THE EFFECT OF FOOD DEPRIVATION AND CROWDING ON THE SEX RATIO IN MICE

by

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ABSTRACT

The theory that female mammals in good condition maximize their inclusive fitness by investing more in male offspring was tested with house mice (Mus musculus). The reproductive performance of six groups of house mice was studied to determine if undernutrition and crowding before and during gestation affects the sex proportion at parturition. Three levels of food availability, Ad libitum, Moderate (80 % of Ad lib) and Low (65 % of Ad lib) and two levels of density, Low (5 mice/bin) and High (20 mice/bin) created six different environmental treatments where there was an advantage to allocating more resources to male or female offspring depending on the dam's physical condition. The results indicated that Ad libitum conditions produced an unbiased sex proportion, Moderate food conditions produced a male biased sex proportion and Low food conditions produced a female biased sex proportion. Density was not a significant factor in sex proportion alteration. Female pups in Low food conditions weighed more than female pups in Moderate food conditions. These results demonstrate that female mice can facultatively alter the sex ratio of their offspring depending on their ability to obtain food.

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PART A

INTRODUCTION

Sex allocation concerns the way that individuals maximize their inclusive fitness by differentially investing in male and female offspring. Measures of allocated resources are sex ratio and sex proportion. The sex ratio is the number of males produced divided by the number of females whereas the sex proportion is the proportion of males. Darwin believed that the sex ratio of a species was a biological characteristic and as such was under genetic control. Artificial selection does not affect the sex ratio (Falconer, 1960) but the capacity to adjust the sex ratio of individuals as a function of the female's physical condition may have been favored in polygynous species. There was reason, therefore, to expect that sex ratio was subject to natural selection. Several theories have been proposed to account for change in the sex ratio. A review of these theories and a discussion of mating systems should reveal which theory is best suited to explain sex allocation in polygynous species.

Sex Allocation Theories

Fisher

Fisher (1930) realized that parental strategies should evolve toward equal investment in males and females by the time they become independent of the parents. His reasoning can be understood intuitively although it is usually expressed mathematically (Charnov, 1982).

Suppose a hypothetical population consists of many females and fewer males. If a pregnant female in this population could choose the sex of her offspring she should choose to produce a male for the following reason. Since each offspring must have two parents of the opposite sex, each sex group will produce the same number of progeny. In our hypothetical population, males are fewer in number than females so each male on the average leaves more progeny. As females raise more and more sons, sons become less rare and therefore of less value in producing grandoffspring. The sex ratio is thus driven back to a 1:1 ratio. This argument is symmetrical. If there are fewer females, there is a selective advantage for any genotype that influences an increased production of females. As females produce more daughters, the sex ratio is driven back to 1:1. This conclusion is not altered by the fact that many females can be fertilized by one male. The average production of offspring for males is still the same as that for females. Fisher's theory is more specific than the above argument indicates since it can be expressed in terms of the amount of parental investment each offspring receives.

Fisher began by noting that parents "invest a certain amount of biological capital" (Fisher, 1930, p.158) that is divided between both male and female offspring and that the total reproductive value of all male progeny is equal to the total reproductive value of all female progeny in a population since each sex supplies one-half of the genes of all future generations. Parental strategies should therefore evolve toward equal investment of "biological capital" in each sex. Where the costs of producing a son and a daughter are equal, parents should produce an equal number of each sex. If one sex is more costly to produce than the other, the investment in that sex should be modified in relationship to the extra cost and fewer of the more expensive sex should be produced by the end of the investment period.

It has been demonstrated that deviations from the 1:1 ratio, inexplicable by Fisher's logic, occur as Fisher's theory involves assumptions that may be inappropriate for some species. He assumed that 1) parents have no information about the competitive abilities of their offspring and 2) mating is random within a homogeneous population. Several authors consider the conditions under which these assumptions are inappropriate.

Trivers and Willard

Trivers and Willard's (1973) theory assumes parents have some information on how reproductively successful their offspring will be and use the information to adjust the sex ratio of their progeny. The theory is one of facultative sex ratio adjustment, alteration of son or daughter production in response to particular environmental conditions. Trivers and Willard (1973) make three basic assumptions.

1. A female in good condition is more likely to produce healthy offspring than a female in poor condition.
2. Healthy offspring have the advantage of greater size and

strength at the end of the period of parental investment, and this advantage endures into adulthood.

3. In species where males compete for access to females, the sons of healthy females are more reproductively successful than the sons of unhealthy females.

Healthy females should therefore invest more in sons than in daughters as sons will leave more grandoffspring than daughters. In other words, allocation of resources should be sensitive to and respond to the relative gains possible through either sex function (Charnov, 1980). Research on opossums (Austad and Sunquist 1986) and woodrats (McClure 1980) provide support for Trivers and Willard's theory and is discussed in a later section.

Local Mate Competition

The previous models are based on a large, homogeneous population of randomly mated individuals. Hamilton (1967) realized that populations with certain spatial restrictions might select for different sex ratios than those selected in a spatially unrestricted population. He considered the case where the world consists of a large number of islands each of which in one generation is colonized by fertilized females. Females produce sons and daughters and mating takes place within each island. The sons die and the newly fertilized females (next generation) disperse to recolonize empty islands. Since generations are discrete, islands are vacant at the end of each generation. Hamilton proved mathematically that if only one female colonizes an island, she should produce only enough sons to ensure insemination of her daughters. As the number of founding females increases, subsequent females produce more sons since these sons must now compete with males unrelated to her. As the number of fertilized females on the island increases, the sex ratio changes to 1:1 (Charnov, 1982).

Nasonia vitripennis is a small wasp that parasitizes fly pupae. Since male offspring of this species fertilize their sisters, the first wasp laying eggs reduces competition among her sons for access to the females by producing only enough males to fertilize their sisters. This particular wasp produces 90 percent females when she is the first to parasitize the fly pupae. If a second female parasitizes the same host and lays only a few eggs, she produces relatively more male offspring which will compete with unrelated males for access to the females on the host. As the number of eggs the second female lays increases, relative number of male offspring she produces decreases (Barash, 1982).

Local Resource Competition

Clark (1974) also reviewed a spatial restriction that might select for different sex ratios than those selected for in a spatially unrestricted population. Using data on the prosimian Galago crassicaudatas, she attempted to explain how local resource competition can affect the sex ratio of progeny. Females remain on the home range of their mother sharing the resources of the range while males in this species disperse. The mother's range can only support a limited number of galagos, so it is to the mothers advantage to decrease the number of daughters she bears and increase the number of sons she bears. Clark found that females of this species bias their sex ratio toward males as expected.

Social Organization of the House Mouse

Mus musculus is a suitable as a model to test sex allocation theories in polygynous species. In general, the social organization of the house mouse involves the division of space into territories. Each territory accomodates one dominant male, a few subordinate males, several females and some offspring. Male and female young disperse from their natal area. Young females may be successful in entering an established territory while young males have great difficulty in establishing a territory or entering an established territory. The mortality rate of dispersing male young is therefore higher than that of dispersing female young (Bronson, 1979). The following facts and conclusions indicate that males have higher variance in reproductive success than females and male reproductive success is influenced by the physical condition of its dam.

- Fact 1: mice are polygynous (Bronson, 1979).
- Fact 2: dominant males do most of the mating (DeFries and McClearn, 1970).
- Fact 3: there is a high mortality among young dispersing males as intense fights occur for territory and dominance

and the loser may be killed (Reimer and Petras, 1967). Small subordinate males are ignored presumably because they don't threaten the dominant males status (Oakeshott, 1974).

- * <u>Fact 4</u>: being a subordinate male on a dominant male's territory does not increase the subordinate male's reproductive fitness. Subordinates are often harrassed by the dominant male and many subsequently die or fail to breed (DeFries and McClearn, 1970).
- * <u>Fact 5</u>: dominant males retain their status for several months (Reimer and Petras 1967).
- * <u>Conclusion 1</u>: the reproductive success of a male varies more than that of a female.
- * <u>Conclusion 2</u>: a dominant male on a territory has higher reproductive fitness than males without territories.
- * <u>Fact 6</u>: larger males win territory and dominance battles (Vessey, 1967).
- * <u>Fact 7</u>: larger body size is correlated with good maternal condition (Clutton-Brock and Albon, 1982).
- * <u>Conclusion 3</u>: females in good condition produce healthy sons that are more likely to win a territory and breed.

Theories of local mate competition and local resource competition are inappropriate for mice since both males and females disperse from their natal area before breeding. Local mate competition requires brother/sister matings which rarely occur in mice since both sexes disperse before breeding. Similarly, local resource competition requires that one sex remain in its natal area. Fisher (1930) and Trivers and Willard (1973) are the two remaining theories that are applicable to mice. From the life history of mice it is apparent that Mus musculus is a species where males compete for access to females. In addition, the sons of healthy females will be more reproductively successful than sons of unhealthy females as larger sons win dominance battles and territories. Females on the other hand show less variability in reproductive success as they are not excluded from well-established territories (Dixon and Mackintosh 1971). A pregnant female mouse should therefore bias the sex ratio of her progeny toward males if she is in good condition and toward females if she is in poor condition. In addition, a recent review by Clutton-Brock and Iason (1986) indicated that a trend existed for female rodents subjected to various forms of stress (one of which was inadequate diet) to produce more female offspring at birth. In other words, it is probable that Trivers and Willard (1973) will best explain the data from this present experiment.

Altering the Sex Ratio

Most experimental studies of the sex ratio have induced poor physical condition in the female during lactation and weaning. McClure (1980) induced poor maternal body condition in lactating woodrats (Neotoma floridana), by restricting the amount of food they received and found that the sex ratio was significantly lower at weaning than at birth. Furthermore, the female woodrats actively rejected male pups at feeding more often than female pups which resulted in increased male pup mortality and lighter male weights at weaning.

Since a female has a large biological investment in gestating progeny, natural selection would favor the ability to alter the sex ratio of progeny before birth. Mice gain approximately 20 g (an 80% increase in body weight) and their food intake increases by 34 % during gestation, a considerable initial investment (Myrcha, Ryszkowski and Walkowa, 1969). If a female in poor condition could bias the primary or secondary sex ratio toward females valuable biological investment would not be wasted producing males that may not reach maturity or breed. Females could alter the sex ratio by: altering the pH levels in the vaginal tract (Roberts, 1940), altering the permeablility of their eggs to X and Y bearing sperm (Barash, 1977), selectively aborting or resorbing fetuses (Bruce, 1963), and altering the timing of insemination (Guerrero, 1974, 1975). These mechanisms leave the possibility open that mammals can facultatively alter the primary sex ratio of their progeny.

