Fig. 6b) by treatments suggest that patterns of weight gain varied with the age of pups. On Days 1 and 2, control and AR males were significantly heavier than RR males. Weights of AR and RR males were similar from Days 3–10, and both groups of food-restricted pups weighed significantly less than control males during those days. AR males weighed significantly less than control males for the remainder of the experiment and less than RR males during Days 11–20. Although control males were always heavier than RR males, this difference was not significant during the final days of lactation (Days 14–16).

Patterns of weight gain for control and RR pups were different for males and females. Whereas control males always weighed more than RR males, RR female pups were comparable to (Days 6–12), or significantly heavier (Days 13–16), than control females. After Day 5, weight gain for AR females was always less than for females from the other two treatments.

Following the period of maternal investment, both male and female control pups gained weight much more rapidly than did offspring from food-restricted mothers (Figs. 6a and b). On Day 17, control males were 33% and 13% heavier than AR and RR males, respectively; control females weighed 18% more than AR females and 3% less than RR daughters. By Day 25, control males weighed 67% more than AR males and 64% more

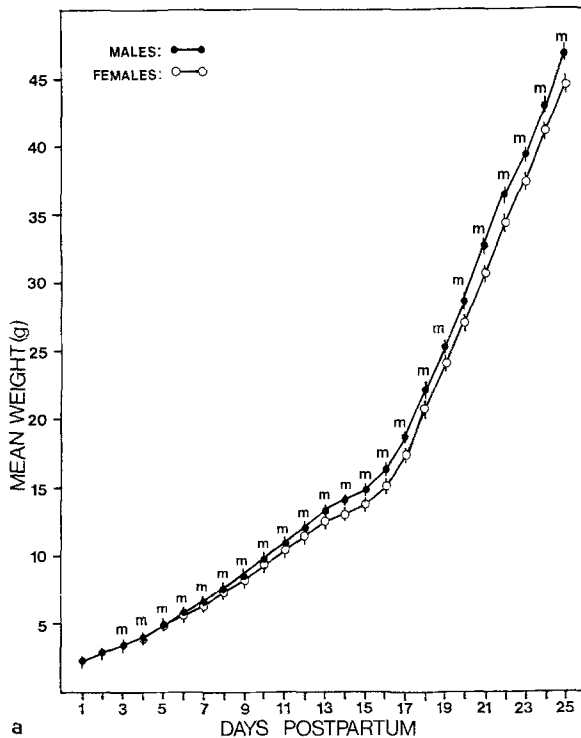
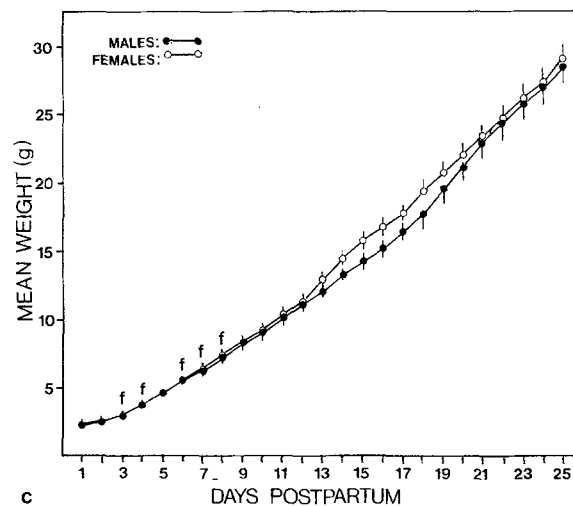
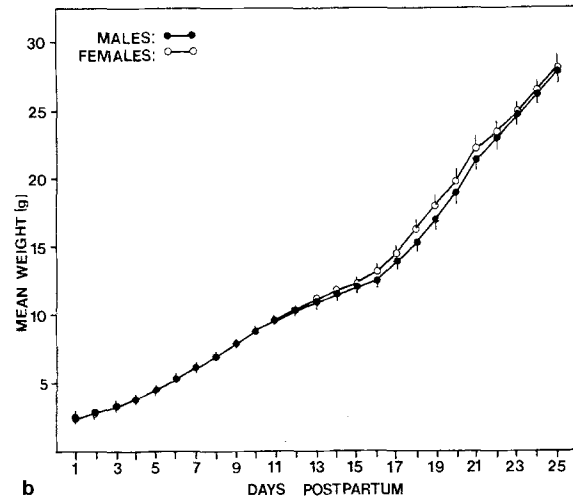