The purpose of my research was to determine if mice have the ability to alter the sex ratio of their offspring during gestation. The house mouse, Mus musculus, was used to test the hypothesis that females in poor physical condition bias their progeny's sex ratio toward females. The factors manipulated were density (crowding) and food intake.

Effects of Crowding on the Dam

Lloyd and Christian (1969) studied the reproductive activity of individual females in three experimental freely growing populations of house mice. Their results indicated that the proportion of the total number of females that successfully reproduced was limited and declined with an increase in population density. Fetal resorptions were apparently a significant factor in contributing to the decline in birth rates. As density increased the intervals between litters born to individual females increased. The limited number of females that had offspring were predominantly older and higher ranking individuals.

Lidicker (1975) studied two populations of freely growing mice and found a substantial reduction in reproductive output in both populations. Most of the effect was due to a failure of young mice to mature reproductively, but also some older mice regressed from reproductive competency. Autopsy revealed that among mice old enough to be reproductively active 44% of the males and 68% of the females were reproductively stunted or regressed. Allen and Haggett (1977) confirmed that significantly fewer offspring are produced by crowded females. Sixty-one percent of crowded parental females gave birth while 100 percent of the control females gave birth. Therefore one of the main effects of crowding was a decrease in the number of reproductive individuals due to reproductive stunting and fetal resorptions.

Effects of Crowding on the Dam's Offspring

Much attention has been given to the effects of crowding the dam and the subsequent effects on male offspring. The most significant findings were, male offspring of crowded dams exhibit sexual behaviour deficits. Harvey and Chevins (1984) found that males from crowded mothers displayed poor copulation behaviours. Both Ward (1972) and Dahlof et al. (1977) found that crowding pregnant rats influenced male offspring to show readiness to display lordosis (a typically feminine behavior) in response to environmental stress. Ward (1972) also found crowding decreased testicular size, and plasma and urine concentrations of testosterone but increased the amount of androgen secreted by the adrenal cortex. He therefore concluded that crowding pregnant dams demasculinized their male offspring. Dahlof et al (1977) discovered that if during the last trimester pregnant rat dams were exposed to various forms of stress (one of which was crowding), at birth male offspring had shortened anogenital distances.

When pregnant albino mice were subjected to stress by crowding, their litters were less active, slower to respond and defecated less than control mice when they encountered unfamiliar stimuli. These differences persisted to 30-100 days of age whether pups were raised by crowded or uncrowded mothers and in spite of starvation (Keeley, 1962). Harvey and Chevins (1985) investigated the attack/threat behaviour of adult male offspring of mouse dams crowded during the final third of pregnancy. The prenatally crowded group of males demonstrated significantly less attack behaviour, an increase in attack latency and a decrease in the number of attacks, bites and amount of time spent attacking. A decrease in threat behaviour was also observed from offspring of crowded dams.

Christian and LeMunyan (1968) studied a crowded population of male and female mice for six weeks. No young were born during the period of crowding. When the crowded mice were paired for breeding and housed in pairs, half of the pups in each litter that ensued were fostered onto a noncrowded dam. Although there was no difference in the birth weights of the pups from crowded and noncrowded dams, pups nursed by crowded dams were 15 percent lighter than pups nursed by noncrowded dams. When this cross-fostering experiment was repeated with the pups in the first experiment, pups nurtured by females that in turn were nurtured by crowded dams were 8 percent lighter than controls at weaning. It was concluded that growth was supressed in progeny nurtured by crowded dams and this effect persisted to the second generation. In addition, crowding resulted in an increase in intrauterine mortality and a decrease in fertility. Therefore, some of the main effects of crowding of the dam on the pups are lower fetal weights, demasculinization of male offspring and an increase in foetal resorptions.

Other Indicators of Stress Due to Crowding

Armarro et al. (1984) found that crowded male adult rats (10/cage) gained less weight than control rats (3/cage).

Crowding decreased food intake and increased water intake. Similarly Gamallo et al. (1986) found that crowded reared rats (10/cage) had body weights significantly lower at the end of the crowding period.

Effects of Food Restriction

Evidence exists which demonstrates that provisioning females with extra food increases their ability to invest in male offspring. Female opossums were provisioned with extra food by leaving 125 g of sardines every two days at the front of their sleeping dens from two weeks before pouch young appeared until the end of the breeding season. Austad and Sunquist (1986) found the number of male offspring of provisioned females increased significantly.

Zamiri (1978) subjected mice to food restriction levels of ad libitum (8 g/mouse/day), 85 % of 8 g, 70 % of 8 g, and 55 % of 8 g. The 55 % level of feeding resulted in an increase in the length of the oestrous cycle and a decrease in the implantation rate. Late embryonic survival decreased at all levels of food restriction. In addition, the 70 % and 55 % levels resulted in a decrease of the littering rate and an increase in foetal resorptions. Infertility has been associated with short periods of total starvation at or about the time of mating (McClure 1958, 1966). Chow and Lee (1964) found restriction during gestation and lactation of dietary intake of rats by as little as 25 % of that consumed by unrestricted rats resulted in growth stunting of progenies, anemia and a decreased resistance to hypothermia. Similar effects occurred when the dietary restrictions were imposed during gestation only. Bronson (1984) found that food restriction of domestic or wild female mice resulted in a decline in growth and reproductive development but did not influence reproductive development in male mice even if growth was inhibited by food restriction. Durst-Zivkovic (1977) and Berg (1965) also found that when rats were food deprived during pregnancy, dams lost weight and fetal weights were subsequently reduced.

The previous two sections on the effects of crowding and food restriction indicate the following.

1. As food restriction increased, birth rate, fetal weights and dam weights decreased, oestrous was suppressed and fetal resorptions increased.
2. Provisioning pregnant dams with food, biased the sex proportion toward males.
3. Dams subjected to crowding lost weight and reduced their reproductive output.
4. Male offspring of crowded dams exhibited smaller weight gains and sexual and aggressive behavioural deficits which would decrease their ability to obtain a territory and sire offspring.

Therefore, male offspring of crowded and food restricted dams would be in poor condition at weaning and be unable to compete successfully for mates against male offspring of uncrowded, well-fed dams. A crowded, food restricted dam would do better to rear daughters under these conditions as daughters are accepted onto territories and do not compete for access to mates. A pregnant dam in a low density situation, provisioned with food would do better to bear male offspring.

Rationale/Hypotheses

The purpose of the proposed research was to determine if mice could alter the sex ratio of their offspring at birth (secondary sex ratio) and weaning (tertiary sex ratio). Mus musculus were used to test the main hypothesis that females in poor physical condition bias their progeny's sex ratio toward females.

In the main experiment, two levels of density (crowding) and three levels of food were manipulated to create six environmental treatments where there was an advantage to biasing the sex ratio toward male or female offspring. The groups had either a low density (Ld) or high density (Hd) and a food intake of ad libitum (Al) or 80 % of ad lib (Moderate food-Mf) or 65 % of ad lib (Low food-Lf). Ad libitum/Low Density (AlLd), Moderate food/Low Denstity (MfLd), and Low food/Low Density (LfLd) had low density and ad libitum , 80 % of ad lib or 65 % of ad lib food restrictions respectively. Ad libitum/High Density (AlLd), Moderate food/High Density (MfHd) and Low food/High Density(LfHd) had high density and ad libitum, 80 % of ad lib or 65 % of ad lib food restrictions respectively. AlLd would be in the best physical condition while LfHd would be in the poorest physical condition. The other groups will be at intermediate levels of physical condition. The six treatments of food and density are illustrated in the following table.

Experimental Design

		Density	
		Low	High
Food	ad lib	AlLd	AlHd
	80 %	MfLd	MfHd
	65%	LfLd	LfHd

Hypotheses

Dams' Weight

Main Effect of Density

1. The mean weight of dams in low density groups was predicted to be higher than the mean weight of dams in high density groups at parturition.

Main Effect of Food Restriction

2. The mean weight of dams in ad libitum food groups was predicted to be higher than the mean weight of dams in moderate food groups and the mean weight of dams in moderate food groups was predicted to be higher than the mean weight of dams in low food groups at parturition.

Litter Size

Main Effect of Density

3. The mean litter size of dams in low density groups was predicted to be higher than the mean litter size of dams in

high density groups.

Main Effect of Food Restriction

4. The mean litter size of dams in ad libitum groups was predicted to be higher than the mean litter size of dams in moderate food groups and the mean litter size of dams in moderate food groups was predicted to be higher than the mean litter size in low food groups.

Sex Proportion

Main Effect of Density

5. The mean sex proportion (proportion of males) of dams in low density groups was predicted to be higher than the mean sex proportion of dams in high density groups.

Main Effect of Food Restriction

6. The mean sex proportion of dams in ad libitum groups was predicted to be higher than the mean sex proportion of dams in moderate food groups and the mean sex proportion of dams in moderate food groups was predicted to be higher than the mean sex proportion of dams in low food groups.

Male Pup Weights

Main Effect of Density

7. The mean male pup weight of dams in low density groups was predicted to be higher than the mean male pup weight of dams in high density groups.

Main Effect of Food Restriction

8. The mean male pup weight of dams in ad libitum groups was

predicted to be higher than the mean male pup weight of dams in moderate food groups and the mean male pup weight of dams in moderate food groups was predicted to be higher than the mean male pup weight of dams in low food groups.

Female Pup Weights

The Main Effect of Density

9. The mean female pup weight of dams in low density groups was predicted to be the same as the mean female pup weight in high density groups.

Main Effect of Food Restriction

10. The mean female pup weight of dams in ad libitum groups was predicted to be the same as the mean female pup weight of dams in moderate food groups and the mean female pup weight of dams in moderate food groups was predicted to be the same as the mean female pup weight of dams in low food groups.

PART B

METHOD

Pilot Studies

The amount of food mice (Mus musculus, CD-1 strain) consumed per day was estimated since food restricted groups were based on ad libitum food intake. Two pilot studies were conducted to determine the amount of food mice consumed on a daily basis. In addition, a third pilot study was conducted to determine the number of mice that had to be housed together to constitute "crowding".

Pilot #1: Food Intake of Mice

Twelve virgin female and twelve male albino mice (Mus musculus) were used to determine the average daily intake of food. Male and female mice were housed separately in standard polypropylene shoe box cages with opaque sides and wire fitted lids. The temperature was maintained at 20 degrees celsius and the humidity at 50 %. A light cycle of 14 L/10 D was used with lights on at 0700 hours. All groups were fed Standard Purina Lab Chow. On day one, 150 grams of food was placed in the feeder and the mice were left for 5 days to consume the food. On the 6th day the remaining food was removed, weighed and any large particles in the bedding on the cage floor were removed. The amount of food consumed per day was determined by averaging. Water was provided ad libitum.

Result

Mice (CD-1 strain) housed separately consumed on average 6.6 g of food per mouse per day. To ensure that this was a reasonable estimate for pregnant mice, Pilot # 2 was conducted.

Pilot #2: Food Intake of Pregnant Mice

To ensure the amount of food determined in Pilot #1 was adequate for pregnant mice, the intake of two groups of 6 females and one male was determined. Housing and lab conditions were the same as above. On day one, 200 g of food was placed in the feeder and was reweighed every two days. The mice were also weighed every two days. On the nineteenth day, mice were separated, and housed separately. The amount of food consumed per day was determined by averaging. Water was provided ad libitum.

Result

Pregnant mice housed in groups consumed an average of 5.0 g of food/mouse/day for approximately the first 16 days. The amount of food consumed by pregnant mice during the last three days of gestation increased to 7 g per day. The value of 5 g/mouse/day was used to represent ad libitum since mice consumed this amount of food for the longest period of time and the 80 % and 65 % restrictions were based on this value.

Pilot #3: Crowding

The intensity of crowding required to detrimentally affect the physical condition of the dams was subsequently determined. Female mice were housed in the same apparatus as in Pilot #1. There was one bin each containing mice housed in groups of 10, 15 or 20. The bins were 45.72 cm x 23.50 cm and allowed 42.29 cm^2/mouse in the 10 mouse treatment, 28.19 cm^2/ mouse in the 15 mouse treatment and 21.16 cm^2/mouse in the 20 mouse treatment.

The ratio of male to female was 1:4. They were fed 200 g every day and any unconsumed food was removed and weighed. Mice were weighed every two days to monitor weight loss. If a mouse decreased in weight below 80 % of its original weight that mouse was removed and replaced by another. Crowding continued from conception to parturition (3 weeks). After 18 days the mice were housed separately. At parturition, day 10 and weaning, the sex proportion, the cumulative weight of male and female offspring, the number of females bearing pups and the weight of the dams was determined. Water was provided ad libitum.

Result

There were no significant differences on the measures as a function of density when the data were analyzed by a one-way anova. The highest density was used on the assumption that in conjunction with food restriction it would have an effect on the mice's physical condition.

Main Experiment

Twenty mice per environmental treatment were used. Ad libitum/Low density, Moderate food/Low density and Low food/Low density were housed in four groups of five female mice. AlLd was fed ad libitum, MfLd was fed 80 % of ad libitum and LfLd was fed 65 % of ad libitum. Ad libitum/High density, Moderate food/High density and Low food/High density were housed in one group each of twenty female mice. AlHd was fed ad libitum, MfHd was fed 80 % of ad libitum and LfHd was fed 65 % of ad libitum. All mice were marked on the tail with waterproof pen for identification. After two weeks four female mice were removed and replaced by four males in the high density group and one female was removed and replaced by a male in the low density group. Mice were weighed every two days and if any fell below 80 % of their original weight that mouse was replaced by another to keep the densities constant. Females were monitored daily for the presence of a vaginal plug and this constituted day one of gestation. Females remained crowded for 18 days of gestation (a total of 32 days in the treatments). Since the females became pregnant at different times, they were removed from the experiment and housed separately at different times. Males were removed after all pregnant females had been housed separately. Water was provided ad libitum throughout the experiment. The dams were weighed just prior to parturition (Dams' Final Weight) and just after parturition. On average, two days before parturition the dams were fed ad libitum due to the fact that the first female that had offspring and was not fed just prior to parturition, consumed her offspring. At parturition, the sex proportion, the weight of the male and female pups, litter size, the number of male and female pups, Total Male Pup Production (the cumulative weight of the male pups in a litter), Total Female Pup Production (the cumulative weight of the female pups in a litter) and the number of females bearing pups were determined. Total Male Pup Production and Total Female Pup Production were overall measures of investment in male pups and female pups. These measures were repeated at day 15 and weaning.

Several measures of the Dams' physical condition were also calculated. Dams' Weight Gain (Weight Before Parturition - Initial Weight), Percent Weight Gain (Weight Before Parturtion - Initial Weight/Weight Before Parturition), Weight Gain due to Pups (Total Weight of Litter), Parturition Weight Gain (Weight After Parturition - Initial Weight) and Residual Weight Gain (Weight Gain - Weight Gain due to Pups) were the values calculated. In addition to the absolute amount of weight gained an index was needed to assess the physical condition of the animal was after parturition. If she was food restricted and still managed to complete a pregnancy, she would need to use her original fat stores to gestate the progeny. It would be expected that the food restricted dam would be lighter in weight after parturition than her well-fed counterpart and would have a smaller increase in weight after parturtion. In other words, she would begin lactation at a lighter weight.

Several planned comparisons of the food groups were conducted to highlight the differences caused by the experimental manipulation.

<u>Planned Comparisons</u>

1. Ad libitum groups were compared with Low food groups.
2. Ad libitum groups were compared with Moderate food groups.
3. Moderate food groups were compared with Low food groups.

PART C

RESULTS

Observations

Although 108 female mice were bred only 85 had litters. The percent of each group that became pregnant is as follows: 95 % of AlLd (19/20), 100 % of AlHd (16/16), 95 % of MfLd (18/20), 93 % of MfHd (15/16), 40 % of LfLd (8/20), and 56 % of LfHd (9/20). It should be noted that 30% of the 40% of the pregnant females from LfLd delivered pups three weeks after the end of the experiment. Only 2 females of 8 had pups within the actual experiment in the LfLd treatment. Thirty-eight percent of the females delivered pups within the experiment in LfHd with another 18 % of the pups delivered 2 weeks after the experiment. In contrast, 69% to 80% of the females had their pups within the actual experiment in AlLd, AlHd, MfLd, and MfHd. In addition, three females in Lfld increased weight steadily gaining 10 to 12 grams and subsequently lost the weight over one night. One of these females delivered pups three weeks later.

Since many females did not become pregnant in LfLd and LfHd and subsequent cell sizes were unequal a two-way analysis of variance with equally weighted cells and food and density as the main factors was used. Dam's Initial Weight, Dam's Final Weight, Weight Gain, Percent Weight Gain, Weight Gain due to Pups, Parturition Weight Gain, Residual Weight Gain, Litter Size, Number of Male Pups, Number of Female Pups, Proportion of Males, Average Male Pup Weight, Average Female Pup Weight, Total Male Pup Production and Total Female Pup Production were the dependent variables. A Kruskal-Wallis, one way analysis of variance was also conducted to ensure that unequal sample sizes were not affecting the analysis. The analysis was kept conservative to ensure the unequal cell sizes were not biasing the results by reporting only those P values below the 0.01 level of significance. Three different time periods yielded three sets of data: newborn pups, 15 day old pups, and 23 day old pups.

Indices of Dams' Condition

Several measures were used to determine if the Dams' physical condition was affected by the manipulations as intended. Table 1 and 2 are a summary of the two-way analysis of variance and include the marginal means, standard errors and P-values for various weight measures of the dams. Figures 1 and 2 highlight the differences found in the two tables. The cell means for these measures at parturition are found in Table 8. Dams' Initial Weight ranged from 21.10 g to 30.68 g and was not significant for the food or density factors (Table 3 and 4). Dam's Final Weight ranged from 34.62 g to 64.26 g and was significant for the food factor (Table 3). In addition, Weight Gain (Weight Before Parturition - Initial Weight), Percent Weight Gain (Weight Before Parturition - Initial Weight /Weight Before Parturition), Weight Gain Due to Pups (Total Weight of Litter), Parturition Weight Gain (Weight After Parturtion-Initial Weight) and Residual Weight Gain (Weight

Gain-Weight Gain Due to Pups) were significant for the food factor (Table 1). Dams were heaviest in the Ad libitum groups and lightest in the Low food groups. Dams' Weight Gain, Percent Weight Gain and Parturition Weight Gain were significant for the density factor (Table 2). Dams gained the most weight in Low density groups and gained the least in High density groups. By 15 days postpartum, there were no significant differences in the dams' weight between the groups.

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Place table 1 and 2 and Figure 1 about here

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<u>Contrasts.</u> When Ad libitum food groups were contrasted with Moderate food groups or Low food groups all of the above measures were significant. When Moderate food groups were contrasted with Low food groups none of the measures were significant (Table 8).

The results of this section indicate that dams in Ad libitum groups were heavier than dams in Moderate or Low food groups and dams in Low density groups gained more weight than dams in High density groups. These results support the first two hypotheses.

Litter Size

Tables 3 to 7 contain a summary of the two-way analysis of variance and include marginal means, standard errors and P-values for the remaining dependent variables. Appendix A contains the cell means for Litter Size, Number of Male Pups, Number of Female Pups, Sex Proportion, Male Pup Weight, Female Pup Weight, Total Male Production and Total Female Production for newborn, 15 day old and 23 day old time periods (Tables 8 to 11). Figure 3 highlights the differences between the groups in litter size and number of male and female pups. The differences between the groups for mean litter size was significant for the food factor but not the density factor and this result persisted until the pups were 23 days old (Table 3 and 4). At parturition, Ad libitum groups had the largest mean litter sizes (11.06) and Moderate food and Low food groups had reduced mean litter sizes (8.92 and 9.16 respectively in Table 3). Tables 5 and 6 demonstrate that when the pups reached 15 and 23 days old the average litter sizes changed slightly (Ad libitum, 10.66, Moderate food, 9.24, Low food 8.95 for 23 days of age).