Fig. 5. a Postpartum weight gain (mean \pm SE) by control male and female pups (dams fed ad libitum during both pregnancy and 25 days postpartum). *m* = days on which male pups were significantly heavier than female pups. **b** Postpartum weight gain (mean \pm SE) by AR male and female pups (dams fed ad libitum during pregnancy and then food-restricted postnatally). **c** Postpartum weight gain (mean \pm SE) by RR male and female pups (dams food-restricted during pregnancy and postpartum period). *f* = days on which female pups were significantly heavier than male pups



than RR males while control females were 56% and 52% heavier than AR and RR females. The significant weight advantage enjoyed by RR pups of both sexes over AR subjects was eliminated after Day 20.

Discussion

The results of this study support the hypothesis that the physiological condition of a female mammal may result in the biased production (Trivers and Willard 1973) and growth (McClure 1981) of young of one gender or the other. Trivers and Willard postulated that females in poor condition should invest more resources in daughters. Tests of their hypothesis have been equivocal. Some studies found no effects of maternal stress on offspring sex ratio (e.g., Myers 1978; Clutton-Brock et al. 1981). Others have reported female-biased litters at birth when laboratory mice (Rivers and

Crawford 1974) and rats (Lane and Hyde 1973) were physiologically stressed during pregnancy, or the selective elimination of male pups when wood rats were malnourished postnatally (McClure 1981). In contrast, studies of Richardson's ground squirrels (Michener 1980), diverse species of primates (Altmann 1980; Silk et al. 1981; Simpson and Simpson 1982; Silk 1983), and white-tailed deer (Verme 1965, 1969) have shown that females suffering from poor nutrition or other forms of stress during pregnancy delivered litters with predominantly male infants (but see Meikle et al. 1984).

Evidence for facultative maternal investment

We did not sacrifice control and experimental dams at various stages of pregnancy to assess survival and development of male and female embryos, nor did we conduct systematic postnatal ob-