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Contrasts. Table 3 shows that when Ad libitum food groups were contrasted with Moderate food groups the mean litter size differences were significant (10.83 and 8.90) and these differences remained until the pups were 23 days old (Table 6). When Ad libitum food groups were contrasted with Low food groups the mean litter size differences were significant (11.06 and 9.17) and they remained until the pups were 23 days old (10.66 Ad Lib, 8.95 in Low in Tables 5 and 6). There were no significant litter size differences between the Moderate food and Low food groups.

Litter size was further partitioned into the number of male and female pups to determine what sex was being under and overproduced when litter sizes declined in the Moderate and Low food groups. This section's purpose was to provide further support for the sex proportion analysis.

Number of Male Pups. The differences between the groups for Number of Male Pups born were significant for the food factor only, with Ad libitum and Moderate food groups having the most male pups (with means of 5.40 and 5.16 respectively) and Low food groups having the least (3.80 from Table 3). However, at 23 days of age, Table 6 shows that there was no significant difference between the groups for number of male pups.

Contrasts. When Ad libitum or Moderate food groups were contrasted with Low food groups significantly fewer males were born to Low food groups (5.40 in Ad lib, 5.16 in Moderate and 3.80 in Low, Table 3). There was no difference in the number of males born to Ad libitum and Moderate food groups. At 23 days of age there was no signficant difference between the groups (Table 6).

Number of Female Pups. Differences between the groups in mean Number of Female pups born were significant for the food factor. The Low food groups had the same mean number female pups born (5.66) as the Ad lib groups (5.67) and the Moderate food groups had the lowest mean number of female pups born (3.77 in Table 3). This result persisted for the 23 day period of lactation and weaning (Table 6).

Contrasts. When Moderate food groups were contrasted with Ad libitum or Low food groups, Moderate food groups had significantly fewer female pups born (Table 3). This result persisted for 23 days (Tables 5 and 6).

The results demonstrated that density did not affect litter size or the number of male and female offspring born. The third hypothesis was therefore not supported. The fourth hypothesis was partially supported as Ad libitum groups had more pups than the Moderate or Low food groups. However, Moderate food groups did not produce significantly more offspring than the Low food groups as predicted. The number of male and female pups born reveal that the litter size reduction was achieved in the Moderate food groups by reducing the number of female offspring born while litter size reduction was achieved in the Low food groups by reducing the number of male offspring born.

Sex proportion

The mean differences between groups for proportion of males was significant with Moderate food groups having the highest proportion of males (0.57) and Low food groups having the lowest proportion of males (0.42 in Table 3). Figure 4 demonstrates that as time elapsed, the sex proportion in all groups increased slightly.

Contrasts. At parturition and 23 days, Tables 3 and 6 show that when Moderate food groups were contrasted with either the Ad libitum or Low food groups, sex proportion was significant. Moderate food groups had the largest sex proportion and low food groups had the smallest sex proportion.

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Place Figure 4 about here

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The fifth hypothesis was not supported since density did not significantly affect the sex proportion. The sixth hypothesis was partially supported. It was predicted that Ad libitum groups would have a higher mean sex proportion than the other two groups but the results revealed that Moderate food groups had the highest sex proportion, and Ad libitum groups had an unbiased sex proportion (approximately 50 % males). However, the Low food groups had the lowest sex proportion as predicted.

Indices of Pup Physical Condition

Male Pup Weight. There were no significant differences between the groups in terms of mean male pup weights for any of the time periods (Tables 3 to 7).

Female Pup Weight. There were no significant differences between groups for mean female pup weight for the three time periods (Tables 3 to 7).

Contrasts. When Ad libitum food groups were contrasted with Low food groups, Low food groups had heavier female pups by 15 days (Table 10) and this result persisted to 23 days of age.

Total Male Pup Production. This measure was not significant for any of the time periods (Tables 3 to 7).

Contrasts. At parturition, the difference between Moderate food and Low food groups was significant (Moderate food 7.54, Low food 6.31). At Day 15 there was a significant difference between Moderate food and Low food groups (Moderate food 36.00, Low food 27.71). As Table 5 shows these difference did not persist to 23 days of age.

Total Female Pup Production. This measure was significant for the food factor at parturition (with means of Ad lib 8.49, Moderate food 5.30, Low food 8.04 in Table 3). Tables 5 and 6 demonstrate that these differences peristed until 23 days of age.

Contrasts. When Ad libitum food groups were contrasted with Moderate groups and when Moderate food groups were contrasted with Low food groups differences between the group means were significant. These results persisted until 23 days of age (Tables 3, 5 and 6).

When male pup weights and total male production were considered, the seventh and eighth hypotheses were not supported as male pup weights and total male pup production were not significantly different for the food or density factors as predicted. Male pup weight was an index of male pup investment and if dams in good condition invested more in male pups they should be heavier in the ad libitum groups. The results demonstrated that the male pups weighed about the same at parturition and weaning. The last hypotheses was supported since female pups weighed the same at parturition and weaning.

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Place Figures 5 and 6 about here

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Kruskal-Wallis ANOVA

This ANOVA was included to ensure that unequal cell sizes were not influencing the results of the previous analysis. Since Kruskal-Wallis is a nonparametric test which does not make assumptions about the distribution of the population, it was included in this analysis to further support the two-way ANOVA with equally weighted cells. For all three sets of data, the Kruskal-Wallis and the two-way anova for unequal cells produced the same results. Specifically, for the parturition data, Dams's Initial Weight was not significant while Dams' Final Weight, Number of Male and Number of Female pups, Litter Size and Proportion of Males was significant. For the 15 day data, Dams' Weight, Male pup Weight and Female Pup weight were not significant. For the 23 day data, Dams' Weight was not significant while Number of Male Pups, Number of Female Pups, Litter Size, Female Pup Weight and Proportion of Males was significant.

PART D

DISCUSSION

Index of Dams' Physical Condition

From the measures used to determine the dams' physical condition in the various treatments, it is evident that the dams' physical condition was manipulated as intended. Although there was no interaction between the factors, there were significant main effects for density and food. Dams in Ad libitum groups gained and retained more weight than either the Moderate food groups or Low food groups. Dams in the Low food groups gained and retained the least amount of weight. Dams in Low density groups gained more weight than dams in High density groups. It was concluded that physical condition varied with density and diet restriction at parturition. All dams recovered from the weight loss by the time the young were weaned.

Pregnancy Blocks

From the observations and the number of mice that became pregnant, Low food conditions resulted in a reduced rate of pregnancy when compared to Ad libitum and Moderate food conditions. This decrease suggested that pregnancy blocks and delays may have occurred in the low food groups. Blocked pregnancies have been associated with food restriction and exposure to strange males. Bruce (1963) supplied mice with no food for one, two or three days. She found that a fast of 24 hours was enough to prevent implantation in nearly half of the treatment animals and estimated that 92 % of the pregnancies were blocked. She found that females housed in small groups were prone to an increased number of spontaneous pseudopregnancies. In the same study, pregnancies were blocked by olfactory stimuli from male mice. After breeding, the female was removed from the sire and placed with a strange male. This had the effect of blocking 63 % of the pregnancies. Several other investigators confirmed that exposure to strange males blocked pregnancies in mice (Chipman et al. 1966 ,Chipman and Fox 1966, Labov 1981). McClure (1959, 1966) also found that infertility in female mice was associated with short periods of starvation. Grouping females together has the effect of lengthening the estrous cycle and delaying pregnancy (Champlin 1971). Both food restriction and exposure to strange males would be consistent with the observed decline in reproductive performance in the Low food groups. Male mice were switched in all groups during the experiment to accomodate male mice that fell below their critical weight in the low food groups and had to be removed.

Litter Size

Litter size reduction was one response to food deprivation in both the Moderate and Low food groups. Density did not have an affect on litter size. The Ad libitum groups had average litter sizes of 11 pups whereas both Moderate and Low food groups reduced the number born to 8.5 pups. Litter size reduction as a response to food restriction has been observed in both mice and hamsters. Rivers and Crawford (1974) restricted the fat content in the diets of a groups of mice and found a marked reduction in litter size that was attributable to a decline in the number of male offspring born. Golden hamsters that were food restricted during pregnancy and lactation produced smaller litters than hamsters restricted during pregnancy only or left unrestricted (Labov et al. 1986). In addition, when wild and domestic stocks of mice were compared, the individual weights of offspring were not significantly different but litter size doubled in the domestic stocks. Domestic stocks produced and weaned larger litters by increasing their food intake (Bronson 1984). Therefore, a possible response to restricted food intake was to reduce the number of pups born once the "decision" to have pups was made.

Sex Proportion

Results of the experiment demonstrated that restriction of food affects the sex proportion of litters. An interaction between the Density factor and the Food factor was absent. The absence of a strong Density effect in all groups was probably due to the treatment not being intense enough as mice can tolerate high densities before any adverse effects result. Although 21.59 cm^2/mouse was believed to be crowded other studies have given mice less space and observed adverse affects on the dam (Christian and LeMunyan (1966) allowed 14.73 cm^2/mouse and Keeley (1962) allowed 12.19 cm^2/mouse).

For the food factor, dams fed an ad libitum diet produced an even sex proportion while dams fed a 20 % reduction in food produced a male biased sex proportion and dams fed a 35 %

reduction in food produced a female biased sex ratio. Since lab mice have been raised on Ad libitum diets, dams have no new information on the quality of their surroundings. In such a situation, their best bet for future offspring is to have unbiased sex proportions. If females produce male biased litters in this environment an advantage accrues to new females who produce female biased sex proportions. When animals have no information about fluctuations in food in their environment, Fisher's theory is the most viable. This is supported by population studies in natural environments.

Reimer and Petras (1968) conducted a trapping census of mice on two farms in Ontario. Food was plentiful on both farms. On Farm A, the buildings were in poor repair and farm animals scattered considerable amounts of food around the buildings. In the summer, the main food source was the granary but by the middle of the summer this source was depleted. The depleted source was replaced by a hayloft. In addition, corn cribs were refilled all year long. Farm B also had corn cribs that contained corn 9 months of the year and a granary where oats were stored year long. The mouse sex ratio in this environment was estimated to be 50 percent males. Smith (1954) censused the wild mouse population in four types of indoor habitats a) food handling establishments b) other businesses c) farm buildings and d)residences. He suggested that more food was present in the food handling establishments and farms than the others but food was indicated to be plentiful in all environments. The sex ratio once again was 50 percent males. Laurie (1946) assessed the mouse population in four different environments a) urban-warehouses, shops, restaurants b) corn ricks c) cold stores and d) Ministry of Food Buffer Depots. Urban, cold stores and buffer depots were stable food sources and in these environments the sex ratio was 50 percent males.

When food is moderately restricted, dams have altered information as to the quality of the environment. Territories are variable, some having better food stores than others and males on good territories have greater access to females (Wolff 1985). If the dam is in good condition she should produce males. Although females in the Moderate food groups did not gain as much weight, their capacity to become pregnant and maintain a pregnancy was similar to ad libitum animals. In addition, pup growth was not stunted in the Moderate food groups. It is proposed that mice in habitats with variable food sources, concentrated in some areas and defendable have more males in the population. Brown (1953) censused mouse populations on a farm and noted there were local areas in the barn where food is super abundant throughout the study. Whereas these areas were focal points for mouse concentration they never reached maximum carrying capacity. Brown discovered through experimentation that dominant male mice were excluding subordinant males from better feeding areas. The sex ratio in this environment was 60 percent males.

When the information the animal is receiving is the environment is poor she should produce females. Females do not have the same potential for reproductive output as males, but when food is scarce and the best territories are established, male offspring have little chance of establishing territories and breeding. In the Low food groups females responded to a decreased food supply by producing females.

Evidence in wild populations of mice inhabiting corn ricks, a temporary and unstable environment, show a female bias in the population (Laurie 1946, Southern and Laurie 1946). In addition, as corn ricks age and decrease in available food, the population becomes female biased. It is unclear, however, if this effect is due to more female offspring being born, or sub-adult and adult males dispersing from the poor food resource (Newsome 1971, Rowe et al. 1964). Evans (1949) censused the mouse population in a seedhouse. Seeds and grains were stored in metal containers with lids but small quantities were scattered on the floor and table affording a limited food supply for mice. He found that the health of the mice in this population was precarious and weight increases of mice were so small that growth was at a standstill. In this population the proportion of males was 40 per cent. Crowecroft and Rowe (1957) fed several populations abundant food and allowed their density to increase until the population asymptoped. They found that early litters were male biased but since later litters were unbiased and male mortality was high the final adult sex proportions were female biased. Labov et al.

(1986) provided direct evidence of manipulation of the sex proportion. Newly mated females were food restricted during pregnancy and lactation or during lactation only while controls were fed ad libitum. The mean sex ratio was significantly less for the animals restricted during pregnancy and lactation. There were 40 per cent males in the restricted groups and 49 percent males in the control groups. As mentioned before Rivers and Crawford (1974), fat restricted pregnant female mice and found a subsequent decline in the number of male pups born.

When no new information about the environment is available, mice produce an unbiased sex ratio and Fisher's theory is confirmed. However, when mice have information that moderate food sources are available (dam is in good condition) more male offspring are produced and when few food sources are available (dam is in poor condition) more female offspring are produced. Therefore Trivers and Willard (1973) operates when information about the environment changes.

Pup Investment

The results demonstrated no difference in male or female pup weights. All the pups born were healthy and viable but investment was not equal among them. Investment was varied by the number of male and female offspring produced. Males received the same amount of investment in the Moderate food conditions and the Ad libitum food conditions and females received the same amount of investment in the Low food conditions and the Ad libitum conditions. This is due to the Low food conditions producing a high number of female pups and fewer male pups, the Moderate food conditions producing a high number of male pups and fewer female pups and the Ad libitum food conditions producing high numbers of both male and female pups. It is interesting to note that by weaning all food groups had the same number of surviving male pups and they were the same weight. By contrast, the number of surviving female pups varied with the lowest number in the Moderate food groups. Dams managed to produce the most male offspring possible by altering the number of females that were viable and survived to weaning. However, it remains unclear if male offspring required more investment than female offspring since all groups managed to produce the same number and weight of male offspring by weaning. If the litter size had not been simultaneously altered what would have happened to pup weights and numbers? The number of pups could have been increased in both the Moderate and Low food groups by increasing the number of females in the Moderate food groups and increasing the number of males in the Low food groups. If after this manipulation the number and weights of male pups decreased it would be evident that male offspring required more investment. Further investigation in this area will need to conducted in the future.

Conclusions

1. Dams physical condition responded to the manipulation as intended. Low density and Ad libitum food produced dams in

the best condition and High density and Low food produces dams in the poorest condition.

2. Litter size reduction was one response to food restriction.
3. When litter size was reduced, biased investment in male or female offspring ensued. Under Ad libitum food conditions males and females received equal investment through producing an equal number of male and female offspring. In Moderate food conditions males received more investment through dams producing more males. In Low food groups females received more investment through dams producing more females and female pups acheiving heavier weaning weights.
4. When a dam had no new information about her environment Fisher's theory of equal investment was supported. The ad libitum group received no new information and produced a sex proportion of 50 percent. When a dam had new information about her environment the Trivers and Willard theory was supported. Moderate food groups produced a male biased sex proportion and Low food groups produced a female biased sex proportion.

PART E

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APPENDIX A

Appendix A. Table 8. Cell Means for the Indices of Dams' Physical Condition (two-way anova) at Parturition

	AILd	AIHd	MfLd	MfHd	LfLd	LfHd
Dams' Weight Gain (g)	27.71	24.55	21.15	18.06	21.20	17.58
Percent Weight Gain (g)	52.74	47.87	43.83	40.13	45.00	40.11
Weight Gain due to Pups (g)	17.41	16.67	14.05	11.99	14.47	13.10
Parturition Weight Gain (g)	8.89	6.77	5.25	4.60	8.13	4.97
Residual Weight Gain (g)	10.29	7.88	7.10	6.07	6.73	4.49
Sample Size	19	16	18	15	8	9

Appendix A. Table 9. Cell Means for the Parturition data (two-way anova)

	AlLd	AlHd	MfLd	MfHd	LfLd	LfHd
Dam's Initial Weight (g)	24.67	26.45	26.13	26.34	25.49	25.53
Dam's Final Weight (g)	52.21	51.00	47.28	44.40	48.39	43.42
Number of Males	5.78	5.00	6.11	4.20	3.71	3.88
Number of Females	5.78	5.56	3.67	3.87	5.71	4.88
Litter Size	11.56	10.56	9.78	8.07	9.57	8.75
Male Pup Weight (g)	1.53	1.62	1.38	1.58	1.77	1.57
Female Pup Weight (g)	1.46	1.56	1.36	1.49	1.53	1.49
Proportion	0.50	0.48	0.62	0.52	0.39	0.44
Total Male Production (g)	8.91	8.04	8.65	6.44	6.57	6.07
Total Female Production (g)	8.34	8.63	5.05	5.55	8.81	7.27
Sample Size	18	16	18	15	7	8

Appendix A. Table 10. Cell Means for the 15 Day Old Pup Data (two-way anova)

	AlLd	AlHh	MfLd	MfHd	LfLd	LfHd
Dam's Weight (g)	44.07	43.39	42.04	41.12	44.11	40.59
Number of Males	5.79	4.94	6.38	4.53	3.85	3.71
Number of Females	5.63	5.38	3.56	3.73	5.43	5.00
Litter Size	11.42	10.31	9.94	8.27	9.29	8.71
Male Pup Weight (g)	6.31	6.86	6.51	7.15	7.93	6.87
Female Pup Weight (g)	6.18	6.70	6.40	6.96	7.68	6.88
Proportion	0.51	0.46	0.65	0.55	0.41	0.43
Total Male Production g	36.17	33.17	41.01	30.99	30.14	25.28
Total Female Production (g)	34.66	35.52	22.40	24.51	44.37	34.21
Sample Size	19	16	16	15	7	7

Appendix A. Table 11. Cell Means for the 23 Day Old Pup Data (two-way anova)

	AlLd	AlHd	MfLd	MfHd	LfLd	LfHd
Dams' Weight (g)	36.47	34.74	35.35	34.44	37.65	34.83
Number of Male Pups	5.69	4.81	6.38	4.53	4.17	4.00
Number of Female Pups	5.38	5.44	3.50	4.00	5.33	4.40
Litter Size	11.06	10.25	9.88	8.60	9.05	8.40
Male Pup Weight (g)	10.83	11.69	10.99	12.06	13.86	12.22
Female Pup Weight (g)	10.39	11.15	10.73	11.40	13.00	12.06
Proportion	0.51	0.47	0.65	0.53	0.44	0.46
Total Male Production (g)	60.53	55.05	68.99	51.46	57.77	48.42
Total Female Production (g)	55.66	89.60	36.31	44.21	67.91	53.63
Sample Size	16	16	16	15	6	5