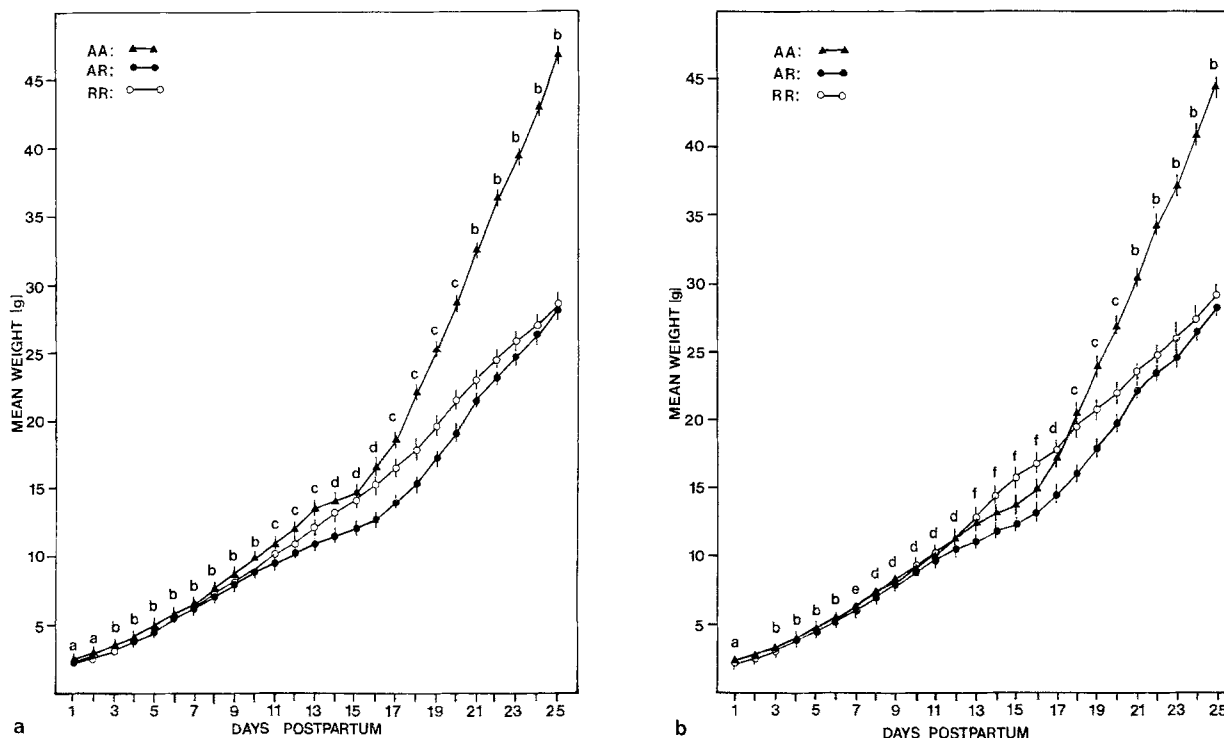


Fig. 6. a Comparison of postpartum weight gain (mean \pm SE) of AA, AR, and RR male pups. AA=Controls: Dams fed ad libitum during both pregnancy and 25 days postpartum; AR=Dams fed ad libitum during pregnancy and then postpartum restriction; RR=Dams food-restricted during both pregnancy and postpartum period. When analysis of variance indicated significant effects of treatment (refer to text), Newman-Keuls' Multiple Range Test indicated the following relationships among treatments: a=AA and AR > RR; b=AA > AR and RR; c=AA > RR > AR; d=AA and RR > AR. **b** Comparison of postpartum weight gain (mean \pm SE) of AA, AR, and RR female pups. AA=Controls: Dams fed ad libitum during both pregnancy and 25 days postpartum; AR=Dams fed ad libitum during pregnancy and then postpartum restriction; RR=Dams food-restricted during both pregnancy and postpartum period. When analysis of variance indicated significant treatment effects (refer to text), Newman-Keuls' Multiple Range Test indicated the following relationships among treatments: a=AA and AR > RR; b=AA > AR and RR; c=AA > RR > AR; d=AA and RR > AR; e=RR > AR; f=RR > AA > AR

servations of mother-offspring and sibling-sibling behavioral interactions. While we cannot conclude unequivocally that dams were directly responsible for manipulating sex ratio and gender-associated patterns of weight gain of their young, our results suggest that female hamsters can compensate, within limits, for food restriction with a continuum of prenatal and postnatal mechanisms that favor the birth and growth of female offspring.

Despite their being restricted to 75% of normal food consumption during pregnancy, all RR females delivered litters. Dams that fed to satiation delivered litters after 16 days, a period of gestation that is characteristic for *M. auratus* (Knigge and Leatham 1950; Orsini 1961), but more than one third of RR females were pregnant for 17–19 days. This prolongation of pregnancy in RR dams is consistent with observations from other species of rodents and domestic livestock when females are food-restricted at the onset of gestation (reviews by Racey 1981; Widdowson 1981). Although not

statistically significant, data from those dams exhibiting extended pregnancies suggest a potential for prenatal adjustment of sex ratio during the final days of gestation. When and how fetuses of one sex or the other are recognized and selectively culled *in utero* is unknown (Charnov 1982).

Male pups were also affected more postnatally by the undernutrition of their mothers than were females. Control males enjoyed a clear weight advantage over their sisters from Day 3 until Day 25. In contrast, weights of male offspring born to food-restricted mothers were similar to (AR), or less than (RR) that of female offspring. Moreover, the percentage of RR males declined from an average of 40.7% males at birth to 34.0% males by Day 16. While not statistically significant, this additional loss of males suggests that dams sacrifice at least some potential reproductive success.

These results conform to the predictions of Trivers and Willard (1973). However, Clutton-Brock et al. (1985) have argued that in sexually

dimorphic species males require greater amounts of nutrition during development than females, and differential mortality may result from reduced viability of males when food is in short supply rather than from prenatal or postnatal maternal rejection. This hypothesis seems unlikely for several reasons. First, increased prenatal mortality of male conceptuses is characteristic for hamsters. The primary sex ratio in this species may approach 64% (i.e., 1.8 males/1 female; Lindahl and Sundell 1958), but sex ratio at parturition is near 50% (control and AR litters) or skewed slightly toward males (Clemens and Witcher 1985). Loss of males during pregnancy is not associated with levels of maternal nutrition since weights of surviving male offspring from well-fed dams are similar to those of female pups at birth. Food-restriction may contribute to the mechanism(s) by which male embryos are eliminated, but it is probably not the direct cause of male mortality.