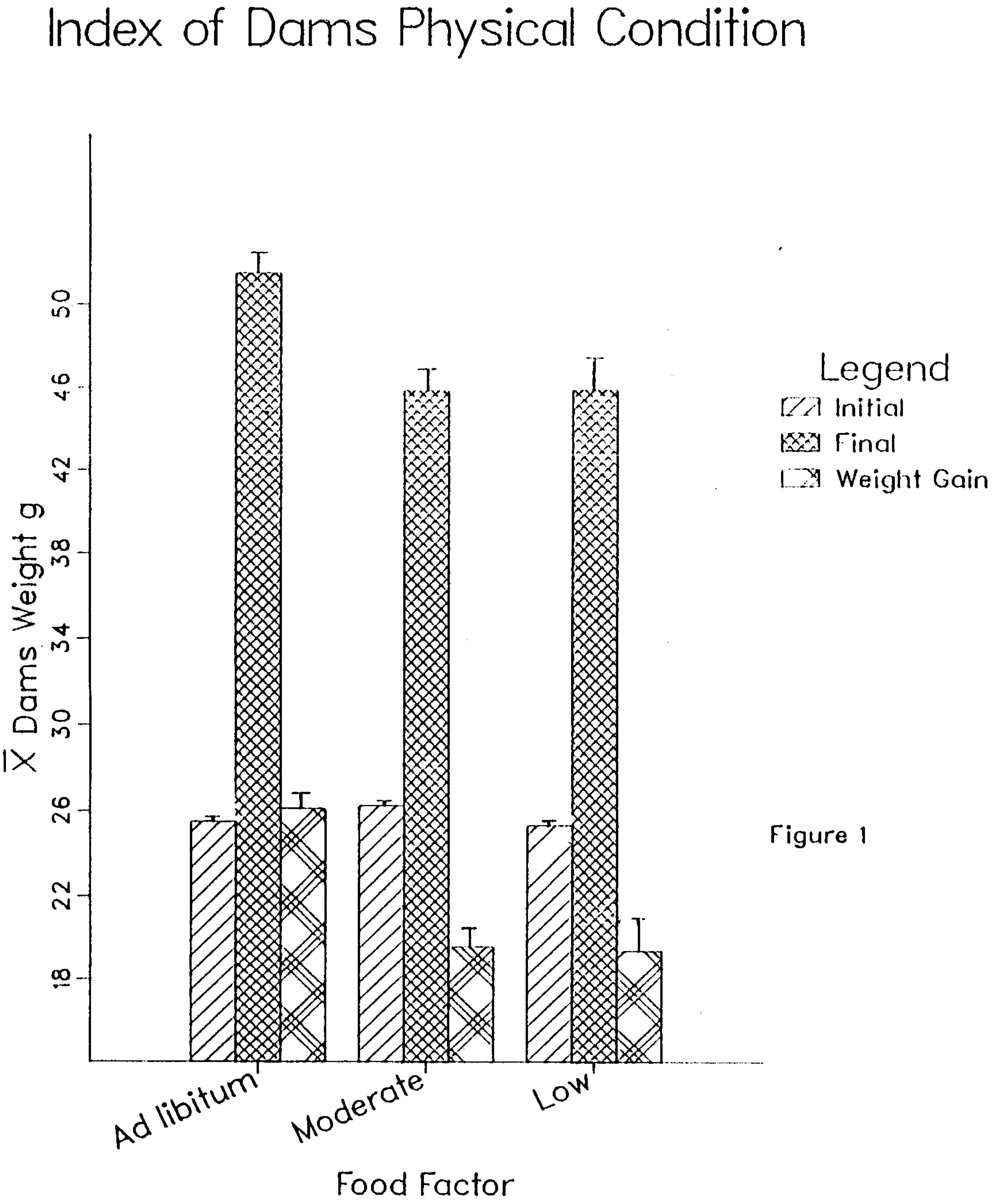

Index of Dams Physical Condition
$\overline{X}$ Dams Weight g
50
46
42
38
34
30
26
22
18
Legend
▨ Initial
▩ Final
⊠ Weight Gain
Ad libitum
Moderate
Low
Food Factor

Figure 1

Index of Dams Physical Condition

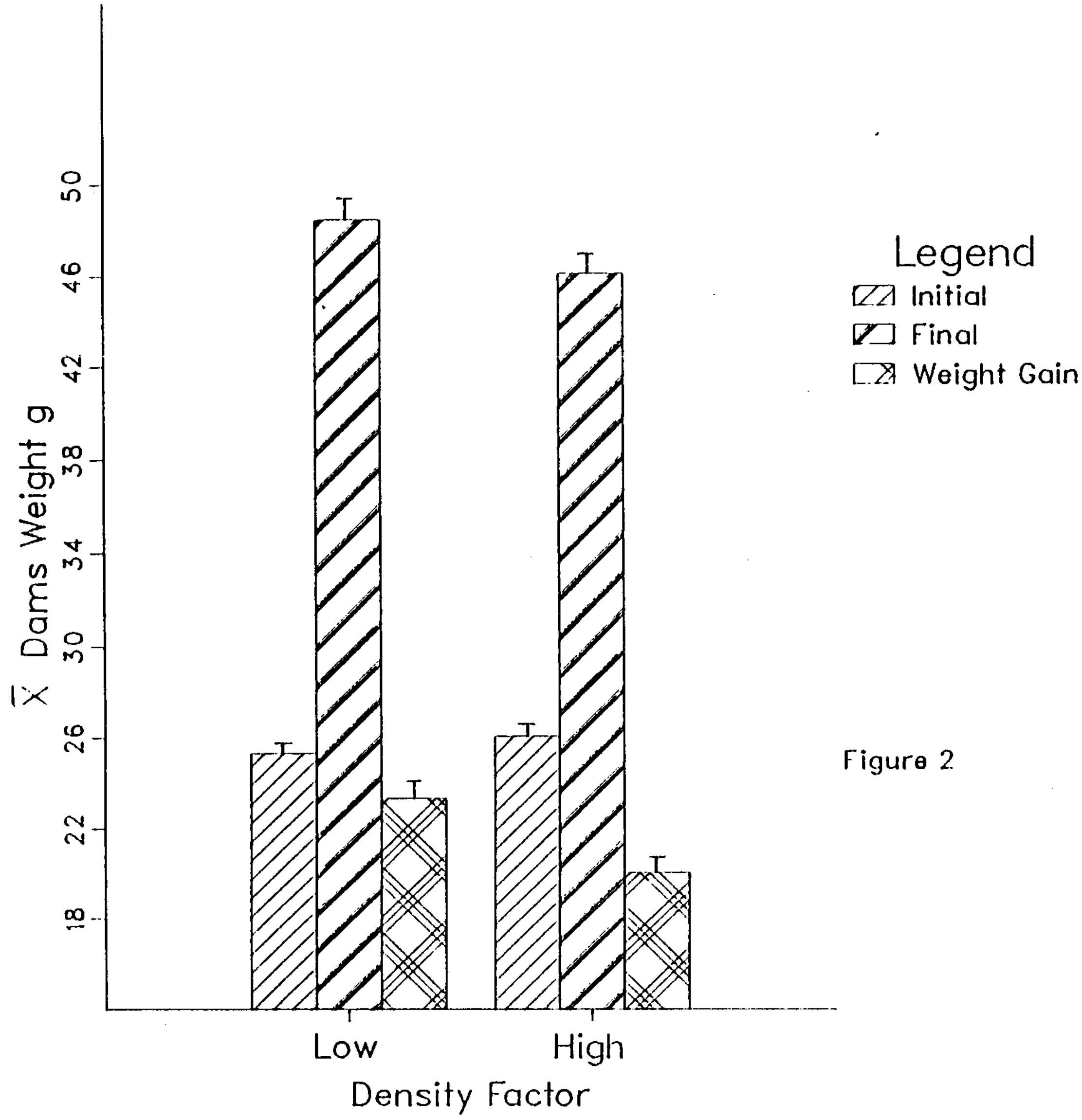


Figure 2

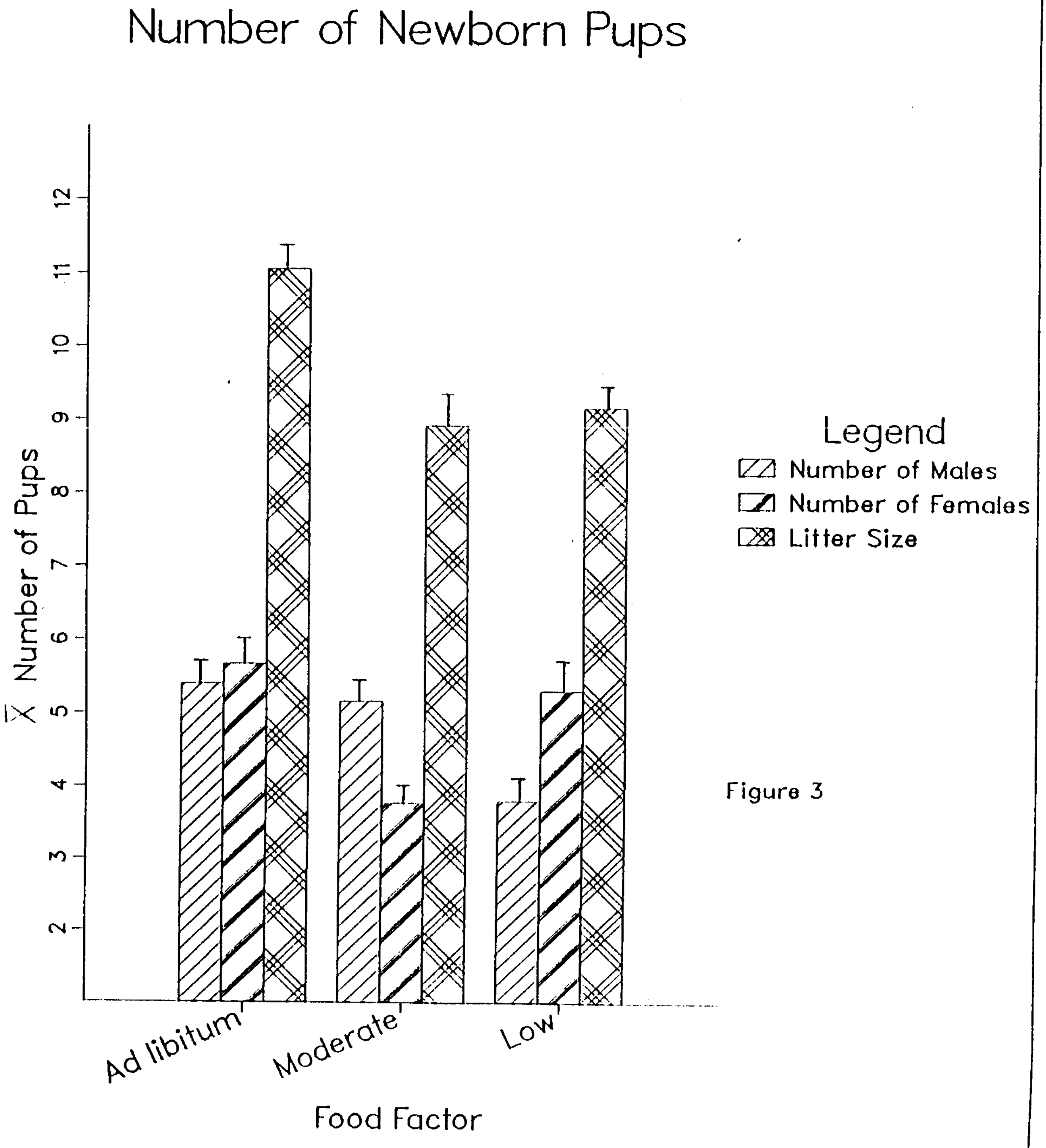

Number of Newborn Pups
X̄ Number of Pups
2
3
4
5
6
7
8
9
10
11
12
Ad libitum
Moderate
Low
Food Factor
Legend
Number of Males
Number of Females
Litter Size

Figure 3

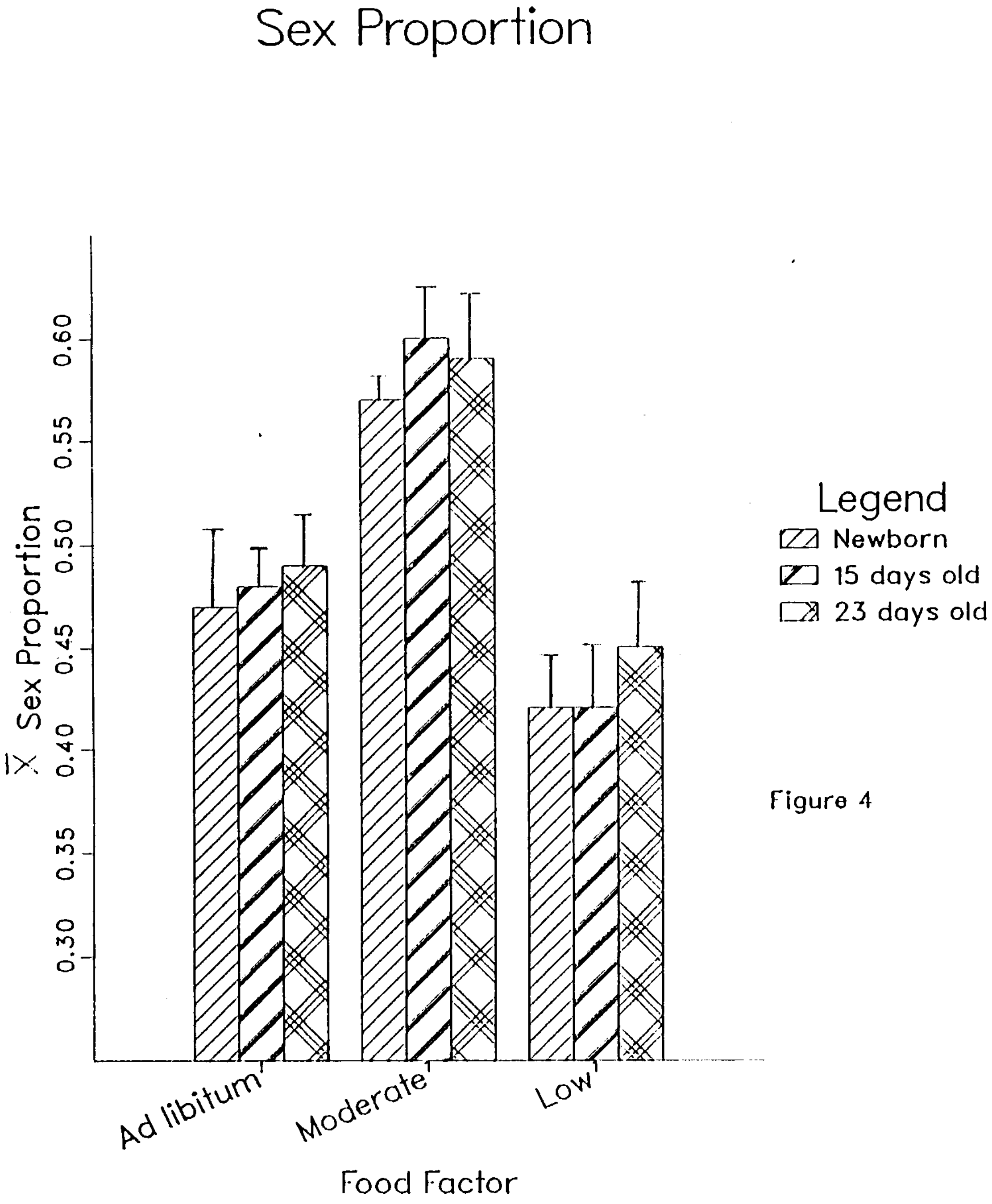

Sex Proportion
X̄ Sex Proportion
0.30
0.35
0.40
0.45
0.50
0.55
0.60
Ad libitum
Moderate
Low
Food Factor
Legend
Newborn
15 days old
23 days old

Figure 4

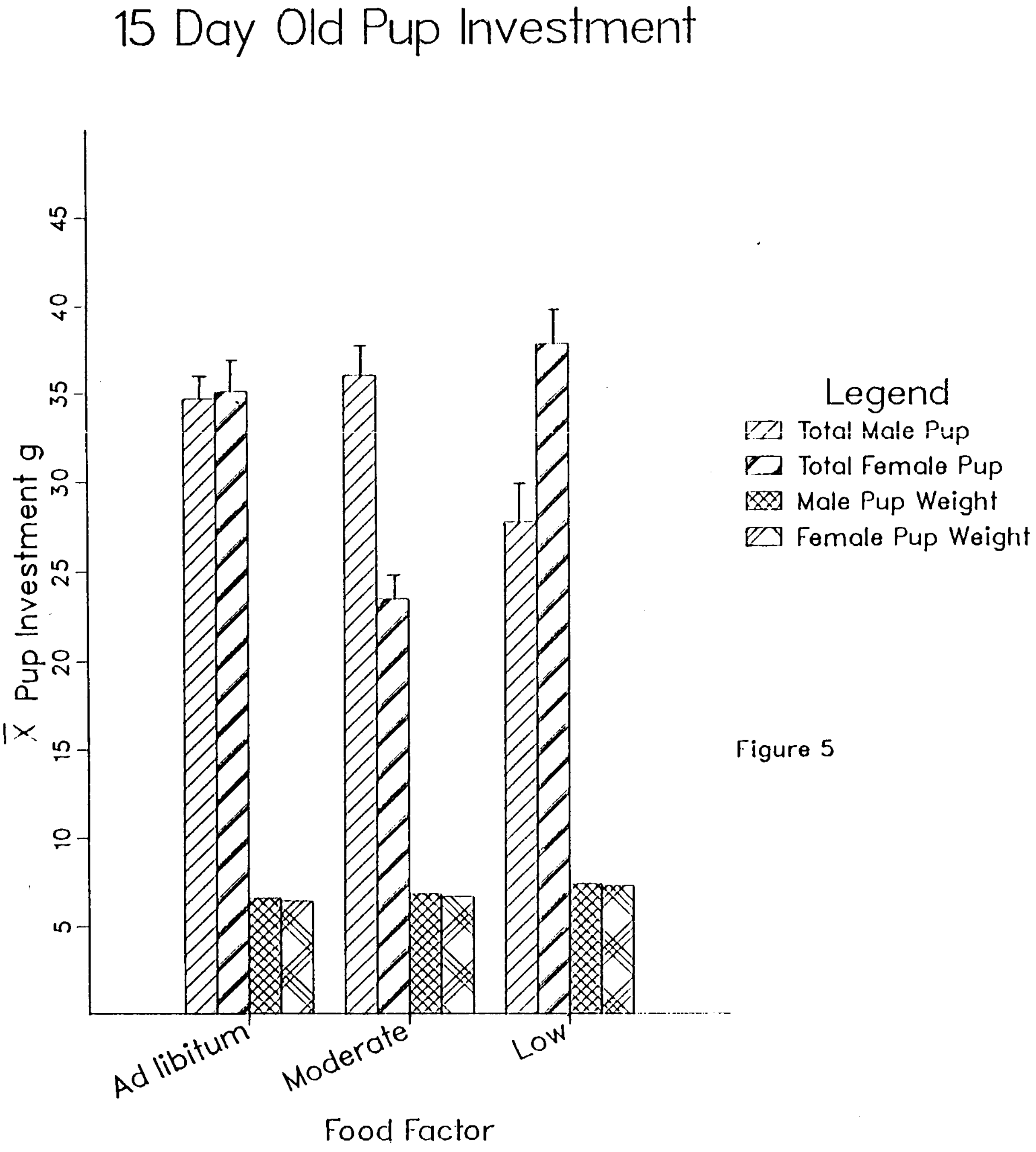
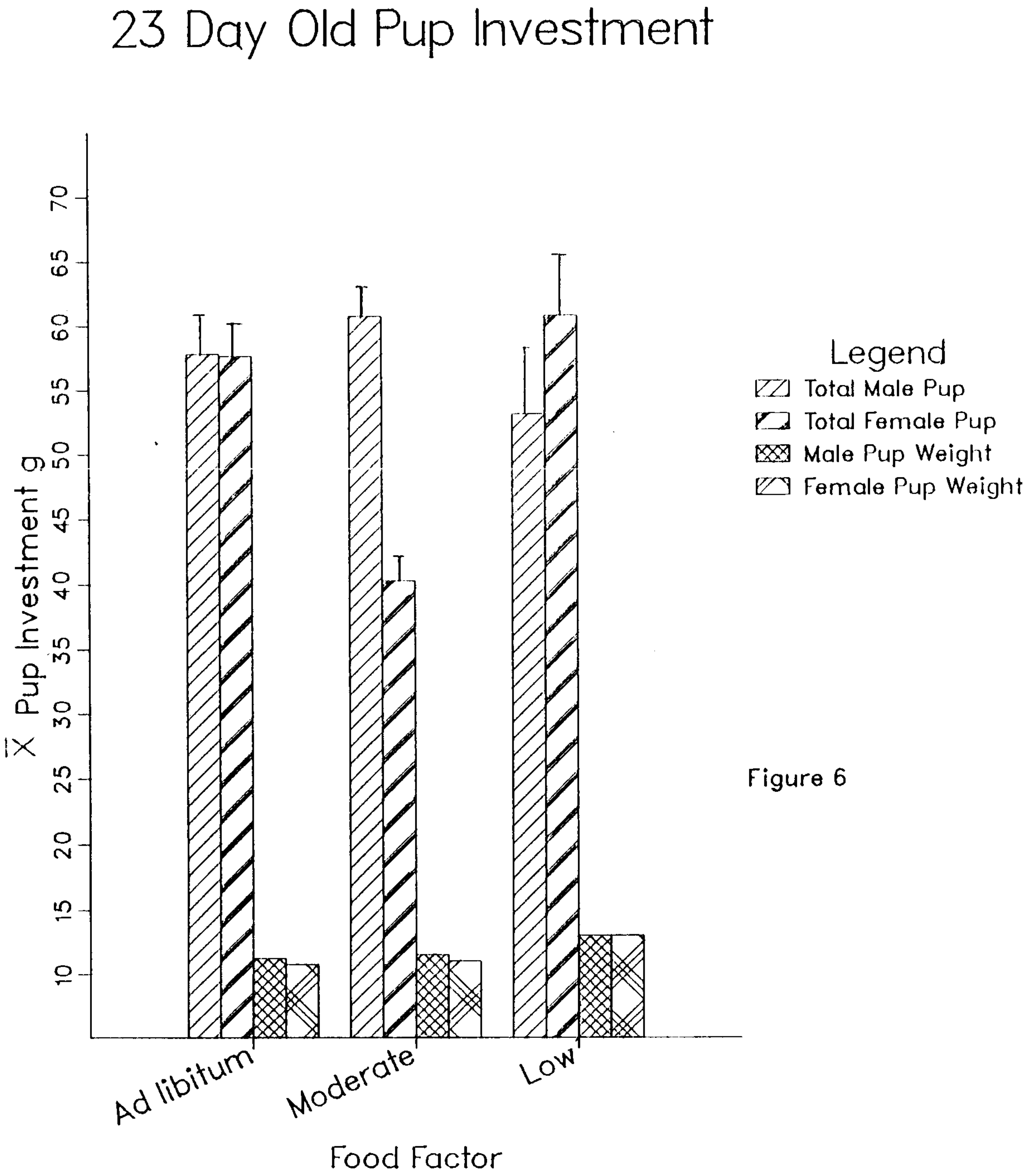