Second, the differences in sex ratio and weight gain that we observed parallel those reported by McClure (1981) for wood rats (*Neotoma floridana*). In that study, control male and female offspring received equal amounts of lactational energy. In experimental litters (food intake of dams restricted to 70–90% of controls), significantly more energy went to daughters and sex ratios of these litters declined to 40%. Importantly, McClure observed her subjects daily and found that differential channeling of maternal investment to daughters resulted because experimental dams ignored or physically removed males from their nests (p. 1059). With one exception, McClure found that every male in food-restricted litters died before any female deaths occurred. We found a similar pattern of postnatal survivorship among AR and RR litters (Table 2).

Third, the average size of RR litters declined rapidly after parturition (Fig. 4) and sibling competition for milk should have abated after several days. However, female pups were significantly heavier than their brothers on five of the first eight days of lactation, suggesting that more resources may have been provided to daughters than to sons during at least part of the period of maternal investment. Indeed, RR females were born weighing significantly less than their control female counterparts, but this difference was eliminated by Day 6 and reversed on Days 13–16 (Fig. 6b).

Fourth, the hypothesis of Clutton-Brock et al. (1985) predicts that 1) sex differences in mortality among stressed individuals should prevail throughout the period of differential growth and that 2) these differences should be observed when juve-

niles are reared on inadequate diets in the absence of their parents (p. 132). Because we observed no significant gender-associated postnatal mortality, our data cannot address the first prediction. However, no mortality was observed in RR litters after Day 14 or in AR litters after Day 15 (Fig. 4), even though food-restriction continued for an additional 10–11 days.

Finally, if patterns of weight gain are suggestive of future success of offspring, AR and RR pups appear at a distinct disadvantage compared to control progeny. Because of continuing food-deprivation, AR and RR males and females gained weight much less rapidly from Days 17–25 than did control juveniles (Figs. 5a and b). We have recently found that these differences in juvenile body weight influence subsequent reproduction. Dams that were food-restricted for at least 25 days during their first 50 days of life gave birth to litters with sex ratios skewed significantly toward daughters (Huck, Labov, and Lisk, in press).

In summary, the differences in sex ratios at birth and postnatal growth that were observed in golden hamsters placed on restricted diets during pregnancy and lactation support the predictions of Trivers and Willard (1973). Whether similar results will emerge from studies with wild-caught or first generation laboratory-reared conspecifics is unknown and should be investigated. Research also must be undertaken to determine whether the patterns noted in this study are typical for other species of rodents, for larger mammals, and for other vertebrates. If facultative alteration of sex ratio and maternal investment have evolved as adaptations to ephemeral resources, then stressed dams that have adjusted their reproductive efforts to favor the production of females prenatally should reverse that strategy if the source of stress is removed postnatally. Although we did not deprive hamsters of food during pregnancy and then permit them ad libitum consumption, we predict that the preparturitional effects on male offspring noted in the present experiments should be negated during lactation and possibly after weaning.

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References

- Altmann J (1980) Baboon mothers and infants. Harvard University Press, Cambridge
- Barash DP (1982) Sociobiology and behavior. 2nd ed. Elsevier, New York