15 Day Old Pup Investment

Figure 5



23 Day Old Pup Investment

Figure 6

Table 1. Indices of Dams' Physical Condition for the Food Factor (two-way anova) at Parturition

	Ad libitum	Moderate Food	Low Food	P Value
	$\bar{X} \pm$ S.E.	$\bar{X} \pm$ S.E.	$\bar{X} \pm$ S.E.	
Dams' Weight Gain (g)	26.13 ± 0.77	19.60 ± 1.00	19.39 ± 1.45	$P<0.01$
Percent Weight Gain (g)	50.30 ± 0.84	41.90 ± 1.10	42.60 ± 2.10	$P<0.01$
Weight Gain due to Pups (g)	17.04 ± 0.42	13.02 ± 0.73	13.80 ± 0.52	$P<0.01$
Parturition Weight Gain (g)	7.70 ± 0.46	4.90 ± 0.44	6.55 ± 0.91	$P<0.01$
Residual Weight Gain (g)	9.10 ± 0.51	6.59 ± 0.59	5.61 ± 1.19	$P<0.01$
Sample Size	35	33	17	

Table 2. Indices of Dams' Physical Condition for the Density Factor (two-way anova) at Parturition

	Low Density	High Density	P Value
	$\bar{X} \pm$ S.E.	$\bar{X} \pm$ S.E.	
Dams' Weight Gain (g)	23.35 ± 0.95	20.06 ± 0.88	$P<0.01$
Percent Weight Gain (g)	47.19 ± 1.07	42.71 ± 1.13	$P<0.01$
Weight Gain due to Pups (g)	15.31 ± 0.57	13.92 ± 0.54	N.S.
Parturition Weight Gain (g)	7.35 ± 0.53	5.45 ± 0.38	$P<0.01$
Residual Weight Gain (g)	8.38 ± 0.57	6.15 ± 0.57	N.S.
Sample Size	45	40	

Table 3. Marginal Means for the Food Factor at Parturition (two-way anova)

	Ad Libitum	Moderate Food	Low Food	P Value
	$\bar{X} \pm$ S.E.	$\bar{X} \pm$ S.E.	$\bar{X} \pm$ S.E.	
Dams' Initial Weight (g)	25.56 ± 0.35	26.24 ± 0.32	25.51 ± 0.36	N.S.
Dams' Final Weight (g)	51.60 ± 0.87	45.84 ± 1.13	45.90 ± 1.49	$P<0.01$
Number of Males	5.40 ± 0.30	5.16 ± 0.36	3.80 ± 0.31	$P<0.01$
Number of Females	5.67 ± 0.34	3.77 ± 0.26	5.30 ± 0.36	$P<0.01$
Litter Size	11.06 ± 0.32	8.92 ± 0.46	9.16 ± 0.27	$P<0.01$
Proportion	0.49 ± 0.14	0.57 ± 0.02	0.42 ± 0.03	$P<0.01$
Male Pup Weight (g)	1.58 ± 0.02	1.48 ± 0.05	1.67 ± 0.06	N.S.
Female Pup Weight (g)	1.51 ± 0.02	1.43 ± 0.05	1.67 ± 0.05	N.S.
Total Male Production (g)	8.50 ± 0.48	7.54 ± 0.55	6.32 ± 0.58	N.S.
Total Female Production (g)	8.49 ± 0.47	5.30 ± 0.40	8.04 ± 0.63	$P<0.01$
Sample Size	34	33	15	

Table 4. Marginal Means for the Density Factor at Parturition (two-way anova)

	Low Density	High Density	P Value
	$\bar{X} \pm$ S.E.	$\bar{X} \pm$ S.E.	
Dams' Initial Weight (g)	25.43 ± 0.31	26.10 ± 0.25	N.S.
Dams' Final Weight (g)	49.29 ± 1.03	46.27 ± 0.92	N.S.
Number of Males	5.20 ± 0.32	4.36 ± 0.23	N.S.
Number of Females	5.05 ± 0.32	4.77 ± 0.27	N.S.
Litter Size	10.30 ± 0.35	9.13 ± 0.35	N.S.
Proportion	0.51 ± 0.03	0.48 ± 0.02	N.S.
Male Pup Weight (g)	1.56 ± 0.04	1.59 ± 0.03	N.S.
Female Pup Weight (g)	1.45 ± 0.04	1.52 ± 0.04	N.S.
Total Male Production (g)	8.04 ± 0.51	6.84 ± 0.34	N.S.
Total Female Production (g)	7.40 ± 0.49	7.15 ± 0.41	N.S.
Sample Size	43	39	

Table 5. Marginal Means for the Food Factor at 15 Days of Age (two-way anova)

	Ad libitum	Moderate Food	Low Food	P Value
	$\bar{X} \pm$ S.E.	$\bar{X} \pm$ S.E.	$\bar{X} \pm$ S.E.	
Dams' Weight (g)	43.73 ± 0.56	41.58 ± 0.56	42.34 ± 0.87	N.S.
Number of Males	5.36 ± 0.32	5.45 ± 0.33	3.76 ± 0.28	$P<0.01$
Number of Females	5.55 ± 0.31	3.65 ± 0.27	5.21 ± 0.28	$P<0.01$
Litter Size	10.87 ± 0.30	9.10 ± 0.44	9.00 ± 0.28	$P<0.01$
Proportion	0.48 ± 0.02	0.60 ± 0.02	0.42 ± 0.03	$P<0.01$
Male Pup Weight (g)	6.59 ± 0.12	6.83 ± 0.22	7.40 ± 0.30	N.S.
Female Pup Weight (g)	6.44 ± 0.14	6.68 ± 0.21	7.28 ± 0.30	N.S.
Total Male Production (g)	34.67 ± 1.85	36.00 ± 1.94	27.71 ± 2.23	N.S.
Total Female Production (g)	35.09 ± 1.92	23.46 ± 1.46	37.80 ± 2.33	$P<0.01$
Sample Size	35	31	14	

Table 6. Mariginal Means for the Food Factor at 23 Days of Age (two-way anova)

	Ad libitum	Moderate Food	Low Food	P Value
	$\bar{X} \pm$ S.E.	$\bar{X} \pm$ S.E.	$\bar{X} \pm$ S.E.	
Dams' Weight (g)	35.60 ± 0.58	34.90 ± 0.59	36.24 ± 0.86	N.S.
Number of Males	5.25 ± 0.34	5.45 ± 0.34	4.08 ± 0.28	N.S.
Number of Females	5.41 ± 0.32	3.75 ± 0.26	4.87 ± 0.31	$P<0.01$
Litter Size	10.66 ± 0.31	9.24 ± 0.40	8.95 ± 0.33	$P<0.01$
Male Pup Weight (g)	11.26 ± 0.28	11.53 ± 0.44	13.04 ± 0.72	N.S.
Female Pup Weight (g)	10.77 ± 0.28	11.06 ± 0.36	12.52 ± 0.65	N.S.
Proportion	0.49 ± 0.03	0.59 ± 0.02	0.45 ± 0.03	$P<0.01$
Total Male Production (g)	57.79 ± 3.45	60.72 ± 3.56	53.09 ± 5.03	N.S.
Total Female Production (g)	57.63 ± 3.21	40.26 ± 2.44	60.77 ± 4.63	$P<0.01$
Sample Size	32	31	11	

Table 7. Marginal Means for the Density Factor at 23 Days of Age (two-way anova)

	Low Density $\bar{X} \pm$ S.E.	High Density $\bar{X} \pm$ S.E.	P Value
Dams' Weight (g)	36.49 ± 0.60	34.70 ± 0.42	N.S.
Number of Males	5.40 ± 0.33	4.45 ± 0.24	N.S.
Number of Females	4.74 ± 0.32	4.61 ± 0.24	N.S.
Litter Size	10.14 ± 0.32	9.08 ± 0.32	N.S.
Male Pup Weight (g)	11.89 ± 0.37	11.99 ± 0.34	N.S.
Female Pup Weight (g)	11.37 ± 0.35	11.53 ± 0.30	N.S.
Proportion	0.53 ± 0.03	0.49 ± 0.02	N.S.
Total Male Production (g)	62.43 ± 3.49	51.98 ± 2.49	N.S.
Total Female Production (g)	53.29 ± 3.45	52.48 ± 2.43	N.S.
Sample Size	38	36	