- Bruning JL, Kintz BL (1977) Computational handbook of statistics. 2nd ed. Scott, Foresman and Co., Glenview
- Burley N (1982) Facultative sex-ratio manipulation. *Am Nat* 120:81-107
- Charnov EL (1982) The theory of sex allocation. Princeton University Press, Princeton
- Clemens LG, Witcher JE (1985) Sexual differentiation and development. In: Siegel HI (ed) The hamster, reproduction and behavior. Plenum Press, New York, pp 155-171
- Clutton-Brock TH, Albon SD (1982) Parental investment in male and female offspring in mammals. In: King's College Sociobiology Group (eds) Current problems in sociobiology. Cambridge University Press, Cambridge, pp 223-247
- Clutton-Brock TH, Albon SD, Guinness FE (1981) Parental investment in male and female offspring in polygynous mammals. *Nature* 289:487-489
- Clutton-Brock TH, Albon SD, Guinness FE (1985) Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature* 313:131-133
- Darwin C (1859) On the origin of species by means of natural selection. John Murray, London
- Day CSD, Galef BG (1977) Pup cannibalism: one aspect of maternal behavior in golden hamsters. *J Comp Physiol Psychol* 91:1179-1189
- Fisher RA (1930) The genetical theory of natural selection. Clarendon, Oxford
- Hedricks C, McClintock MK (1982) Regulation of mating and sex ratios during postpartum estrus. Abstract, Animal Behavior Society Meetings
- Huck UW, Labov JB, Lisk RD (in press) Food-restricting young hamsters (*Mesocricetus auratus*) affects sex ratio and growth of subsequent offspring. *Biol Reprod*
- Knigge KM, Leatham JH (1950) Length of gestation period and ovum size in developing follicle of the golden hamster (*Cricetus auratus*). *Anat Rec* 106:278
- Labov JB, Huck UW, Elwood RW, Brooks RJ (1985) Current problems in the study of infanticidal behavior of rodents. *Q Rev Biol* 60:1-20
- Lane EA, Hyde TS (1973) Effect of maternal stress on fertility and sex ratio: a pilot study with rats. *J Abnormal Psychol* 82:73-80
- Layne JN (1968) Ontogeny. In: King JA (ed) Biology of *Peromyscus* (Rodentia). Special Publication No. 2. The American Society of Mammalogists, Norman, pp 148-253
- Lindahl PE, Sundell G (1958) Sex ratio in the golden hamster before uterine implantation. *Nature* 182:1392
- McClure PA (1981) Sex-biased litter reduction in food-restricted wood rats (*Neotoma floridana*). *Science* 211:1058-1060
- McGinley MA (1984) The adaptive value of male-biased sex ratios among stressed animals. *Am Nat* 124:597-599
- Meikle DB, Tilford BL, Vessey SH (1984) Dominance rank, secondary sex ratio, and reproduction of offspring in polygynous primates. *Am Nat* 124:173-188
- Michener GR (1980) Differential reproduction among female Richardson's ground squirrels and its relation to sex ratio. *Behav Ecol Sociobiol* 7:173-178
- Myers JH (1978) Sex ratio adjustment under food stress: maximization of quality or numbers of offspring? *Am Nat* 112:381-388
- Orsini MW (1961) The external vaginal phenomena characterizing the stages of the estrous cycle, pregnancy, pseudopregnancy, lactation, and the anestrus hamster, *Mesocricetus auratus*. *Proc Anim Care Panel* 11:193-206
- Racey PA (1981) Environmental factors affecting gestation lengths in mammals. In: Gilmore D, Cook B (eds) Environmental factors in mammal reproduction. University Park Press, Baltimore, pp 197-213
- Ray AA (ed) (1982) SAS user's guide: statistics. SAS Institute, Inc., Cary
- Rivers JPW, Crawford MA (1974) Maternal nutrition and the sex ratio at birth. *Nature* 252:297-298
- Silk JB (1983) Local resource competition and facultative adjustment of sex ratios in relation to competitive abilities. *Am Nat* 121:56-66
- Silk JB, Clark-Wheatley CB, Rodman PS, Samuels A (1981) Differential reproductive success and facultative adjustment of sex ratios among captive female bonnet macaques (*Macaca radiata*). *Anim Behav* 29:1106-1120
- Simpson MJA, Simpson AE (1982) Birth sex ratios and social rank in rhesus monkey mothers. *Nature* 300:440-441
- Swanson HH (1983) Parental behaviour and population control. In: Elwood RW (ed) Parental behaviour of rodents. Wiley and Sons, Chichester, pp 259-291
- Trivers RL, Willard DE (1973) Natural selection of parental ability to vary the sex ratio. *Science* 179:90-92
- Verme LJ (1965) Reproduction studies on penned white-tailed deer. *J Wildl Manag* 29:74-79
- Verme LJ (1969) Reproductive patterns of white-tailed deer related to nutritional plane. *J Wildl Manag* 33:881-887
- Widdowson EM (1981) The role of nutrition in mammalian reproduction. In: Gilmore D, Cook B (eds) Environmental factors in mammal reproduction. University Park Press, Baltimore, pp 145-159